Meiofauna at a tropical sandy beach in the SW Atlantic: the influence of seasonality on diversity (#92413)

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Meiofauna at a tropical sandy beach in the SW Atlantic: the influence of seasonality on diversity

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Background. Sandy beaches are dynamic environments that houses a large diversity of organisms and provide important environmental services. Meiofaunal metazoan are small organisms that play a key role in the sediment and its diversity, distribution and composition are driven by sedimentary and oceanographic parameters. Understanding the diversity patterns of marine meiofauna is critical in a changing world. **Methods.** In this study, we investigate the influence of seasonality of environmental variables (rainfall, total organic matter, carbonate, carbohydrate, protein, lipids, protein-to-carbohydrate, carbohydrate-to-lipids, and biopolymeric carbon) and changes on marine seascapes dynamics (characterized by temperature, salinity, absolute dynamic topography, chromophoric dissolved organic material, chlorophyll-a, and normalized fluorescent line height) on meiofaunal metazoans at a tropical sandy beach. We used metabarcoding (V9 hypervariable region from 18S gene) from sediment samples to assess the meiofaunal assemblage composition and calculate diversity metrics (phylogenetic diversity and Shannon’s diversity) over a year. **Results.** Meiofauna was dominated by Crustacea (46% of sequence reads), Annelida (28% of sequence reads) and Nematoda (12% of sequence reads) in periods of the year with high temperatures (> 25 °C), high salinity (>31.5 ppt), and calm waters. Our data support our initial hypotheses revealing a higher meiofaunal diversity (phylogenetic and Shannon’s Diversity) and different composition during warmer periods of the year. Meiofaunal diversity is not drive by a unique variable, but by a complex set of variables, including biological variables (biopolymeric carbon) and organic matter quality (protein content, lipid content, and carbohydrate-to-lipid ratio), and may be influenced by ecological interactions among taxa.

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Abstract

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Keywords: benthos; seascape; environmental DNA; temporal change

Introduction

Sandy beaches are the most predominant coastal ~~ecosystem~~ worldwide ~~and form~~ an intricate environment between marine and terrestrial realms, with a large diversity of organisms supporting important biogeochemical processes and providing key ecosystem services (McLachlan and Brown, 2006; Defeo et al., 2009; Wu et al., 2018; Okamoto et al., 2022; Corte et al., 2023). ~~Sandy beaches are dynamic~~ environments ~~with structure and topography~~ influenced by global and local oceanographic and physical processes (e.g., granulometric characteristics, wave regime, tides, and currents) (Di Domenico et al., 2009), which in turn shape the community structure of these habitats (Maria et al., 2016). In addition, sandy beaches are under a range of anthropogenic impacts (including climate change) with signs of declining diversity in numerous areas worldwide (Bellwood et al., 2004; McLachlan and Defeo, 2018). However, this ecosystem still the ~~less~~ studied coastal environment (Lercari, 2023), and understanding how marine diversity varies at local scales, and how global and local ~~impacts~~ may affect sandy beach~~es~~ biodiversity contributes to the conservation of these ecosystems, ~~and is crucial to~~ ~~support~~ efficient management and conservation strategies (Gaston, 2000; Defeo et al., 2021). Furthermore, understanding which environmental factors are the main drivers of marine diversity, including spatial and seasonal variations, is critical to establish a strong baseline that can be used in future comparisons.

Sandy beache~~s~~ morphodynamics may change at different timescales: along several decades to hundreds of years; from several years to decades, also referred as interannual variability; seasonal variability, which repeats on an annual cycle, also referred as intra-annual variability; short-term variability, generally associated with extreme events (Senechal and Alegría-Arzaburu, 2020). The interest in understanding long and medium-term processes (inter- and intra-annual patterns) in marine ecosystems has increased recently (Blue and Kench, 2017; Vos et al., 2019), boosted by frequency and intensity of climate change events. It is well known that the southern hemisphere lacks long-term data in tropical and subtropical environments, what represents a risk to the development of a worldwide synthesis regarding the biological diversity and dynamics of marine ecosystems (Odebrecht et al., 2017). Nonetheless, seasonal variation has been less investigated, even though it plays key roles on the beach system ~~and understanding it is essential to development of beach surveying~~ (Basanta et al., 2017; Senechal and Alegría-Arzaburu, 2020). Long-term studies are the only way to obtain accurate description of changes in the ecosystem, rigorous monitoring of cycles and trends, and an acceptable assessment of the status of living resources, so that seasonal variations can be captured and fully understand this ecosystem under constant pressure (e.g., anthropogenic activities and climate change) (Coppo, 2023).

Meiofauna is composed by organisms ranging from 42 to 500 µm, comprising at least 22 phyla, and often displaying high abundance and diversity in marine benthic systems (Higgins and Tiel, 1988; Giere, 2009; McIntyre, 1969; Hakenkamp and Palmer, 2000). These organisms play crucial ecological roles in marine sediments through nutrient recycling, thus transferring energy and matter into benthic and pelagic trophic food webs and linking different trophic levels (Giere, 2009). Due to its ecological importance, meiofaunal communities reflect the overall health of the marine benthos and are considered excellent bioindicators to ~~monitoring~~ marine environmental health~~,~~ and ~~testing~~ ~~general~~ ecological hypotheses (Bonaglia et al., 2014).

In benthic marine communities from coastal habitats, spatial-temporal diversity patterns are mostly driven by substrate and oceanographic parameters (Blanchette et al., 2008; Griffiths et al., 2017; Mazzuco et al., 2019;2020). It is recognized that sediment grain size, coastal hydrodynamics, and food availability are typical drivers of meiofaunal coastal communities (Giere, 2009). In sandy beaches, the distribution and abundance of infaunal benthos are expected to respond to the swash climate and sediment characteristics (McLachlan et al., 1993; McLachlan and Brown, 2006). Wave action also plays an important role on spatial variability (i.e., patchiness) of density and diversity of meiofauna due to the hydrodynamic stress (Covazzi et al., 2001). Along the intertidal zone of sandy beaches, temperature and salinity are highly variable and can also influence the distribution and composition of organisms (Olafsson, 1991). In tropical areas seasonal changes are less markedly defined, but meiofaunal organisms show some seasonality, with greater abundance during the warmest/rainy months (Coull, 1988; Albuquerque et al., 2007).

However, meiofaunal taxa may have specific adaptations and respond differently to environmental conditions, due to their differential ability of dispersion, locomotion, nutrition, development, and reproduction (Curini-Galletti et al., 2012). A number of studies demonstrated that benthic species richness increases from temperate to tropical sandy beaches for macrofauna (McLachlan et al., 1996; McLachlan and Dorvlo, 2005; Defeo and McLachlan, 2013) and meiofauna (Lee and Riveros, 2012). However, temperature can act as main driver on intertidal benthic communities, reducing their diversity, when it surpasses species' physiological limits (Vafeiadou et al., 2018; Starko et al., 2019). In tropical humid regions, rainfall may additionally work as a major factor structuring meiofauna diversity in sandy beaches (Gomes and Rosa-Filho, 2009; Venekey et al., 2014; Baia and Venekey, 2019). Previous studies have demonstrated that meiofaunal communities respond to warming in aquatic ecosystems (O'Gorman et al., 2012; Gingold et al., 2013), causing the mortality of dominant species in subtropical environments (Gingold et al., 2013), changes in biomass (Alsterberg et al., 2011), and altering body-size structure (Jochum et al., 2012).

~~At~~ Brazilian sandy beaches, grain size has been reported to be the variable that best explains meiofaunal community in pristine (Todaro and Rocha, 2004; Albuquerque et al., 2007) and polluted areas (Maria et al., 2013a). Meiofaunal metazoan species may respond differently to different environmental conditions (Oliveira and Soares-Gomes, 2003). Temperature and salinity seasonal fluctuations may also influence on meiofaunal distribution (Esteves et al., 1998), and biological interactions may affect meiofaunal community with seasonal effect (Curvelo and Corbisier, 2000; Maria et al., 2013b).

