Effects of seascape dynamics on the sand beach meiofauna in the SW Atlantic coast (#92413)

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Effects of seascape dynamics on the sand beach meiofauna in the SW Atlantic coast

Gabriel C Coppo Corresp., 1 , **Araiene P Pereira** 1 , **Sérgio A Netto** 2 , **Angelo F Bernardino** 1

1 Grupo de Ecologia Bentônica, Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil

2 Marítima Estudos Bênticos, Laguna, Santa Catarina, Brazil

Corresponding Author: Gabriel C Coppo
Email address: coppogabriel@gmail.com

Background. Understanding the diversity patterns of marine meiofauna is critical in a changing world. Here we investigate the seasonality of a sandy beach meiofaunal assemblage in response to coastal oceanography dynamics based on the Seascapes remote sensing dataset.

Methods. We used metabarcoding from sediment samples to assess the meiofaunal assemblage composition and diversity during one year. Our data support our initial hypotheses revealing a higher abundance of reads, phylogenetic diversity, and Shannon's diversity during warmer periods of the 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. The association between meiofauna abundance of reads and diversity to seascape dynamics suggest that large-scale changes in ocean heat and productivity may have importance to the sand beach biodiversity in this tropical ecoregion.

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Gabriel C. Coppo[1], Araiene P. Pereira[1], Sérgio A. Netto[2], Angelo F. Bernardino[1]

[1]Grupo de Ecologia Bentônica, Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil.

[2]Marítima Estudos Bênticos, Laguna, Santa Catarina, Brazil

Corresponding Authors:

Gabriel C. Coppo[1]

Av. Fernando Ferrari 514, CCHN, Vitória, Espirito Santo, 29075-910, Brazil

Email address: coppogabriel@gmail.com

Abstract

Brackground.

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Methods.

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Keywords: benthos; seascape; environmental DNA; temporal change

Introduction

In benthic marine communities, 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 communities (Giere, 2009). 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). Additionally, 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; Mazzuco et al., 2020). In tropical humid regions, rainfall may additionally work as a major factor structuring meiofauna diversity in ~~tropical~~ sandy beaches (Gomes and Rosa-Filho, 2009; Venekey et al., 2014; Baia and Venekey, 2019).

Sandy beaches form an intricate ecosystem between marine and terrestrial environments, with a large diversity of organisms supporting important biogeochemical processes (Wu et al., 2018; Okamoto et al., 2022). Sandy beaches are influenced by global and local oceanographic processes, which in turn shape the community structure of these habitats. 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). Understanding how marine diversity varies at local scales contributes to the conservation of these ecosystems (Gaston et al., 2000). ~~Also,~~ understanding which environmental factors are the main drivers of marine diversity and abundance, including spatio-temporal variations, is critical to establish a strong baseline that can be used in future comparisons.

Sandy beache~~s morphodynamic~~ may change ~~in~~ different timescales: (1) 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) has increased recently (Blue and Kench, 2017; Vos et al., 2019), boosted ~~by~~ frequency and intensity of global climate change. 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).

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; ~~Higgins & Thiel 1988;~~ Hakenkamp and Palmer, 2000). These organisms play crucial ecological roles in ~~the~~ marine ~~sediment, such as~~ nutrient recycling, ~~and~~ transferring energy and matter into benthic and pelagic trophic food webs~~,~~ linking different trophic levels (Coull, 1999; 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).

Meiofaunal organisms may have a strong direct impact on benthic properties, modifying interactions between macrofaunal species and the environment (Zeppilli et al., 2015). In some shallow marine environments, such as tidal flats, meiofaunal secondary production may exceeds macrofaunal production (Warwick et al., 1979; Kuipers et al., 1981), contributing up to 40% of the total benthic metabolism in sandy beaches (Fenchel, 1978). 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).

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). Wave action also plays an important role on spatial variability (i.e., patchiness) of ~~density and diversity~~ 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).

Monitoring marine seascapes using satellite data has recorded alterations on different ocean ~~depth,~~ from surface to the deep (Boyce et al., 2010; McCauley et al., 2015; Mazzuco and Bernardino, 2022). Under a changing marine ecosystem, seascapes can be tracked by assessing biotic and abiotic variables, such as benthic-pelagic association and important environmental variables to benthic fauna (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 ~~on~~ benthic ~~composition and diversity~~ (Fagundes et al., 2020; Pittman et al., 2021; Mazzuco and Bernardino et al., 2022).

Predicting changes in diversity patterns from local to global scales is ~~a research prime concern~~ 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. Here, we aimed to assess meiofaunal diversity in a tropical sandy beach to test whether or not (i) the phylogenetic diversity is influenced by seasonality; (ii) ~~if~~ the local diversity and assemblage composition would be related to regional (larger- scale influences) in marine seascapes. We addressed the following hypotheses in this study: meiofaunal phylogenetic diversity and abundance of sequences is higher during warmer months in Gramuté beach.

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). ~~It is a~~ tropical region ~~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 ~~area~~ has experienced significant warming in the last 40 years (Bernardino et al., 2015; Mazzuco et al., 2020).

Sediment samples (approximately 200 g) were collected monthly in triplicate at three stations 20 meters distant from each other (n = 9 sediment samples per month) in the subtidal zone, always during the low-tide (Figure 1B) ~~for~~ one year (December 2019 to November 2020). Sediment samples were collected manually using sterile, DNA-free corers, over all seasons during the sampling period (Summer = December 2019 to February 2020; Autumn = March 2020 to May 2020; Winter = June 2020 to August 2020; Spring = September 2020 to November 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). We used similar sample sizes ~~between~~ stations to be able to compare them without sampling artifacts. Total monthly rainfall data ~~for~~ ~~sample~~ period (December 2019 - November 2020) ~~were~~ 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 ~~away~~ from ~~the~~ Gramuté beach.

Sediment analysis

~~We dried s~~ediment samples ~~for~~ ~~48 hours~~ at 60°C for 48 h~~ours~~ before all granulometric analysis. ~~Then the dry~~ 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 determinat~~e~~ total protein (PRT) content according to Hartree (1972) ~~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. 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 hours.

