

# Diversity of benthic fauna of rhodoliths and sediments deposited on sandstone reefs in Southeast Brazil

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## ABSTRACT

Sandstone reefs play an important role in sheltering a great diversity of organisms. In the north sector of the state of Espírito Santo, southeastern Brazil, the beaches are characterized by ferruginous sandstone reefs in the intertidal zones. These structures have unconsolidated sediment deposited over the reefs, mainly composed of bioclastic fragments of shells and seaweed, like the rhodolith. Rhodoliths are free-living calcareous algae with three-dimensional structures. By modifying the environment's physical characteristics, they create new microhabitats capable of being inhabited by several organisms, such as meio- and macrobenthonic invertebrates. This study sought to investigate the diversity of benthic fauna (macro- and meiofauna) on different substrates (rhodoliths vs. unconsolidated sediment) in the sandstone reef and investigate whether there are differences in benthic community structure between reef zones on Gramuté Beach in the Costa das Algas Environmental Protection Area in Aracruz, Espírito Santo, Brazil. Uni and multifactor analyses showed significant differences in the composition of the benthic fauna between the substrates ( $p < 0.05$ ). Meiofauna and macrofauna had higher numbers of taxa and diversity associated with rhodoliths compared to with sediments. A multivariate analysis corroborates the results of the univariate, showing variations between substrates and beach zones. The presence of rhodoliths at Gramuté Beach contributes to the heterogeneity of the ecosystem and increases the richness and diversity of the benthos. The character of the benthic community and its dynamic aspects are discussed herein and are extremely important for conservation actions.

**Descriptors:** Costa Das Algas environmental protection area, Faunal assemblage, Macrofauna, Meiofauna, Biodiversity.

## INTRODUCTION

Sandstones reefs play an important role in the coastal zone, providing habitats for a great variety of organisms such as algae and benthic invertebrates sessile and motile (Martinez, Mendes and Leite, 2012; Teodoro and Costa, 2018). This environment features spatial

heterogeneity, with high associated biodiversity and complex biological interactions (Soares et al., 2017; Queiroz et al., 2016). Sandstone reefs differ from coral reefs by their sediment composition and typical rocky shore, mainly due to their gentle slope (Rabelo et al., 2015). Despite its ecological and socio-economic importance given that it shelters species of commercial interest, intertidal sandstone reefs are less studied than other hard bottom environments (Soares et al., 2017), with a resulting knowledge gap about reef biodiversity, mainly when we refer to mobile fauna.

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In the state of Espírito Santo, southeastern Brazil, the north sector of the inner shelf is associated with abrasion terraces formed by lateritic concretions (Albino and Suguio, 2011). The beaches of this region are characterized by ferruginous sandstone reefs in the intertidal, and the sedimentary composition is predominantly bioclastic material, such as fragments of carbonate organisms like bryozoans, coralline algae, benthic foraminifera, and mollusks (Albino, Neto and Oliveira, 2016). Rhodolith nodules also contribute to local sedimentation, which are brought to the beach by storms or strong currents (Dias and Villaça, 2012; Andrades et al., 2014) brought in from adjacent rhodolith beds.

Rhodoliths are free-living nodules composed of coralline algae (Bosence, 1983) with three-dimensional structures and can be classified as 'ecosystem engineers' because they alter the physical features of the habitat (Bruno and Bartness, 2001; Nelson, 2009). The different growth forms and structures of the nodules form a microhabitat by providing a hard substrate for epibionts like other algae, sessile organisms, and small cryptic invertebrates that live inside the nodules, called cryptofauna (Steller et al., 2003; Amado-Filho and Pereira-Filho, 2012; Gondim et al., 2014). The cryptofauna of rhodoliths is generally composed of small annelids, crustaceans, mollusks, nematodes, and other groups that use the host substrate as shelter and food (Figueiredo et al., 2007; Costa et al., 2019; Sánchez-Latorre et al., 2020; Otero-Ferrer et al., 2019; Neto, Bernardino & Netto, 2021; Stelzer et al., 2021). The cryptofauna associated with the rhodoliths is represented by two ecological compartments, macro- and meiofauna. A joint analysis of both components of the benthic fauna is necessary due to the lack of information on the role of rhodoliths as a shelter for smaller organisms and larval stages.