Monitoring marine seascapes using satellite data (e.g., MBON Marine Seascapes) has recorded alterations on different ocean depths, from surface to the deep (Boyce et al., 2010; McCauley et al., 2015; Mazzuco and Bernardino, 2022). Sandy beaches are expected to be drastically affected by ~~environmental changes associated to~~ climate change in an under pressure marine ecosystem (e.g., warming and sea-level rising), seascapes can be tracked by assessing biotic and abiotic variables, such as benthic-pelagic association and important environmental variables to benthic fauna (Maria et al., 2016; Ehrnsten et al., 2019). The use of this approach to ecological assessments can help marine spatial planning, conservation efficiency, and improve our capacity to understand and predict alterations of benthic ecosystems (Fagundes et al., 2020; Pittman et al., 2021; Mazzuco and Bernardino, 2022). Marine seascapes are associated to different components of the marine ecosystem, such as benthic-pelagic interactions and essential ocean variables (Centurioni et al., 2019; Ehrnsten et al., 2019. Marine biodiversity in coastal ecosystems is strongly associated to oceanographic and ecological processes that may impact larval supply and recruitment, which is a key factor ~~once~~ many marine animals have a life cycle with larval/juvenile stage (Caley et al., 1996; Strathmann et al., 2002; Mazzuco and Bernardino, 2022). Processes that fluctuate seasonally and spatially in relation to pelagic conditions may have an impact on benthic recruitment. Consequently, variations in the number of benthic recruits might be a reaction to modifications in marine pelagic seascapes, which would impact the regional total biodiversity. (Fogarty et al., 1991; Gilg et al., 2003; Wahle, 2003; D'Aloia et al., 2015).

Predicting changes in diversity patterns from local to global scales is ~~a~~ paramount in a scenario of global environmental change, and it has been added to the protocols of diverse ocean observatories (Muller-Karger et al., 2017; Bax et al., 2019; Mazzuco et al., 2020). To predict how these assemblages will respond in the future, firstly it is necessary to understand the drivers of local-scale diversity patterns, and how organisms respond to environmental parameters and seasonality. Portions of this text were previously published as part of a thesis (Coppo, 2023). Here, we aimed to assess meiofaunal diversity in a tropical sandy beach ~~to test~~ whether or not (i) there is seasonal differences ~~on~~ meiofaunal assemblage composition and diversity (phylogenetic and Shannon's diversity) along one year ~~at a sandy beach on the SW Atlantic coast,~~ (ii) the marine seascapes conditions, rainfall, and sediment parameters (total organic matter, carbonate, carbohydrate, protein, lipids, protein-to-carbohydrate, carbohydrate-to-lipids, and biopolymeric carbon) affect significatively meiofaunal diversity metrics ~~(phylogenetic and Shannon's diversity) at a sandy beach on the SW Atlantic coast~~. We addressed the following hypotheses in this study: (i) meiofaunal diversity ~~(phylogenetic and Shannon's diversity)~~ is higher during warmer months and its composition changes significatively among seasons along a year at Gramuté beach, and (ii) meiofaunal diversity metrics ~~(phylogenetic and Shannon's diversity)~~ are significantly explained by marine seascapes characteristics and sediment parameters.

Materials & Methods

Study area and sampling

The study was carried out at ~~the~~ Gramuté sandy beach~~,~~ located within a marine protected area in the Eastern Brazilian Marine Ecoregion (Figure 1A). The region is geomorphically characterized by abrasion terraces of Barreiras Formation from the coast to the inner continental shelf (Martin et al., 1996). Gramuté beach is marked by scattered intertidal lateritic reefs (Mazzuco et al., 2020), with the presence of carbonate secreting organism which contributes to ~~deposit layer~~ of bioclastic sediment (Albino and Suguio, 2011). Additionally, Gramuté beach ~~region~~ is marked by strong internal tidal currents, and E-SE wave swells with upwelling events occurring mostly during spring and summer (Pereira et al., 2005). This tropical region is marked by dry winters and rainy summers (Bernardino et al., 2015), with sea surface temperatures ranging between 21 °C and 27 °C, and salinity ranging from 34.6 to 36 ppt (Quintana et al., 2015; Mazzuco et al., 2019;2020). This region has also experienced significant warming in the last 40 years (Bernardino et al., 2015; Mazzuco et al., 2020).

The study region is marked by frequent exposure to waves generated mainly by the South Atlantic Subtropical Anticyclone (ASAS), with northeast (NE) swells mainly. Although there is dominance of NE waves throughout the year, in the autumn and winter period the wind regime changes to E-SE, strengthening the presence of waves from these directions (E-SE), with average heights of 1.5 m. During winter, the region is also affected by the passage of frontal systems, making it susceptible to wave action coming from the south-southwest (S-SW) (Silva et al., 1982).

During a year (December 2019 to November 2020), we monthly collected sediment samples (approximately 200 g each replicate) on three different stations (n = 9 sediment samples per month) at Gramuté beach on the low-tide shoreline, spaced 20 meters apart (Figure 1B). Sediment samples were collected manually using sterile, DNA-free corers, over all seasons during the sampling period (Summer = December 12th, 2019, January 12th, 2020, and February 11th, 2020; Autumn = March 11th, 2020, April 7th, 2020, and May 26th, 2020; Winter = June 22nd, 2020, July 23rd, 2020, and August 22nd, 2020; Spring = September 20th, 2020, October 15th, and November 28th, 2020). Additionally, we collected samples for sediment analysis (grain size, total organic matter, carbonate content, and sedimentary organic biopolymers). All samples were transported in thermic bags with ice, and stored at -20 °C until analysis. Field sampling was authorized by the Biodiversity Authorization and Information System of the Brazilian Institute for the Environment and Renewable Natural Resources (SISBIO-IBAMA, sampling license number 24700-1). Total monthly rainfall data for the sampling period (December 2019 – November 2020) was obtained from the National Water Resources Information System (SNIRH) portal, made available by the National Water and Sanitation Agency (ANA – https://www.snirh.gov.br/hidroweb/), considering the station of Santa Cruz -Litoral (code: 1940002; Lat: -19.9578, Lon: -40.1544), which is approximately 4 Km from Gramuté beach.

Sediment analysis

Sediment samples were dried at 60 °C for 48 h before all granulometric analysis. Dried sediment was macerated and sieved in mesh openings of -1.5 Φ to 4 Φ (with 1Φ intervals) in a sieve shaker to determinate the carbonate content by muffle combustion at 550 °C for 4 h with an additional hour at 800 °C. Additionally, we quantified total organic matter (TOM) by weight loss after combustion (500 °C for 3 h) (Suguio, 1973).

Sedimentary organic biopolymers (proteins, carbohydrates, and lipids) ~~we~~ analyzed following Danovaro (2010). After extraction with NaOH 0.5 M we determinated total protein (PRT) content according to Hartree (1972) as modified by Rice (1982) to compensate for phenol interference. For total carbohydrates (CHO) analysis, we followed the protocol from Gerchacov and Hatcher (1972). Total lipids (LIP) were extracted from 1 g of homogenized sediment lyophilized by ultrasonication in 10 ml of chloroform: methanol (2:0 1 v/v) and analyzed according to Marsh and Weinstein (1966). The concentrations of PRT, CHO, and LIP are presented respectively as bovine serum albumin, glucose, and tripalmitin equivalents. Protein (PRT), CHO, and LIP concentration were converter to carbon equivalents following Fabiano and Danovaro (1994) using conversion factors of 0.49, 0.40, and 0.75, respectively. The sum of PRT, CHO, and LIP carbon equivalents are presented as biopolymeric carbon (BPC) (Fabiano et al., 1995). Further, protein to carbohydrate (PRT: CHO) and carbohydrate to lipid (CHO: LIP) ratios were used to assess biochemical degradation processes (Galois et al., 2000). All analyzes were performed in triplicate and blanks were carried out for all analysis with pre-combusted sediments at 450 and 480 ºC for 4 h.

Seascape characterization

The Marine Biodiversity Observation Network (MBON) Seascapes are obtained from satellite and modeled data that comprises different oceanic parameters (sea surface temperature – SST, sea surface salinity – SSS, absolute dynamic topography – ADT, chromophoric dissolved organic material – CDOM, surface chlorophyll-a – Chl-a, and normalized fluorescent line height – NFLH). These variables are used ~~to~~ a categorization system of 33 water masses that represents different marine scenarios/conditions (Montes et al., 2020).

Oceanographic conditions were characterized according to the variation in MBON Seascape Pelagic Habitats Classification (Kavanaugh et al., 2014; 2016; Mazzuco and Bernardino, 2022) using the database available in the NOAA Coast and Ocean Watch Programs, with monthly frequency on a 5 Km^2 grid (Kavanaugh et al., 2014; 2016), to characterize the seascapes for the Área de Proteção Ambiental Costa das Algas (~ 30 km coastline, 465 Km^2, Longitude – 40.3º to – 39.8º, Latitude 20.3º to 19.8º) for the study period (December 2019 – November 2020). Additionally, to determine seasonal SST and SSS for the study area, we calculated a weighted average based on the monthly coverage area of each identified MBON marine seascape.