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 – CHLA, and normalized fluorescent line height – NFLH). These variables are used to a categorization system of 33 water masses (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 ~~disponible on~~ 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 – 40.3° to – 39.8°, Latitude 20.3° to 19.8°) for the study period (December 2019 – November 2020). Additionally, to determine seasonal ~~mean sea surface temperature (~~SST~~)~~ and ~~sea surface salinity (~~SSS~~)~~ for the study area, we calculated a weighted average based on the monthly coverage area of ~~each~~ MBON marine seascape ~~identified.~~

DNA extraction and sequencing

Previously to the DNA extraction, sediment samples were elutriated using sieves of 45 µm mash, then aliquoted to 20 mL in an attempt to increase the meiofaunal abundance and enrich metazoan ~~ASVs after elutriation, and~~ suggested by Brannock and Halanych (2015) ~~for studies focused on metazoan meiofauna assessments, instead of extract the DNA directly from sediment~~.

1L flasks were filled with 950 mL of filtered seawater and ~~sediment and~~ sediment samples were added to it, then homogenized and let to sit before decanting the liquid over the sieve. ~~It~~ was repeated ~~ten~~ times~~, then the~~ sediment retained on the sieve was ~~rinsed~~ to Falcon tubes and centrifuged at room temperature for 3 minutes at 1342 ~~X~~ g in an Eppendorf Centrifuge 5430. ~~Alliquots~~ of 1mL ~~aliquots~~ were stored ~~them~~ at -20°C (Brannock and Halanych, 2015) (Figure 2). All glassware was sterilized between samples to avoid cross contamination. DNA were extracted from ~~the~~ 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 (Life Technologies-Invitrogen, Carlsbad, CA, USA). Negative controls were carried in triplicate for each step before metabarcoding sequencing (sediment elutriation, DNA extraction, and integrity, purity, and concentration checking).

PCR, ~~metabarcoding sequencing and amplicon libraries~~ were conducted by ©NGS Genomic Solutions (Piracicaba, SP, Brazil). To perform a PCR reaction, were used the 18S selected primers (Illumina_Euk_1391 forward and Illumina_EukBr reverse) synthesized with Illumina adaptors. The products of this PCR were observed in a 1.5% agarose gel, then purified using AMPure Beads (Beckman Coutler, Life Sciences). After that the Illumina adapters are connected in a second PCR reaction (index Nextera XT Index Primer 1 (N7xx) and Nextera XT Index Primer 2 (S5xx)), then purified again using the AMPure Beads, and the products visualized in a 1.5% agarose gel. After that, the PCR products are quantified by NanoDrop and then normalized to the same concentration, and mixed in an equimolar pool of all samples. This sample pool is quantified by qPCR for validation and quantification using a KAPA Library Quantification kit for Illumina (Roche). Additionally, the mix of reagents for PCR reaction and its condition are described below. PCR reaction conditions in the thermal cycler were 94 °C for 3 minutes followed by 30 cycles at 94 °C for 30 seconds, 57 °C for 30 seconds, 72 °C for 30 seconds, 72 °C for 10 minutes, and 4 °C hold.

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 FastQC 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 ~~composition~~ of amplicon sequence variants (ASV) generated by the DADA2 plugin was ~~determined by~~ machine learning Python library scikit-learn ~~to determine the taxonomic composition of the~~ (Pedregosa et al., 2011). A pre-trained Naïve Bayes classifier trained ~~on~~ Silva 132 database (Quast et al., 2013) clustered at 99% similarity was used to identify taxonomically the ~~sequences.~~ Datasets ~~were~~ normalized to allow analysis and comparisons under similar sampling depth (1384 reads), and resampled each sample to the same depth, and these normalized datasets were used to calculate all diversity metrics. We performed rarefaction curves for all four sampled seasons (summer~~,~~ winter, spring, and autumn) with ~~the observed amplicon sequence variants (~~ASVs~~)~~ at each sampling depth. We calculated the Faith's Phylogenetic Diversity (PD) for each sample using the diversity core-metrics-phylogenetic pipeline. Shannon diversity was calculated using the qiime diversity alpha pipeline and setting the p-metric parameter to "shannon". Raw sequences ~~data~~ are ~~disponible~~ online ~~in~~ NCBI (SRR24675047).

Statistical analysis

~~For s~~tatistical analysis ~~we only considered~~ meiofaunal metazoan sequences. 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), as previously ~~realized~~ in other studies (Brannock and Halanych, 2015; Bernardino et al., 2019; 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 its~~ biopolymeric composition), seascape coverage, and meiofaunal data (diversity metrics - Shannon's diversity index ~~and~~ phylogenetic diversity, and abundance of sequence reads) among sampled seasons (summer, autumn, winter, and spring) at Gramuté beach. A canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003) ordination plot was made with environmental 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~~ dissimilarity ~~between~~ seasons. A linear model was calculated using Shannon’s diversity Index and phylogenetic diversity as response variables, and the assessed environmental variables as predictive variables. Significative differences were defined ~~when~~ $p<0.05$. All graphical and analytical ~~processes~~ were performed in the R environment (R Core Team, 2022).