Operationally, benthic invertebrates are classified according to the mesh opening size used to retain them. The meiofauna comprises organisms retained in the 45-63 µm mesh size, while the macrofauna are organisms 500-5000 µm in size (Giere, 2009; Ruiz-Abierno and Armenteros, 2017). In addition to body size, the

life history traits of the components are different (Gallucci et al., 2020). Macrofauna is more mobile and has a planktonic larval stage, which enables greater dispersal. In contrast, meiofauna has direct benthic development and less mobility in the substrate (Schratzberger et al., 2008). Meio- and macrofauna contribute fundamentally to the ecosystem processes and functioning of marine environments (Neto, Bernardino and Netto, 2021; Lam-Gordillo, 2020). They act in nutrient cycling, decomposition of organic matter, energy transfer to higher trophic levels, bioturbation of sediments, and are commonly used as bioindicators due to their sensitivity to environmental disturbances (Schratzberger and Ingels, 2018; Baldrighi and Manini, 2015).

In general, the presence of rhodoliths in the environment increases the biotic and structural complexity of the habitat, making more niches available (Figueiredo et al., 2007; Berlandi, Figueiredo and Paiva, 2012) and significantly increasing local biodiversity (Riosmena-Rodríguez, 2017). Some studies indicate that rhodoliths have higher richness and associated diversity compared to those in the surrounding sandy bottom and/or under the beds (Steller et al., 2003; Foster et al., 2013; Gabara et al., 2018; Stelzer et al., 2021). However, these works focus on macrofauna, with studies involving meiofauna as an important promoter of biodiversity associated with rhodoliths being scarce (Neto, Bernardino & Netto, 2021). Moreover, sampling is mostly carried out on beds, which are massive agglomerations of rhodoliths (Foster, 2001), constantly submerged, and at greater depths. Investigations of biodiversity associated with these algae in shallow intertidal or subtidal environments are neglected.

Therefore, the objective of the present study was to investigate the diversity of the benthic fauna (macro- and meiofauna) on different substrates (rhodoliths vs. unconsolidated sediment) in the sandstone reef. We expected that the fauna associated with the rhodoliths to be more diverse compared to unconsolidated sediment. We also investigated whether there are differences in benthic community structure between reef zones.

## METHODS

### STUDY AREA

The study was conducted on Gramuté Beach in the state of Espírito Santo, on the southeast coast of Brazil (19°58'21.48"S, 40°08'14.32"W) (Figure 1). The area is in the Environmental Protected Area (EPA) of Costa das Algas and is considered of high conservation importance. The site was created to protect biological diversity, mainly environments colonised by algae and associated benthic fauna, mangroves, coastal vegetation, and sedimentary formations (MMA/ICMBio, 2019).

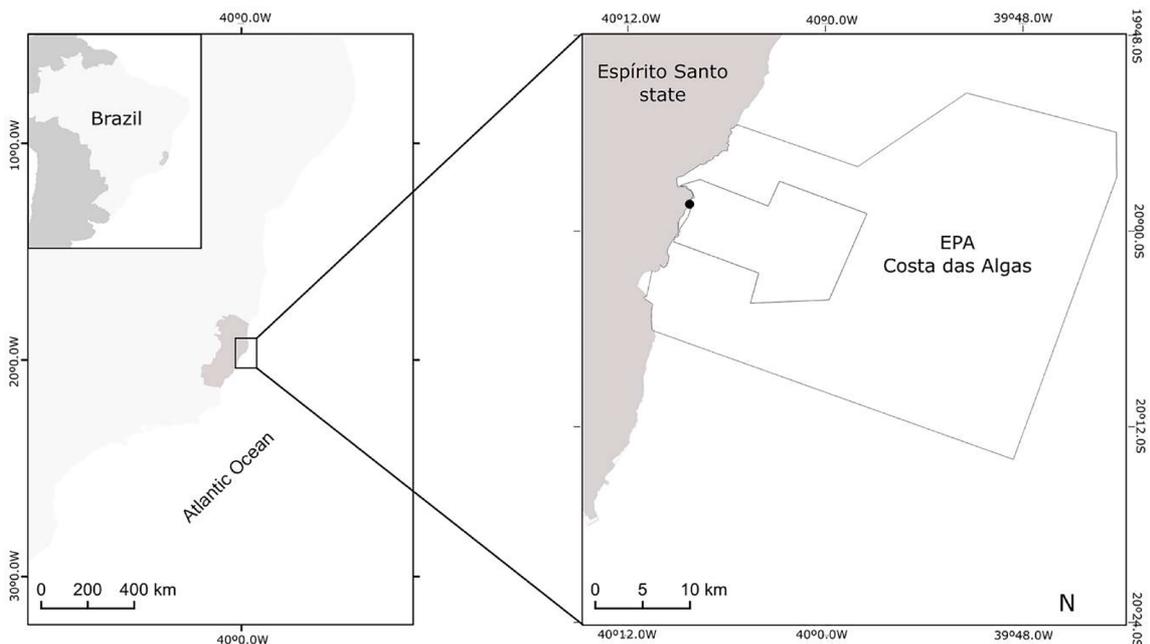
The region's geomorphology is characterized by abrasion terraces of the Barreiras Formation (Martin et al., 1996) that extend from the inner continental shelf to the coast. The intertidal and subtidal zones of Gramuté beach are mainly composed of ferruginous sandstone reefs. The reef structures, which are less than one meter in height, are exposed during low tide, and extensive tide pools form in the eroded reef spaces. In some places on the reefs, deposits of bioclastic sediment occurs, resulting from the intense fragmentation or encrustation of carbonate secreting organisms (Albino and Suguio, 2011). This deposit forms a

layer of unconsolidated sediment a few centimeters in thickness.

### FIELD AND LABORATORY PROCEDURES

To investigate the diversity of the benthic fauna of the unconsolidated sediments and associated rhodoliths, we sampled at three-month intervals for one year (May, August, and December 2013 and February 2014) in three beach zones: shallow subtidal (<1m depth), intertidal, and tidal pool. We collected four replicates of each substrate per zone. Samples were always collected during low spring tides. This study was authorised by the Instituto Chico Mendes de Conservação da Biodiversidade–ICMBio, under SISBIO (Biodiversity Information and Authorization System) license number 23658-2. Although sampling occurred over time, this work avoided a temporal analysis of the fauna.

To sample the unconsolidated sediment, we used 15cm x 15cm PVC squares randomly distributed in each zone to sample the macrofauna. We scraped the sediment from the delimited area with a spatula and immediately placed it in 0.5mm mesh bags to ensure organism retention. We fixed the contents in the field with 10% formaldehyde. Due to the irregularity of the



**Figure 1.** Location map of the study area. Black circle indicates Gramuté Beach.

sandstone reefs, the sampled sediment layers had different thicknesses, all greater than 5cm. Adjacent to the squares, we collected meiofauna with a plastic syringe (2 cm in diameter to a depth of 5 cm), added them to plastic jars, and fixed them immediately in 10% formalin. To analyze the meio- and macrofauna communities associated with the rhodoliths, we collected individual nodules with average sizes between 3.5 and 8.5. We placed each nodule in labeled plastic bags containing 7% magnesium chloride to anesthetize the associated fauna. After two hours, they were fixed with 10% formaldehyde.

## DATA ANALYSIS

To compare the contribution of each taxonomic group of macrofauna and meiofauna between substrates, the relative abundance of each was calculated. Univariate measures for both components of invertebrate fauna included number of taxa, Shannon-Wiener diversity ( $H' - \text{Log}2$ ), and rarefaction (ES50). The rarefaction index was less dependent on sample size (Soetaert and Heip, 1995) and based on the Sanders rarefaction technique, as modified by Hurlbert (1971). Using this index, the expected number of species (ES) for each sample was calculated for a given number of individuals. To compare univariate measures between different substrates (sediments and rhodoliths) and different zones, variance analysis using a generalised linear model (GLM) was conducted. After applying normality and homoscedasticity tests and residue analysis, we built models with the appropriate distribution in accordance with the data set, Gaussian for normal data, or Poisson for non-normal count data. The ecological descriptor data were analysed using 'VEGAN' (Oksanen et al., 2013), and models were analysed using the GLM and ANOVA functions of the R package 'CAR' in the R program environment (R Development Core Team, 2013).

Because of differences in sample size and units of density between the substrates (volumetric ( $\text{ind./cm}^3$ ) for rhodoliths and area ( $\text{ind./cm}^2$ ) for sediment), we used relative abundance data for multivariate analysis. We calculated the relative abundance of each taxon on the two substrates using the formula  $Ra (\%) = (n_i \times 100)/N$ , where  $n_i$

is the total abundance of the taxon  $i$  and  $N$  is the total abundance of the sample.

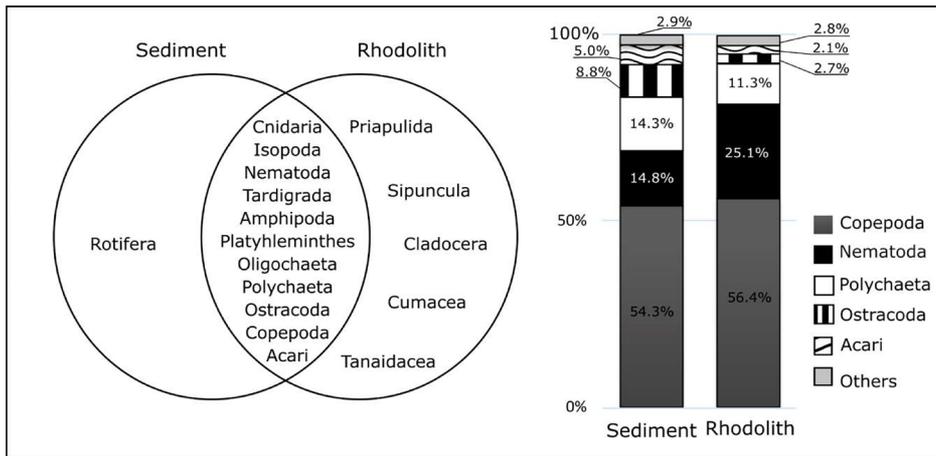
To examine variations in species composition between unconsolidated sediment and rhodoliths and in different zones, we applied nonmetric multidimensional scaling (nMDS). A similarity matrix was constructed using square root transformation and the Bray–Curtis coefficient. To assess differences in the composition of benthic fauna between substrates and zonation, a repeated-measure permutational analysis of variance (PERMANOVA) was used (Anderson, Gorley and Clarke, 2008). When PERMANOVA showed significant differences ( $p < 0.05$ ), a pair-wise comparison (999 permutations) was conducted to explore differences among pairs of levels of the selected factor. Similarity percentage analysis SIMPER (Clarke, 1993) was used to identify invertebrate taxa contributing to differences in the main factors identified by PERMANOVA. All multivariate and diversity analyses were performed using PRIMER v.7 and its add-on package PERMANOVA+ (Clarke and Warwick, 2001; Anderson, Gorley and Clarke, 2008).

## RESULTS

### MEIOFAUNA

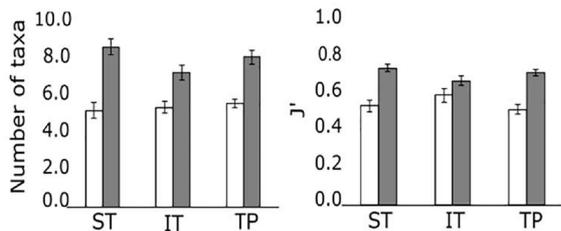
For meiofauna, 3,061 organisms and 12 taxa were recorded in the sediment, and 21,933 organisms and 16 taxa were associated with rhodoliths, totaling 24,994 individual organisms registered in the present study. The mean density found in sediment and rhodoliths was 203  $\text{ind./100 cm}^3$  and 1790  $\text{ind./100 cm}^3$ , respectively. Copepoda dominated the meiofauna, with 54.3% in sediment and 56.4% in rhodoliths). Numerically, nematodes ranked second among taxons with 14.8% in sediment and 25.1% in rhodoliths (Figure 2). The list of taxonomic groups associated with the unconsolidated sediment and rhodoliths on the sandstone reef at Gramuté Beach can be seen in Supplementary Table S1.

The number of meiofauna taxonomic groups was significantly higher in rhodoliths ( $16.145 \pm 6.115$ ) than in sediments ( $9.45 \pm 4.71$ ;  $\text{Pr}(>\text{Chi})$

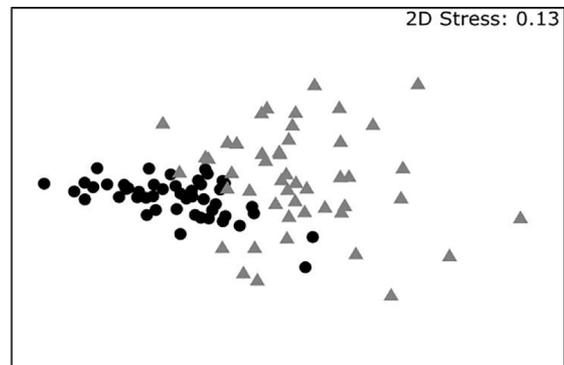


**Figure 2.** Taxonomic groups found in the present study and relative contribution of the main groups of meiofauna associated with rhodoliths and unconsolidated sediment.

= <0.001). Equitability ( $J'$ ) was also higher in rhodoliths ( $J' = 0.723 \pm 0.133$ ), demonstrating greater uniformity in the distribution of taxa compared to unconsolidated sediment ( $J' = 0.5604 \pm 0,087$ ;  $F = 52.013$ ,  $p <0.001$ ) (Figure 3). Equitability was also significantly different in sediment vs. zonation interaction ( $F = 3.190$ ,  $p <0.04$ ). Though diversity and ES50 were also higher in the rhodoliths, the difference was not statistically significant. The exploratory analysis nMDS (Figure 4) and PERMANOVA multifactorial found significant differences in the meiofaunal community structure between substrates (Table 2). A-posteriori pairwise comparisons indicate clear distinctions between meiofauna of unconsolidated sediment and rhodoliths ( $t = 5.570$ ;  $p =0.001$ ). However, zonation did not show well-defined groupings; there was no significant difference. SIMPER showed an average dissimilarity of 45.6% in meiofauna composition between substrates, mainly due to differences in abundance of Nematoda and Copepoda (Table 1).



**Figure 3.** Number of taxa and equitability ( $J'$ ) of meiofauna in sediment (white) and rhodolith (grey) in subtidal (ST), intertidal (IT) and tidal pool (TP) zones.



**Figure 4.** nMDS ordination for meiofauna density in rhodoliths (black circles) and sediments (grey triangles).

**Table 1.** Percentage similarity (SIMPER) of meiofauna associated with rhodoliths and unconsolidated sediment.

**Average dissimilarity = 45.67**

Taxonomic group	Rhodolith		Sediment	
	Av. dens	Av. Dens	Cont.%	Cum.%
Copepoda	93.24	41.38	30.68	30.68
Nematoda	61.32	20.03	23.49	54.17
Polychaeta	40.76	20.34	14.19	68.35
Acari	17.27	11.37	6.44	74.79

Cut-off for low contribution: 70%. Av. dens., average density; Cont. %, percentage contribution of each species to the group similarity; Cum. %, cumulative percentage contribution to group similarity.

**MACROFAUNA**

A total of 128 macrobenthic taxa were recorded in this study, 74 in sediment (22 exclusive) and 104 in rhodoliths (52 exclusive). In total, 8,252 macrofauna individuals were found in

**Table 2.** Results from the multivariate repeated measure PERMANOVA to test effects of substrate (sediment/rhodoliths) and zonation (subtidal/intertidal/tidal pool) on faunal descriptors and pair-wise comparisons for meio- and macrofauna; macrofauna as presence/absence data only. Significant P-values are in bold.

<b>Meiofauna</b>						
Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Substrate	1		13554	18.08	<b>0.001</b>	999
Zonation	2		1047.2	1.39	ns	998
Substrate x Zonation	2		944.72	1.26	ns	999
Residual	90		749.38			
<b>Macrofauna</b>						
Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Substrate	1	30015	30015	15.64	<b>0.001</b>	999
Zonation	2	13571	6785.4	3.53	<b>0.001</b>	997
Substrate x Zonation	2	9721.6	4860.8	2.53	<b>0.001</b>	999
Residual	88	1.688E5	1919.1			
<b>Pair-wise test</b>						
	t	P (perm)				
Sediment v Rhodolith	3.9547	<b>0.001</b>				
Subtidal v Intertidal	1.4218	<b>0.003</b>				
Subtidal v Tidal pool	2.2024	<b>0.001</b>				
Intertidal s Tidal pool	2.0426	<b>0.001</b>				
Subtidal (Rhodolith v Sediment)	2.1251	<b>0.001</b>				
Intertidal (Rhodolith v Sediment)	2.1928	<b>0.001</b>				
Tidal pool (Rhodolith v Sediment)	3.9187	<b>0.001</b>				

df, degrees of freedom; SS, square sum; MS, ns, non-significant.

both substrates, with 5,374 organisms occurring as infauna in the unconsolidated sediment and 2878 organisms associated with rhodoliths. The taxonomic list of macrofauna organisms can be seen in Supplementary [Table S2](#).

Polychaeta and Crustacea were the most abundant group in both substrates. In total, 31 families of polychaetes were identified, of which Syllidae and Spionidae were the most abundant (80.1 and 4.9%, respectively). In both substrates, Syllidae polychaetes were present in all samples.

Among crustaceans, Tanaidacea and Amphipoda were dominant in both substrates. Amphipoda, with 11 identified families, was the most abundant order associated with rhodoliths, mainly represented by *Globosolembos* sp. Tanaidacea was the most abundant taxon in unconsolidated sediments, represented by 4 families, with the genus *Leptocheilia* sp. being the most abundant.

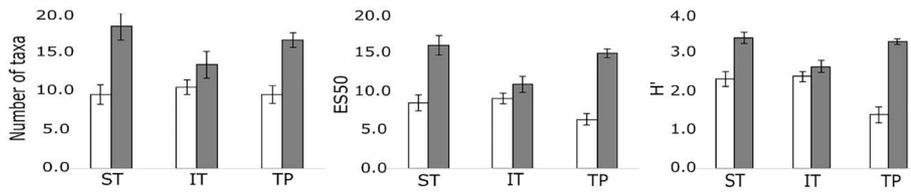
GLMs showed that both substrates and zonation had a significant effect on the macrofauna community structure. The number of taxa ( $F = 36.653$ ,  $p < 0.0001$ ) ES50 ( $F = 67.048$ ,  $p < 0.0001$ ) and diversity ( $\text{Pr}(>\text{Chi}) = 0.0002$ ) were significantly higher in rhodoliths ( $S = 16.145 \pm 6.115$ ; ES50

$= 13.771 \pm 4.396$ ;  $H' = 3.109 \pm 0.597$ ) than in sediments ( $S = 9.479 \pm 4.766$ ; ES50 =  $8.406 \pm 3.965$ ;  $H' = 1.941 \pm 0.915$ ) (Figure 5). According to nMDS ordination, there was a clear distinction in macrofauna structure between substrate. As such, PERMANOVA detected significant results between substrates and zonation (Table 2, Figure 6).