MBON Seascapes are presented as seascape coverage (%), which represents the extent of an area that is encompassed within any of the MBON Marine Seascapes categories. This percentage represents how much of the area of the Área de Proteção Ambiental Costa das Algas (which is a Marine Protected Area) is encompassed with one of the seascape categories. Each MBON Seascape category is defined by a fixed value for each oceanic variable, and the seascape product is generated as monthly and 8-day composites at 5 Km spatial resolution. In this manuscript we used the seasonal mean, calculated as the mean of the monthly seascape coverage for all three months per season.

DNA extraction and sequencing

~~Previously~~ to ~~the~~ DNA extraction, sediment samples were elutriated using sieves of 45 µm mash in an attempt to increase the meiofaunal abundance and enrich metazoan DNA recovery as suggested by Brannock and Halanych (2015).

1L flasks were filled with 950 mL of filtered seawater and sediment samples were added to it, then homogenized and let to sit before decanting the liquid over the 45 µm sieve. This procedure was repeated 10 times for each sediment sample. The sediment retained on the sieve was transferred to Falcon tubes and centrifuged at room temperature for 3 minutes at 1342 X g in an Eppendorf Centrifuge 5430, then the excess water was discarded and samples were aliquoted to 20 mL. We mixed the samples in the Falcon tube~~d~~, then aliquots of 1mL were stored at -20 °C (Brannock and Halanych, 2015). All glassware was sterilized between samples to avoid cross contamination. DNA ~~were~~ extracted from 1mL aliquots using the PowerSoil DNA® (Qiagen) kit following the manufacturer's instructions. DNA integrity was verified in 1% agarose gel, and purity using NanoDrop One spectrophotometer (Thermo Fisher Scientific Inc., Waltham, MA, USA). We measured DNA concentration using the Qubit® 4 Fluorometer (Qubit™ 1X dsDNA HS Assay Kit – Life Technologies-Invitrogen, Carlsbad, CA, USA). Blank samples were carried in triplicate for each step before metabarcoding sequencing (sediment elutriation, DNA extraction, and integrity, purity, and concentration checking).

DNA samples extracted from the same sediment sampling station, for each month separately, were combined into a single pool, totaling three samples per month (nine samples per season). PCR, library preparation, and sequencing were conducted by ©NGS Genomic Solutions (Piracicaba, SP, Brazil). Metabarcoding sequencing was performed using the MiSeq Illumina platform (2 x 250 bp, with a coverage of 100,000 paired-end reads per sample), sequencing the V9 hypervariable region from 18S SSU rRNA gene using the primers Euk_1391 forward (GTACACACCGCCCGTC) and EukBr reverse (TGATCCTTCTGCAGGTTCACCTAC) (Medlin et al., 1988; Amaral-Zettler et al., 2009; Stoeck et al., 2010).

Bioinformatic pipeline

Bioinformatic analysis were conducted using an AMD Ryzen 1950x Crucial 64 GB (16x4) DDR4 2666MHz computer. We used the QIIME2 2022.8 software to identify sequences with the demultiplexed raw paired-end reads (Bolyen et al., 2018). Firstly, we imported FastQ files as QIIME2 artifacts, then denoised them via DADA2 (Callahan et al., 2016) using the *denoise-paired* plugin, and removed low-quality bases and primer sequences.

The taxonomic assignment of amplicon sequence variants (ASV) generated by the DADA2 plugin (p-trim = 10, p-trunc = 160, and mean phred score = 39±1; Table S1) was performed using the machine learning Python library scikit-learn (Pedregosa et al., 2011). A pre-trained Naïve Bayes classifier trained on the Silva 132 database (Quast et al., 2013) clustered at 99%

similarity was used to identify taxonomically the DNA sequences. Due to the difference on the number of identified sequences, the dataset was normalized to allow analysis and comparisons under equal sampling depth. We used the spring dataset minimum sampling depth (1384 reads) and resampled each sample to the same depth. This normalized dataset was used to calculate all diversity metrics. We performed rarefaction curves for all four sampled seasons (summer. Winter, spring, and autumn) with the ASVs. We calculated the Faith's Phylogenetic Diversity (PD) for each sample using the *diversity core-metrics-phylogenetic* pipeline from QIIME2. The PD was calculated based on phylogenetic trees generated using the *align-to-tree-mafft-fasttree* pipeline from the *q2-phylogeny* plugin from QIIME2. Shannon diversity was calculated using the *qiime diversity alpha pipeline* and setting the p-metric parameter to "~~9hannon~~". Raw sequences are available online on NCBI (SRR24675047).

Statistical analysis

Statistical analysi~~s~~ were only considered meiofaunal metazoan sequences. The dataset was subset to contain only metazoan sequences based on taxonomic annotations using the *qiime taxa filter-table* function from the QIIME2 *q2-taxa* plugin. Here we considered ~~meiofaunal metazoans~~ all the exclusively meiofaunal phyla (Gnathostomulida, Kinorhyncha, Loricifera, Gastrotricha, and Tardigrada) and other metazoans that can be meiofaunal~~ size~~ during ~~life~~ (temporary meiofaunal taxa) (Higgins and Tiel, 1988; Giere, 2009). After this filtering, the final dataset contained 10 phyla (Annelida, Cnidaria, Crustacea, Echinodermata, Gastrotricha, Mollusca, Nematoda, Nemertea, Platyhleminthes, and Rotifera) as previously implemented in other studies (Brannock and Halanych, 2015; Bernardino et al., 2019; Fais et al., 2020; Bellisario et al., 2021; Castro et al., 2021; Coppo et al., 2023). Permutational Analysis of Variance (PERMANOVA; Anderson et al., 2008) was performed to compare environmental variables (rainfall, temperature, salinity, carbonate content, grain size, total organic matter , and biopolymeric composition), seascape coverage (the extent of an area that is encompassed within any of the MBON Marine Seascapes categories), and meiofaunal data (diversity metrics – Shannon's diversity index, phylogenetic diversity, and abundance of sequence reads) among sampled seasons (summer, autumn, winter, and spring) and sampled stations at Gramuté beach. All multiple comparisons corrections were done using the Bonferroni correction (Bonferroni, 1936). A canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003) ~~ordination plot was made~~ with environmental variables (rainfall and sediment variables) and the meiofaunal assemblage composition at Phylum level (square-root transformed). Additionally, a similarity percentage routine (SIMPER; Clarke, 1993) was applied to define the taxa that most contributed to the dissimilarity among seasons, based on a Bray-Curtis dissimilarity matrix. A multiple linear regression was fit using Shannon's diversity Index and phylogenetic diversity as response variables, and the assessed environmental variables as predictive variables. After testing for multicollinearity among variables, we removed carbohydrate content (CHO) ~~because it~~ was highly correlated to carbohydrate-to-lipids ratio (CHO:LIP) and biopolymeric carbon (BPC). Normality tests were run on model's residuals ~~though~~ QQ-plots and Shapiro-Wilk normality tests. After obtaining the multiple linear regression values, we used the Akaike Information Criterion (AIC), though a stepwise backward model configuration and the final model was chosen based on the lowest AIC

(Akaike, 1979). Significative differences were defined at $p<0.05$. All graphical and analytical procedures were performed in the R environment (R Core Team, 2022).

Results

Environmental conditions and seascape coverage

Significant seasonal variability was observed at Gramuté beach during the period studied (PERMANOVA, df = 3; Pseudo-F = 6.916; p = 0.001; Table S2), with higher LIP content on autumn (Figure 2; Table S2) and lower on spring (Figure 2; Table S2), meanwhile the CHO:LIP ratio was higher on spring than on other seasons (Figure 2; Table S2). Total rainfall ranged from 80.2±35.6 mm in winter to 193.0±42.2 mm in summer (Figure 2). The sediment is completely composed of sand, mainly by medium and coarse sand, with carbonate content ranging from 19% during autumn to 64% in spring (Figure 2). Total organic matter (TOM) had its lower concentration in summer (8.6±3.8%), and higher in spring (10.4±7.9%) (Figure 2; Table S2). The protein fraction of the organic matter content in the sediment ranged from 48.2±25.0 mg/g in summer to 96.9±17.1 mg/g in winter (Figure 2; Table S2), while the carbohydrate fraction ranged from 997.1±223.5 mg/g in summer to 2102.0±1435.5 mg/g in spring (Figure 2; Table S2). The labile fraction of the organic matter, which is represented by the biopolymeric carbon (BPC), peaked in winter (1562.6 mg C.g-1) and lowered in spring (241.1 mg C.g-1) (Figure 2; Table S2).