Results

Environmental conditions and seascape coverage

We observed significant seasonal variability in lipids content (LIP) and in carbohydrate-to-lipids ratio (CHO:LIP). LIP was 33.0±18.8 in spring, ~~and~~ 444.9±78.1 in summer, 518.8±120.5 in autumn, and 362.8±80.7 in winter (representing differences of 13.5-fold, 15.7-fold, and 11.0-fold, respectively; Table 1). Consequently, the CHO:LIP ratio was higher in spring (98.0±67.9) than in summer (2.25±0.23), autumn (1.87±1.52), and winter (3.78±1.94), which represent differences of 43.6-fold, 34.8-fold, and 25.9-fold, respectively (Table 1). These ~~significative~~ differences contributed to seasonal changes at Gramuté beach, SE Brazil (PERMANOVA, df = 3; Pseudo-F = 6.916; p = 0.001; Table 2). Additionally, ~~the~~ total rainfall ranged from 80.2±35.6 mm in winter to 193.0±42.2 mm in summer (Table 1). The sediment is completely composed of sand (1.2±0.6% very fine sand, 17.9±6.1% fine sand, 31.5±5.5% medium sand, 31.9±6.9% coarse sand, 17.5±5.8% very coarse sand), and its carbonate content ranges from 19% during autumn to 64% in spring (Table 1). Total organic matter (TOM) had its lower concentration in summer (8.6±3.8)~~,~~ and higher in spring (10.4±7.9) (Table 1). ~~P~~rotein fraction ~~of~~ organic matter content ~~in~~ sediment ranged from 48.2±25.0 in summer to 96.9±17.1 in winter (Table 1), ~~mean~~while carbohydrate fraction ranged from 997.1±223.5 in summer to 2102.0±1435.5 in spring (Table 1). The ~~content of~~ labile fraction of organic matter, which is represented by the biopolymeric carbon (BPC), ~~had its highest~~ peak ~~during~~ winter (1562.6 mg C.g-1)~~,~~ and lower ~~during~~ spring (241.1 mg C.g-1) (Table 1).

Overall, the Seascapes categories in this region ~~are~~ 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 ~~have~~ 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 3). 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 2).

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 2). This marine seascape is usually characterized by high temperatures (25.4 °C) and salinity (35.4 psu) (Figure 2), 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, 24.3±0.1 °C, respectively, and mean salinity of 36.0±0.1 psu, 35.6±0.3 psu, 35.4±0.1 ps[illegible]espectively. During Spring (Sep – Nov), the dominance of seascapes changed from Tropical to Subtropical (class 13 - 42.7% of area coverage; Figure 2), which is usually characterized by lower temperature (23.5 °C) and higher salinity (35.9 psu)~~, and~~ at Gramuté beach ~~was~~ observed a mean temperature of 24.5±0.2 °C and mean salinity of 36.0±0.2 psu.

Meiofaunal assemblage

A total of 9692 sequences from meiofaunal taxa were identified in the dataset, showing seasonal changes in assemblage composition and abundance of reads (PERMANOVA, df = 3; Pseudo-F = 2.353; p = 0.001; Table 4). Higher abundance of meiofaunal sequence reads was observed in summer (3347 sequence reads) and in winter (3160 sequence reads), which ~~are~~ significantly different when compared to spring (565 sequence reads) (Figure 3A), representing differences of 5.9-fold and 5.6-fold, respectively. Abundance of sequence reads in autumn (2620 sequence reads) ~~was similar to~~ all other seasons (Figure 3A). Furthermore, meiofaunal assemblage composition was significantly different among all seasons ~~besides~~ summer and winter~~;~~ and winter and spring (Table 4).

Crustacea and Annelida typically dominated the assemblage during summer (35% and 40% of reads, respectively), autumn (43% and 34% of reads, respectively), and spring (59% and 27% of reads). ~~While d~~uring winter, the most abundant taxa were Crustacea (57% of reads) and Nematoda (17% of reads) (Figure 3B). Sequence ~~reads~~ from Nemertea were not detected during autumn, Gastrotricha was not detected in spring, and Rotifera was not detected in neither. Only 11 taxa (26.19% of all detected taxa) - Annelida miscellaneous, Echiuroinea (Annelida), Phyllodocida (Annelida), Maxillopoda miscellaneous, Harpacticoida (Crustacea), Podocopida (Crustacea), Holothuroidea (Echinodermata), Pterioida (Mollusca), Chromadorea miscellaneous (Nematoda), Rhabditida (Nematoda), and Rhabdocoela (Platyhelminthes) – were detected on all four sampled seasons (Table S1). On the other hand, 14 taxa (33.33% of all detected taxa) – Aspidosiphonidormes (Annelida), Golfingiida (Annelida), Protodrilidae (Annelida), Spionida (Annelida), Calanoida (Crustacea), Zoantharia (Cnidaria), Ophiuroidea (Echinodermata), Chaetonida (Gastrotricha), Heterobranchia (Mollusca), Desmodorida (Nematoda), Monhysterida (Nematoda), Enoplida (Nematoda), Platyhelminthes miscellaneous, and Bdelloidea (Rotifera), were detected only on one sampled season (Table S1).

Rarefaction curves suggest that the number of meiofaunal taxonomic groups detected during ~~S~~pring was lower when compared to summer, autumn, and winter (Figure 4). We observed significant differences in diversity patterns among seasons in Gramuté beach. ~~P~~hylogenetic diversity presented a marked seasonal variation, with lower diversity in spring (9.23±1.88) and in autumn (11.88±1.82), when compared to summer (17.93±3.11) and winter (19.37±4.85) (PERMANOVA; Pseudo-F = 18.863; df = 3; $p < 0.001$; Figure 3C; Table 5). Similarly, Shannon's diversity was lower in spring (2.38±0.91) when compared to autumn (4.03±0.53), summer (4.82±0.72), and winter (4.56±1.13), representing differences of 1.7-fold, 2.0-fold, and 1.9-fold, respectively (PERMANOVA; Pseudo-F = 13.129; df = 3; $p < 0.001$; Figure 3D; Table 6).

The meiofaunal assemblage differs significantly ~~between~~ the ~~sampled~~ seasons in Gramuté beach (PERMANOVA, df = 3; Pseudo-F = 2.353; p = 0.001; Table 4; Table S2). 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 ~~sampled~~ seasons. SIMPER analysis revealed that Annelida (ranging from 16.5% to 28.3%; Table S2), Crustacea (ranging from 21.8% to 26.7%; Table S2) and Nematoda (ranging from 13.9% to 21.8%; Table S2) 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 S2). Annelids, crustaceans and nematodes were more abundant in summer and winter ~~samples~~. ~~Further,~~ 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 5).

