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Do human impacts and environmental factors shape intertidal meiobenthic communities across freshwater, estuarine, and oceanic beaches in Uruguay?

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ABSTRACT

Meiofauna comprises small benthic metazoans that play a crucial role in aquatic ecosystems and reflect the ecological condition of marine, estuarine, and freshwater environments. In this study, intertidal meiobenthic communities were examined across three coastal environment types along the Uruguayan coast (freshwater, estuarine, and oceanic), and the influence of anthropogenic impact on biodiversity and community structure was evaluated. Three pairs of dissipative sandy beaches were sampled (one impacted and one less impacted per environment type), and the main meiobenthic taxa were quantified, calculating richness, Shannon exponential diversity, Pielou's evenness, total abundance, and nematode abundance. Physicochemical water variables (dissolved oxygen and pH) and sediment characteristics (mean grain size and organic matter content) were also measured. Generalized linear models showed that biodiversity indices were significantly associated with sediment properties and water parameters, with richness and abundance increasing in finer sediments and with higher organic matter content, and diversity and evenness decreasing under higher organic enrichment. Dissolved oxygen was positively related to richness, Shannon exponential diversity, and evenness. Nematodes, copepods, gastrotrichs, turbellarians, and nauplii dominated the assemblages, with nematodes being the most abundant group overall. Multivariate analyses (NMDS based on Bray–Curtis dissimilarities, PERMANOVA, and beta-dispersion) revealed a clear structuring of communities according to environmental type and the level of anthropogenic impact. In particular, the group of less impacted beaches exhibited a more homogeneous community composition (lower dispersion), whereas impacted beaches showed greater heterogeneity (higher dispersion), reflecting increased variability in composition among their samples. Indicator value analysis identified taxa associated with specific environments and impact levels. Overall, these results highlight that meiobenthic communities on Uruguayan sandy beaches respond to both natural environmental gradients and human disturbance, supporting the use of meiofauna as a sensitive tool for coastal ecosystem assessment.

Keywords: Sandy beaches; Meiofauna; Environment Anthropogenic impact; Biodiversity

INTRODUCTION

Meiofauna comprises small benthic metazoans that play a crucial role in aquatic ecosystems, reflecting the ecological condition of marine, estuarine, and freshwater environments (Coull, 1999; Milner, 2003; Giere, 2009; Balsamo et al., 2012; Somerfield and Warwick, 2013; Alves et al., 2013). Their high biodiversity and abundance, particularly in intertidal zones, make them essential components of food webs and key contributors to matter and energy flow in coastal ecosystems (Coull and Chandler, 2001; Schratzberger and Ingels, 2018).

Due to their small body size, short life cycle, and close association with sediments, meiofauna is highly sensitive to both natural and anthropogenic changes, making it valuable for ecosystem assessment (Warwick et al., 1990; Kennedy and Jacobi, 1999; Moreno et al., 2008; Alves et al., 2013; Zeppilli et al., 2015; Leasi et al., 2021; Schratzberger et al., 2023; Zhou et al., 2023). The sensitivity of meiobenthos to environmental variability makes biodiversity indices important indicators for evaluating ecosystem condition (Warwick et al., 1990; Palmer et al., 2000; Ruellet and Dauvin, 2007; Leasi et al., 2021; Checon et al., 2023; Brannock et al., 2023; Zhou et al., 2023). Among the most relevant environmental factors are salinity and sediment properties, which have a significant effect on the composition and structure of meiobenthic communities (Broman et al., 2019; Baia et al., 2021; Giere and Schratzberger, 2023). Sediment grain size also plays a critical role, as certain organisms prefer finer sediments, promoting the dominance of more adaptable groups (Giere, 2009). Fine-grained sediments particularly benefit nematodes, which can reach densities of thousands per 10 cm^2 (Bezerra et al., 1997; Pinto and Santos, 2006; Kandratavicius et al., 2015). In contrast, coarser grain sizes tend to reduce meiofaunal densities and shift dominance toward other groups, such as harpacticoid copepods, tardigrades, and turbellarians (Bezerra et al., 1997; Kandratavicius et al., 2015). Altogether, these factors highlight the complex interactions that shape meiofaunal communities (Zeppilli et al., 2015).

In addition to environmental factors, human activities, such as urbanization and agriculture, have significantly altered coastal environments, affecting the biodiversity of benthic communities (Barros, 2001; Brown and McLachlan, 2002; Pagán et al., 2017). The Uruguayan coast, characterized by sandy beaches, beach arcs, and rocky headlands, encompasses a wide variety of ecosystems resulting from the confluence of the Rio de la Plata with the Atlantic Ocean, forming a unique estuarine region (Calliari et al., 2003; Lercari and Defeo, 2003; Defeo et al., 2009; García-Alonso et al., 2019). In this context, a high degree of anthropogenic disturbance is observed, mainly associated with urbanization and agriculture (Muniz et al., 2015; García-Alonso et al., 2019; Orlando et al., 2020; Vermeiren et al., 2021). The Rio de la Plata's freshwater beaches, such as those in Colonia city with a harbor, are expected to be potentially affected, although no studies on benthic communities are reported. The estuarine coast, particularly Montevideo's beaches, faces severe environmental degradation due to contamination and urban expansion with negative impact on micro, meio- and macro-benthic communities (Piccini and García-Alonso, 2015; Felix et al., 2016; García-Alonso et al., 2017; Castiglioni et al., 2018). At the oceanic coast, a freshwater discharge with agrochemical pollutants impacts the quality and benthic fauna of La Coronilla beach (Lercari et al., 1999; 2002; Sauco et al., 2010, Jorge-Romero et al., 2019).

This study aims to examine meiobenthic communities across different intertidal coastal ecosystems (freshwater, estuarine, and oceanic) and to evaluate how specific human activities influence meiofauna, using response variables such as diversity indices and community structure to explain spatial and environmental patterns. Biodiversity indices are hypothesized to be influenced by environment types, with higher taxonomic richness and diversity (Shannon index) in oceanic environments and lower values in freshwater environments. Similarly, impacted beaches are predicted to exhibit reduced richness, diversity, and evenness (Pielou index) compared to less impacted beaches. Regarding taxonomic composition, greater similarity is anticipated among beaches belonging to the same environmental type and among those with lower levels of anthropogenic impact, reflected in a higher homogeneity of community composition. In contrast, beaches exposed to higher levels of anthropogenic impact are expected to exhibit greater heterogeneity in community composition, expressed as higher dispersion among samples, reflecting differential community responses to the intensity or type of anthropogenic disturbance.

Finally, it is proposed that the structure of meiobenthic communities is determined by both physicochemical water variables and sediment characteristics. Specifically, higher dissolved oxygen (DO) levels and pH values close to neutrality are predicted to promote greater richness and diversity, whereas low DO and extreme pH conditions are associated with reduced diversity and changes in community composition. Concerning sediment properties, fine- to medium-grained sands are expected to support higher meiobenthic richness, abundance, and diversity due to their greater capacity to retain organic matter (OM).

METHODS

STUDY AREA AND SAMPLING DESIGN

Three pairs of dissipative sandy beaches along the Uruguayan coast were selected to represent different environmental contexts and levels of anthropogenic impact: two freshwater beaches (Honda and Matamoras, Colonia), two estuarine beaches (Punta Yeguas and Capurro, Montevideo), and two oceanic beaches (Punta La Coronilla and La Coronilla, Rocha). Each pair consisted of one impacted and one less impacted beach (Figure 1). At each beach, three sampling sites were selected in the swash zone of the intertidal area to represent the corresponding beach arc. At each site, three random replicates were collected for meiofauna analysis (nine total per beach), along with a sediment sample (three total per beach). For analyses focused on biodiversity indices, replicate values were averaged at the site level and then across the three sites per beach, considering the beach as the unit of analysis. In contrast, for analysis focused on community composition and variability among beaches, individual replicates from each site were used, allowing a more detailed assessment of community structure and dispersion within each beach. For the statistical analysis, conductivity was not considered as a continuous variable in the association between meiofauna and environmental factors. Instead, it was categorized according to the different environments (freshwater, estuarine, and oceanic), as salinity in estuarine beaches fluctuates significantly on a daily basis. This decision is justified because the study constitutes a snapshot, i.e., a single-time assessment of the natural conditions of each environment at the moment of sampling. Although this approach may reduce resolution, it avoids spurious associations driven by short-term estuarine variability and is consistent with the snapshot nature of the sampling design. This design aims to evaluate how meiobenthic communities respond to different natural environmental conditions and levels of anthropogenic impact.