Overall, the Seascapes categories in this region were characterized by high sea surface temperature (SST > 20.9 °C), high sea surface salinity (SSS> 33.6 psu) and calm waters (absolute dynamic topography - ADT ranging from 0.51 to 0.83m). The seascapes had wide ranges in dissolved organic matter (CDOM; 0.00 to 0.07 m^{-1}), chlorophyll-a concentration (CHLA; 0.07 to 2.09 $mg.m^{-3}$), and fluorescence (NFLH; 0.02 to 0.24 $W.m^{-2}.um^{-2}sr^{-1}$) (Figure 2). We observed changes in the frequency of seascapes in the studied area along the year (PERMANOVA, df = 3; Pseudo-F = 8.014; p = 0.001; Table 1). Seascapes Tropical Seas (class 15 – 38.4% of area coverage during sampling period), Subtropical Gyre Transition (class 5 – 19.0% of area coverage during sampling period), Subtropical Gyre Mesoscale Influenced (class 13 – 18.3% of area coverage during sampling period), and Warm, Blooms, High Nutrients (class 21 – 12.4% of area coverage during sampling period) were the most frequent, with more than 80% of area coverage during the study period (Figure 3).

Water masses at Gramuté beach during summer (Dec – Feb), autumn (Mar – May) and winter (Jun – Aug) were dominated by the Seascape Tropical Seas (class 15), with 40.9%, 43.1%, and 45.1% of area coverage respectively (Figure 3). This marine seascape is usually characterized by high temperatures (25.4 °C) and salinity (35.4 psu) (Figure 3), but in summer, autumn and winter the marine seascape at Gramuté beach was characterized by mean temperature of 24.6±0.1 °C, 24.4±0.1 °C, and 24.3±0.1 °C, respectively, and mean salinity of 36.0±0.1 psu, 35.6±0.3 psu, and 35.4±0.1 psu, respectively. During spring, the dominance of seascapes at Gramuté changed due to an intrusion of subtropical a water mass (class 13 - 42.7% of area coverage; Figure 3), characterized by lower temperature (23.5 °C) and higher salinity (35.9 psu). At Gramuté beach we observed a temperature of 24.5±0.2 °C and salinity of 36.0±0.2 psu during the intrusion of this subtropical water mass.

Meiofaunal assemblage

A total of 9692 sequences from meiofaunal taxa were identified in the dataset. We did not observe significative differences ~~on~~ meiofauna composition and abundance of reads among sampled stations (PERMANOVA, df = 2; Pseudo-F = 0.963; p = 0.491; Table 2). Nonetheless, there ~~are~~ significant seasonal variations (PERMANOVA, df = 3; Pseudo-F = 2.307; p = 0.002; Table 2). Meiofaunal sequence reads abundance was 5.9-fold and 5.6-fold higher on summer and in winter, respectively, than on spring (Figure 4A). Meanwhile, the abundance of sequence reads in autumn did not differ from all other seasons (Figure 4A). Furthermore, meiofaunal assemblage composition was significantly different among all seasons, excepts between summer and winter and between winter and spring (Table 2).

During the summer (35% and 40% of reads), autumn (43% and 34% of reads), and spring (59% and 27% of reads), Crustacea and Annelida were the most prevalent taxa ~~in the assemblage.~~ The two taxa with the highest abundance throughout the winter were Crustacea (57% of reads) and Nematoda (17% of reads) (Figure 4B). Nemertea was not detected during autumn, Gastrotricha was not detected in spring, and Rotifera was not detected in neither. Only 11 taxa (e.g., Harpacticoida, Podocopida, and Chromadorea) were detected on all seasons (Table S3), meanwhile 14 taxa were detected only on one sampled season (Table S3).

~~Less~~ meiofaunal taxa was detected ~~on~~ spring than ~~on~~ all other seasons (Figure 5), influencing on significant seasonal differences on diversity patterns in Gramuté beach. Lower phylogenetic diversity was registered in spring (9.23±1.88) and in autumn (11.88±1.82) than in summer (17.93±3.11) and winter (19.37±4.85) (PERMANOVA; Pseudo-F = 18.863; df = 3; p < 0.001; Figure 4C; Table 3). Similarly, Shannon's diversity was 1.7-fold, 2.0-fold, and 1.9-fold lower in spring than in autumn, summer, and winter, respectively (PERMANOVA; Pseudo-F = 13.129; df = 3; p < 0.001; Figure 3D; Table 4).

~~The m~~eiofaunal assemblages differed significantly among ~~the~~ seasons in Gramuté beach (PERMANOVA, df = 3; Pseudo-F = 2.353; p = 0.001; Table 2; Table S4). Dissimilarity levels ranged from 49.7% (between winter and summer) to 68.6% (between autumn and summer), and winter had distinct assemblage composition compared to the others seasons. SIMPER analysis revealed that Annelida (ranging from 16.5% to 28.3%; Table S3), Crustacea (ranging from 21.8% to 26.7%; Table S4) and Nematoda (ranging from 13.9% to 21.8%; Table S4) were the taxa that most contributed to the differences among ~~all~~ seasons. Platyhelminthes contributed 15.4% to the total dissimilarity of 49.5% between autumn and spring (Table S4). Annelids, crustaceans, and nematodes were more abundant in summer and winter. Furthermore, these taxa were highly associated with higher organic matter content and quality (total organic matter content, biopolymeric carbon, protein content, and protein-to-carbohydrate ratio; Figure 6).

Protein content (PRT), lipid content (LIP), biopolymeric carbon (BPC), and carbohydrate-to-lipids ratio (CHO:LIP) composed a significant model of variables likely to drive meiofauna diversity (Shannon's diversity Index and phylogenetic diversity) at Gramuté beach (Adjusted R^2

= 0.602; F = 7.319; p<0.001; Table 5). We observe significant positive relationship between meiofaunal diversity (Shannon's diversity and phylogenetic diversity) and lipid content (LIP) (t = 2.513; p = 0.018; Table 5). Biopolymeric carbon content – BPC showed a significant negative relationship to diversity (t = -2.584; p = 0.015; Table 5), as well as protein content (PRT), although it was not significative (t = -1.719; p = 0.096; Table 5).

Discussion

This study investigated the influence of seasonal changes on meiofaunal diversity in a sandy beach in the SW Atlantic, advancing ~~on~~ the current knowledge on meiofaunal assemblages, understanding which factors act as main drivers of meiofaunal diversity in a local-scale. Traditionally, benthic sandy beach diversity is expected to be controlled by physical factors (e.g., grain size and tidal action) (McLachlan et al., 1993; Todaro and Rocha, 2004; McLachlan and Brown, 2006; Albuquerque et al., 2007; Di Domenico et al., 2009; Maria et al., 2013a; Maria et al., 2016). However, previous studies suggested that the sandy beach benthic macrofauna is not structured by a unique physical factor, but by a complex set of drivers including biological factors (e.g., food availability) (Lastra et al., 2006; Rodil et al., 2012). Our metabarcoding and environmental data demonstrate that this may be similar for sandy beach meiofauna, ~~once~~ biopolymeric carbon (labile fraction of organic matter) and lipid content ~~act as~~ the main drivers of meiofaunal diversity at Gramuté beach.

Although seasonal variations of environmental parameters are less markedly defined in tropical environments (Coull, 1988; Albuquerque et al., 2007), we observed variation on sediment biopolymers content and biopolymeric carbon. Lower quality organic matter was higher during spring and autumn (higher carbohydrate content, lower PRT:CHO, and high CHO:LIP), due to accumulation of aged and degraded organic matter (Danovaro et al., 1993; Joseph et al., 2008). The multiple regression fitted showed that food availability (BPC content; Danovaro et al., 1993; Fabiano et al., 1995) and organic matter quality (PRT, LIP, and CHO:LIP) are the main variables that drive meiofaunal diversity. This result may ~~represent~~ that the accumulation of aged and degraded organic matter (higher CHO:LIP) is associated to lower meiofaunal diversity, similar to what was reported by Venturini et al. (2012). Similarly, Cisneros et al. (2011) observed seasonal changes ~~on~~ organic matter content and nutrients associated to differences ~~on~~ benthic abundance and diversity at a tropical sandy beach. Surprisingly, high-quality organic matter (PRT) that is usually first consumed (Joseph et al., 2008) is also negatively associated to meiofaunal diversity. It may be caused by biological interaction among taxa, such as Crustacea and Annelida, which are the main components of the meiofaunal assemblage at Gramuté beach, also known to be strong predators that competitively may suppress the overall diversity. Similar ~~relationships pointing up to~~ the relation between food supply and benthic diversity and abundance ~~was reported by previous studies~~ (Antón et al., 2011; Neto et al., 2021).