~~The assessed e~~nvironmental variables (rainfall; organic matter content; carbonate content; biopolymeric fractions and ratios - carbohydrate, protein, lipids, CHO:LIP, and PRT:CHO; and biopolymeric carbon content) compose a significant model of variables likely to drive meiofauna diversity (Shannon's diversity Index and phylogenetic diversity) at Gramuté beach (Adjusted R^2 = 0.423; F = 4.21; p=0.002; Table 7). We observe significant positive relationship between meiofaunal diversity (Shannon's diversity and phylogenetic diversity) and biopolymeric carbon content - BPC (t = 2.303; p = 0.030; Table 7), ~~meanwhile~~ carbohydrate-to-lipids ratio (CHO:LIP) was negatively correlated to meiofaunal diversity (t = -2.347; p = 0.027).

Discussion

Our findings suggest a marked seasonality of the meiofaunal assemblage composition, abundance of reads, and diversity (phylogenetic and Shannon's index) ~~along the year~~ at Gramuté beach. The observed seasonal differences at Gramuté beach reveal that meiofaunal assemblages in this tropical region ~~support~~ marked oscillations in the coastal oceanography, recruitment, and possibly productivity regimes (Mazzuco et al., 2015; 2019; Mazzuco and Bernardino, 2022). We observed 5.9-times more sequences during summer when compared to spring, and the dissimilarities on assemblages between seasons reflected in differences of 1.9 and 2-times in phylogenetic diversity and Shannon's index, respectively. Higher phylogenetic diversity was observed during summer and winter, as well as higher abundance of sequences and Shannon diversity.

We observed higher content of organic matter during spring, which presented higher values of carbohydrate, that is associated to accumulation of aged organic matter, once protein (PRT) is usually consumed first (Joseph et al., 2008). Meanwhile, winter presented lower values of organic matter content with higher values of protein in sediment. Autumn had the lower organic matter quality, represented by the protein-to-carbohydrate ratio (PRT:CHO), which ~~mean~~ more degraded organic matter (Danovaro et al., 1993). Additionally, rainfall data showed higher values during summer and lower during winter, as reported previously by Bernardino et al. (2015).

Water masses detected in the study area had its higher temperature and salinity on summer when compared to the other seasons, and MBON marine seascape coverage markedly changes seasonally, with dominance of four MBON marine seascapes: Tropical Seas (class 15), Subtropical Gyre Transition (class 5), Subtropical Gyre Mesoscale Influenced (class 13), and Warm, Blooms, High Nutrients (class 21), similar to Mazzuco and Bernardino (2022)'s findings at the same area. This seascape dynamics are 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. The study region is predominantly represented by a mixing of Tropical Water (mass of hot and saline surface water) and Coastal Waters (less saline water mass) (Silva et al., 1982; Perenco, 2009).

Furthermore, the study region is marked by frequent exposure to waves generated mainly by the South Atlantic Subtropical Anticyclone (ASAS), with northeast (NE) ~~as main direction,~~ 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).

We observed that the dominant seascapes are associated to abundance of reads, Shannon's diversity, and phylogenetic diversity patterns at local scale, supporting our initial hypothesis. These biological parameters (e.g., abundance of reads, Shannon's diversity index, and phylogenetic diversity) showed higher values ~~associated to~~ the presence of tropical water masses ~~associated to higher abundance and diversity of meiofaunal taxa~~, which are followed by the intrusion of subtropical water masses rich in nutrients. Similar patterns were observed by Mazzuco and Bernardino (2020) for benthic recruitment at Gramuté beach, with Seascapes on the Eastern Brazil Marine Ecoregion correlated with patterns of larval recruitment of reef benthic species at multiple temporal scales. The observed peaks of abundance of reads and diversity may be influenced by larval recruitment, even though some meiofaunal taxa ~~does~~ not have a larval phase (e.g, nematodes) but some temporary meiofauna may have a larval or juvenile stage of life (with the size a meiofaunal organism), playing key roles in the sediment. This result highlights the relation between food supply and benthic abundance and diversity, as observed in previous studies (Antón et al., 2011; Neto et al., 2021).

Meiofaunal assemblage at Gramuté beach was overall mainly dominated by Crustacea and Annelida (46% and 28% of ~~sequence~~ reads), with Nematoda representing only 12% of the meiofauna over the year. ~~Differently, in general is expected to nematodes~~ ~~to~~ dominate meiofauna in benthic habitats, representing more than 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 dry period (57% and 17% of sequence reads, respectively, in winter), while annelids are less ~~representative~~ (11% of sequence reads). ~~Meanwhile, during~~ the rainy period annelids and crustacean were more representative (40% and 35% of sequence reads, respectively, in summer), and nematodes represented 14% of the sequence reads, differently from what was indicated by Coull (1988) for temperate regions.

We did not observe differences on richness (at Phylum level) between dry and rainy periods (winter and summer, respectively), ~~we~~ observed differences ~~between~~ seasons, with higher richness in summer and winter (9 phyla) and lower ~~on~~ 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 ~~dependent on time (~~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, highlighting that rainfall, although is important on 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.

Shannon’s Diversity index and phylogenetic diversity were positively influenced by the biopolymeric carbon (BPC) content, which represents the labile fraction of organic matter in sediment (Danovaro et al., 1993; Fabiano et al., 1995), showing that meiofaunal diversity is associated to food availability. Similarly, Cisneros et al. (2011) ~~found~~ observed seasonal changes on organic matter content and nutrients associated to differences on benthic abundance and diversity at a tropical sandy beach. ~~However, c~~arbohydrate-to-lipids ratio (CHO:LIP) was negatively related to meiofaunal diversity, ~~which represents a~~ lower meiofaunal diversity associated to higher content of aged organic matter (CHO) (Venturini et al., 2012 as observed on spring. Additionally, CHO:LIP may be related to ~~a~~ low lipids (LIP) income from anthropogenic sources such as petroleum and domestic sewage input (Joseph et al., 2008; Venturini et al., 2012).

