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Environmental and human impacts on fish assemblages in shallow bay areas of South-eastern Brazil

Wagner Uehara, Gustavo Henrique Soares Guedes, Marcia Cristina Costa de Azevedo, Victória de Jesus Souza, Francisco Gerson Araújo *

Universidade Federal Rural do Rio de Janeiro, Departamento de Biologia Animal, Laboratório de Ecologia de Peixes, Km 7, BR-465, 23897-030, Seropédica, RJ, Brazil

A R T I C L E I N F O

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A B S T R A C T

Environmental and human influences strongly shape fish assemblages in coastal marine ecosystems, yet their combined effects remain unclear. This study examines how anthropogenic activities and environmental variables (e.g., salinity, substrate roughness, beach dimensions, and water renewal) influence fish assemblage descriptors (species composition, abundance, richness, taxonomic diversity, and trophic guilds) in two bays, two types of sandy beaches (continental vs. insular), across two seasons (winter and summer) in southeastern Brazil. We hypothesized that (H1) fish assemblage characteristics vary between bays, beach types, and seasons due to differing environmental features, and (H2) ecological and anthropogenic factors have distinct effects on assemblage descriptors. We conducted 312 beach-seine samples and analyzed the data using PERMANOVA and Generalized Additive Mixed Models (GAMMs). Results show that fish assemblages differ significantly by bay, beach type, and season, with significant interactions between bays and beach types, supporting H1. Fish abundance and richness, as well as the abundance of benthivorous and planktivorous species, were higher on continental beaches. Environmental factors differentially influenced assemblage descriptors, supporting H2. For example, human impact (Human Footprint Index) was a major predictor of fish abundance, richness, and specific trophic guilds (e.g., planktivores and opportunists). Species richness peaked at intermediate salinity (∼30), substrate roughness positively affected planktivores but negatively affected benthivorous, beach length was negatively associated with total abundance and opportunistic species, and depth negatively correlated with taxonomic distinctness and benthivore abundance. These findings highlight the role of local environmental conditions in structuring fish assemblages and emphasize the need for conservation strategies that preserve habitat complexity in tropical marine ecosystems.

1. Introduction

Transitional zones between terrestrial and aquatic systems are vital nurseries for ichthyofauna (Beck et al., 2001; Lefcheck et al., 2019; Whitfield, 2020a). They provide environmental diversity that supports spawning, reproduction, juvenile growth, and shelter from predators and adverse conditions, enhancing survival and recruitment into new generations (Gomes-Gonçalves and Araújo, 2023; Harrison and Whitfield, 2024; Sheaves et al., 2015). Recognized as some of the most productive ecosystems on the planet, they are characterized by high biodiversity and organism density (Cardoso, 2021; Carvalho Junior, 2025; Costanza et al., 1997), but they face severe impacts from the unregulated growth of human activities in their surroundings (Defeo et al., 2021; Lotze et al., 2006; Osinaga et al., 2025), leading to habitat degradation and pollution caused by the discharge of effluents directly into estuarine systems via rivers and drainage channels (Araújo et al., 2018; Damasceno et al., 2025), thereby compromising the integrity of these ecosystems (Davenport and Davenport, 2006; Defeo and McLachlan, 2013). Urban and industrial expansion further worsens this situation, negatively affecting local biodiversity, particularly the ichthyofauna that inhabits shallow waters, resulting in changes in taxonomic composition and structure (Araújo et al., 2018). The success of species that rely on these habitats is directly linked to the maintenance of their fitness, measured by the reproductive contribution of individuals to future generations (Bozzeda et al., 2023).

Sandy beaches in estuarine areas mark the transition between

* Corresponding author.
E-mail addresses: wagneruehara81@gmail.com (W. Uehara), gustavohsg@outlook.com (G.H.S. Guedes), mazevedoufrrj@gmail.com (M.C.C. de Azevedo), victoriadejsouza@ufrrj.br (V. de Jesus Souza), gerson@ufrrj.br (F.G. Araújo).

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aquatic and terrestrial environments and play a crucial role in the marine ecosystem. The dynamic nature and constant interaction between land and sea create unique conditions for marine biodiversity (Defeo et al., 2009; Whitfield, 2021). This type of habitat contributes significantly to the maintenance of fish populations and, consequently, to the health of marine ecosystems. Understanding fish distribution and the interactions between species and their environment is a challenging task due to the high spatial-temporal variability of the fauna and the inherent complexities of the environment, yet it is fundamental for conserving marine biodiversity and maintaining ecosystem services.