Oceanographic conditions and marine seascapes in study area ~~are~~ mainly characterized by high temperatures, salinity, and nutrients during summer, winter and autumn. However, this tropical water mass is substituted by an intrusion of a subtropical water mass on spring. This corroborates ~~to~~ Silva et al. (1982) and Perenco (2009). This seascape dynamic is influenced by the Brazil Current occurring outside the continental shelf; drift currents generated by winds on the platform up to the wave breaking zone, and currents generated by waves. A similar seascape seasonal pattern was observed by Mazzuco and Bernardino (2022) ~~that~~ reported ~~that~~ seasonality on benthic recruitment, with higher abundance correlated to warmer water masses and high nutrient content. Changes ~~on~~ marine seascapes are associated to benthic-pelagic interactions and oceanic variables (Centuroni et al., 2019; Ehrnsten et al., 2019) that may impact larval supply and recruitment, and consequently the coastal ecosystems biodiversity once many marine animals that live in sandy beach environments have a life cycle with larval/juvenile stage (Caley et al., 1996; Strathmann et al., 2002; Mazzuco and Bernardino, 2022). This higher recruitment observed by Mazzuco and Bernardino (2022) at Gramuté beach corroborates with the higher sequence abundance - 5.9-times more when compared to spring, and diversity (phylogenetic and Shannon's diversity) – 2-times higher in comparison to spring, ~~we~~ observed in this study during the same period of the year, and associated with a similar marine seascape pattern.

Meiofaunal assemblage at Gramuté beach was overall mainly dominated by Crustacea and Annelida (46% and 28% of reads), with Nematoda representing only 12% of the meiofauna over the year. Nematodes often dominate meiofauna in benthic habitats, representing 50% - 90% of the total individuals in medium to fine sandy sediments (Coull, 1988; Giere, 2009; Merckx et al., 2009). However, crustaceans and nematodes become more representative during the winter (57% and 17% of sequence reads), while annelids are less (11% of sequence reads). During the summer annelids and crustacean were more representative (40% and 35% of sequence reads), and nematodes represented 14% of the sequence reads, differently from what was indicated by Coull (1988) for temperate regions.

Crustacea and Annelida are typically macrofaunal groups, however, most crustacean ~~sequence~~ reads observed are from Harpacticoida (21% of the meiofaunal sequences) and Podocopida (13% of the meiofaunal sequences). Harpacticoids are usually one of the most abundant meiofaunal metazoan in sediment samples, that have been reported to represent 35% of the meiofaunal assemblage in tropical beaches, and Podocopida is composed by many marine benthic forms that are meiobenthic size. Some Annelids (Polychaeta) are meiobenthic size as adults, ~~but~~ many polychates have a juvenile phase in meiobenthic size range (temporary meiofauna; McIntyre, 1969), such as juvenile Syllidae and Capitellidae (Giere, 2009). Most Annelida sequence reads observed in this study are identified as capitellids (16% of the meiofaunal sequences).

We did not observe differences ~~on~~ meiofaunal taxon richness (at Phylum level) between dry and rainy periods (winter and summer, respectively), but we observed differences among seasons, with higher richness in summer and winter (9 phyla) and lower in spring and autumn (8 phyla). Differently, Cavalcanti et al. (2023) found lower meiofaunal richness during dry months than during rainy months, at a sandy beach ~~on~~ NE Brazil. Meiofaunal structure, abundance of reads, Shannon's diversity index, and phylogenetic diversity were significatively different among seasons, showing that these biological parameters are influenced by seasonal variability, as observed by previous studies in different sandy beaches around the world (McLachlan and Brown, 2006; Baia and Venekey, 2019; Baldrighi et al., 2019). Shannon's diversity was lower during spring, but with no significant differences between summer, autumn, and spring. Phylogenetic diversity was higher in summer and winter than in autumn and spring. These differences ~~on~~ diversity metrics shows that, at Gramuté beach, meiofaunal diversity changes seasonally but is not different among dry and rainy periods (at Phylum level), highlighting that rainfall, although is known to be important for assemblage structuring, did not play a key role on meiofaunal diversity at the study area, differently ~~of~~ what was ~~observed~~ by Gomes and Rosa-Filho (2009) and Venekey et al. (2014) for nematofauna structure on tropical region.

This metabarcoding assessment is the first molecular record of benthic animals registered for this region, and can be used as a baseline dataset for future research. We understand that metabarcoding approaches are influenced by PCR errors, primer biases, and sequence length (Adams et al., 2019; Beng and Corlett, 2020). Also, the taxonomic identification refinement obtained using DNA-based techniques are directly influenced by the lack of DNA sequences broadly representing meiofauna (Steyaert et al., 2020; Castro et al., 2021), incomplete DNA-barcodes deposited in molecular databases, and methodological practices (Cahill et al., 2018; Pawlowski et al., 2022; Keck et al., 2022; Willassen et al., 2022). ~~It~~ is important to emphasize the necessity to follow environmental DNA standards, particularly in sample collection, DNA extraction, genetic marker selection, and reduce or avoid false and negative detection (Shu et al., 2020). Additionally, metagenomic data should follow the FAIR principles, being findable, accessible, interoperable, and reusable.

Our study revealed a distinct meiofaunal structure with seasonal influences on diversity and abundance of sequence reads at a tropical beach within a Marine Protected Area (MPA), which needs to be considered as a priority area for conservation and management. Understanding diversity patterns and how it changes seasonally ~~in~~ a local-scale (as well as regional and global) is a key factor for conservation strategies, and associated to it, identifying priority areas for conservation (Strassburg et al., 2020; Pittman et al., 2021). The number of ~~sandy beaches ecological~~ studies in Brazil ha~~ve~~ increased significantly over the last ten years, but only the scientific knowledge acquired is not enough to effectively protect this ecosystem, once management and governance are extremely important in protecting priority areas and maintaining diversity and ecosystems services (Harris and Defeo, 2022). Open access information and data (published in open-access databases, such as OBIS and GBIF) should be accompanied by management and participatory decision-making process to allow a sustainable management and protection of ecosystem services and benefits from sandy beach ecosystems (Fanini et al., 2020).

Our findings also highlight the importance of using multivariable approaches, including sedimentary variables associated to climatic and water parameters, such as marine seascapes. Additionally, we highlight the importance of long-term studies to understand how meiofaunal assemblages may vary temporally in tropical regions. Long-term ecological studies in sandy beaches still scarce in Brazil, even with the production of monitoring protocol (e.g., MBON Pole-to-Pole and ReBentos) (Corte et al., 2023). ~~This~~ scarcity of long-term ecological studies contribute to the limited ~~information~~ on ~~diversity and~~ ecological role of meiofaunal species ~~from~~ sandy beach~~es~~ (Fanini et al., 2020; Corte et al., 2023). Several benthic ecological processes (e.g., recruitment, zonation, intra- and inter-specific interactions) may change during long-term temporal scale (years to decades), and can only be detected and understood ~~by~~ long-term monitoring studies (Turra et al., 2014).

Conclusion

We observed seasonal influence on meiofaunal diversity (phylogenetic and Shannon's diversity) at Gramuté beach, where the marine seascape is characterized by high temperatures, high salinity, and calm water masses with high nutrient supply. Higher abundance of reads and diversity were observed during the warmer months of the year (summer), associated to changes in food supply and it was lower when happened a subtropical water mass intrusion. Additionally, our results reveal that meiofaunal diversity is not drive by a unique variable, but by a complex set of variables, including biological variables like food supply (biopolymeric carbon – labile fraction of organic matter) and organic matter quality (protein content, lipid content, and carbohydrate-to-lipid ratio), and may be influenced by ecological interactions among taxa. We highlight the necessity of long-term monitoring programs to continue understanding which environmental factors are the main drivers of marine diversity, including spatial and seasonal variations, and how marine benthic organisms will respond to future warmer environmental scenarios.

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Table 1(on next page)

PERMANOVA Results.

Permutational Multivariate Analysis of Variance results from MBON Seascapes coverage at local scale (~ 30 km coastline, 465 Km2) at SE Brazil, during all seasons (summer, autumn, winter, and spring). Significative results are considered when p<0.05, and are presented in bold. df = Degrees of Freedom; SS = Sum of Squares; MS = Mean of Squares.

Source	df	SS	MS	Pseudo-F	*p*
Season	3	120.1	40.0	8.014	**0.001**
Residual	32	159.9	5.00		
Total	35	280.0			

Pair-wise tests

Groups	t	*p*
Summer X Autumn	1.478	0.106
Summer X Winter	3.467	**0.001**
Summer X Spring	3.003	**0.002**
Autumn X Winter	2.461	**0.001**
Autumn X Spring	2.589	**0.002**
Winter X Spring	3.573	**0.001**

Table 2(on next page)

PERMANOVA Results.

Permutational Multivariate Analysis of Variance results from meiofaunal composition at Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring) and sampled stations. Significative results are considered when $p<0.05$, and are presented in bold. Df = Degrees of Freedom; SS = Sum of Squares; MS = Mean of Squares.

Source	df	SS	MS	Pseudo-F	*p*
Season	3	11842.0	3947.5	2.307	**0.002**
Station	2	3296.2	1648.1	0.963	0.491
Season X Station	6	9315.7	1552.6	0.907	0.657
Residual	24	41070.0	1711.3		
Total	35	65525.0			
Pair-wise tests					
Groups				t	*p*
Autumn X Spring				1.356	**0.044**
Autumn X Summer				1.074	0.312
Autumn X Winter				1.403	0.062
Spring X Summer				1.950	**0.001**
Spring X Winter				1.880	**0.001**
Summer X Winter				0.988	0.488
Station 1 X Station 2				1.198	0.214
Station 1 X Station 3				0.852	0.698
Station 2 X Station 3				0.922	0.575
Autumn, Station 1 X Station 2				0.958	0.611
Autumn, Station 1 X Station 3				0.322	1.000
Autumn, Station 2 X Station 3				0.946	0.502
Spring, Station 1 X Station 2				1.015	0.497
Spring, Station 1 X Station 3				1.349	0.205
Spring, Station 2 X Station 3				1.203	0.396
Summer, Station 1 X Station 2				0.792	0.606
Summer, Station 1 X Station 3				0.365	0.885
Summer, Station 2 X Station 3				0.703	0.906
Winter, Station 1 X Station 2				1.113	0.429
Winter, Station 1 X Station 3				0.776	0.785
Winter, Station 2 X Station 3				0.652	0.886

Table 3(on next page)

PERMANOVA Results.

Permutational Multivariate Analysis of Variance results from meiofaunal phylogenetic diversity at Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring). Significative results are considered when $p<0.05$, and are presented in bold. Df = Degrees of Freedom; SS = Sum of Squares; MS = Mean of Squares.

Source	df	SS	MS	Pseudo-F	*p*
Season	3	1545.9	515.3	18.863	**0.001**
Residual	32	573.69	27.3		
Total	35	2119.6			

Pair-wise tests

Groups	t	*p*
Summer X Autumn	3.699	**0.022**
Summer X Winter	0.508	0.657
Summer X Spring	6.186	**0.001**
Autumn X Winter	3.303	**0.017**
Autumn X Spring	2.219	0.054
Winter X Spring	6.012	**0.001**

Table 4 (on next page)

PERMANOVA Results.

Permutational Multivariate Analysis of Variance results from meiofaunal Shannon’s Diversity index at Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring). Significative results are considered when $p<0.05$, and are presented in bold. Df = Degrees of Freedom; SS = Sum of Squares; MS = Mean of Squares.

Source	df	SS	MS	Pseudo-F	*p*
Season	3	1954.2	651.4	13.129	**0.001**
Residual	32	1587.6	49.6		
Total	35	3541.8			

Pair-wise tests

Groups	t	*p*
Summer X Autumn	2.598	**0.026**
Summer X Winter	0.719	0.544
Summer X Spring	4.906	**0.001**
Autumn X Winter	0.899	0.412
Autumn X Spring	3.861	**0.001**
Winter X Spring	3.806	**0.003**

Table 5(on next page)

Linear model results.

Linear model statistical values from relation between meiofaunal diversity (Shannon’s diversity index and phylogenetic diversity) and environmental variables (biopolymeric carbon, carbohydrate-to-lipid ratio, lipid content, and protein content) collected in Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring). This model was chosen based on the lowest AIC. Significative results are considered when $p<0.05$.

	Estimate	Standard Error	*t*	*p*
Intercept	-8.429	7.993	-1.055	0.300
Biopolymeric Carbon (BPC)	-0.002	0.001	-2.584	**0.015**
Carbohydrate-to-lipid (CHO:LIP)	0.015	0.009	-1.530	0.137
Lipid (LIP)	0.006	0.002	2.513	**0.018**
Protein (PRT)	-0.015	0.009	-1.719	0.096

Figure 1

Study area location.

(A) Location of Gramuté beach in the SE Brazilian coast, within the marine protected areas Refúgio da Vida Silvestre de Santa Cruz and Área de Proteção Ambiental Costa das Algas (polygon areas) (B) sampling design in Gramuté beach, with sampling stations 20 m apart from each other.

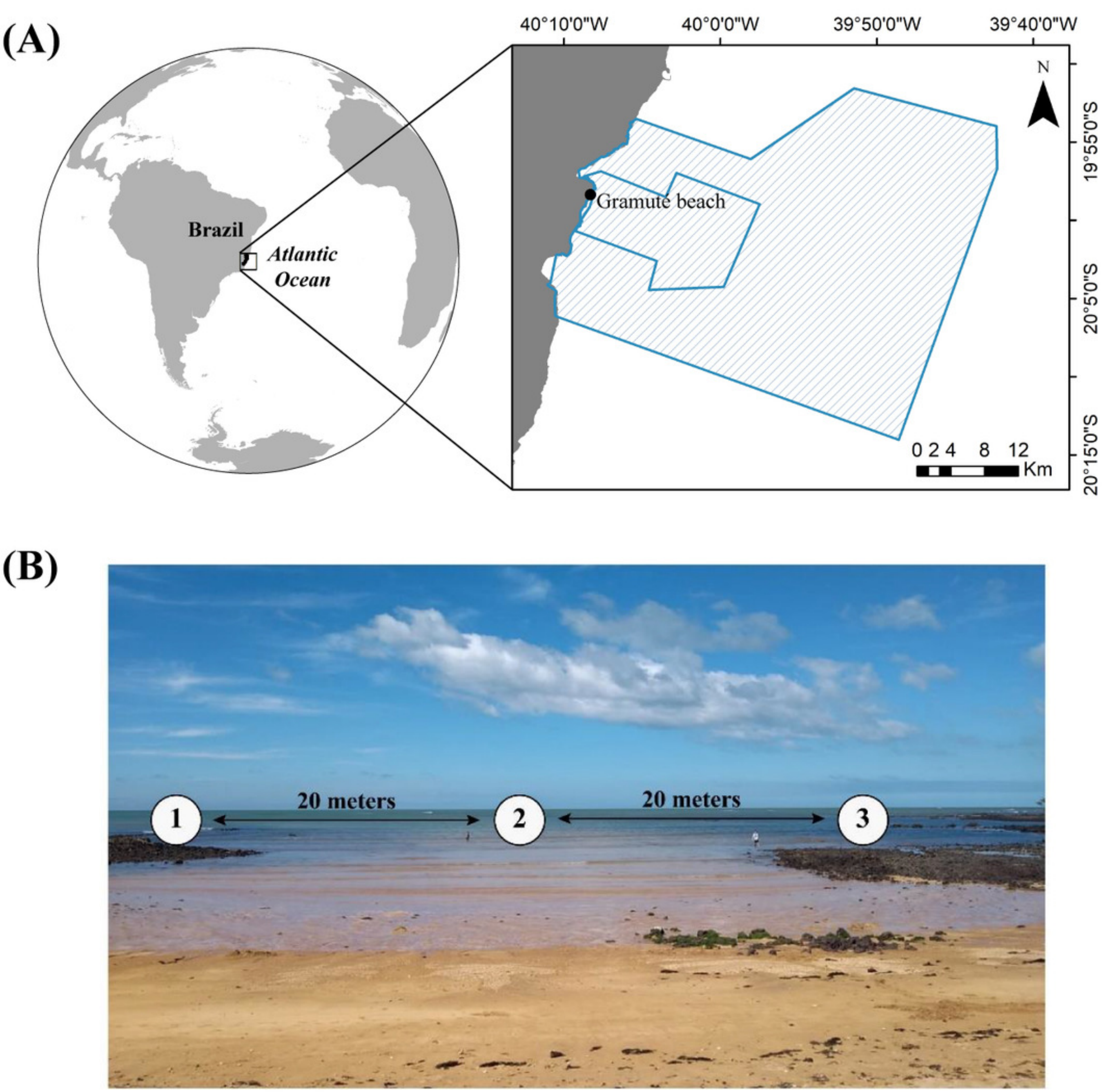

(A)
Brazil
Atlantic Ocean
40°10'0"W
40°0'0"W
39°50'0"W
39°40'0"W
N
19°55'0"S
20°5'0"S
20°15'0"S
Gramute beach
0 2 4 8 12
Km
(B)
1
20 meters
2
20 meters
3

Figure 2

Environmental variables barplots

Environmental variables (mean±SD) from Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring).

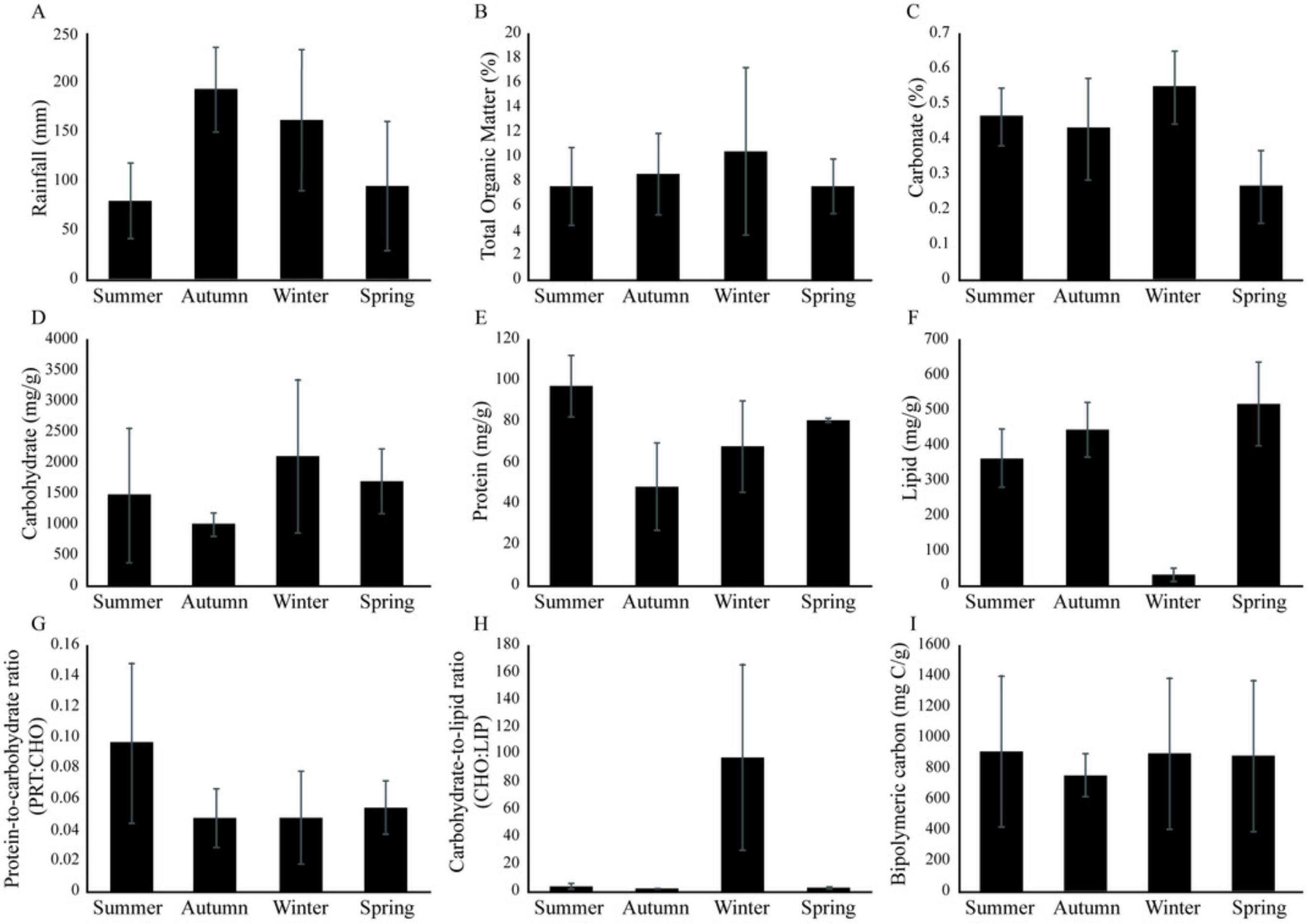
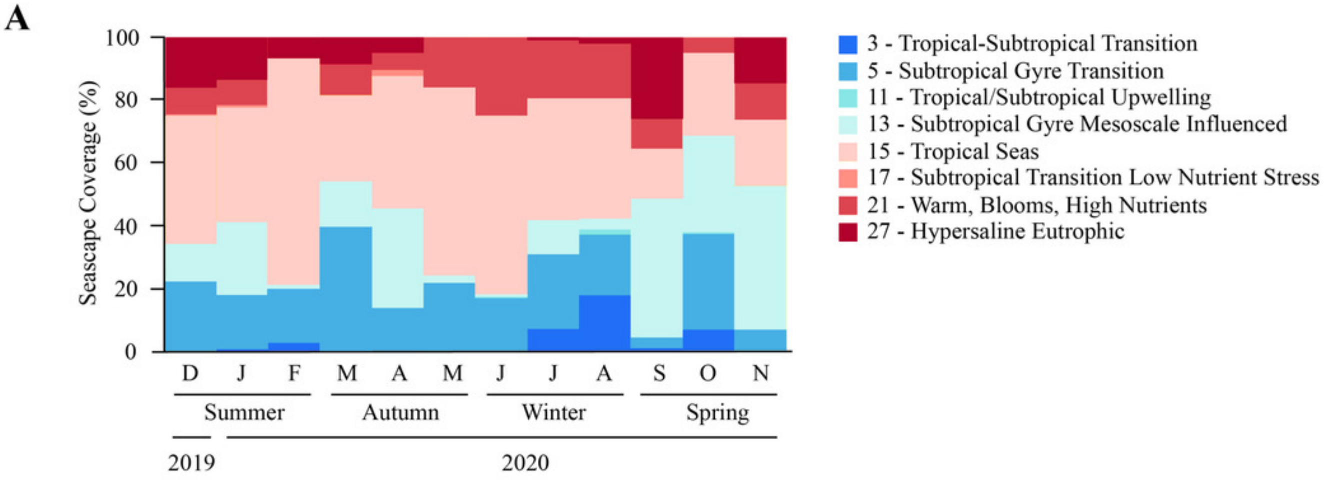


Figure 3

Seascape coverage.

Monthly (A) and seasonal (B – E) variation in Seascapes coverage (%) between December 2019 to November 2020 in Gramuté beach, SE Brazil. Mean oceanographic values from oceanographic variables that identify each MBON Seascape water mass (class). SST - sea surface temperature, SSS - sea surface salinity, ADT - absolute dynamic topography, CDOM - chromophoric dissolved organic material, CHLA - chlorophyll-a, NFLH - normalized fluorescent line height.



	SST (°C)	SSS (psu)	ADT (m)	CDOM (m^{-1})	NFLH (W m^{-2} um^{-2} sr^{-1})	CHLA (mg m^{-3})	NFLH: CHLA
🟦 3 - Tropical-Subtropical Transition	24.12	35.34	0.68	0.01	0.06	0.15	0.40
🟦 5 - Subtropical Gyre Transition	23.95	35.89	0.71	0.00	0.04	0.07	0.50
🟦 11 - Tropical/Subtropical Upwelling	22.94	34.79	0.83	0.01	0.11	0.27	0.39
🟦 13 - Subtropical Gyre Mesoscale Influenced	23.47	35.89	0.52	0.01	0.02	0.10	0.19
🟥 15 - Tropical Seas	25.35	35.40	0.51	0.02	0.06	0.32	0.20
🟥 17 - Subtropical Transition Low Nutrient Stress	20.89	33.59	0.64	0.01	0.02	0.17	0.15
🟥 21 - Warm, Blooms, High Nutrients	22.54	34.46	0.57	0.07	0.24	2.09	0.12
🟥 27 - Hypersaline Eutrophic	25.95	38.14	0.54	0.07	0.11	1.15	0.09

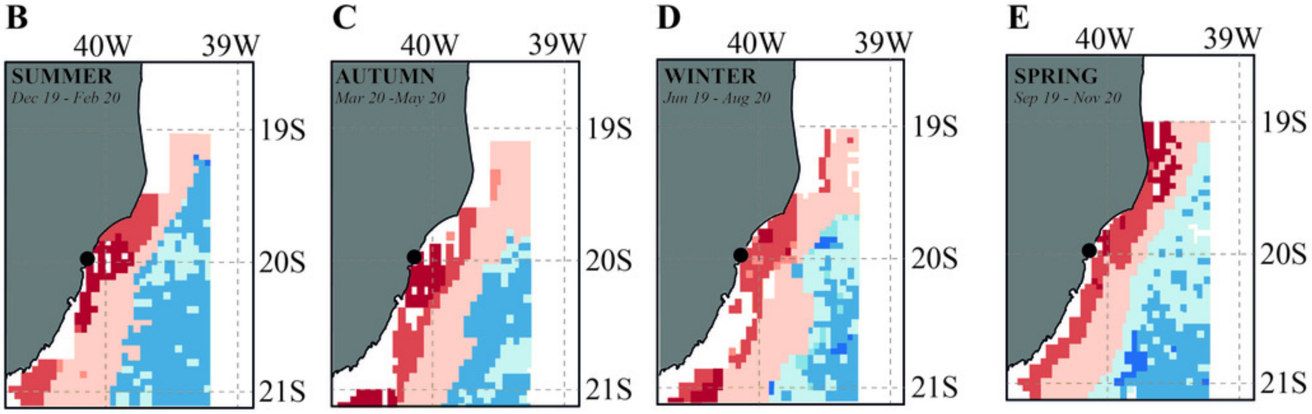


Figure 4

Meiofaunal abundance of sequences, assemblage composition, and diversity metrics.

(A) Number of meiofaunal sequence reads (mean±SD) (B) Meiofaunal taxa proportion (%) (C) Faith’s Phylogenetic Diversity (mean±SD) (D) Shannon’s Diversity index (mean±SD), obtained after metabarcoding sediment samples from Gramuté beach, SE Brazil, in each season. Different letters represent significative statistical differences (p<0.05).

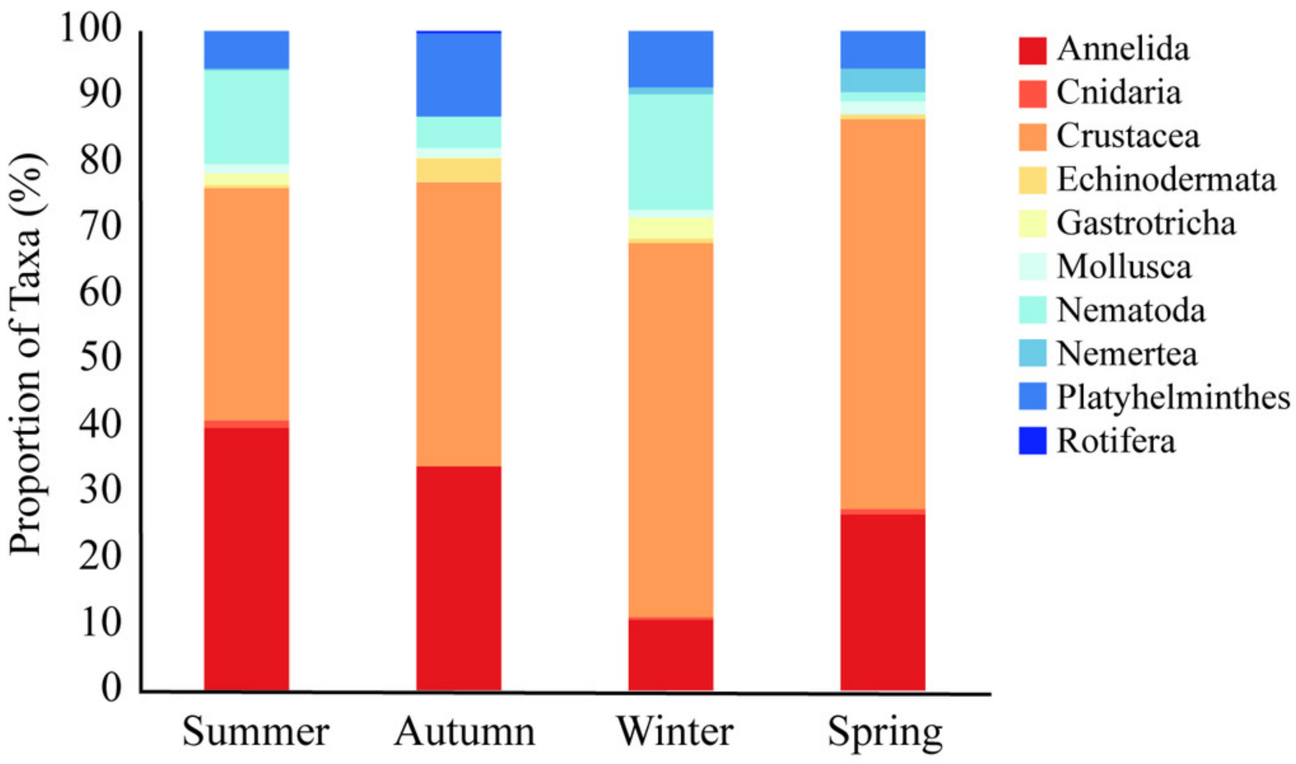


Figure 5

Rarefaction curves.

Rarefaction curves obtained from sediment samples metabarcoding collected at Gramuté beach, SE Brazil, during all seasons on a 1-year sampling. Solid lines represent a mean of observed ASVs at each sampling depth, and the shaded area represents the standard deviation.

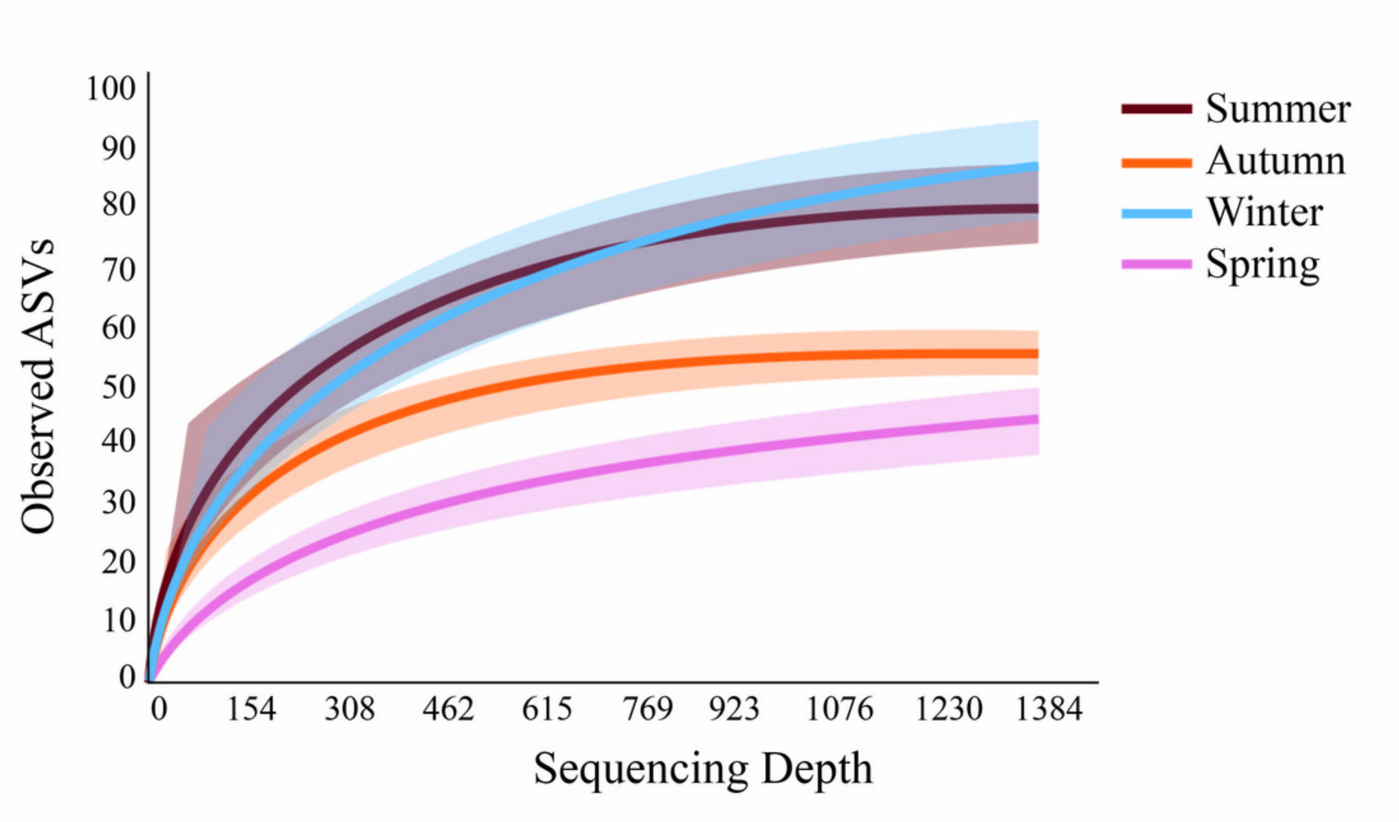


Figure 6

CAP ordination.

Canonical Analysis of Principal Coordinates (CAP) of main meiofaunal phyla and environmental variables (rainfall, carbonate content, organic matter, and biopolymers) at Gramuté beach, SE Brazil, during all seasons.