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 (Fais et al., 2020; Steyaert et al., 2020; Castro et al., 2021), incomplete DNA-barcodes deposited in molecular databases, and different methodological practices followed by research groups (Cahill et al., 2018; Pawlowski et al., 2022; Keck et al., 2022; Willassen et al., 2022).

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 ~~tracked~~ as a priority area for conservation and management. Understanding diversity patterns, how it changes seasonally in a local-scale is important for conservation strategies, and associated to it, identifying priority areas is one of the key objectives of ecologists around the world (Strassburg et al., 2020; Pittman et al., 2021). ~~The results obtained~~ 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 ~~with temporal replication~~ to understand how meiofaunal assemblages ~~varies~~ ~~along a temporal scale~~ ~~at the~~ tropical region, ~~once most part of studies in Brazilian beaches have the duration of less than one year, and are mainly only one sampling event per site.~~ Several benthic ecological processes (e.g., recruitment, zonation, intra- and inter-specific interactions) may change ~~in a~~ long-term temporal scale (years to decades), and can only be detected and understood by long-term monitoring studies (Turra et al., 2014).

Conclusion

~~In conclusion, we~~ observed seasonal influence on meiofaunal diversity and abundance of sequence reads at Gramuté beach, where the marine seascape is characterized by high temperatures, high salinity, calm water masses with high nutrient supply. Although richness does not differ significantly among seasons, meiofaunal assemblage composition, abundance of reads and diversity (Shannon's Diversity index and phylogenetic diversity) ~~depend on time in a long-term scale~~ (seasonal variability). Higher abundance of reads and diversity were observed during the warmer months of the year (summer), associated to changes ~~on environmental parameters such as~~ food supply and variation on water mass intrusion. Additionally, our results reveal that meiofaunal diversity is driven by food supply (biopolymeric carbon – labile fraction of organic matter) and organic matter quality. We highlight the necessity of long-term monitoring programs to continue understanding how marine benthic organisms will respond to future warmer environmental scenarios.

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Table 1(on next page)

Environmental data.

Environmental variables data, presented as mean ± standard deviation, obtained at Gramuté beach, SE Brazil over the seasons (summer, autumn, winter, and spring) during 1-year sampling.

Variable	Season			
	Summer	Autumn	Winter	Spring
Rainfall (mm)	193.0±42.2	95.3±65.6	80.2±35.6	162.3±71.5
Total Organic Matter (TOM)	8.6±3.3	7.60±2.21	7.59±3.25	10.43±6.80
Carbonate (%)	42.9±14.4	26.4±10.3	46.3±8.0	54.7±10.4
Carbohydrate (CHO)	997.1±193.5	1134.1±999.2	1476.9±1015.1	2102.0±1243.0
Protein (PRT)	48.3±21.6	80.6±0.7	96.9±15.8	67.7±22.2
Lipids (LIP)	444.9±78.1	518.8±120.5	362.8±80.7	33.0±18.8
PRT:CHO	0.05±0.02	0.04±0.03	0.10±0.05	0.05±0.03
CHO:LIP	2.25±0.23	1.87±1.53	3.78±1.94	98.0±67.9
Biopolymeric Carbon (BPC)	756.1±140.1	882.2±489.9	910.4±454.7	898.7±493.6

Table 2(on next page)

PERMANOVA Results.

Permutational Multivariate Analysis of Variance results from environmental data (rainfall. grain size, carbonate, organic matter, biopolymers) collected in 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	123.9	41.3	6.916	**0.001**
Residual	32	191.1	5.97		
Total	35	315.0			

Pair-wise tests

Groups	t	*p*
Summer X Autumn	2.698	**0.001**
Summer X Winter	2.874	**0.001**
Summer X Spring	2.632	**0.005**
Autumn X Winter	1.923	**0.027**
Autumn X Spring	3.009	**0.001**
Winter X Spring	2.476	**0.002**

Table 3(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**

1

Table 4(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). 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	3947.5	2.353	**0.001**
Residual	32	53682	1677.6		
Total	35	65525			

Pair-wise tests

Groups	t	*p*
Summer X Autumn	1.330	**0.049**
Summer X Winter	1.142	0.271
Summer X Spring	1.463	**0.046**
Autumn X Winter	1.918	**0.002**
Autumn X Spring	1.830	**0.001**
Winter X Spring	1.044	0.392

Table 5(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**

1

Table 6(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**

1

Table 7(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 (rainfall. temperature, salinity, grain size, carbonate, organic matter, biopolymers) collected in Gramuté beach, SE Brazil, during all seasons (summer, autumn, winter, and spring). Significative results are considered when $p<0.05$.

	Estimate	Standard Error	*t*	*p*
Intercept	2.25e+01	1.00e+01	2.245	**0.033**
Carbonate	2.81e+01	8.68e+00	3.232	**0.003**
PRT	3.86e-01	1.94e-01	1.989	0.057
LIP	-1.10e-02	1.08e-02	-1.019	0.317
BPC	3.90e-01	1.70e-01	2.303	**0.030**
PRT:CHO	-2.83e+02	1.59e+02	-1.780	0.086
Rainfall	-3.44e-04	1.54e-02	-0.022	0.982
TOM	-2.36e-01	2.95e-01	-0.798	0.432
CHO	-1.16e-02	6.65e-03	-1.739	0.093
CHO:LIP	-1.02e-01	4.35e-02	-2.347	**0.027**

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.

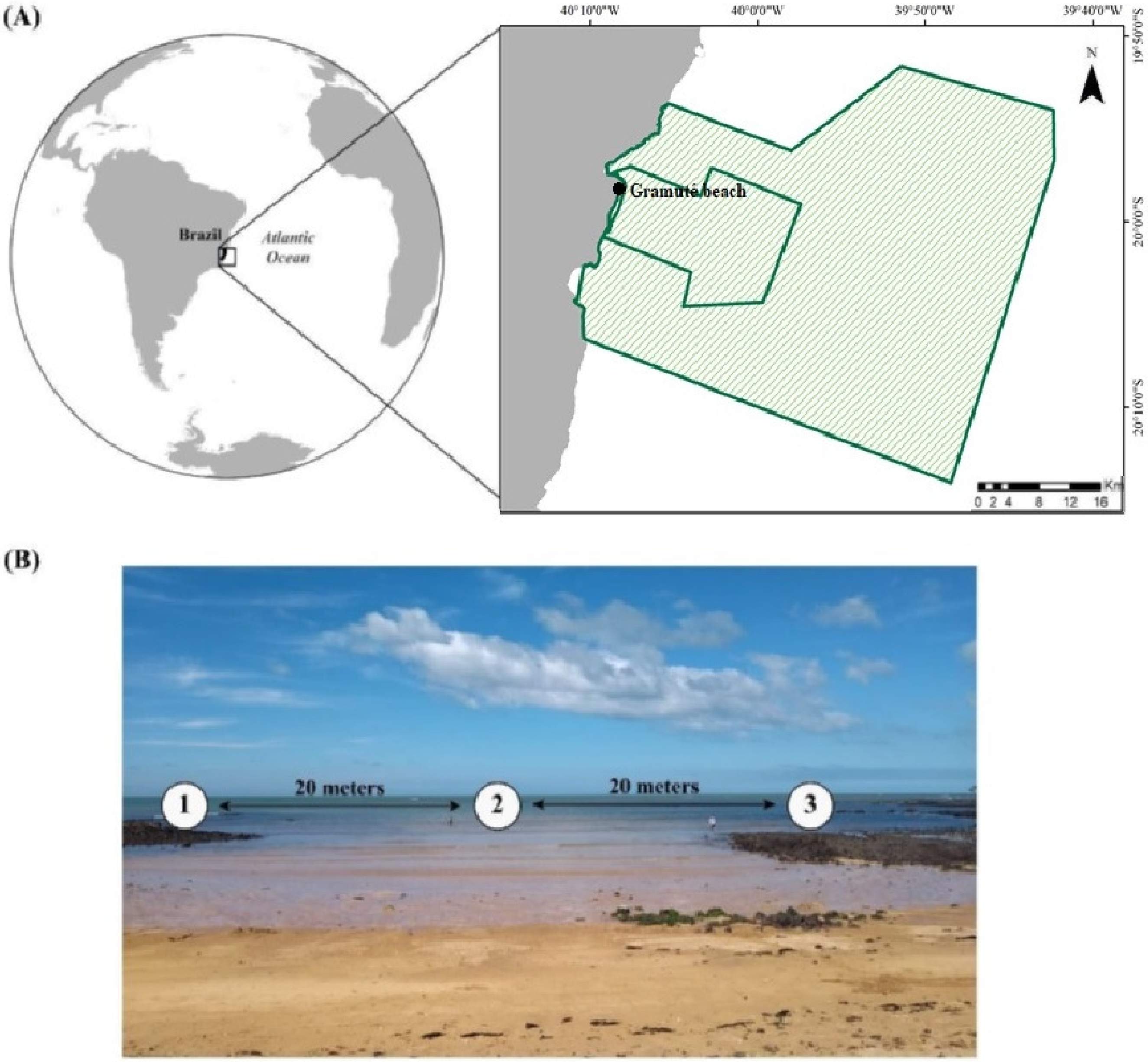
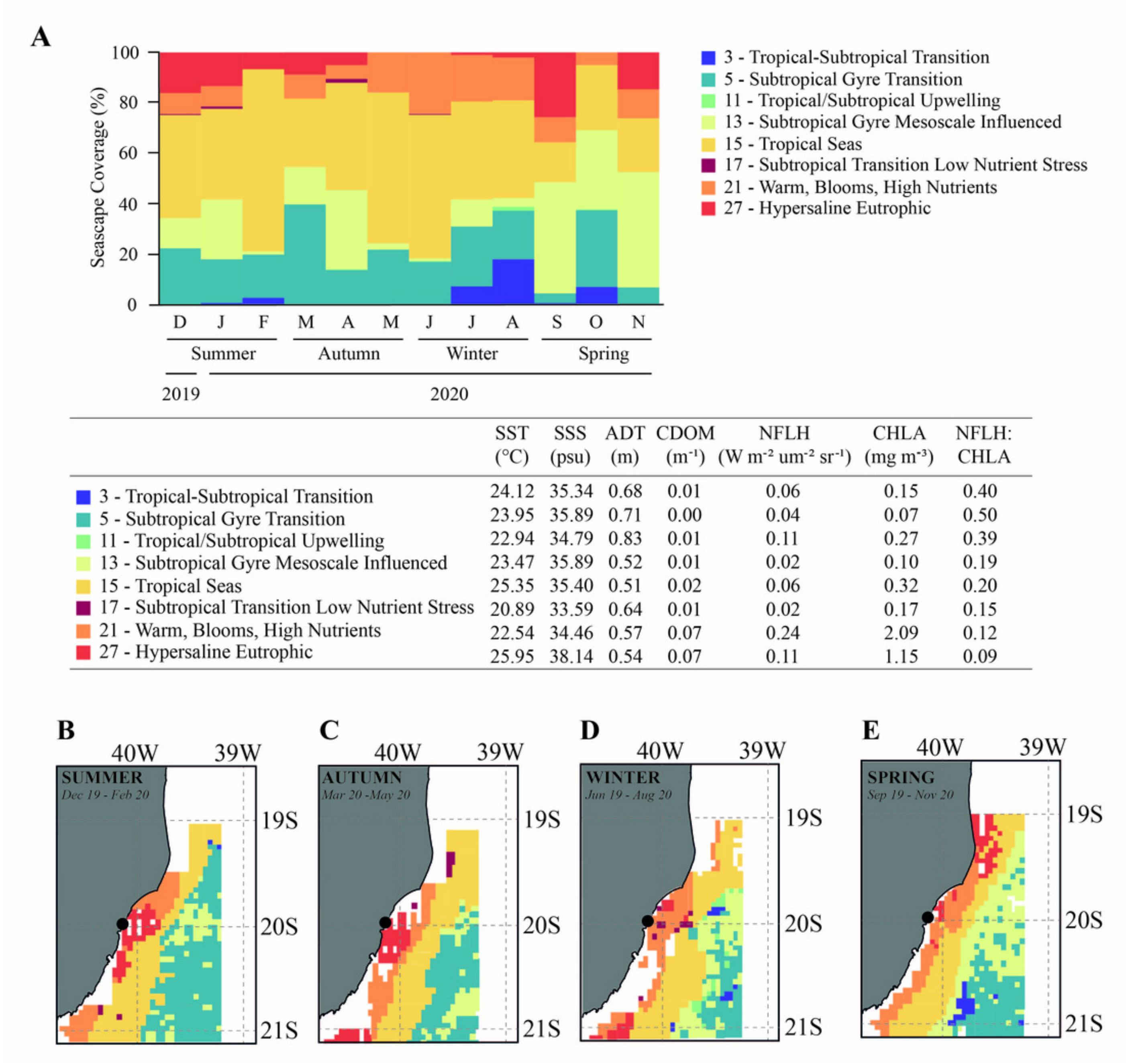