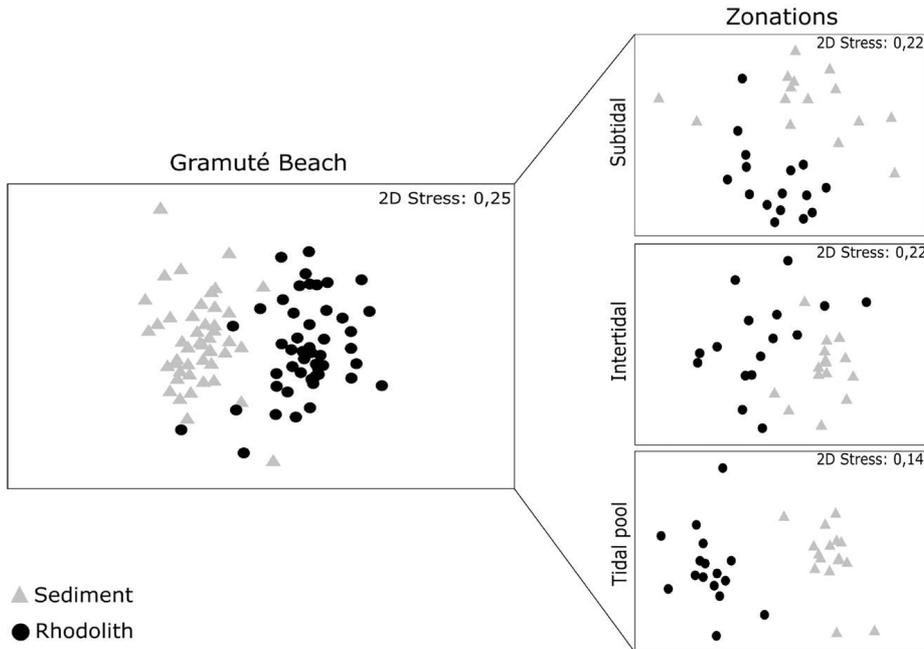
SIMPER analyses of relative abundance data showed a considerable dissimilarity (74.71%) in average species composition between substrates. The amphipod *Globosolembos* sp., the polychaete *Nematonereis* sp., and the echinoderms of the Ophiuroidea class had higher relative abundance in the rhodolith samples, while polychaetes of the family Syllidae and Nematoda were more frequent in unconsolidated sediment. These five taxa were mainly responsible for the dissimilarity between the substrates (Table 3).

## DISCUSSION

Structurally more complex environments favour the presence of a diverse benthic fauna (Yanovski *et al.*, 2017; Otero-Ferrer *et al.*, 2019). In rhodoliths, the properties that provide complexity to microhabitats are shape, volume, porosity, size of the nodules, amount of sediment



**Figure 5.** Number of taxa, ES50 and diversity (H') of macrofaunal at sediment (white) and rhodolith (grey). Zones: ST = subtidal, IT = intertidal, TP = tidal pool



**Figure 6.** nMDS ordination for macrofauna relative abundance data in Gramuté Beach and for zones (tidal pool, intertidal and subtidal). Representation of rhodoliths (dark circles) and sediments (grey triangles).

**Table 3.** Percentage similarity (SIMPER) of macrofauna associated with rhodoliths and unconsolidated sediment.

Average dissimilarity = 74.71%

Species	Sediment		Rhodolith	
	Av. Ab.	Av.Ab.	Cont. %	Cum. %
Syllidae (Polychaeta)	6.57	4.95	6.2	6.2
<i>Globosolembos</i> sp. (Amphipoda)	0.33	2.55	5.89	12.09
Nematoda	2.71	0.54	5.66	17.74
<i>Nematonereis</i> sp. (Polychaeta)	0.37	1.78	3.96	21.7
Ophiuroidea	0.05	1.52	3.51	25.21
<i>Cirolana</i> sp. (Isopoda)	0.87	1.36	3.36	28.57
<i>Leptochelia</i> sp. (Tanaidacea)	1.24	0.59	3.11	31.68
Ostracoda	0.62	1.03	2.82	34.5
<i>Bunakenia</i> sp. (Tanaidacea)	0.10	0.10	2.76	37.26
<i>Parhyale</i> sp. (Amphipoda)	0.62	0.80	2.61	39.88

Cut-off for low contribution: ten species with the highest contributions. Av. ab. = average density; Cont. % = percentage contribution of each species to the group similarity; Cum. % = cumulative percentage contribution to group

trapped in the holes, and epiphytic algae adhered to surfaces (Amado-Filho *et al.*, 2010; Veras *et al.*, 2020). Thus, the presence of free nodules on the abrasion terrace on Gramuté Beach increases the possibility of shelter and protection for various organisms and corroborates the hypothesis that benthic fauna richness and diversity (meiofauna and macrofauna) in sandstones reefs is higher in rhodolith beds than in the sediment deposited in the surroundings.

Steller *et al.* (2003) and Robinson (2015) also demonstrated that greater species richness and diversity are typically associated with live rhodoliths rather than unconsolidated gravelly sediments and algae fragments. More recently, Stelzer *et al.* (2021) investigated the fauna associated with rhodolith beds on the continental shelf adjacent to Gramuté Beach at the isobath of approximately 50m and compared it to the sediment under the beds. As expected, the authors found higher numbers of species in the algae and higher functional diversity. Our results demonstrate that, in the same way as on a rhodolith bank on the continental shelf, rhodoliths of shallow intertidal or subtidal environments also increase the richness and diversity of the benthos.

The present study is the first to include meiofauna in a comparison between rhodolith nodules and adjacent sediment in a beach environment with intertidal sandstone reefs. Although knowledge about rhodolith beds has developed over the past few decades in various aspects, such as geological, taxonomic, and ecological (Amado-Filho *et al.*, 2017; Costa *et al.*, 2021a; Otero-Ferrer, *et al.*, 2019; Riul *et al.*, 2009; Rocha *et al.*, 2020), the interaction patterns and processes with the benthic cryptofaunal communities, especially the meiofauna, remain poorly studied.

Shratzberger and Ingels (2017) highlighted the importance of knowledge about the role of meiofauna in benthic ecosystems. In the coastal region, where the environment is constantly subject to anthropogenic stressors (Lu *et al.*, 2018), meiofaunal communities are less vulnerable to disturbance than macrofauna. Due to their continuous reproduction strategy, recolonization of disturbed sediments by meiofauna is facilitated

(Costa and Netto, 2014) in contrast to the slower recolonization of macrofauna. Therefore, meiofauna activities may increase the resilience of ecosystem processes, such as energy transfer and nutrient regeneration (Baldrighi and Manini, 2015).

Multivariate analyses (nMDS, PERMANOVA and SIMPER) showed variations in macrofauna and meiofauna community structure between substrates, as well as spatial differences between the subtidal, intertidal, and tidal pools for the macrofauna. Stelzer *et al.* (2021) also observed differences in macrofauna composition between sediments under beds and rhodoliths. The authors attribute these changes to a high turnover of taxa between substrates and to the fact that macrofauna of the unconsolidated sediment is not a subgroup of species inhabiting the nodules (and vice versa). Differences in faunal composition and community descriptors between zonations were expected. Because it is an intertidal environment alternating between emersed and submerged periods, the zones have different hydrodynamics, daily variations in salinity and temperature, and availability of food (Correia *et al.*, 2018). Therefore, the taxonomic composition of the community may be different among the beach zones due to the distinct responses and adaptations of the taxa to environmental variations (Celentano *et al.*, 2019).

Regarding the meiofauna taxonomic groups composition, we highlight that the higher richness in the rhodoliths is due to the exclusive presence of juveniles of the groups Priapulida, Sipuncula, Cladocera, Cumacea, and Tanaidacea, which are components of the temporary meiofauna (Bianchelli *et al.*, 2010). Thus, when they achieve the adult stage, with a larger body size, these can become components of the macrofauna.

The taxonomic groups that contributed the most to meiofauna density were the same for both substrates studied. High densities of Copepoda and Nematoda, such as those recorded in the present study, were also found in studies of carbonate sediments deposited on the coral reefs of Atol das Rocas (Netto, Attrill and Warwick, 1999; Pereira *et al.*, 2008), which has granulometric characteristics similar to Gramuté Beach. Sarmiento, Barreto and Santos (2011), investigating the meiofauna

associated with sediments adjacent to sandstone reefs in Porto de Galinhas (northeast of Brazil), also verified the dominance of these two groups. In sediments characterized by the predominance of coarse sand, copepods are generally the dominant group because they are well adapted to high energy environments due to their brief life cycle and preference for oxygen-rich environments (Hicks, 1985; Higgins and Thiel, 1988). The meiofauna associated with algae is also dominated by copepods, mostly of the order Harpacticoida (Sarmiento and Santos, 2012).

Nematoda, the second most abundant group of meiofauna, also occurred as macrofauna in the unconsolidated sediment as the third taxonomic group in total number of individuals. Diversity in mouth parts and the small and elongated body of Nematoda allow them to occupy interstitial spaces in several ecosystems with unique characteristics (Kiontke and Fitch, 2013; Venekey and Santos, 2017).

In both substrates, polychaetes contributed most to the abundance of macrofauna, corroborating several studies investigating the community of associated invertebrates (Figueiredo et al., 2007; Costa et al., 2021b; Stelzer et al., 2021). In this study, the Syllidae family was predominant among polychaetes. This family is one of the most diverse and widely distributed in the world and can be found in high densities on various substrates, including calcareous algae and corals reefs (Antoniadou and Chintiroglou 2006), mainly in shallow water. General feeding and reproduction strategies, active and mobile lifestyles, and the ability to move in interstitial spaces are factors that may contribute to the success of this family in various environments (Martins et al., 2013; Fukuda, 2017).

The subphylum Crustacea was the second most abundant macrofauna in both substrates. Peracarid crustaceans are commonly associated with algae and carbonaceous sediments (Bueno et al., 2016) due to a wide variety of life modes, such as free-living or tube-building, and various feeding modes, suggesting that organisms in this group can exploit a range of resources (Guerra-Garcia et al., 2014). The great abundance of amphipods associated with rhodoliths was also described by

other authors, who pointed out that amphipods and polychaetes were the most dominant cryptofauna (De Grave, 1999; Figueiredo et al., 2007; Neill et al., 2015; Robinson, 2015). In unconsolidated sediment, there was a greater representation of Tanaidacea, most of which belonging to the genus *Leptochelia* sp., considered the best adapted and most abundant genus found in shallow waters worldwide (Hiebert, 2015; Larsen, Gutu and Sieg, 2015).

The echinoderms of the Ophiuroidea class were also represented in the fauna associated with rhodoliths. Gondim et al. (2014) had already observed that echinoderms have a preference for rhodoliths. On a rhodolith bank in Paraíba, Brazil, these authors recorded greater richness and diversity of echinoderms than in other marine environments within the same geographical region. More data on species assemblages of echinoderms and other phyla are needed to understand lifestyles and life cycles. Do they complete the entire life cycle inside the nodule or just part of early development? Can they migrate to other environments (Prata et al., 2017)? These are but two of the many questions to be addressed in future studies of this unique environment and its ecology.

In studies with rhodoliths, care should be taken when comparing results because estimates of ecological indices depend on sample design (Sciberras et al., 2009). Research investigating cryptofauna associated with rhodoliths use different methodological approaches. For example, Steller et al. (2003) and Trejo et al. (2020) sampled random rhodoliths arranged in different transects on different beds in California and New Zealand. The sampling unit for the density of associated organisms was  $\text{ind}/\text{cm}^3$ , and they already used the size measurements of each nodule. However, Neto, Bernardino & Netto (2021), and Stelzer et al. (2021) delimited squares on beds in southeastern Brazil and collected all individuals. The sampling unit for density of organisms was per unit area ( $\text{m}^2$ ). In this study, we randomly collected individual rhodoliths in different zonations of a sandstone reef between seas and the unconsolidated sediment per square. The difference in units of measurement between substrates ( $\text{cm}^3$  for

rhodolith nodules vs. cm<sup>2</sup> for sediment of squares) used to analyze macrofauna in the present study did not allow for a more detailed comparison between abundance and density of the associated fauna. When comparing distinct substrates (such as unconsolidated sediment and rhodolith beds), we suggest that a sampling strategy be devised to measure parameters in a common unit of measurement, preferably volume to quantify both substrates (i.e., cm<sup>3</sup>).

In terms of significance, this study was the first to verify the composition of benthic macrofauna and meiofauna in rhodolith in intertidal environments. The scarcity of information on the subject makes it difficult to discuss the interaction between fauna associated with rhodoliths and unconsolidated sediments and the processes involved, such as turnover and species and interspecies interactions. Gramuté Beach is an environment composed of a mosaic of habitats, with structural elements such as hard-bottom, sandy beach, tide pools, and a great diversity of algal fronds in the infralittoral. Carvalho and Barros (2017) state that habitats with a wide variety of elements support greater richness and abundance of organisms. As a conservation unit with scant information on local biodiversity, still without a management plan, and with scarce studies on the faunal composition (Mazzuco *et al.*, 2019; Pimentel *et al.*, 2019), there is a need for more information to consolidate conservation status.

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## AUTHOR CONTRIBUTIONS

S.B.N.: Investigation; Methodology; Writing - original draft; Writing - review & editing.

K.G.C.: Conceptualization; Supervision; Writing - review & editing.

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