The analysis of fish community descriptors is essential for understanding the ecological dynamics of these aquatic ecosystems. They characterize the communities by providing valuable information about the health and structure of fish populations while reflecting the environmental conditions in which these communities exist. Abundance is a critical metric for understanding population density in aquatic ecosystems (Vieira et al., 1998; Yan et al., 2025). Factors such as habitat quality, biotic interactions, and environmental conditions influence abundance, while human activities like overfishing and pollution can significantly reduce populations (Brown et al., 2018; Pessanha et al., 2021). Similarly, species richness, which indicates the diversity within a community, depends on the variety of habitats and environmental conditions (Henderson et al., 2022; Melo, 2008). Environments characterized by the presence of multiple types of habitats tend to exhibit higher richness, whereas anthropogenic impacts can lead to species extinction. Thus, fish communities assume different structures and compositions in different habitat types, following environmental heterogeneity in aquatic systems (Medeiros et al., 2024).

Community descriptors such as abundance, richness and taxonomic distinctness are fundamental to understanding community dynamics (Clarke and Warwick, 1998). Taxonomic distinctness refers to the diversity of taxonomic groups within a community, encompassing the variety of families, genera, and species (Clark and Gorley, 2006). This descriptor is pivotal for understanding community structure and its resilience to disturbances (Clark and Gorley, 2006; Colombo et al., 2017). Communities with high taxonomic distinctness tend to be more resilient to environmental changes due to the presence of a broader range of species performing diverse ecological functions (Passos et al., 2013; Vilar et al., 2011). Additionally, the presence of keystone species can influence community dynamics, while temporal changes driven by environmental factors or human activities may affect taxonomic distinctness.

Bays generally offer protection against strong currents and waves, creating a more stable environment, which can favor the presence of species that prefer calm and sheltered waters (Borland et al., 2017). Insular beaches inside bays tend to have greater exposure to ocean waves and currents, while continental beaches may be more protected depending on their location (Gibran and Moura, 2012; Silva et al., 2019). Beaches near river mouths may present salinity variations, affecting the presence of estuarine and marine species (Whitfield, 2021). Continental beaches may be more influenced by human activities (pollution, habitat degradation), negatively affecting fish assemblages. On islands, there is generally less anthropogenic pressure compared to continental areas, resulting in more preserved ecosystems. The unique characteristics of each beach make comparisons between different systems difficult, in addition to understanding the simultaneous influence of multiple sources of disturbances, associated with the scarcity of historical data makes it even more difficult (Defeo and McLachlan, 2005; Defeo et al., 2009; Schlacher et al., 2008).

Regardless of the specific characteristics of each bay or beach, the fish community is influenced by a complex combination of anthropogenic and environmental factors. These impacts are often exacerbated by natural environmental variables, such as changes in hydrodynamic conditions or the physical and chemical characteristics of the environment, resulting in significant changes in the structure, composition, and dynamics of fish assemblages. For example, variations in salinity can exacerbate the negative effects on fish health, increasing mortality and reducing reproduction (Olds et al., 2018). Physical variables such as length, width, and depth and roughness of beaches, as well as water renewal and chemical variables such as pH and conductivity, can interact and influence the different descriptors and trophic groups of the ichthyofauna in different ways (Ferreira et al., 2015; Gutiérrez-Martínez et al., 2021).

Variation in some physical and chemical factors or variables that co-vary with these factors have a great influence on fish assemblages than anthropogenic stressors such as contamination (Inui et al., 2010; McKinley et al., 2011). Marine landscape metrics of length, depth, and width have been referred to as predictors of the fish community on sandy beaches (Moustaka et al., 2024). The composition and diversity of fish along a shallow beach depend on the extent of the beach, which contributes significantly to species diversity (Frischknecht et al., 2023; Olds et al., 2018). Longer beaches provide varied environmental conditions and abundant resources, resulting in greater species diversity (Able et al., 2013). The extent of the intertidal zone, defined by its length, width, and depth, represents the temporal variation in the amount of habitat available for fish within a marine landscape. Intertidal habitats can also serve as refuges against predators for small fish or as feeding areas (Gibson and Yoshiyama, 1999; Teichert et al., 2018).

Environmental disturbances interfere with the structure of the fish assemblage, modifying local conditions and affecting the adjustment of species to the environment (Santos et al., 2017; Villéger et al., 2010; Zeng et al., 2021). The HFI (Human Footprint Index) summarizes the influence of several human activities, such as population density, number of buildings, proportions of crops and pastures, extent of roads, railroads, and waterways, and electrical infrastructure, in a weighted average variable that represents human pressure on the environment (Mu et al., 2022). Human activities, such as pollution or organic enrichment, have direct and indirect impacts on biodiversity and the structure of assemblages (Capp Vergès et al., 2022; Moustaka et al., 2024; Tran et al., 2024).

Seasonality is another factor modifying the structure of communities and the effects of their predictors (Gurgel-Lourenço et al., 2025). Seasonal changes imposed by rainfall levels are often related to key ecosystem processes in tropical areas, especially for coastal and estuarine habitats. Souto-Vieira et al. (2024) demonstrated that coastal habitat mosaics exhibit significant spatial and temporal variations in fish assemblage, with remarkable differences in between-habitat responses to the onset of the tropical rainy season. Hernández-Álvarez et al. (2023) showed that fish assemblages in the estuarine systems of the Tropical Eastern Pacific respond to the specific seasonal water conditions, with seasonal changes related to the fluctuations in temperature and rain into the system.

The south-eastern coast of Brazil has two large bays (Sepetiba and Ilha Grande), which contain several islands and exhibit different environmental conditions. While Sepetiba Bay is relatively semi-enclosed, receives a higher input of continental drainage waters, and is situated in an area of increasing urban and industrial development, Ilha Grande Bay has a broader connection to the sea, with a comparatively more preserved surrounding area, though it also faces pressure from large-scale enterprises. These two environments provide a suitable setting for investigating the fish community and its local influences. The present study had two main objectives: 1) to compare the ichthyofauna and its descriptors (richness, abundance, taxonomic distinctness, and trophic guilds) of sandy beaches between two large bays (Sepetiba and Ilha Grande) in southeastern Brazil, as well as between two types of beaches (continental and insular) and seasons (winter and summer), and, 2) to assess how environmental variables (e.g., salinity, anthropogenic impact, substrate roughness, beach depth-width-length, and water renewal rate) modulate the patterns of fish assemblage descriptors. The hypotheses tested were: (H1) fish assemblage descriptors vary between the two bays, beach types (insular and continental), and seasons (winter/summer) due to their different environmental characteristics;

and (H2) different environmental and anthropogenic variables have distinct impacts on assemblage descriptors. It is expected that anthropogenic, physical, and chemical factors will interact in a complex way, modulating the distribution patterns and behavior of fish species.

2. Material and methods

2.1. Study area

The study area encompasses two adjacent coastal bays, Sepetíba and Ilha Grande, located in the state of Rio de Janeiro, Southeastern Brazil (22°53′-23°25′ S; 43°60′-44°30′ W; Fig. 1). Sepetíba Bay, with a drainage area of 3816 km^2, functions as a semi-enclosed system due to the presence of a natural sand barrier approximately 40 km long (Marambaia Restinga) along its southern edge, which separates it from the open ocean (Azevedo et al., 2017). This bay is experiencing increasing anthropogenic pressure, with high population and industrial density in its surroundings, exposing its waters to diffuse pollution (Carvalho et al., 2022). Sepetiba Bay, located on the southeast coast of Brazil, is a crucial ecosystem for coastal fish populations (Azevedo et al., 2007), featuring a diversity of habitats such as mangroves and rocky shores. However, the bay faces serious environmental pressures, including overfishing, eutrophication (Fonseca et al., 2013; Freitas and Rodrigues, 2014), pollution, and degradation caused by civil construction (Molisani, 2006). Urban and industrial developments, such as the dredging of the Sepetiba Port access channel to a depth of 20 m, aiming at the operation of larger ships (Araújo et al., 2018) and the establishment of industries, have intensified the occupation of the shores, resulting in habitat destruction and increased pollution (Carneiro et al., 2013; Ribeiro et al., 2013). Also, the Submarine Development Program (PROSUB), created with the proposal to expand the national defense structure, for the manufacture of four conventional submarines and one with nuclear propulsion, was implemented in the area. This program encompasses the construction of a Metallic Structures Manufacturing Unit, two Shipyards, a Radiological Complex and a Naval Base. Currently, Sepetiba Bay is facing serious environmental damage, such as deforestation of its surrounding areas and water warming, resulting from the installation of fluctuating Thermal Power Plants in the inner bay area.

Ilha Grande Bay has a smaller drainage area of 2356 km^2 and is an open system that includes a complex of approximately 350 islands (Teixeira-Neves et al., 2016). Ilha Grande Bay covers an area of 652.58 km^2 and the main freshwater inputs are the Mambucaba and Bracuí rivers, with mean annual discharges of 25.58 $m^3\ s^{-1}$ and 11.20 $m^3\ s^{-1}$, respectively (Signorini, 1980). Sepetiba Bay, with an area of approximately 450 km^2, receives only from the Guandu River a mean annual discharge of about 287 $m^3\ s^{-1}$, exceeding the combined discharge of all tributaries flowing into Ilha Grande Bay. Ilha Grande Bay is more preserved compared to Sepetíba Bay due to lower population and industrial density, as well as the presence of terrestrial and marine conservation units. However, Ilha Grande Bay hosts major naval and port activities, including the BrasFELS Shipyard, the Port of Angra dos Reis, and the Ilha Grande Bay Maritime Terminal (TEBIG). The region also contains Brazil's only operating nuclear power complex, comprising three plants (Angra 1, 2, and 3), with Angra 3 currently under construction. In addition, the scenic beauty of Ilha Grande Bay has driven its growth as a major tourist destination, which has promoted rapid and largely unplanned urban development and increased real estate investment, particularly since the 1990s (Damasceno et al., 2025; Silva et al., 2021a).

The circulation pattern of Sepetiba Bay results in a relatively short water residence time (4–17 days), characterized by intense water-column mixing and little to no stratification. In contrast, Ilha Grande Bay has stronger connectivity with the open ocean and functions as a more open system, with enhanced east–west water transport that promotes higher water renewal. During winter, increased oceanic water intrusion driven by the more frequent passage of cold fronts enhances water renewal in both bays (Kjerfve et al., 2021; Pereira et al., 2024; Rodrigues et al., 2022).

The region has a tropical climate with hot, rainy summers and dry winters (Köppen Aw). In Sepetiba Bay, mean water temperature ranges from 19.7 ± 1.3 °C in winter to 28.1 ± 1.5 °C in summer, with annual precipitation between 1000 and 2230 mm; average rainfall is approximately 195–275 mm in summer and decreases to less than 31–35 mm in winter (Gomes-Gonçalves and Araújo, 2023; Kjerfve et al., 2021). In Ilha Grande Bay, water temperature varies from 20.0 ± 1.4 °C in winter to 31.0 ± 2.7 °C in summer, and mean annual rainfall is about 1770 mm, exceeding 230 mm during summer (December–March) and dropping below 100–180 mm in winter (June–August) (Alvares et al., 2013; Dias and Bonecker, 2008; Kjerfve et al., 2021).

2.2. Fish sampling

Fish from continental and insular sandy beaches of the bays were sampled using beach seine nets (12 × 2.5 m; mesh size 5 mm), with three replicates per site. The three replicates within each site were spatially independent, with trawls conducted approximately 100 m apart. This

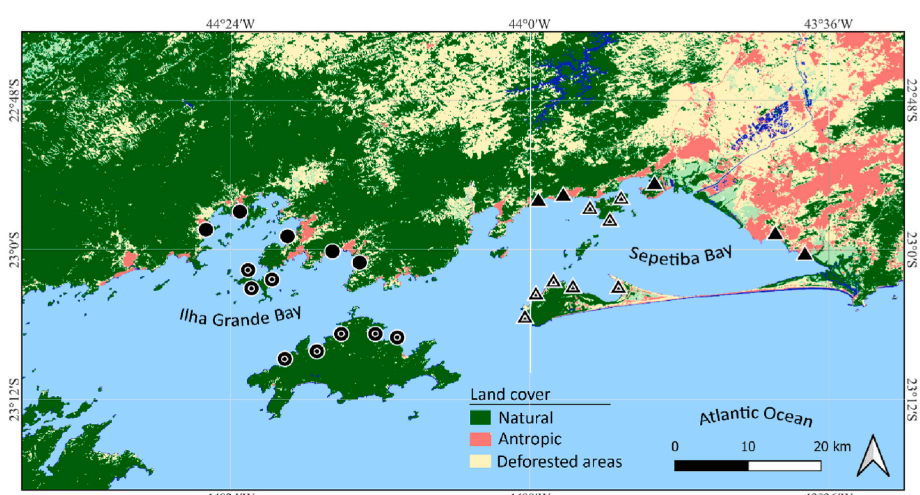

Fig. 1. Map of the study area highlighting the sampling sites and the geographical location of Ilha Grande and Sepetíba bays, situated in the state of Rio de Janeiro (Southeast Brazil). Sites: Sepetiba Bay, continental beaches, filled triangles; island beaches, open triangles; Ilha Grande Bay, continental beaches, filled circles; island beaches, open circles.

spacing was adopted to minimize any influence of previous collections on subsequent trawls. The seine net was operated to a maximum depth of 1.5 m and pulled perpendicular to the shoreline, using a 30 m line at each end of the net (Fig. 2). Sampling was conducted during the day, between 6:00 a.m. and 5:00 p.m., during neap tide. The temporal sequence of sampling sites was randomized on each sampling occasion; therefore, samples from the same location were not consistently collected at the same time of day, reducing potential systematic bias related to diel variation. