Community Ecology (2026) 27:35–44
https://doi.org/10.1007/s42974-026-00292-7

ORIGINAL ARTICLE

Influence of the structural complexity of phytal substrates on intertidal meiofaunal community structure in a tropical system (NE Brazil)

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Received: 25 November 2024 / Accepted: 17 February 2026 / Published online: 17 February 2026
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Abstract

Phytal environments harbor meiofaunal communities due to the variety of available niches and resources. Meiofauna play essential roles in aquatic ecosystems, contributing to energy transfer in food webs, recycling organic matter, and serving as bioindicators of environmental changes. Despite their ecological importance, studies on phytal meiofauna remain scarce in tropical systems, especially along the Amazonian coast of Brazil. In this context, the present study analyzed the effects of the structural complexity of *Spartina alterniflora* and *Ulva lactuca* from the Maranhão Gulf (Maranhão, Brazil) on meiofaunal community structure. Ten specimens from each species were collected over a period of five months, totaling 100 samples. Eighteen taxa were recorded, with 16 associated with S. alterniflora and 13 with *U. lactuca*. Mean densities were 3.22 ± 1.17 ind. 10 cm^{-2} in S. alterniflora and 2.8 ± 2 ind. 10 cm^{-2} in *U. lactuca*. Nematoda, Copepoda, and Amphipoda dominated, with nematodes more abundant in S. alterniflora and amphipods in *U. lactuca*. Structural complexity did not significantly affect meiofauna density; however, it strongly influenced taxonomic richness and community composition. These findings highlight the relevance of substrate complexity in shaping tropical meiofaunal communities and provide a baseline for future ecological and monitoring studies in Amazonian coastal ecosystems.

Keywords Benthos · Macrotidal · *Spartina alterniflora* · Spatial heterogeneity · Tropical environment · *Ulva lactuca*

Introduction

Benthic meiofauna is an important food source for both macrofauna and ichthyofauna, comprising part of the total energy required by their consumers (de Tito and Bondiou 1984). In addition, meiofaunal organisms are regularly employed in environmental monitoring studies (Allouche et al. 2021; Michelet et al. 2021; Gheller and Corbisier 2022), due to close associations and dependence on sediment, short life cycle with benthic larval stages and high density, diversity, and sensitivity to environmental changes (Zarghami et al. 2020).

Besides inhabiting sediments, meiofauna organisms can also occupy other substrates (Cerrano et al. 2015; Vieira et al. 2018). However, for the meiofauna to colonize a certain type of substrate, both colonizable space and the accumulation of degradable organic matter for feeding are required (Fonsêca-Genevois et al. 2006).

Complex phytal substrates provide a greater variety of food resources (Hicks 1980) and better protection from predators (Coull and Wells 1983), desiccation, and wave action (Hooper and Davenport 2006; Norderhaug et al. 2014), facilitating sediment trapping (Giere 2009). Therefore, meiofauna associated with complex substrates generally exhibit greater abundance and diversity than those associated with less complex ones (Hooper and Davenport 2006; Frame et al. 2007; Veiga et al. 2016; Ape et al. 2018a).

The architecture of phytal substrates plays a fundamental role in the structure of meiofaunal communities, as it

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provides a variety of microhabitats and niches for these organisms (Duarte et al. 2020). In macroalgae, where colonization by meiofauna is better documented (Santos et al. 2025), the organisms stay at the base of the fronds and in the interstices between the rhizoids (da Rocha et al. 2006).

Among the various taxa of invertebrates that occur in the meiofauna, Copepoda, Halacaridae, Nematoda, and Ostracoda are the principal representatives of the so-called "phytal meiofauna" (Hicks 1985). The presence of these groups in phytal substrates is well reported in the literature, given their occurrence and representativeness in studies that analyze the colonization of substrates by meiofauna (Santos et al. 2025).

Most quantitative phytal meiofauna studies focus on specific taxa, such as Copepoda Harpacticoida, Nematoda, Turbellaria, and Ostracoda (Veiga et al. 2016), and few consider the entire community structure (Ape et al. 2018a, b; Gan et al. 2019). In this regard, studies regarding meiofauna associated with phytal substrates for the Brazilian coast are scarce, especially compared to macrofauna or even meiofauna assessments in sedimentary environments (Vieira et al. 2018). This is especially true for the state of Maranhão (Brazil), with still insufficient studies concerning this community available.

The state of Maranhão has the second longest coastline in Brazil (El-Robrini et al. 2006). This coastal region is divided between two coastlines, divided by the Bay of São Marcos. The western portion of the state belongs to the Amazon coast and the eastern portion to the northern northeastern coast (Villwock et al. 2005). Maranhão Island is located in the transition region between these two distinct types of coastlines (Silveira 1964). The coast of Maranhão is characterized by a variety of vegetated coastal environments, including wetlands, dune fields, mangroves, beaches, and sandbanks (Santos et al. 2024). Despite the diversity of environments and vegetated substrates found there, there are no published studies on the colonization of these substrates by meiofauna in Maranhão or other regions of the Amazon Coast.

To analyze the influence of phytal substrate complexity on meiofaunal community structuring, the present study considered two native plant species, the salt marsh plant *Spartina alterniflora* Loisel 1807 and the algae *Ulva lactuca* Linnaeus 1753. *Spartina alterniflora* is a facultative pioneer halophyte, dominant in saline sites that serves as a substrate for many epiphytic organisms (Gleason 1986; Lin et al. 2015). Differences in the shape and spatial dispersal of its stalks can lead to structural changes of associated fauna, due to the reduced foraging efficiency of large predators (Macy et al. 2019). *Ulva lactuca* (considered to be a synonym of *U. fasciata* Delile, 1813 by Guiry and Guiry 2022) is exposed during low tides for long periods of time, resisting desiccation due to the shape of its thallus, allowing it to maintain inter-fold moisture, serving as food, refuge, and protection against desiccation for numerous microinvertebrates (Vieira et al. 2018; Liu et al. 2020).

Banks of *S. alterniflora* are common environments in the coastal-estuarine zone off the coast of the island of Maranhão (Brazil). They are usually found in the upper mediolittoral in front of mangrove banks and tidal flats, forming homogeneous and/or mixed fields, with the presence of mangrove seedlings growing alongside them (Rebelo 2000; Ferreira et al. 2012). *U. fasciata* is also a fairly common species on the coast of Maranhão. They are commonly found on rocky shores and tidal pools, in the surf zone. In certain months of the year, this macroalga quickly colonizes large stretches of rock, adding color to the landscape (Correia and Brandão 1974).

In this sense, this study analyzed the effect of the structural complexity of these two phytal substrates on the structures of intertidal meiofaunal communities in two Maranhão Gulf regions located on Brazilian Amazon Coast. We hypothesize that density, taxa richness, and community structure differ between phytal substrates as a function of their structural complexity, with higher density and richness values found in more complex substrates.

Materials and methods

Study area

The coastal vegetation of the Maranhão Gulf is composed of mangroves, beach vegetation, and leafy trees (dos Santos et al. 2014) (Fig. 1). *Spartina alterniflora* specimens were sampled from Caúra beach (2°33′25″S; 4°2′19″W), in São José Bay, municipality of São José de Ribamar, in the northeast of Maranhão Island (Brazil). This beach is about 1 km long and undergoes intense wind, sea and riverine activity, generating waves and currents that shape local cliffs, mangroves, and local islands (Mederiros 1988). It has a flat surface, with no elevated sandy deposits. The area has a dry period from August to December, and a rainy period that begins in January and continues until June (Amorim et al. 2023). The climate in the region is Aw (tropical) (Alvares et al. 2013), with average rainfall of around 2000 mm/year and an average temperature of 28 °C, with a minimum of 25 °C and a maximum of 33 °C (INMET, 2023).

Ulva lactuca specimens were sampled at Medo Island (01°27′S; 44°12′W), in São Marcos Bay. The island lies in the portion of the bay with an active estuary, with a well-developed central channel dominated by ebb currents (Muehe 2006; Castro et al. 2014). Its geomorphological structure includes cliffs, streambeds, beaches, dunes, talus

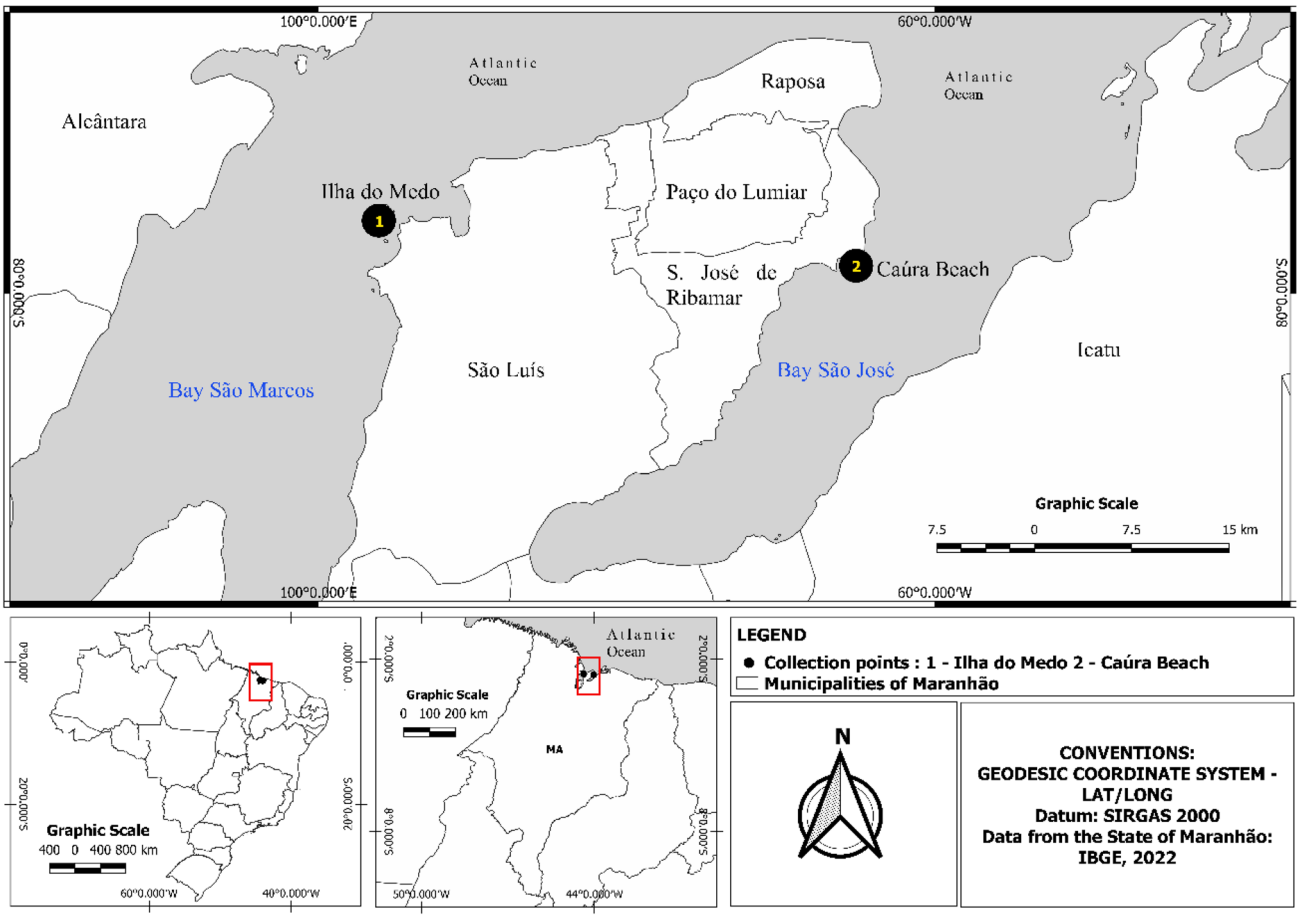


Fig. 1 Location of the *Ulva lactuca* and *Spartina alterniflora* sampling areas, Maranhão Gulf, Maranhão, Brazil

deposits, and tidal flats. The island's vegetation is made up of mangroves, beach vegetation, and leafy trees and its soil varies from clayey to sandy (dos Santos et al. 2014).

Phytal morphology

Spartina alterniflora Loisel (1807) is a cespitose herb with thick rhizomes and stout, erect aerial stems, ranging from 100 to 150 cm in length (Caetano et al. 2017). This species exhibits alternate, glabrous linear-lanceolate leaves, 10–30 cm long and 4.5 mm wide (Soriano-Sierra et al. 2014). Its flowers consist of 5 to 14 cm long white inflorescences ending in spikes and exhibiting two to three spikelets, some oval and aristate (Bortolus and Schwindt 2018). It is found near igarapés (streams), forming dense spots bordering mangroves (Bortolus and Schwindt 2018).

Ulva lactuca Linnaeus (1753) exhibits a rigid membranous consistency, reaching 2 to 10 cm in height with a foliaceous, irregular, and lobed thallus (Aguilar-Rosas et al. 2005). The most frequent form is a 1 to 4 cm wide-band attached to the substrate by a tiny holdfast and fronds consisting of two cell layers 0.065 to 0.096 mm thick and thick cuticles ranging from 0.004 to 0.009 mm (Kazi et al. 2016).

Sampling and sample processing

Ten specimens from each phytal substrate were collected during low tide for five months (May, June, August, September, and October 2014), totaling 50 samples of each substrate. *S. alterniflora* specimens were collected manually from the same bank in the supralittoral zone each month. The samples were extracted from the base and wrapped in plastic bags, while *U. lactuca* specimens were collected manually of tide pools and packaged in 500 mL plastic bottles for transport. To ensure independence of the samples, replicates of *S. alterniflora* were sampled in different areas of the bank and each replicate of *U. lactuca* was collected in different pools.