(A)
Brazil
Atlantic Ocean
40° 10'0"W
40°0'0"W
39°50'0"W
39°40'0"W
19°50'0"S
20°0'0"S
20°10'0"S
N
Gramuté beach
Km
0 2 4 8 12 16
(B)
1
20 meters
2
20 meters
3

Figure 2

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 3

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).

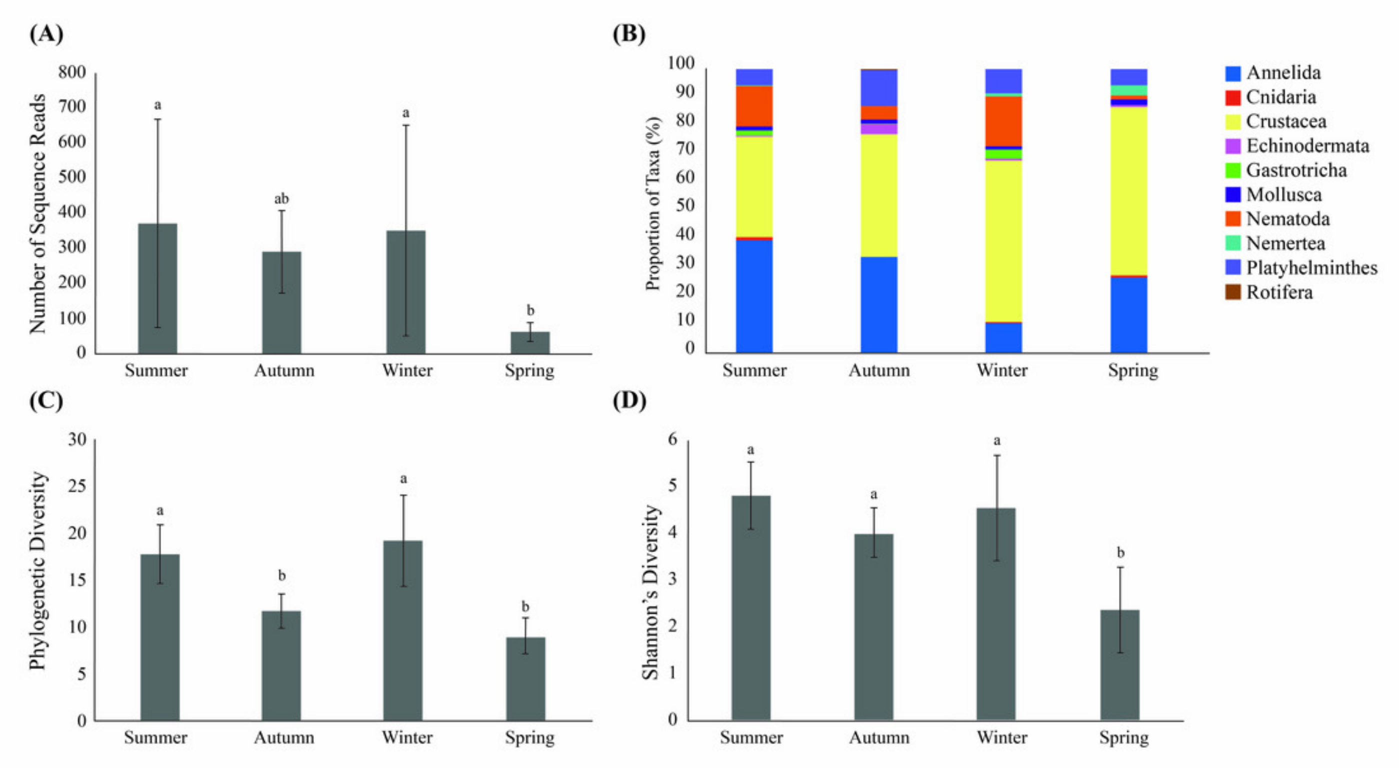


Figure 4

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.