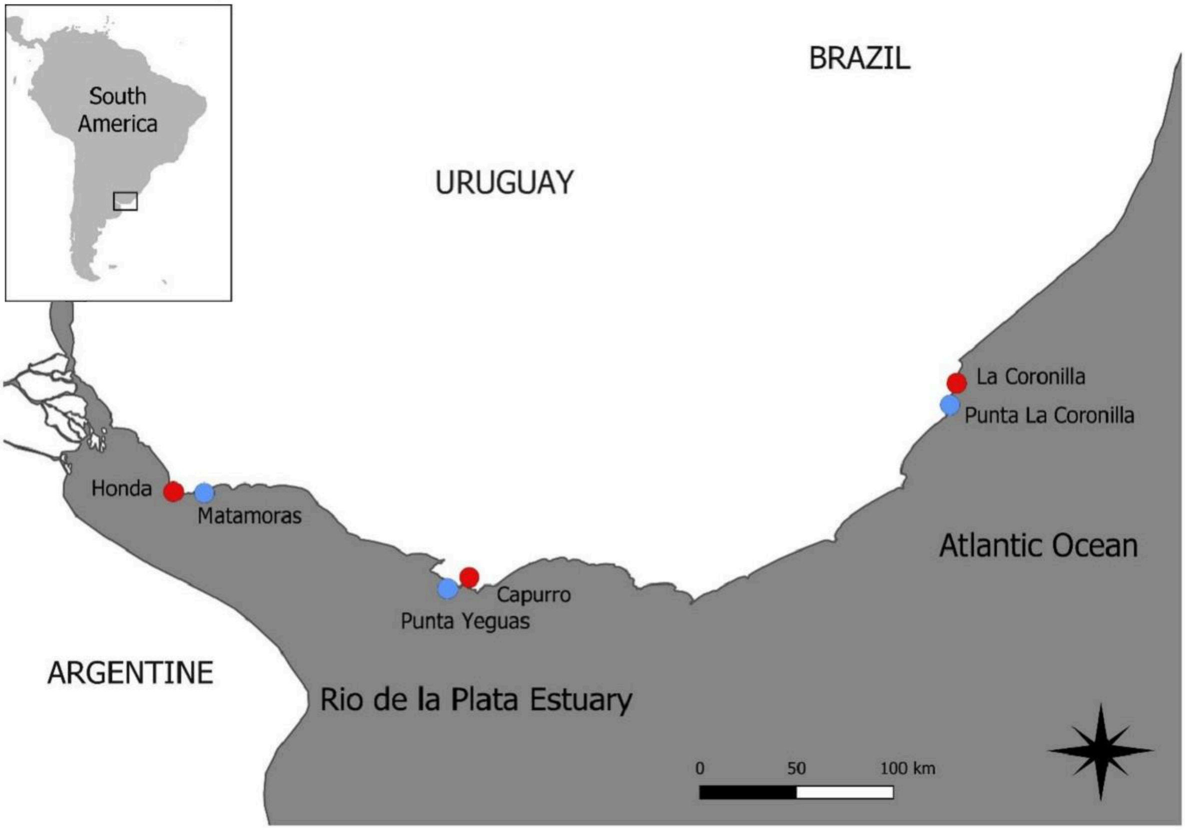

Figure 1. Map of the study area with sampling location at the Rio de la Plata and Atlantic coast. Honda and Matamoras beaches (freshwater), Punta Yeguas and Capurro beaches (estuarine), Punta La Coronilla and La Coronilla beaches (oceanic). Impacted beaches are shown in red, while less impacted ones are shown in blue.

Honda (freshwater), Capurro (estuarine) and La Coronilla (oceanic) were designated as impacted beaches due to their proximity to urban areas, industrial zones, ports, or pollution sources, including agrochemical runoff (Muniz et al., 2004; Sauco et al., 2010; Piccini and García-Alonso, 2015; Castiglioni et al., 2018). Honda is an urban freshwater beach near the port of Colonia, which receives approximately 3,300 vessels per year (ANP, 2024). Capurro, located in the urban bay of Montevideo, is close to an oil refinery and streams contaminated with solid waste and high nutrient loads (Muniz et al., 2004; Piccini and García-Alonso, 2015; Castiglioni et al., 2018). La Coronilla Beach is affected by artificial freshwater discharge and agricultural runoff from a 270,000-ha watershed created in the late 19th and early 20th centuries (Lercari et al., 2002; Sauco et al., 2010; Jorge-Romero et al., 2019). In contrast, Matamoras (freshwater), Punta Yeguas (estuarine), and Punta La Coronilla (oceanic) were identified as less impacted beaches, located away from urban and industrial activities. Matamoras is a lightly urbanized beach with natural areas, Punta Yeguas has green spaces and camping areas, and Punta La Coronilla is part of the Cerro Verde National Protected Area (Table 1).

Table 1. Classification of beaches, categorized by environments and degree of anthropogenic impact. Impacted (+) or less impacted (-). Additionally, a brief description and georeferencing of each beach are provided.

Beaches	Environment	Impact	Description	Location
Honda	Freshwater	+	Urban/Harbour	34°28'24.0"S 57°50'26.9"W
Matamoras	Freshwater	-	Countryside	34°26'47.5"S 57°40 '52.5"W
Punta Yeguas	Estuarine	-	Countryside	34°54'02.1"S 56°18 '42.1"W
Capurro	Estuarine	+	Urban/Harbour/ Indusrty	34°52'31.6"S 56°12'41.4"W
Punta La Coronilla	Oceanic	-	Countryside	33° 55'19.6"S 53°30'40.4"W
La Coronilla	Oceanic	+	Artificial freshwater discharge/ Agrochemicals pollutants	33°53'57.2"S 53°30'29.9"W

COLLECTION OF SAMPLES, LABORATORY ANALYSIS AND MEIOFAUNA IDENTIFICATION

DO, pH, conductivity, and temperature were measured in situ using a Thermo multiparameter (Orion Star A325) and a Thermo oximeter (Orion Star A223). Sediment samples for grain size and OM content analyses were collected using a 15 cm diameter PVC corer inserted 10 cm into the sediment. Grain size analysis followed the mechanical method described by Suguio (1973), using a Ro-Tap (RX-29-16) with a series of sieves differing by 1 Ø (phi) in mesh size. Each sediment fraction was weighed with a precision balance to 0.01 g, and the Gradistat program was used to calculate the percentage of each fraction as well as the mean grain size (μm).

OM content was estimated using the Loss on Ignition (LOI) technique (Byers et al., 1978). Two grams of wet sediment were dried at 60 ºC for 48 hours, followed by calcination at 450 ºC for 3 hours. Total OM concentration was calculated as the weight difference between the dried and calcined samples and expressed as a percentage of total OM.

Meiofauna was collected using a 2.7 cm diameter "mini corer" inserted 5 cm into the surface sediment (Higgins and Thiel, 1988). Samples were preserved in 4% formaldehyde in phosphate buffer solution, transported to the laboratory, and stored at room temperature until analysis.

In the laboratory, a small amount of Rose Bengal was added to the meiofauna samples to achieve a final concentration of 1%. Samples were processed using the elutriation method, sieving the sediment through 500 μm and 63 μm meshes, and separating organisms from the sand based on density differences (Platt and Warwick, 1983; Boisseau, 1957). Meiobenthic organisms were counted, and the main taxonomic groups were identified following Higgins and Thiel, (1988) and Giere, (2009). Identification focused on the principal taxa according to the World Register of Marine Species (WoRMS, www.marinespecies.org) as meiofauna identification at finer taxonomic levels is complex and time-consuming (Heip et al., 1988). Taxonomic classifications are essential to understand meiofaunal community structure and to highlight compositional differences, particularly in response to disturbances (Gee et al., 1985; Heip et al., 1988; Herman and Heip, 1988; Warwick and Clarke, 1993; Quintana et al., 2010; Kandratavicius et al., 2015). Rare taxonomic groups representing less than 1% of the total abundance were also considered.

The number of individuals per sample was quantified under the assumption of homogeneous distribution of the fauna ind/10 cm^2 following Higgins and Thiel (1988), and selected taxa were photographed using topographic magnification.

BIODIVERSITY INDICES AND STATISTICAL ANALYSIS

The composition of the meiobenthic community was assessed, and several biodiversity indices were calculated, including richness (number of taxa), Shannon (exponential), Pielou, total abundance per beach (ind/10 cm^2), and absolute abundance of nematodes per beach. The Shannon index was transformed into its exponential form (Shannon exponential) to express diversity as the effective number of equally abundant taxa, facilitating ecological interpretation and enabling meaningful comparisons among beaches (Jost, 2006).

These indices were fitted to different probability distribution functions using distribution curves and QQ-plots (Figure S1, S2). Richness was evaluated using Poisson and negative binomial distributions, with Poisson ultimately selected as the most appropriate. The Shannon exponential index, total abundance, and absolute abundance of nematodes were modeled using a Gamma distribution. The Pielou's evenness index was assessed with a Beta distribution, a family of continuous distributions defined on the interval (0, 1).

Generalized linear models (GLMs) were constructed for each group of explanatory variables based on a priori ecological hypotheses (Zuur et al., 2009; Inchausti, 2023). Continuous variables included water parameters (DO and pH) and sediment characteristics (OM and mean grain size). Categorical factors, Environment (freshwater, estuarine, and oceanic) and Impact (impacted vs. less impacted) were analyzed in separate models, as they represent distinct ecological hypotheses.

Given the limited number of beaches (n = 6), it was not feasible to perform a full multimodel inference in the univariate analyses. However, the models were structured to incorporate the main a priori identified explanatory abiotic variables. Their relative importance was assessed within these global models, also considering the Akaike Information Criterion (AIC) to compare the relative fit of the models. This approach allows for a robust ecological interpretation of variable effects, avoiding reliance solely on single-variable GLMs. Post-hoc Tukey comparisons were performed for models involving the categorical variables of "Environments" and "Impact".

Before including the explanatory variables in the GLMs, pairwise correlations among the continuous abiotic variables (DO, pH, OM, and mean grain size) were assessed to rule out potential multicollinearity issues. All correlation coefficients were below 0.7, indicating the absence of problematic collinearity (Table S1); therefore, these variables were retained in the models. For the sediment variables, an interaction term (OM * mean grain size) was additionally included, as the ecological effect of OM enrichment on the meiofauna may vary depending on sediment grain size (Figure 2).