At the laboratory, the samples were washed under running water over superimposed 0.5 mm and 0.053 mm mesh sieves, according to Boisseau (1975). The material retained in the 0.053 mm sieve was conserved in a 4% formalin

saline solution in plastic recipients and elutriated manually in a beaker. The supernatant was then transferred to a Dollfus plate. All meiobenthic organisms were counted and categorized into major groups employing a stereomicroscope.

Structural complexity of phytal substrates

Structural complexity was measured using biomass and fractal dimensions of substrates as proxies for habitat size and architecture, respectively (Gee and Warwick 1994; Hooper and Davenport 2006; Veiga et al. 2014, 2016; Torres et al. 2015; Ape et al. 2018a). The substrates were dried for 48 h at 60 °C and then weighed to determine the biomass in grams (Veiga et al. 2014, 2016; Torres et al. 2015; Ape et al. 2018a).

Each substrate replica was lightly crushed and photographed with a digital camera Canon EOS Rebel T7 EF-S 18-55 f/3.5–5.6 IS II BR, to obtain the fractal dimensions. Fractal dimensions were calculated according to McAbendroth et al. (2005). Each photograph was converted to TIFF format and transferred to grayscale. A threshold was set to produce a binary image used to quantify the fractal dimensions of area (Da) and perimeter (Dp) for each image, using ImageJ software (Rasband 1997–2012). Da is a measure of the spaces between the branches, so higher values indicate a higher degree of branching (McAbendroth et al. 2005; Torres et al. 2015). Dp is a measure of the contour of the macroalgae or the degree of convolutions of its edges, so larger values indicate more divisions at smaller scales (McAbendroth et al. 2005; Torres et al. 2015).

Biomass was used here as a proxy for habitat size, while fractal dimensions were considered descriptors of habitat architecture. Although biomass and fractal dimensions may covary to some degree, they represent distinct descriptors: biomass reflects habitat size, whereas Da and Dp quantify the branching degree and edge convolutions of the substrate, i.e., its architectural complexity. These attributes are not strictly dependent on biomass, since substrates with similar weight can differ markedly in morphology and fractal geometry. Thus, we analyzed biomass and fractal measures separately to disentangle the effects of size and architecture on meiofaunal assemblages.

We hypothesized that differences in meiofaunal assemblages would be more influenced by architectural complexity (Da, Dp) than by total habitat size (biomass), in agreement with previous studies (Attrill et al. 2000; Christie et al. 2009).

Data analysis

The normality of the biomass, fractal area (Da), and fractal perimeter (Dp) data transformed log(x) was tested by the Shapiro-Wilk test. Statistical differences on these descriptors were determined by a Student's t-test performed for each data set.

The relative abundance, density, richness, and occurrence frequency of each taxon were calculated. To determine the influence of structural complexity (i.e. biomass, Da, and Dp) on density, taxa richness (measurement in the number of taxa), and community structure, a mixed linear model using 9999 permutations with a Type I (sequential) sum of squares was used to calculate p-values from a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2014). In the analysis, the sampling areas were considered random effects and substrate identity was a fixed factor with two levels (*S. alterniflora* and *U. lactuca*), and biomass, Da and Dp were covariates. Interactions between categorical variables (identity of phytal substrates) and continuous predictor variables (biomass, Da, and Dp) were included in the analyses (Veiga et al. 2014). The analyses were done on the basis of Euclidean similarity matrices for abundance and richness and Bray-Curtis similarity matrices for multivariate data (Veiga et al. 2014).

A non-metric multi-dimensional scaling (nMDS) plot was constructed to better visualize inter-group relationships (Clarke 1993). A Similarity Percentages (SIMPER) test was then performed to identify the groups that most contributed to significant effects (Clarke 1993). All analyses were performed using the R software (R Core Team 2022) packages car (Fox and Weisberg 2019), ggplot2 (Wickham 2016), lattice (Sarkar 2008), permute (Simpson et al. 2022), and vegan (Oksanem et al. 2022).

Results

Structural complexity of phytal substrates

Biomass values and fractal measurements varied considerably among the studied phytal substrates, with the highest values found in *S. alterniflora* for all three variables. (Fig. 2). Student's t-test revealed the two substrates studied differed significantly for biomass ($t_{91}=6.233$; $p=7^{-12}$), fractal area ($t_{91}=4.025$; $p=0.0002$), and fractal perimeter ($t_{91}=1.105$; $p=0.003$).

Taxonomic composition

A total of 27.502 organisms and 18 taxa were identified in both substrates, of which 14.852 organisms and 16 taxa were associated with *S. alterniflora*, and 12.650 organisms and 13 taxa with *U. lactuca*. The mean density of *S. alterniflora* individuals was 3.22 ± 1.17 ind.10 cm^{-2}, and of *U. lactuca*, 2.8 ± 2 ind.10 cm^{-2}. Nematoda, Copepoda, and Amphipoda

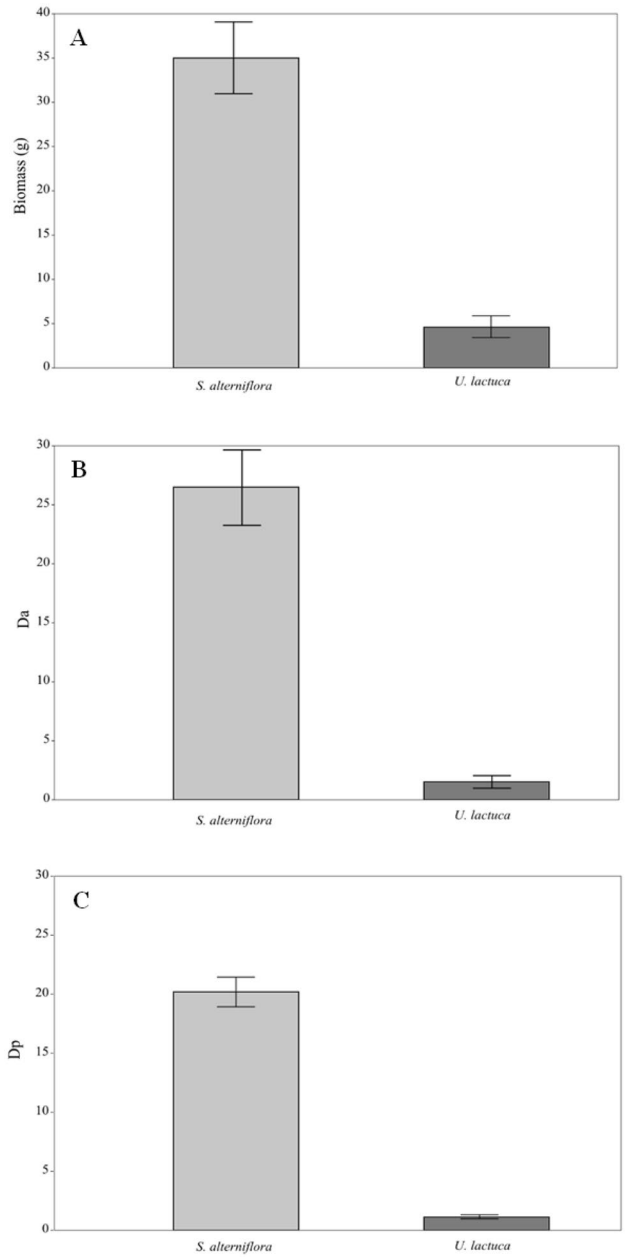


Fig. 2 Means (±standard deviation) of biomass (**A**), fractal dimensions based on area (Da) (**B**), and fractal dimensions based on perimeter (Dp) (**C**) of *S. alterniflora* and *U. lactuca*

were the most abundant and frequent groups, with the first two more representative in *S. alterniflora* and the latter two more representative in *U. lactuca*. Copepoda occurred in all the samples in both substrates. (Table 1).

The structural complexity of the phytal substrates did not affect meiofauna density during the study period. Richness, on the other hand, was significantly affected, with pairwise comparisons indicating that taxa richness in *S. alterniflora* was significantly higher than in *U. lactuca* (Fig. 2; Table 2).

Table 1 Relative abundance (Rel.ab) and occurrence frequency (OF) for each taxa detected in each phytal substrate

Taxa	Spartina alterniflora		Ulva lactuca	
	Rel.ab (%)	OF (%)	Rel.ab (%)	OF (%)
Acari	4.75	85	3.25	30
Amphipoda	0.6	30	16.65	95
Bivalve	3.4	90	0	0
Cnidaria	0	0	3.09	10
Copepoda	18.8	100	39.43	100
Echinodermata	0.41	10	0	0
Gastropoda	0.93	70	3.25	20
Gastrotricha	2.52	45	4.2	20
Insecta	0.6	45	0	0
Isopoda	0.6	10	4.09	60
Nematoda	62.87	100	6.39	70
Oligochaeta	0.74	20	4.23	50
Ostracoda	0.91	50	3.29	70
Polychaeta	0.7	60	5.2	65
Pycnogonida	0.56	5	0	0
Rotifera	0.8	25	2.99	10
Tardigrada	0.8	5	0	0
Turbellaria	0	0	3.93	40

Meiofaunal communities also differed among the substrates according to the PERMANOVA results (Table 2).

In addition, both richness and community structure showed significant interactions with Da, Dp, and Bi. These interactions are ecologically relevant because they indicate that the response of richness to structural complexity depends on the identity of the phytal substrate. In other words, fractal dimensions and biomass do not exert a uniform effect, but instead modulate meiofaunal diversity differently across substrates, highlighting the combined influence of habitat architecture and substrate type on community organization. These results indicate that the effect of structural complexity descriptors differed among the substrates studied, regardless of their identity (Table 2).

The observed multivariate pattern indicates a clear separation between substrates in the nMDS ordering (Fig. 3). The groups that contributed most to substrate type differences were Nematoda, Copepoda, Amphipoda, and Polychaeta (Table 3). Nematoda was the taxonomic group that contributed most to the dissimilarity between the two substrates, with a significant difference in average abundance between *S. alterniflora* and *U. lactuca*. Therefore, the presence or absence of nematodes explains almost half of the difference between the two substrates (Fig. 4).

Discussion

The findings indicate that phytal substrate complexity plays a significant role in meiofauna community diversity and structure, partially supporting the hypothesis of this study.

Table 2 PERMANOVA results concerning taxa richness and density and meiofaunal community structure associated with *S. alterniflora* and *U. lactuca*, respectively

	Richness			Density		Community structure	
	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Da	1	0.341	2.979*	0.07	0.95	1.43	31.51***
Dp	1	0.138	1.209**	0.33	0.44	2.97	9.102***
Bi	1	0.065	0.567**	0.025	0.223	1.376	33.341*
Pi	1	0.249	2.178***	0.02	0.176	2.739	24.76***
Da x Pi	1	0.006	0.056*	0.042	0.367	0.124	20.511**
Dp x Pi	1	0.141	1.231	0.033	0.289	0.05	12.639
Bi X Pi	1	0.137	1.202**	0.092	0.810	0.023	6.61
Residual	91	0.05		0.018		0.091	

Da dimensions of area, *Dp* dimensions of perimeter, *Bi* biomass, *Pi* phytal identity

*$p<0.05$; **$p<0.01$; ***$p<0.001$

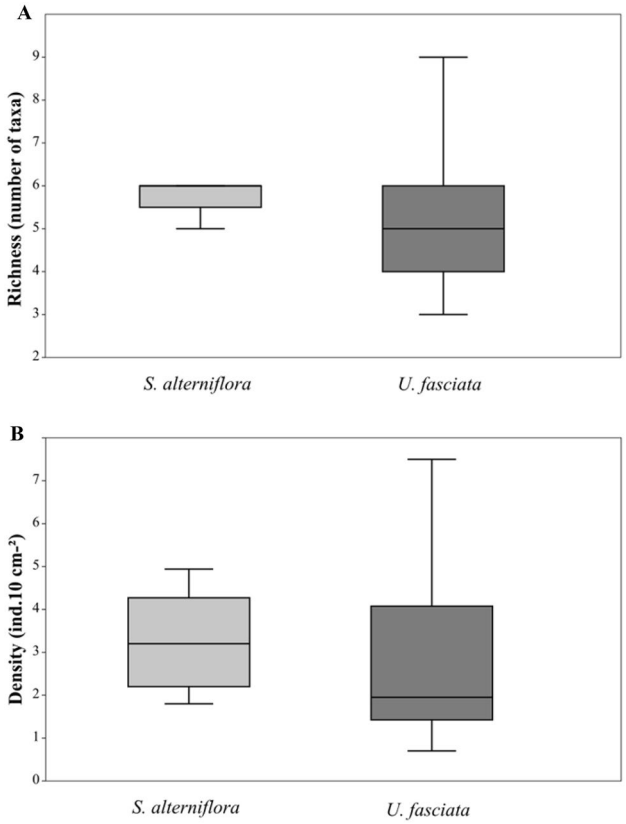


Fig. 3 Box–Whisker plots showing the distribution of (**A**) taxa richness (number of taxa) and (**B**) density (ind.10 cm^{-2}) of meiofaunal communities associated with *Spartina alterniflora* and *Ulva lactuca*

Table 3 SIMPER results indicatings the relative contribution (%) of the four taxonomic groups that contributed the most to significant differences between the faunas associated with *S. alterniflora* (S) and *U. lactuca* (U)

Taxa	Dissimilarity	Contribution (%)	Mean abundance of *S. alterniflora*	Mean abundance of *U. lactuca*
Nematoda (S)	28.32	41.8	62.9	6.38
Copepoda (U)	12.17	17.95	18.8	39.4
Amphipoda (U)	8.024	11.84	0.6	16.6
Polychaeta (U)	2.251	3.321	0.7	5.19

The abbreviations in front of each taxa represent the substrate in which the group was the most abundant

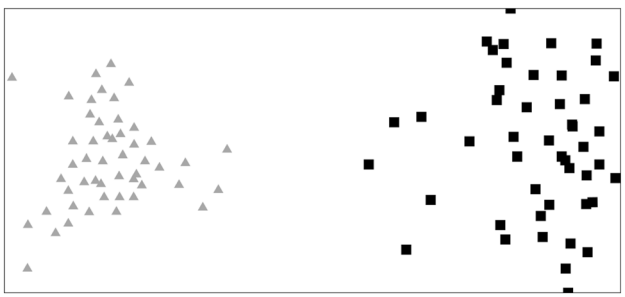


Fig. 4 nMDS ordination based on the abundances of all taxonomic groups detected in the sampled meiofaunal communities and Bray–Curtis similarity associated with *S. alterniflora* and *U. lactuca* (triangles and squares, respectively). 3D Stress: 0.04533

Considering biomass, fractal area, and fractal perimeter as structural complexity descriptors, *S. alterniflora* presented a higher complexity, when compared to *U. lactuca*. Community richness and structure differed among substrates as a function of structural complexity, as confirmed by PERMANOVA results (Table 2) and by the significantly higher richness observed in *S. alterniflora* compared to *U. lactuca* (Fig. 3A). Despite this, the most complex substrate (i.e., *S. alterniflora*) harbored the highest meiofaunal abundance and density.

Our results differ from most previous studies, which have identified effects of complexity on abundance but not on richness (Veiga et al. 2016; Ape et al. 2018a; Vieira et al. 2018). Although no structural complexity effect was observed concerning meiofaunal density, which differs from most studies on the colonization of substrates by meiofauna, organism abundance and community structure were noted as particular to each substrate.

Habitat complexity is of great importance in characterizing the spatial distribution of intertidal species (Beck 1998, 2000; Veiga et al. 2014, 2016; Ape et al. 2018a). Complex substrates are expected to provide multiple resources, allowing for the maintenance of more abundant and diverse communities with different survival requirements (Hicks 1977; Gibbons 1991). Branched substrates such as *Spartina* spp. can support higher faunal abundances by providing additional surface area for attachment or offering greater interstitial volume (Bueno et al. 2017).

It is worth noting that Attrill et al. (2000; although they worked only with macrofauna) and Christie et al. (2009) suggest that fauna composition depends mainly on habitat architecture, while fauna abundance depends on habitat size. In this study, habitat size was used as one of the descriptors of structural complexity, and although the biomass was significantly higher in *S. alterniflora*, there were no significant interactions between density and biomass.

The difference in invertebrate abundance and richness associated with *Ulva lactuca* can be explained, among other factors, by its foliaceous morphotype, with relatively little space available for colonization (Dubiaski-Silva and Masunari 1995). Thus, the lower number of individuals in *U. lactuca*, compared to *S. alterniflora* may be due to an effect of reduced surface roughness, with animal requiring higher efforts to anchoring themselves (Hacker and Steneck 1990).

Among the four major groups that make up the phytal meiofauna (Hicks 1985), two were the most representative herein, namely Nematoda and Copepoda. Acari and Ostracoda, which complete the above category, were also present, albeit at lower densities. Tuberllaria and Polychaeta, which also comprise important phytal meiofauna taxa (da Rocha et al. 2006), contributed to data dissimilarity, along with Amphipoda, Copepoda, and Nematoda.

The dominance of Amphipoda and Copepoda has been reported in several meiofauna studies (Venekey et al. 2008; Pérez-García et al. 2015; Veiga et al. 2016), and its higher abundance in *U. lactuca* can be explained by easy adhesion to this substrate conferred by appendages (Fenwick 1976; Hicks 1977, 1980; Hacker and Steneck 1990; Ayala and Martin, 2003; Lacerda and Masunari 2011). Nematoda dominance in *S. alterniflora* can be associated with the accumulation of fine sediments on this substrate, favoring colonization through a high availability of microhabitat conditions (Warwick 1981; Curvêlo and Corbisier 2000; da Rocha et al. 2006). High Da and Dp values in *S. alterniflora* indicate higher divisions in the total substrate space, and additional divisions of space at smaller scales, respectively (McAbendroth et al. 2005). These divisions facilitate sediment trapping.

The effect of beach hydrodynamics was not tested in the present study, but it is important to point out that the area where *U. lactuca* was collected is highly exposed to wave action, making organism adhesion difficult. In addition, this macroalgae was sampled from tide pools, which harbor a variety of meiofauna predators, such as fish and crabs (Dethier 1980), confined in relatively high densities for a long time (Gibbons 1991). Thus, the low abundance and richness of *U. lactuca* meiofauna may have been influenced by the sampling area, although it is possible that the amount of microflora, microorganisms, and detritus associated with phytal substrates may differ naturally, leading to a substant significantial effect on the associated meiofauna (Frame et al. 2007; Veiga et al. 2016).

Although it was not possible to increase taxonomic refinement, the data presented corroborates both the conclusion of studies on the colonization of substrates by meiofauna that used specific taxonomic levels (Hull 1997; da Rocha et al. 2006; Hooper and Davenport 2006; Lacerda and Masunari 2011; Tavares et al. 2013) and studies that used higher taxonomic categories (Logan et al. 2008; Bohórquez et al. 2013; Veiga et al. 2016; Ape et al. 2018a; Vieira et al. 2018; Lutz et al. 2019). This finding suggests that different taxonomic levels show the same results under the influence of complexity measures. The taxonomic sufficiency of the upper groups was observed by Rodrigues (2017) when he analyzed the epifaunal community in large groups and the amphipod community at the species level in the macroalga *Sargassum filipendula*.

In summary, the results suggest that phytal structural complexity affects the composition of benthic communities. Although our results are a first step in elucidating the dynamics of meiofaunal communities in coastal Maranhão ecosystems in Brazil, we recognize the need to adopt further measures tailored to the target organisms. In contrast to previous studies, which generally test the effect of structural complexity on different species of macroalgae, in this study, we tested this effect on more taxonomically distant substrates. And although no significant differences in density were identified, numerically the more complex substrate harbored the greatest number of individuals, corroborating previous studies carried out with macroalgae (Buschbaum et al. 2006; Veiga et al. 2016; Ape et al. 2018a; Gan et al. 2019) and macrophytes (Rutledge and Fleeger 1993; Atrill et al. 2000; McAbendroth et al. 2005; Mascart et al. 2015; Daudi et al. 2023).

The interaction between macroalgae, macrophytes, and meiofauna is complex and not yet fully understood. However, it is clear that phytal substrates play important roles in supporting meiofauna. The results of this study suggest that substrate identity is less important than complexity in structuring meiofaunal associations. The inclusion of different physicochemical variables such as organic matter and chlorophyll content in sediments, suspended particulate

matter, or inorganic nutrient concentrations as additional descriptors, combined with meiofaunal densities, would have enable to identify which environmental factors exert the greatest influence on community patterns through multivariate approaches (e.g., Principal Components Analysis), a tool that will be taken into account in future studies.

Although biomass differed significantly between the two substrates, it was not the main driver of meiofaunal diversity and community patterns. This finding supports the hypothesis that habitat size alone is insufficient to explain faunal assemblages, since richness and composition were more strongly related to fractal dimensions, reflecting microhabitat heterogeneity. Therefore, structural complexity, expressed through habitat architecture, better explains meiofaunal diversity than substrate quantity (biomass), reinforcing the ecological role of phytal morphology in shaping benthic communities.

The significant differences in Da and Dp between substrates could be interpreted as a byproduct of biomass variation; however, our analyses indicate otherwise. While S. alterniflora presented higher biomass, the strongest effects on richness and community structure were linked to fractal descriptors, not to biomass. This suggests that architectural heterogeneity, rather than substrate quantity, plays a central role in shaping meiofaunal communities. In other words, greater surface divisions and interstitial spaces (Da, Dp) enhance niche availability independently of total habitat size. Similar patterns have been reported by Attrill et al. (2000), Christie et al. (2009) and Veiga et al. (2016), who showed that habitat architecture, more than size, governs faunal assemblage composition.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

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References

Aguilar-Rosas R, Aguilar-Rosas LE, Pedroche FF (2005) Ulva fasciata Delile (Ulvaceae, Chlorophycota): a species newly introduced into Pacific Mexico. Bot Mar 48:46–51. https://doi.org/10.1515/BOT.2005.005

Allouche M, Ishak S, Nasri A, Hedfi A, Ben Ali M, Albogami B, Boufahja F (2021) What is the impact of microplastics and lipid regulators on marine meiofauna? Case study of polyvinyl chloride, atorvastatin, and simvastatin. Sustainability 13(23):13190. https://doi.org/10.3390/su132313190

Alvares CA et al (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschriftm 22(6):711–728

Amorim IFF, Guterres AVF, da Silva AF, de Almeida EB Jr (2023) Arranjo estrutural e diversidade da flora herbácea das dunas da Praia do Caúra, São José de Ribamar, Maranhão. Biodiversidade Brasileira 13(1):1–10. https://doi.org/10.37002/biobrasil.v13i1.2011

Anderson MJ (2014) Permutational multivariate analysis of variance (PERMANOVA). Wiley StatsRef Stat Ref Online. https://doi.org/10.1002/9781118445112.stat07841

Ape F, Gristina M, Chemello R, Sarà G, Mirto S (2018a) Meiofauna associated with vermetid reefs: the role of macroalgae in increasing habitat size and complexity. Coral Reefs 37(3):875–889. https://doi.org/10.1007/s00338-018-1714-x

Ape F, Sarà G, Airoldi L, Mancuso FP, Mirto S (2018b) Influence of environmental factors and biogenic habitats on intertidal meiofauna. Hydrobiologia 807(1):349–366. https://doi.org/10.1007/s10750-017-3410-1

Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? Ecography 23(1):114–121. https://doi.org/10.1111/j.1600-0587.2000.tb00266.x

Ayala Y, Martín A (2003) Relaciones entre la comunidad de anfípodos y las macroalgas a las que están asociados, en una plataforma rocosa del litoral central de Venezuela. Boletín Instituto Español de Oceanografía 19(1–4):171–182

Beck MW (1998) Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar Ecol Prog Ser 169:165–178. https://doi.org/10.3354/meps169165

Beck MW (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. J Exp Mar Biol Ecol 249(1):29–49. https://doi.org/10.1016/S0022-0981(00)00171-4

Bohórquez J, Papaspyrou S, Yúfera M, Van Bergeijk SA, García-Robledo E, Jiménez-Arias JL, Corzo A (2013) Effects of green macroalgal blooms on the meiofauna community structure in the Bay of Cádiz. Mar Pollut Bull 70(1–2):10–17. https://doi.org/10.1016/j.marpolbul.2013.02.002

Boisseau JP (1975) Techenique pour l'estude quantitative de la fauna interstitielle des sables. In: Higgins RP et al (eds) Introduction to the study of meiofauna. Smithsonian Institution, Washington DC

Bortolus A, Schwindt E (2018) Marine-coastal exotic species of Argentina, 1a ed. Alejandro Bortolus, Puerto Madryn

Bueno M, Dias GM, Leite FP (2017) The importance of shore height and host identity for amphipod assemblages. Mar Biol Res 13(8):870–877. https://doi.org/10.1080/17451000.2017.1306650

Buschbaum C, Chapman AS, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar Biol 148(4):743–754. https://doi.org/10.1007/s00227-005-0128-9

Caetano VL, Greis G, de Azevedo AG, Costa CSB (2017) Variação na altura e na abundância de colmos e estruturas reprodutivas em populações pioneiras e maduras de Spartina alterniflora Loisel. e S. densiflora Brongn.(Poaceae) do sul do Brasil. Iheringia Série Botânica 72(2):229–238

Castro E, Moraes A, Pinheiro E, Pontes J (2014) Zoneamento Geomorfológico da Ilha do Medo – MA. Revista Geonorte 5(15):150–155

Cerrano C, Bianchelli S, Di Camillo CG, Torsani F, Pusceddu A (2015) Do colonies of *Lytocarpia myriophyllum*, L. 1758 (Cnidaria, Hydrozoa) affect the biochemical composition and the meiofaunal diversity of surrounding sediments? Chem Ecol 31(1):1–21. https://doi.org/10.1080/02757540.2014.966699

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–234. https://doi.org/10.3354/meps08351

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18(1):117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Correia MMF, Brandão MDS (1974) Flora ficológica marinha da Ilha de São Luís (Estado do Maranhão, Brasil): I – Chlorophyta. Arquivos de Ciências do Mar 14(2):67–80

Coull BC, Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64(6):1599–1609. https://doi.org/10.2307/1937513

Curvêlo RR, Corbisier TN (2000) The meiofauna asssociated whith *Sargassum cymosum* at Lázaro Beach, Ubatuba, São Paulo. Revista Brasileira de Oceanografia 48(2):119–130. https://doi.org/10.1590/S1413-77392000000200003

da Ferreira ED, da Silva FMC, Lobato C (2012) Orla marítima de São Luís - MA: uso de espaços litorâneos e seus impactos ambientais na vegetação de restinga. VII CONNEPI – Congresso Norte Nordeste de Pesquisa e Inovação. Anais

da Rocha CMC, Venekey V, Bezerra TNC, Souza JRB (2006) Phytal marine nematode assemblages and their relation with the macrophytes structural complexity in a Brazilian tropical rocky beach. Hydrobiologia 553(1):219–230. https://doi.org/10.1007/s10750-005-0923-9

Daudi LN, Uku JN, De Troch M (2023) Effects of habitat complexity on the abundance and diversity of seagrass leaf meiofauna communities in tropical Kenyan seagrass meadows. Aquat Bot 187:103651. https://doi.org/10.1016/j.aquabot.2023.103651

de Tito L, Bodiou JY (1984) Predation on meiofauna by juvenile fish in a western Mediterranean flatfish nursery ground. Mar Biol 82(2):209–215. https://doi.org/10.1007/BF00394104

des Sables In: Higgins, R. P. *Introduction to the study of meiofauna*. Smithsonian Institution Press, Washington D. C. 138p

Dethier MN (1980) Tidepools as refuges: predation and the limits of the harpacticoid copepod *Tigriopus californicus* (Baker). J Exp Mar Biol Ecol 42(2):99–111. https://doi.org/10.1016/0022-0981(80)90169-0

dos Santos SR, Pinto PA, dos Santos PC (2014) Ilha do Medo: proposta de uma nova opção de produto turístico para a cidade de São Luís (MA). Rev Bras Ecoturismo (RBEcotur). https://doi.org/10.34024/rbecotur.2014.v7.6090

Duarte RCDS, de Barros G, Milesi SV, Dias TLP (2020) Influence of macroalgal morphology on the functional structure of molluscan community from hypersaline estuary. Hydrobiologia 847:1107–1119. https://doi.org/10.1007/s10750-019-04171-3

Dubiaski-Silva J, Masunari S (1995) Ecologia populacional dos amphipoda (Crustacea) dos fitais de Caiobá, Matinhos, Paraná, Brasil. Revista Brasileira de Zoologia 12:373–396. https://doi.org/10.1590/S0101-81751995000200015

El-Robrini M, Alves MAMS, Souza Filho PWM, El-Robrini MHS, Silva Júnior OG, França CF (2006) Atlas de erosão e progradação da zona costeira do Estado do Pará – Região Amazônica: Áreas oceânica e estuarina. In: Muehe D (ed.) Atlas de erosão e progradação da Zona Costeira Brasileira. São Paulo, p. 1-34.

Fenwick GD (1976) The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownii*. J Exp Mar Biol Ecol 25(1):1–18. https://doi.org/10.1016/0022-0981(76)90072-1

Fonsêca-Genevois VD, Somerfield PJ, Neves MHB, Coutinho R, Moens T (2006) Colonization and early succession on artificial hard substrata by meiofauna. Mar Biol 148(5):1039–1050. https://doi.org/10.1007/s00227-005-0145-8

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. SAGE, Thousand Oaks

Frame K, Hunt G, Roy K (2007) Intertidal meiofaunal biodiversity with respect to different algal habitats: a test using phytal ostracodes from Southern California. Hydrobiologia 586(1):331–342. https://doi.org/10.1007/s10750-007-0707-5

Gan SX, Tay YC, Huang D (2019) Effects of macroalgal morphology on marine epifaunal diversity. J Mar Biol Association United Kingd 99(8):1697–1707. https://doi.org/10.1017/S0025315419000900

Gee JM, Warwick RM (1994) Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Mar Ecol Prog Ser 103:141–150

Gheller PF, Corbisier TN (2022) Monitoring the anthropogenic impacts in Admiralty Bay using meiofauna community as indicators (King George Island, Antarctica). Acad Bras Cienc. https://doi.org/10.1590/0001-3765202220210616

Gibbons MJ (1991) Rocky shore meiofauna-a brief overview. Trans Royal Soc South Afr 47:595–603

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments. Springer, Berlin

Gleason DF (1986) Utilization of salt marsh plants by postlarval brown shrimp: carbon assimilation rates and food preferences. Mar Ecol Prog Ser 31:151–158

Guiry MD, Guiry GM (2022) *Algae Base*. World-wide electronic publication. National University of Ireland, Galway. http://www.algaebase.org accessed 13.07.2022)

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology 71(6):2269–2285. https://doi.org/10.2307/1938638

Hicks GR (1980) Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J Exp Mar Biol Ecol 44(2):157–192. https://doi.org/10.1016/0022-0981(80)90151-3

Hicks GR (1985) Meiofauna associated with rochky shore algae. In: Moore PG, Seed R (eds) The Ecology of Rocky Coasts. Hodder & Stoughton, London, pp 36–56

Hicks GRF (1977) Observations on substrate preference of marine phytal harpacticoids (Copepoda). Hydrobiologia 56(1):7–9. https://doi.org/10.1007/BF00023278

Hooper GJ, Davenport J (2006) Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion. J Mar Biol Association United Kingd 86(6):1297–1304. https://doi.org/10.1017/S0025315406014329

Hull SL (1997) Seasonal changes in diversity and abundance of ostracods on four species of intertidal algae with differing structural complexity. Mar Ecol Prog Ser 161:71–82

INMET (2023) Instituto Nacional de Meteorologia. http://www.inmet.gov.br. Accessed 10 Sept 2023

Kazi MA, Kavale MG, Singh VV (2016) Morphological and molecular characterization of Ulva chaugulii sp. nov., U. lactuca and U. ohnoi (Ulvophyceae, Chlorophyta) from India. Phycologia 55(1):45–54. https://doi.org/10.2216/15-11.1

Lacerda MB, Masunari S (2011) Substrate selection of the caprellid Caprella dilatata (Crustacea, Amphipoda). Revista de Biología Mar y Oceanografía 46(2):207–218

Lin HJ, Hsu CB, Liao SH, Chen CP, Hsieh HL (2015) Effects of *Spartina alterniflora* invasion on the abundance and community of meiofauna in a subtropical wetland. Wetlands 35(3):547–556. https://doi.org/10.1016/j.marpolbul.2018.12.031

Liu J, Zhuang M, Zhao L, Liu Y, Wen Q, Fu M, He P (2020) Taxonomy and Genetic Diversity of Amphipods Living on *Ulva lactuca* L. from Gouqi Coast, China1. Pac Sci 74(2):137–146. https://doi.org/10.2984/74.2.3

Logan D, Townsend KA, Townsend K, Tibbetts IR (2008) Meiofauna sediment relations in leeward slope turf algae of Heron Island reef. Hydrobiologia 610:269–276. https://doi.org/10.1007/s10750-008-9442-9

Lutz ML, Minchinton TE, Davis AR (2019) Differences in architecture between native and non-indigenous macroalgae influence associations with epifauna. J Exp Mar Biol Ecol 514:76–86. https://doi.org/10.1016/j.jembe.2019.03.006

Macy A, Sharma S, Sparks E, Goff J, Heck KL, Johnson MW, Cebrian J (2019) Tropicalization of the barrier islands of the northern Gulf of Mexico: A comparison of herbivory and decomposition rates between smooth cordgrass (*Spartina alterniflora*) and black mangrove (*Avicennia germinans*). PLoS ONE 14(1):e0210144. https://doi.org/10.1371/journal.pone.0210144

Mascart T, Lepoint G, Deschoemaeker S, Binard M, Remy F, De Troch M (2015) Seasonal variability of meiofauna, especially harpacticoid copepods, in Posidonia oceanica macrophytodetritus accumulations. J Sea Res 95:149–160. https://doi.org/10.1016/j.seares.2014.07.009

McAbendroth L, Ramsay PM, Foggo A, Rundle SD, Bilton DT (2005) Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions? Oikos 111(2):279–290. https://doi.org/10.1111/j.0030-1299.2005.13804.x

Mederiros TCC (1988) Contribuição ao estudo da fisiografia de mesolitoral do Golfão Maranhense. Bol do Laboratório de Hidrobiologia 8(1):81–96

Michelet C, Zeppilli D, Hubas C, Baldrighi E, Cuny P, Dirberg G, Michaud E (2021) First assessment of the benthic meiofauna sensitivity to low human-impacted mangroves in French Guiana. Forests 12(3):338. https://doi.org/10.3390/f12030338

Muehe D (2006) Erosão e degradação do litoral brasileiro. MMA, Brasília

Norderhaug KM, Christie H, Fredriksen S (2007) Is habitat size an important factor for faunal abundances on kelp (*Laminaria hyperborea*)? J Sea Res 58(2):120–124. https://doi.org/10.1016/j.seares.2007.03.001

Norderhaug KM, Christie H, Rinde E, Gundersen H, Bekkby T (2014) Importance of wave and current exposure to fauna communities in *Laminaria hyperborea* kelp forests. Mar Ecol Prog Ser 502:295–301. https://doi.org/10.3354/meps10754

Oksanem J et al (2022) *Vegan*: Community Ecology Package. Version 2.6-2. R package. Disponível em: https://CRAN.R-project.org/package=vegan

Pérez-García JA, Ruiz-Abierno A, Armenteros M (2015) Does morphology of host marine macroalgae drive the ecological structure of epiphytic meiofauna. J Mar Biol Oceanogr, 4(1), 2. http://dx.doi.org/10.4172/2324-8661.1000139

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rasband WS (1997–2012) Image J. U. S. Natl. Inst. of Health, Bethesda. http://rsb.info.nih.gov/ij/

Rebelo FM (2000) Caracterização e mapeamento de marismas associados aos estuários e manguezais da baía de Turiaçu, Maranhão, Brasil, usando sensoriamento remoto. V Workshop ECOLAB – Ecossistemas Costeiros Amazônicos. Boletim de resumos, Macapá/AP

Rodrigues CW (2017) Dimensão fractal e métodos quantitativos aplicados ao estudo de comunidades do macrobentos marinhos. Tese (Doutorado, Universidade de São Paulo, São Paulo

Rutledge PA, Fleeger JW (1993) Abundance and seasonality of meiofauna, including harpacticoid copepod species, associated with stems of the salt-marsh cord grass. Spartina alterniflora Estuaries 16(4):760–768. https://doi.org/10.2307/1352434

Santos MEM, Silva TC, Ferreira Sirqueira, J et al (2024) Spatial marine meiofauna variations in areas undergoing different disturbance levels on the Amazon coast. Biologia 79, 483–494. https://doi.org/10.1007/s11756-023-01536-x

Santos MEM, Spenassato D, de Azambuja AMV, Nunes JLS, de Camargo MG (2025) Trends for Research on Hard Substrate Colonization by Meiofauna. Mar Ecol 46:e70010. https://doi.org/10.1111/maec.70010

Sarkar D (2008) Lattice: multivariate data visualization with R. Springer, New York. https://doi.org/10.1007/978-0-387-75969-2

Silveira JD (1964) Morfologia do litoral. In: Azevedo A (ed.). Brasil, a terra e o homem. São Paulo. 1964. p. 253-305.

Simpson LG et al (2022) *Permute*: Functions for Generating Restricted Permutations of Data. Version 0.9-7. R package. Disponível: https://CRAN.R-project.org/package=permute

Soriano-Sierra E, Ribeiro GC, Larissa A, Fonseca D O (2014) Guia de campo: vegetação e peixes das lagoas costeiras de Santa Catarina. Editora Insular, Florianopolis

Tavares MR, Grande H, Jacobucci GB (2013) Habitat and food selection by herbivorous amphipods associated with macroalgal beds on the southeast coast of Brazil. Nauplius 21:09–15

Torres AC, Veiga P, Rubal M, Sousa-Pinto I (2015) The role of annual macroalgal morphology in driving its epifaunal assemblages. J Exp Mar Biol Ecol 464:96–106. https://doi.org/10.1016/j.jembe.2014.12.016

Veiga P, Rubal M, Sousa-Pinto I (2014) Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species. Mar Environ Res 101:115–123. https://doi.org/10.1016/j.marenvres.2014.09.007

Veiga P, Sousa-Pinto I, Rubal M (2016) Meiofaunal assemblages associated with native and non-indigenous macroalgae. Cont Shelf Res 123:1–8. https://doi.org/10.1016/j.csr.2016.04.007

Venekey V, da Fonseca Genevois VG, da Rocha CMC, dos Santos PJP (2008) Distribuiçao espaço-temporal da meiofauna em sargassum *Polyceratium montagne* (Fucales, Sargassaceae) de um costão rochoso do nordeste do brasil. Atlântica (Rio Grande) 30(1):53–67

Vieira EA, Filgueiras HR, Bueno M, Leite FPP, Dias GM (2018) Co-occurring morphologically distinct algae support a diverse associated fauna in the intertidal zone of Araçá Bay, Brazil. Biota Neotrop. https://doi.org/10.1590/1676-0611-BN-2017-0464

Villwock JA, Lessa GC, Suguio K, Angulo RJ, Dillenburg SR (2005) Geologia e geomorfologia de regiões costeiras. In Quaternário do Brasil (p. 378). Ribeirão Preto: Holos. https://repositorio.usp.br/directbitstream/dae31707-e0af-411e-87df-17826638ec03/2161752.pdf

Warwick RM (1981) Survival strategies of meiofauna. IN: Feeding and survival srategies of estuarine organisms. Springer, Boston, pp 39–52. https://doi.org/10.1007/978-1-4613-3318-0_4

Wickham H (2016) Programming with ggplot2. ggplot2. Springer, Cham, pp 241–253. https://doi.org/10.1007/978-3-319-24277-4_12

Zarghami M, Nazarhaghighi F, Moghaddasi B (2020) Using meiobenthos for biomonitoring of ecological health in southern Caspian Sea shores, Mazandaran, Iran. Proc Int Acad Ecol Environ Sci 10(3):56–74