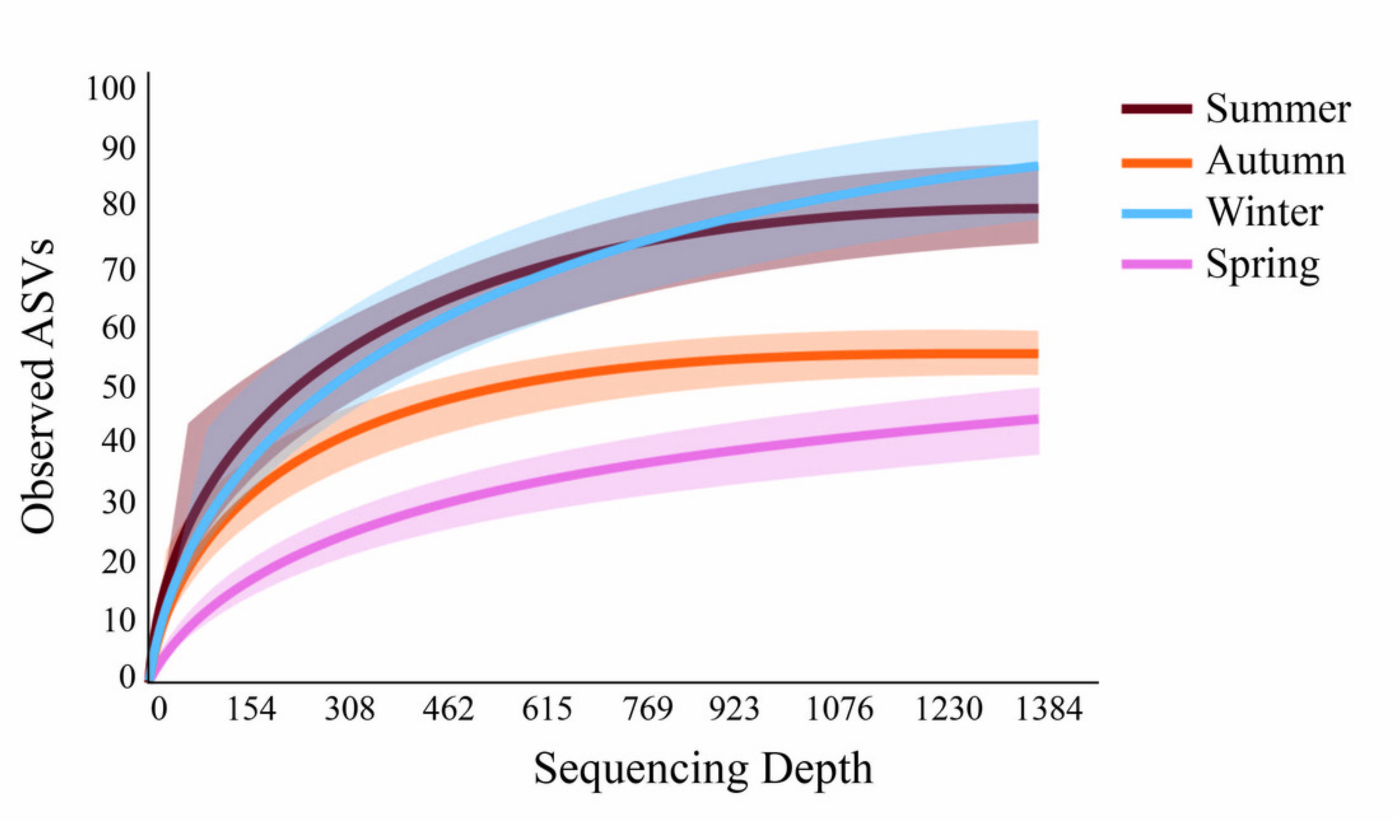
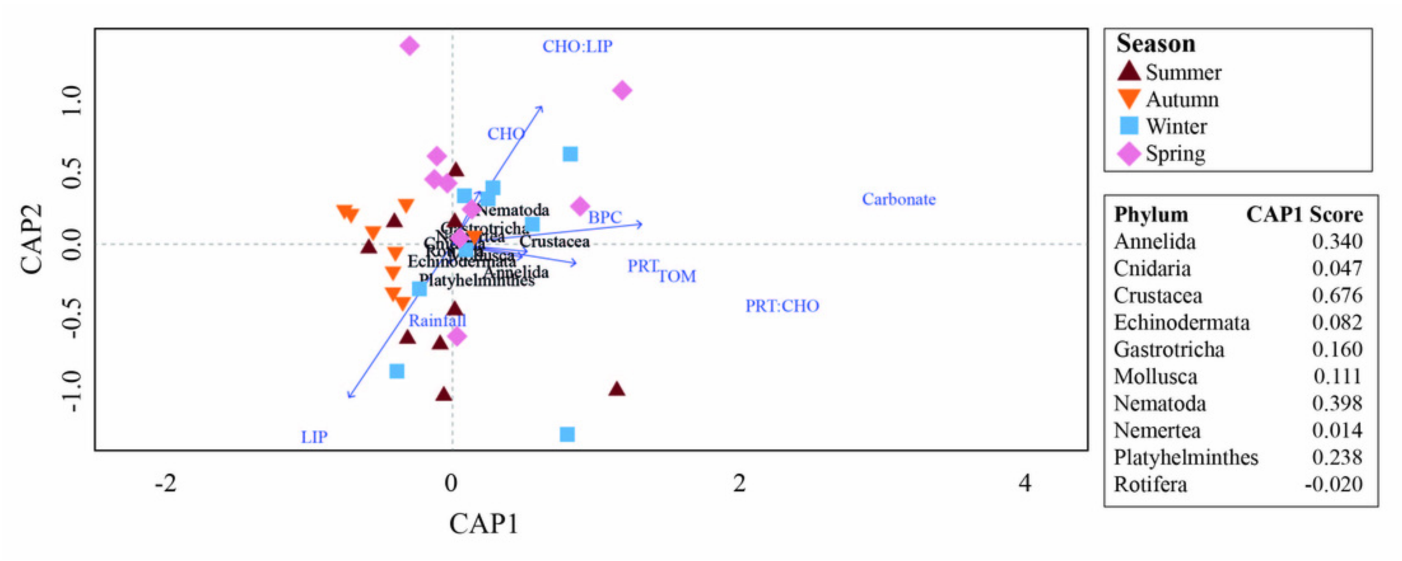


Figure 5

CAP ordination.

Canonical Analysis of Principal Coordinates (CAP) of assemblage composition and environmental variables (rainfall, grain size, carbonate, organic matter, biopolymers) at Gramuté beach, SE Brazil, during all seasons.



Phylum	CAP1 Score
Annelida	0.340
Cnidaria	0.047
Crustacea	0.676
Echinodermata	0.082
Gastrotricha	0.160
Mollusca	0.111
Nematoda	0.398
Nemertea	0.014
Platyhelminthes	0.238
Rotifera	-0.020