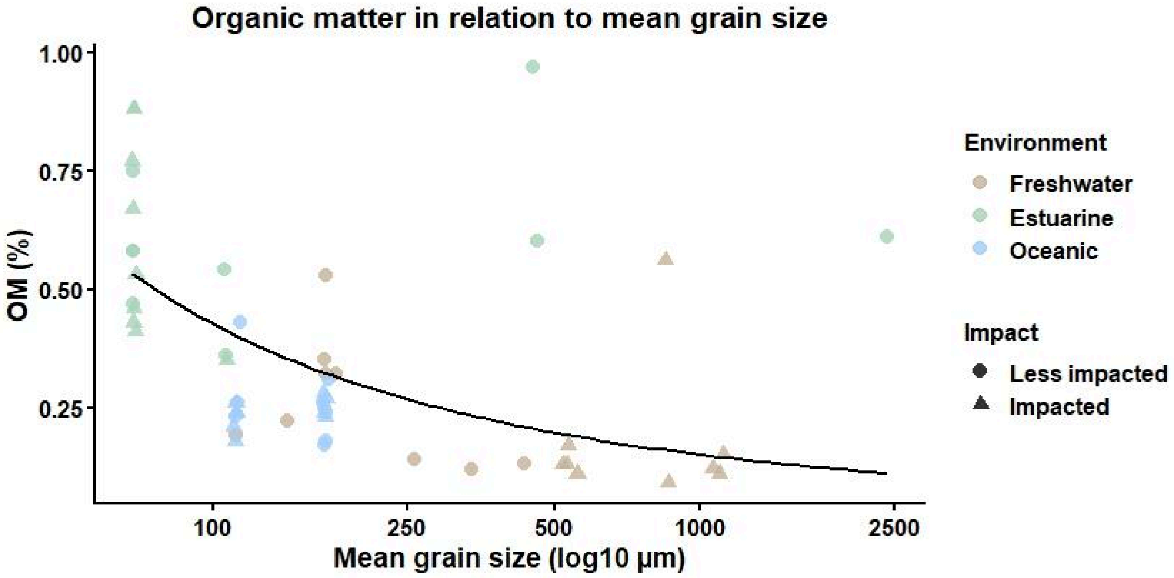

Figure 2. Organic matter concentration (%) in relation to mean sediment grain size (µm, logarithmic scale) at intertidal sandy beaches along the Uruguayan coast. Colors indicate environment type and symbols represent anthropogenic impact. The curve shows the general trend, with higher organic matter associated with finer sediments

MULTIVARIATE ANALYSIS OF COMMUNITY COMPOSITION AND WITHIN BEACH VARIABILITY

To complement the univariate analyses, differences in meiobenthic community composition and variability among beaches were evaluated. A Bray–Curtis dissimilarity matrix was calculated from square-root-transformed taxa abundances. Community composition ordination was performed using non-metric multidimensional scaling (NMDS) to visualize patterns of similarity and separation among beaches according to different environments type (freshwater, estuarine, and oceanic) and levels of impact (impacted vs. less impacted). Continuous environmental variables, including OM, pH, and DO, were fitted onto the NMDS ordination to aid in interpreting the main environmental gradients structuring community patterns.

Differences in community composition among environments and impact levels were assessed using PERMANOVA, based on the same Bray–Curtis dissimilarity matrix. In addition, a beta-dispersion analysis (*betadisper*) was applied to evaluate how similar or variable communities were within each category: lower dispersion indicates more homogeneous communities, whereas higher dispersion reflects greater internal heterogeneity.

Additionally, a beta-dispersion analysis (betadisper) was applied to evaluate how similar or variable meiobenthic communities are within each category. Specifically, this analysis estimates the degree of dispersion of samples within each environment (freshwater, estuarine, and oceanic) and within each impact level (impacted and less impacted beaches). Lower dispersion reflects more homogeneous communities, whereas higher dispersion indicates greater variability in community composition among samples within the same category.

To complement these multivariate analyses, an indicator value analysis (IndVal) was conducted to identify taxa significantly associated with each type of environment or impact level, enabling the detection of organisms representative of specific environmental conditions or anthropogenic disturbance.

Analyses were conducted using R version 4.1.2 software.

RESULTS

ABIOTIC CHARACTERIZATION OF THE BEACHES

On the sampling day, the observed mean conductivity values were 0.20, 42, and 45 mS/cm for freshwater, estuarine, and oceanic beaches respectively. The high salinity in estuarine beaches suggests marine water intrusion during this period. This likely reflects the strong short-term salinity variability typical of the Río de la Plata estuary and does not necessarily represent long-term average conditions.The remaining abiotic characteristics of the studied sandy beaches are shown in Figure 3. DO levels ranged from 6.6 to 9 mg/L at Capurro and Punta La Coronilla, respectively (Figure 3A). Impacted beaches exhibited lower DO concentrations compared to those classified as less impacted. pH values were lowest in freshwater environments, with Honda beach recording the minimum value of 7.64 (Figure 3B). Most beaches were categorized as fine to medium grained sands based on mean grain size (Figure 3D). Freshwater beaches showed the largest mean grain size, with Honda averaging 790.5 µm, composed mainly of 65.8% coarse sand, 16.7% medium sand, and 12.3% gravel. Matamoras followed with a mean grain size of 219.8 µm, composed of 25.2% coarse sand, 15.6% medium sand, and 6.4% gravel. The remaining beaches showed higher proportions of fine and medium sand; however, Punta Yeguas (estuarine) had a mean grain size of 423 µm, with the highest proportion of gravel among all beaches (13.7%). Among the three ecosystems, the lowest average OM content in the sediment was found in freshwater and oceanic beaches, while the highest concentrations were observed in estuarine beaches (Figure 3C).

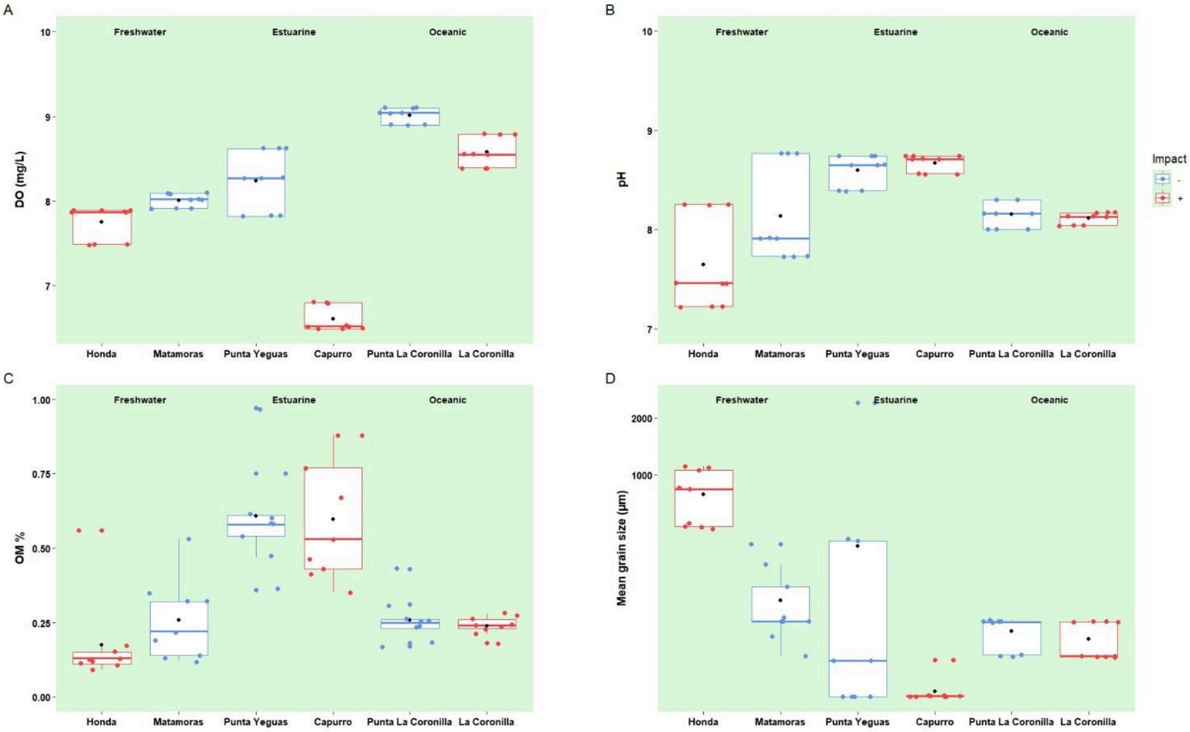

Figure 3. Abiotic descriptions of intertidal sediment from sandy beaches from different environments (freshwater, estuarine, and oceanic). Mean (black dots), median, interquartile range, and outliers of A, dissolve oxygen (DO); B, pH; C, organic matter (OM) in percentage; D, mean grain size of sediments (µm). Impacted beaches are shown in red, while less impacted ones are shown in blue.

MEIOBENTHIC COMMUNITY

A total of 25712.13 ind/10 cm² belonging to 19 taxa distributed across 11 invertebrate phyla were identified. Some of these organisms were photographed, as mentioned in the methodology, under topographic magnification (Figure 4). The lowest taxonomic richness was observed at Capurro Beach (estuarine, impacted), while the highest was recorded at Punta La Coronilla (oceanic, less impacted).

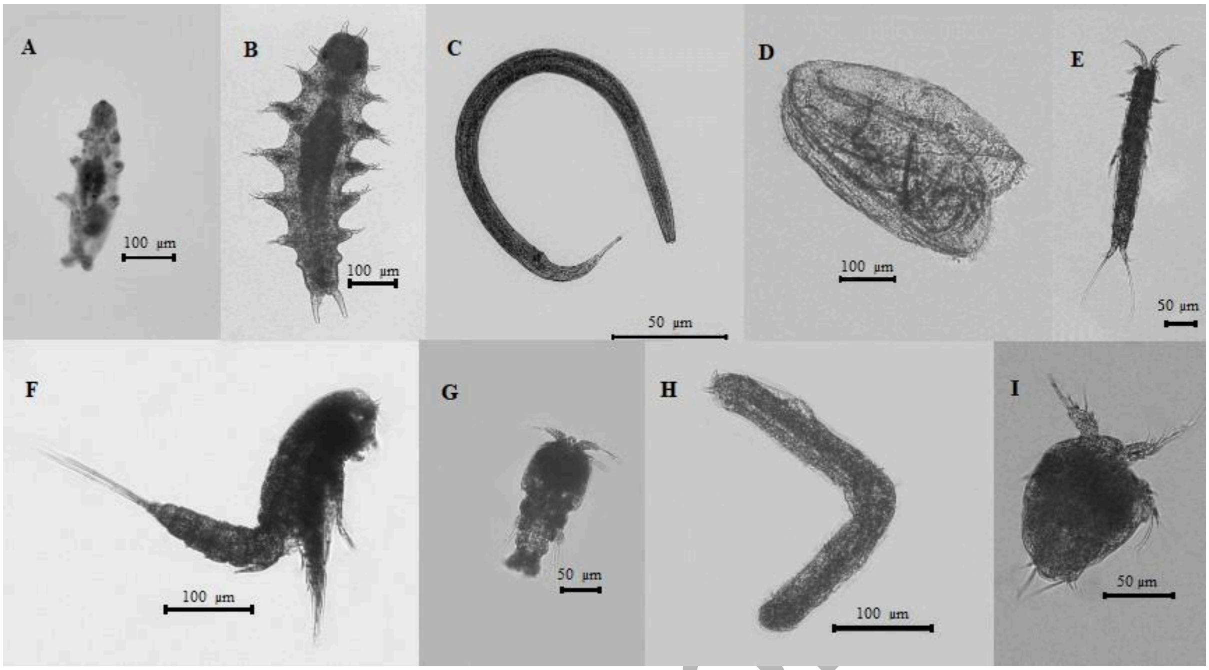

Figure 4. Photomicrographs of different taxa found on the beaches from different environments (freshwater, estuarine, and oceanic) at the Uruguayan coast. A: Tardigrade; B: Polychaete; C: Nematode; D: Ostracod; E, F, G: Copepods; H: Gastrotrich; I: Nauplii.

The total abundance of individuals varied among beaches, with Punta Yeguas (estuarine, less impacted) showing the highest abundance (8110.51 ind/10 cm^2) and Honda (freshwater, impacted) the lowest (995.63 ind/10 cm^2; Table 2).

Nematodes, copepods, gastrotrichs, turbellarians, and nauplii (of copepods) accounted for 95.5% of the total abundance. Oligochaetes, polychaetes, and ostracods made up 3.6%, while the remaining groups were considered rare, representing the remaining 0.8% (gastropods, priapulids, bivalves, insects, aplacophorans, tardigrades, gnathostomulids, amphipods, mites, sipunculids, and bryozoans). Nematodes were the most abundant taxon, representing 58.14% of the total with a total abundance of 14714.35 ind/10 cm^2 (Table 2). Copepods accounted for 12.6% (3267.87 ind/10 cm^2), gastrotrichs made up 9.13% (2165.8 ind/10 cm^2), and nauplii represented 7.94% (2054.07 ind/10 cm^2). Turbellarians represented 7.6% with a total abundance of 1937.71 ind/10 cm^2. Oligochaetes, polychaetes, and ostracods each accounted for approximately 1% of the total, with abundances of 798.62, 260.47, and 276.34 ind/10 cm^2, respectively (Table 2).

Nematodes dominated four of the six beaches: Capurro (96.6%), Matamoras (86.5%), Punta La Coronilla (54.3%), and Punta Yeguas (43%, Table 2, Figure 5A). At Honda Beach, copepods and oligochaetes were the most abundant, each representing 34% of the total abundance (Table 2, Figure 5B, E). In contrast, turbellarians (31.5%) and copepods (31.1%) were the most abundant taxa at La Coronilla (Table 2, Figure 5 B, D). Within the “rare” taxa group (<1% of the total abundance), the main representatives were gastropods (30.3%), priapulids (30%), bivalves (14.6%), insects (7.2%), and aplacophorans (6.4%, Table 2). The remainder included tardigrades (3.6%), gnathostomulids (3%), amphipods (2.5%), acari (1.8%), and bryozoans (0.6%, Table 2).

Table 2. Means of absolute abundances and standard deviations (SD) of each taxon (ind. 10 cm^2) present on the analyzed beaches, corresponding to their type of environment (freshwater, estuarine, oceanic) and degree of

impact (impacted + and less impacted -). The sum of the organism abundances on each beach is presented (total abundance^1), as well as the sum of the abundances of each organism across all beaches (total abundance^2). Additionally, taxon richness is included, which indicates the richness of taxa present on each beach; and the total taxon richness 19* refers to the number of taxa present without repetition.

Beaches	Honda	Matamoras	Punta Yeguas	Capurro	Punta La Coronilla	La Coronilla	Total abundance^2
Environment	Freshwater	Freshwater	Estuarine	Estuarine	Oceanic	Oceanic	
Impact	+	-	-	+	-	+	
Nematodes	9,7 ± 2,45	250,5 ± 278,1	368,7 ± 150,5	788,3 ± 356,3	169,6 ± 164	82,7 ± 8,56	14714,35
Copepods	23,5 ± 16,9	0	115,3 ± 83,8	1,76 ± 0,44	63,3 ± 84,4	159,1 ± 8,39	3267,87
Gastrotrichs	0	5,14 ± 0,67	165,7 ± 261,8	0	24,5 ± 21,7	66,84 ± 32,3	2165,8
Nauplii	3,9 ± 4,66	0	203,3± 171,9	0,44 ± 0,76	1,76 ± 2,68	18,5 ± 9,84	2054,07
Turbellarians	0	20,9 ± 14,7	10,4 ± 3	0	25,6 ± 20,1	160,6 ± 164	1937,71
Oligochaetes	23,5 ± 104,9	10,9 ± 2,69	0	0,22 ± 0,22	12,2 ± 10,7	0,58 ± 0,5	798,62
Ostracods	0	0,14 ± 0,25	30,1 ± 8,61	0	0	0	276,34
Polychaetes	0,44 ± 0,44	0,88 ± 0,88	0,88 ± 0,76	0,66 ± 0,66	13,3 ± 8,94	12,34 ± 11,9	260,47
Gasteropods	3,67 ± 3,56	0,29 ± 0,25	3,38 ± 3,6	0	0	0,29 ± 0,5	72,72
Priapulids	0	0,14 ± 0,25	0	0	0,58 ± 1	6,75 ± 10,9	67,43
Bivalves	2,49 ± 2	0,14 ± 0,25	0,73 ± 0,67	0,14 ± 0,25	0,14 ± 0,25	0	39,66
Insects	1,17± 2,03	0,14 ± 0,25	0,29 ± 0,50	0	0,14 ± 0,25	0	15,86
Aplacophoran	0	0	0	0	0	1,61 ± 0,91	14,54
Tardigrades	0,14 ± 0,25	0,44 ± 0,76	0	0	0,29 ± 0,50	0	7,93
Gnatostomulids	0	0	0,58 ± 0,25	0	0,14 ± 0,25	0	6,61
Amphipods	0	0	0	0	0	0,58 ± 0,67	5,28
Acarii	0	0	0	0	0,14 ± 0,25	0,29 ± 0,50	3,96
Sipunculids	0	0	0	0	0,14 ± 0,25	0,14 ± 0,25	2,64
Bryozoa	0	0	0,14 ± 0,25	0	0	0	1,32
Total abundance^1	995,63	2607,42	8110,51	6838,56	2614,03	4607,94	25713,25
Richness	9	11	12	6	14	13	19*

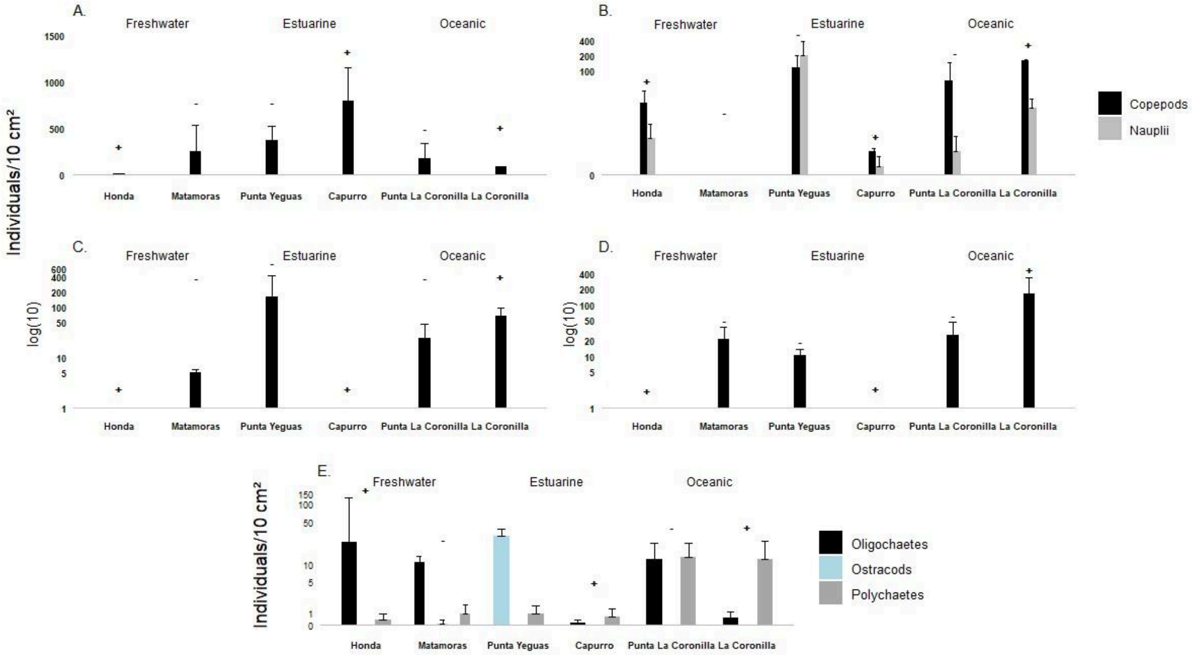

Figure 5. Mean absolute abundances of the most abundant taxa and of taxa with intermediate abundances in intertidal beaches across different environments (freshwater, estuarine, and oceanic) ± SD. Data are expressed as the number of individuals per 10 cm² of sediment. A, Nematodes; B, Copepods + Nauplii; C, Gastrotrichs; D, Turbellarians; and E, Oligochaetes, Ostracods, and Polychaetes. Impacted beaches are indicated by '+' and less-impacted beaches by '–'.

MEIOFAUNA COMPOSITION AND ENVIRONMENTAL DESCRIPTORS

Biodiversity indices were significantly correlated with at least one of the two sediment variables analyzed: mean grain size (μm) and OM content (Table S2). Taxonomic richness was inversely related to mean grain size and positively associated with OM concentration (Figures 6A and 6B, Table S2). The exponential Shannon index and Pielou's evenness index showed a negative relationship with OM concentration (Figures 6C and 6F, Table S2). Additionally, total abundance per beach and nematode abundance were significantly negatively associated with mean grain size and a positively assocation with OM concentration (Figures 6D, 6E, 6G, and 6H, Table S2).

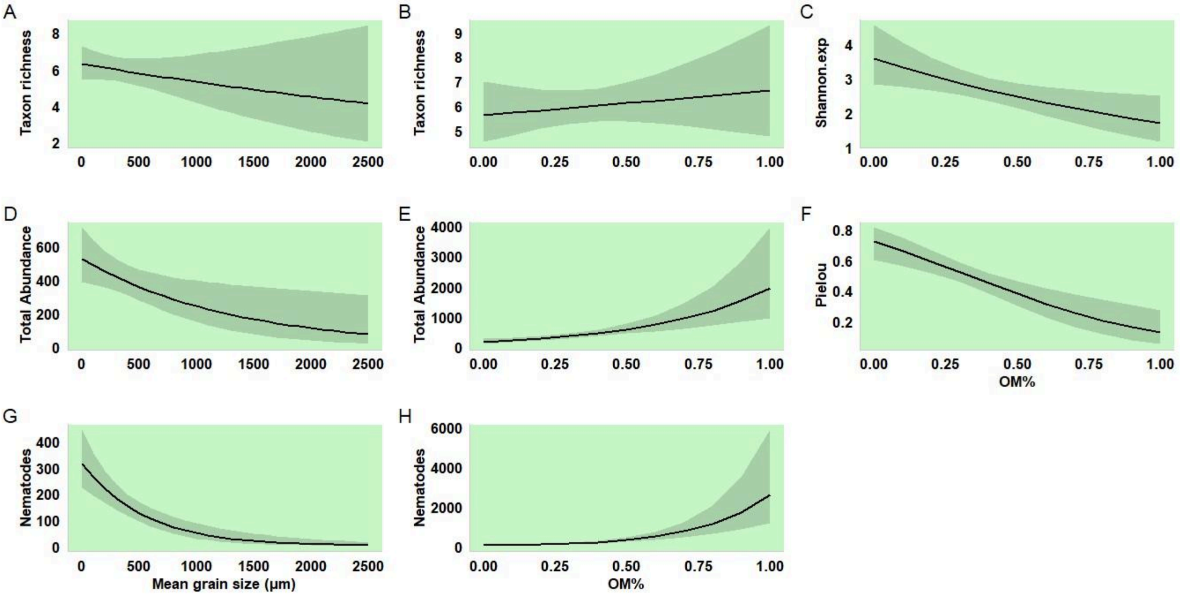

Figure 6. Predicted association of biodiversity indices with the sediment characteristics on intertidal beaches from different environments (freshwater, estuarine, and oceanic) and with varying levels of human impact. A, nTaxas with mean grain size (μm); B, nTaxas with organic matter OM (%); C, Shannon exponential with OM; D, Total abundance with mean grain size; E, Total abundance with OM; F, Pielou with OM; G, Nematodes with mean grain size and H, Nematodes with OM.

Taxonomic richness, the exponential Shannon index, and Pielou's evenness index were positively related to DO concentration in the water (Figures 7A, 7B, and 7C, Table S3). Regarding pH values, Pielou's index was negatively correlated, whereas total abundance and nematode abundance showed a positive association (Figures 7D, 7E, and 7F, Table S3).

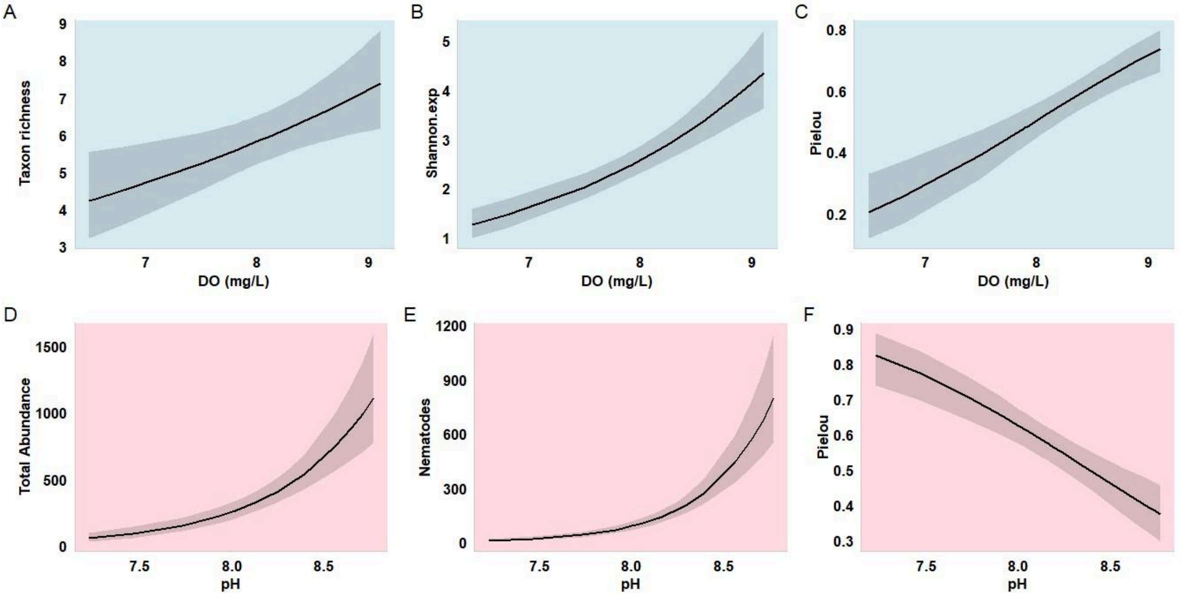

Figure 7. Predicted association of biodiversity indices with water predictors across different environments (freshwater, estuarine, and oceanic) with varying levels of human impact. A, nTaxas; B, Shannon exponential; C,

Pielou with DO, while D, nTaxas; E, Shannon exponential and F, Pielou with pH.

The analyzed biodiversity indices were significantly associated with different types of coastal environments (Figure 8, Table S4). Significant differences in taxonomic richness were observed between freshwater and oceanic environments, with the lowest and highest richness recorded, respectively (Figure 8A, Table S4). Oceanic environments showed the highest values of exponential Shannon index, significantly different from freshwater and estuarine environments (Figure 8B, Table S4). Pielou's evenness index was lowest in estuarine environments, showing significant differences compared to freshwater and oceanic environments (Figure 8C, Table S4). Estuarine environments also exhibited the highest total abundance (Figure 8D, Table S4). Nematodes followed a pattern similar to total abundance, with no significant differences observed between oceanic and freshwater beaches (Figure 8E, Table S4).

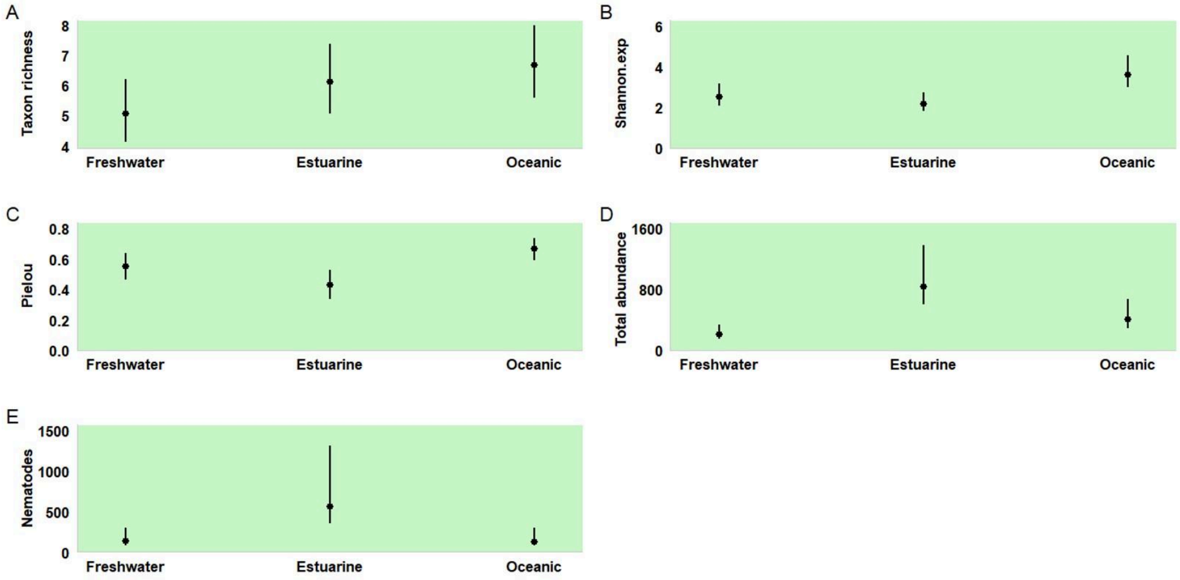

Figure 8. Association of biodiversity indices in relation to the different environments: freshwater, estuarine, and oceanic. A mean value for each pair of beaches is shown.

The impact of anthropogenic activities on the intertidal meiobenthic community was assessed by comparing pairs of beaches within each environment type (freshwater, estuarine and oceanic) along the coast. In estuarine beaches, taxonomic richness and the Shannon index of the meiofauna were significantly lower at the impacted Capurro Beach compared to Punta Yeguas (Figure 9A, Table S5). Similarly, the Shannon index showed significant differences between oceanic beaches Punta La Coronilla (less impacted) and La Coronilla (impacted), with the latter having the highest value (Figure 9B, Table S5). Regarding evenness, Capurro presented the lowest Pielou index, significantly differing from Punta Yeguas (Figure 9C, Table S5). Total abundance also varied notably among freshwater beaches (Figure 9D, Table S5). Nematode abundance showed significant differences between estuarine and freshwater beaches, being higher at Capurro and lower at Honda (Figure 9E, Table S5).

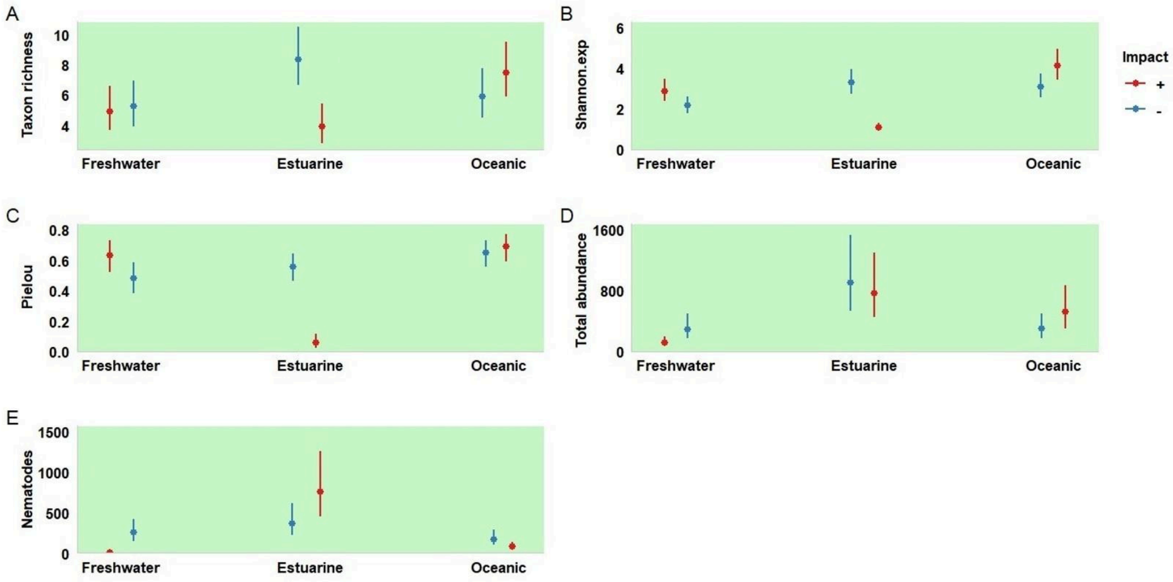

Figure 9. Association between biodiversity indices and beach environments with differing levels of anthropogenic impact: red denotes impacted beaches, while blue represents less impacted beaches. Mean values are shown for each pairwise comparison.

MULTIVARIATE ANALYSIS OF COMMUNITY COMPOSITION

The bidimensional ordination using NMDS, based on a Bray–Curtis dissimilarity matrix calculated from square root transformed taxa abundances, showed a clear separation of meiobenthic communities among environments (freshwater, estuarine, and oceanic) and between impact levels (impacted vs. less impacted beaches), indicating that each category presents a distinct community structure (stress = 0.15). In particular, environmental variables such as mean grain size explained a considerable portion of the variation observed in community structure, especially at Honda beach.

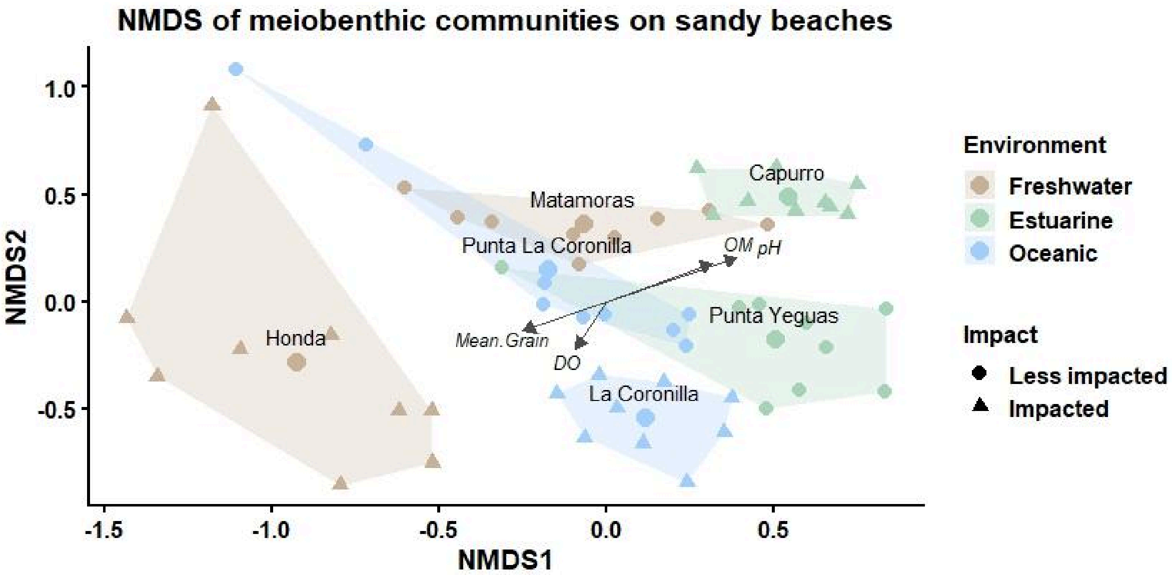

Figure 10. NMDS of meiobenthic communities at intertidal sandy beaches along the Uruguayan coast. Colors indicate environment type and symbols represent anthropogenic impact. Large circles correspond to group centroids, and polygons delineate the clustering of the beaches. The axes represent the two NMDS dimensions.

Arrows indicate environmental variables (mean grain size, organic matter, dissolved oxygen, and pH), showing their direction and strength of association with the ordination.

PERMANOVA showed that environmental type and impact level significantly influenced community composition (Table S6). Beta-dispersion analysis revealed significant differences in community variability among environments and between impact levels (Table S7): less impacted beaches showed lower dispersion at the scale of the sample set (more homogeneous communities), whereas impacted beaches exhibited higher dispersion of the dataset (greater heterogeneity). Differences in dispersion were also detected among environments, suggesting contrasts in the degree of internal heterogeneity of meiobenthic communities along the environmental gradient.

Indicator value analysis (IndVal) identified taxa significantly associated with specific environments and impact levels (Table S8). Among environments, the main indicator taxa were oligochaetes in freshwater beaches, ostracods in estuarine beaches, and turbellarians, polychaetes, and priapulids in oceanic beaches. Some taxa, such as gastropods and bivalves, were associated with both freshwater and estuarine environments, while copepods, nauplii, and gastrotrichs were linked to estuarine and oceanic environments, indicating their capacity to thrive under different environmental conditions. In less impacted beaches, the main indicator taxa were gastrotrichs and ostracods, characteristic of communities under lower anthropogenic pressure, supporting the inferences derived from the multivariate analyses regarding the structure of meiobenthic communities.

DISCUSSION

The results of this study provide a comprehensive understanding of the spatial variability of meiobenthic communities on Uruguayan sandy beaches through the analysis of biodiversity indices and community composition, highlighting how environmental and anthropogenic factors can modulate the structuring of these communities.

WATER AND SEDIMENT PARAMETERS

Salinity, categorized into freshwater, estuarine, and oceanic environments, was representative of the environmental conditions of each beach, reflecting the spatial and temporal dynamics influenced by meteorological, hydrological, oceanographic, and topographic factors (Garcia-Alonso et al., 2019). DO levels remained within expected ranges, with the lowest values observed at the impacted estuarine beach Capurro (Figure 3A), likely associated with the urban and industrial influence of Montevideo Bay (Gray and Elliott, 2009;Muniz et al., 2015).

These low oxygen levels may result from organic enrichment that stimulates bacteria production and, consequently, increases oxygen consumption, affecting benthic and meiobenthic communities (Piccini and García-Alonso, 2015; Kandratavicius et al., 2018).

The range of pH values found was similar to those reported in monitoring studies by García-Alonso et al. (2017) and Castiglioni et al. (2018) in beaches along the Uruguayan coast. Water pH can be used to detect contaminated areas (Pérez-Castillo and Rodríguez, 2008). In this case, the urbanized freshwater beach Honda exhibited the lowest pH values. In most samples, pH remained close to neutrality, with a slight tendency toward more basic values in more saline environments

(Figure 3B), which likely reflects patterns of water alkalinity associated with the salinity gradient rather than effects of anthropogenic impact.

Fine to medium sands, typical of dissipative beaches (Lercari and Defeo, 2006; Short and Jackson, 2013; García-Alonso et al., 2017), predominated at most of the study sites. However, Honda beach exhibited coarser sediments, probably due to the presence of coarse sand, whereas Punta Yeguas showed greater grain size heterogeneity, with fine sand predominating along with the presence of pebbles (Figure 3D).

The sediment OM content was higher in estuarine beaches, consistent with the characteristics of these environments, where variations in salinity and pH favor the deposition of suspended particles (Gray and Elliott, 2009). However, despite this trend, no significant differences in OM content were observed between paired beaches, suggesting that OM accumulation may be influenced not only by local factors but also by larger scale processes, such as hydrodynamics and human activities along the Uruguayan coast (García-Alonso et al., 2019). The higher OM in estuarine beaches, compared to freshwater and oceanic beaches (Figure 3C) may be attributed to the predominance of fine sediments in these environment, which have a greater capacity to retain OM, as noted by Nybakken, (1996) and Giere, (2009), and is reflected in the relationship observed in Figure 2.

STRUCTURE OF MEIOBENTHIC COMMUNITY AND ENVIRONMENTAL FACTORS

In general, the biodiversity patterns of the meiobenthic community on beaches along the Uruguayan coast were consistent with those previously reported for beaches on the southwestern Atlantic coast (Coppo et al., 2024). At the estuarine beaches of the Rio de la Plata (Capurro and Punta Yeguas), richness was higher than in the meiobenthic communities of estuarine coastal lagoons in Uruguay (Kandratavicius et al., 2015).

Nematodes and copepods were the most abundant taxa on Uruguayan beaches (Figures 5A, B, Table 2), which aligns with previous studies highlighting their dominance in various coastal environments (Coull et al., 1979; Nicholas, 2001; Giere, 2009; Kandratavicius et al., 2015). Nematodes, which often represent more than half of the total meiofauna abundance (Dye, 1983; Silva et al., 1997; Kotwicki et al., 2005; Pinto and Santos, 2006), are highly adaptable organisms capable of occupying interstitial spaces, tolerating various stressors, and employing diverse feeding strategies (Kandratavicius et al., 2015; 2024). They are especially abundant in fine sediments, whereas other groups, such as copepods and ostracods, tend to prevail in coarser sediments (Gourbault et al., 1995; Kandratavicius et al., 2015). These patterns were observed when analyzing both freshwater and estuarine beaches. In particular, Matamoras and Capurro exhibited smaller mean grain sizes and higher average OM content compared to their counterparts, Honda and Punta Yeguas. Matamoras and Capurro showed higher nematode abundance and lower copepod abundance, whereas Honda and Punta Yeguas, characterized by larger mean grain sizes and lower OM content, exhibited higher abundances of copepods and nauplii relative to nematodes. These results are consistent with previous studies highlighting sediment grain size and OM content as key factors structuring meiobenthic communities (Kandratavicius et al., 2015; 2024).

According to Alongi (1987), free-living flatworms (also known as "Turbellarians") can be as abundant as nematodes, but they are often underestimated due to sampling and processing techniques that tend to destroy them, resulting in inaccurate abundance estimates. We found the highest mean abundance of this taxon (160.6 ind/10 cm², Table 2) at the oceanic beach of La Coronilla (Figure 5D), and they were also observed at all less impacted beaches. The freshwater input from the artificial Andreoni channel does not appear to influence the turbellarian community. Therefore, at La Coronilla, it is not possible to determine whether the turbellarians present originate from freshwater input or oceanic source. The observation that turbellarians are absent from impacted urban beaches such as Honda (freshwater) and Capurro (estuarine) (Figure 5D), but present at less disturbed sites, suggests that this taxon may be sensitive to anthropogenic disturbances. This pattern is consistent with previous studies indicating that some freshwater planarians serve as bioindicators of environmental quality (Alonso and Camargo, 2011).

Similar pattern was observed for Gastrotrichs (Figure 5C), a group described as one of the most abundant taxa within meiobenthic communities of intertidal sandy beaches (Giere, 2009; Martinez et al., 2024). Despite their ecological importance, gastrotrich populations are often overlooked in monitoring studies (Schmidt-Rhaesa et. al., 2019). It is noteworthy that they exhibit high temporal variability, as observed throughout the year on intertidal beaches of southern Brazil (Coppo et al., 2024), which may result in their underrepresentation depending on the timing of sampling. According to the IndVal results, gastrotrichs are mainly associated with less impacted beaches, as presented in the following multivariate analysis section (Table S8).

Biodiversity indices, including taxon richness, total abundance, and nematode abundance, were positively correlated with finer sediment grain sizes and higher OM content (Figure 6, Table S1).

Shannon diversity and Pielou's evenness indices were negatively correlated with OM, suggesting that high levels of OM, associated with organic enrichment, may reduce biodiversity. High levels of OM alter the redox conditions of the sediment, favoring the development of microbial communities tolerant to organic enrichment, which in turn generate changes in the meiobenthic community, promoting the predominance of tolerant taxa, such as some nematode species resistant to these conditions (Pearson, 1978; Venturini et al., 2012; Kandratavicius et al., 2018).

A similar trend was observed across all beaches: richness, Shannon exponential index, and Pielou's evenness showed a positive association with DO. Low DO levels, indicative of organic enrichment that drives oxygen consumption, were associated with lower biodiversity indices (Kandratavicius et al., 2018). These results were observed at the impacted estuarine beach Capurro and are consistent with previous studies documenting DO reduction associated with industrial pollution sources and organic enrichment (Gray and Elliott, 2009), a pattern reinforced by the higher OM concentration observed at this beach compared to others. In particular, nematodes, known for their tolerance to low DO levels (Vopel et al., 1998; Veit-Köhler et al., 2009), were more abundant at Capurro under hypoxic conditions, whereas harpacticoid copepods, which are more sensitive to environmental stress (Kotwicki et al, 2005), were less abundant (Table 2). These patterns support our hypotheses: fine sands and higher OM favor taxonomic richness and abundance of nematodes, coarser sediments tend to favor mobile interstitial groups such as harpacticoid copepods and other taxa adapted to larger pore spaces. Similarly, higher levels of DO were associated with greater overall diversity, confirming the importance of both sediment and water variables in structuring the meiobenthic community.

When evaluating the meiobenthic community across the two beaches, regardless of anthropogenic impact, it was observed that community responses, both in terms of biodiversity indices and composition, were influenced by salinity associated with the different environment types along the Uruguayan coast. This environmental gradient (freshwater, estuarine, and oceanic) was mainly reflected in taxon richness, with oceanic and estuarine environments showing higher richness compared to freshwater environments (Figure 8A). This is consistent with previous studies that indicate that oceanic environments exhibit greater diversity than freshwater ones (Broman et al. 2019). As expected, oceanic beaches showed higher values of richness and Shannon exponential (Figure 8A and 8B). In contrast, freshwater beaches exhibited the lowest richness values. However, the Shannon exponential index did not follow this pattern, showing lower values in estuarine beaches. Estuarine beaches, characterized by fluctuating salinity and higher OM content, showed reduced biodiversity, likely due to the high abundance of a few euryhaline species, particularly nematodes, capable of tolerating these conditions (Elliott and Whitfield, 2011). The dominance of these tolerant taxa appears to suppress the occurrence of less resilient species, explaining the observed decrease in overall biodiversity. These patterns support our hypothesis that biodiversity indices are influenced by the type of environment, with higher taxonomic richness and diversity expected in oceanic environments and lower values in freshwater environments.

IMPACT OF ANTHROPOGENIC ACTIVITIES ON THE MEIOFAUNAL COMMUNITY

Impacted beaches, such as Capurro Beach, exhibited lower species richness and diversity (Figures 9A and 9B), with nematodes as the dominant group (Figures 5A and 9D). In contrast, Punta Yeguas, which is less impacted, showed higher biodiversity, with a more diverse community that included ostracods, copepods, and gastrotrichs (Figures 5 and 9B). Crustaceans such as copepods and ostracods have been reported as sensitive to pollutants, and are therefore considered reliable indicators of anthropogenic impacts (Van Damme et al., 1984; Ruiz et al., 2005; Amorri et al., 2022), which partly explains the observed patterns.

Oceanic beaches, characterized by stable salinity and lower human disturbance, generally displayed greater biodiversity. In particular, La Coronilla may be receiving exogenous meiofauna through freshwater input from the artificial Andreoni canal, which could contribute to the high values observed in richness and diversity indices. This external influence contrasts with what was recorded at Punta La Coronilla Beach (Figure 9B), which, although classified as a less impacted environment, showed lower values for these indices (Figures 9A and 9B). This suggests that, beyond the level of anthropogenic impact, other factors such as hydrological connectivity and the influx of organisms from adjacent environments could play an important role in shaping meiofaunal community structure. This pattern partly contrasts with the expected reduction in diversity at impacted sites, suggesting that site-specific processes such as hydrological connectivity and exogenous inputs may override the general impact signal.

Beaches such as Honda, which showed the lowest densities but higher evenness in meiofaunal distribution compared to Matamoras (Figures 9C and 9D), had communities dominated by oligochaetes and copepods. The dominance of oligochaetes reflects their tolerance to chemical and physical pollution resulting from urban runoff and crushed stone substrates (Armendáriz et al., 2011). In contrast, the presence of copepods organisms generally more sensitive to chemical pollution (Amorri et al., 2022) appears to be more influenced by sediment type than by chemical contamination itself. This pattern may be related to human activities and to the prevalence of disturbance-tolerant taxa. Overall, these observations support our hypothesis that within the same environmental type, more impacted beaches show lower taxonomic richness, lower Shannon diversity, and lower Pielou evenness, while tolerant taxa are more abundant in impacted sites. It should be noted that "impact" encompasses different stressor types across sites, and thus the observed responses likely reflect a combination of pressure-specific mechanisms.

MULTIVARIATE ANALYSIS AND INDICATOR TAXA

Multivariate analyses showed that meiobenthic communities are clearly structured by both environment type and the level of anthropogenic impact (Zeppilli et al., 2015; Broman et al., 2019; Leasi et al., 2021; Schratzberger et al., 2023; Zhou et al., 2023). Accordingly, NMDS ordinations consistently separated communities according to these categories, revealing well-defined patterns in community composition. PERMANOVA results confirmed that both environment type and anthropogenic impact act as significant predictors of community composition.

The inclusion of continuous environmental variables strengthened the interpretation of these patterns. Mean grain size emerged as a key factor structuring freshwater beaches, particularly at Honda, in agreement with the characteristics of the meiofauna recorded in this environment. In estuarine beaches, organic matter content and pH were relevant variables, reflecting the greater capacity of these systems to accumulate organic matter and generate distinctive physicochemical conditions (Nybakken, 1996; Giere, 2009). In contrast, dissolved oxygen contributed partially to community structuring on oceanic beaches, consistent with the high hydrodynamic energy and the generally well-oxygenated conditions characteristic of these environments (McLachlan & Defeo, 2017).

Beta-dispersion analyses indicated that less impacted beaches harbored more homogeneous communities at the scale of the overall sample set, whereas impacted beaches exhibited higher within-group dispersion, reflecting increased heterogeneity, possibly associated with different types or intensities of anthropogenic disturbance. In this context, exploratory inspection of the NMDS ordinations allowed a broad visualization of intrabeach variability, suggesting differences in replicate-level dispersion within beaches that may reflect differential community responses to disturbance intensity or type; however, this pattern should be interpreted with caution and is presented here for descriptive purposes only. At a broader conceptual level, such patterns have been associated with local disturbances that generate mosaics of microhabitats with variable physicochemical conditions, thereby increasing community variability (Gray and Elliott, 2009; Pearson, 1978). In contrast, the higher homogeneity observed in less impacted beaches may reflect more stable conditions, in which natural environmental filters consistently select the taxa present. Nevertheless, these inferences should be interpreted with caution, as the sampling design and the spatial scale considered impose certain limitations, which are addressed in the "Limitations and perspectives" section.

In this context, indicator value (IndVal) analyses complemented the multivariate patterns by identifying taxonomic associations consistent with both environment type and impact level. Oligochaetes were identified as characteristic taxa of freshwater environments, ostracods showed affinity for estuarine beaches, whereas turbellarians, polychaetes, and priapulids were mainly associated with oceanic beaches. In addition, gastrotrichs and ostracods were preferentially linked to less impacted beaches, while dominant nematodes were associated with disturbed sites, in agreement with their well-documented relative tolerance to organic and chemical pollution. Altogether, these results reinforce the value of meiofauna as an integrated bioindicator of the ecological status of coastal environments (Alonso and Camargo, 2011; Kandratavicius et al., 2018; Leasi et al., 2021)..

LIMITATIONS AND PERSPECTIVES

A major limitation of this study was the small sample size, which restricted the use of full multimodel inference and model averaging approaches to evaluate predictor importance. Therefore, results should be interpreted as exploratory but ecologically consistent patterns, grounded in a priori hypotheses and supported by convergent univariate and multivariate analyses. To minimize overfitting, models were defined a priori based on ecological hypotheses, analyzing continuous environmental variables (DO, pH, mean grain size, and OM) separately from categorical factors (Environment and Impact). It should be noted that, within each environment type, the degrees of freedom for the Impact factor were limited to one, so interpretations of its effect should be made with caution.

Future studies could increase the number of sampled beaches and apply more detailed impact scales for each site, allowing finer-resolution analyses of human impacts. Additionally, the use of molecular tools (e.g., eDNA or metabarcoding) could complement traditional meiofauna surveys, improving taxonomic resolution and detecting cryptic or rare taxa. Expanding sample size and methodological approaches would enable the application of full multimodel inference to explore both within and between beach variation more thoroughly.

CONCLUSION

The structure of meiobenthic communities on sandy beaches along the Uruguayan coast appears to reflect a combination of natural factors (including differences among coastal environment types associated with the salinity gradient, sediment grain size, organic matter content, and oxygen availability) and possible anthropogenic stressors. Fine sediments and higher organic matter levels generally support greater total and nematode abundances, whereas coarser sediments tend to favor copepods and other meiofaunal groups. In contrast, organic enrichment and reduced dissolved oxygen, particularly on impacted beaches, are associated with lower diversity and evenness, often resulting in nematode-dominated assemblages.

Multivariate analyses showed that meiobenthic community composition is structured by both environment type and the level of anthropogenic impact. Less impacted beaches, considered as a group, exhibited more homogeneous communities, whereas impacted beaches showed greater compositional dispersion, reflecting increased heterogeneity associated with disturbance. Indicator taxa analyses identified groups characteristic of specific environments and, in particular, taxa associated with less impacted beaches, suggesting that these organisms are sensitive to anthropogenic disturbance and may serve as indicators of more conserved environmental conditions.

This study provides the first integrated evidence of how anthropogenic pressures, together with natural environmental gradients, shape meiobenthic communities along the Uruguayan coast. Our findings highlight the value of meiofauna as effective bioindicators for monitoring the ecological health of sandy beach ecosystems and establish a baseline for future studies incorporating broader spatial coverage, temporal replication, and higher taxonomic resolution.

AI USE DISCLOSURE

The authors declare that no artificial intelligence tools were used in the writing or editing of this manuscript.

DATA AVAILABILITY STATEMENT

All data are available from the corresponding author upon reasonable request.

SUPPLEMENTARY MATERIAL

Figure S1: Residuals analysis of GLM models with CDF and QQ-plot for each biodiversity indicator.

Figure S2: Residuals analysis of GLM models with CDF and QQ-plot for total abundance and absolute nematode abundance.

Table S1: Pairwise correlation matrix among abiotic explanatory variables (DO, pH, mean grain size, and organic matter).

Table S2: GLMs for biodiversity indices in relation to mean grain size (µm) and organic matter (%). Includes distributions, coefficients, significance, and AIC.

Table S3: GLMs for biodiversity indices in relation to water parameters (DO, mg/L, pH). Includes distributions, coefficients, significance, and AIC.

Table S4: GLMs for biodiversity indices in relation to environments (freshwater, estuarine, oceanic). Tukey post-hoc for oceanic vs. freshwater included.

Table S5: GLMs for biodiversity indices in relation to human impacted (“+”) and less impacted (“−”) beaches. Includes distributions, coefficients, significance, and AIC.

Table S6: PERMANOVA results for meiofaunal community composition in relation to Environment (freshwater, estuarine, and oceanic) and Impact (impacted vs. less impacted). Includes degrees of freedom (Df), sum of squares, proportion of variance explained (R^2), F-statistics, and significance (p-values).

Table S7: Beta-dispersion analysis for meiofaunal community composition in relation to Environment (freshwater, estuarine, and oceanic) and Impact (impacted vs. less impacted). Includes degrees of freedom (Df), sum of squares, mean squares, F-statistics, and significance (p-values).

Table S8: Indicator species (IndVal) analysis for meiofaunal taxa associated with Environment (freshwater, estuarine, and oceanic) and Impact level. Includes associated groups, taxa, IndVal statistic (Stat), and significance (p-values).

These materials are available online via the Ocean and Coastal Research platform and are cited in the main text as Figure S1, Figure S2, and Table S1–S8.

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AUTHOR CONTRIBUTIONS

B.G.: Conceptualization; Investigation; Sampling; Data analysis; Writing – review & editing;
N.K.: Supervision; Taxonomic support; Investigation; Data analysis; Writing – review & editing;
J.G-A.: Supervision; Sampling; Investigation; Writing – review & editing.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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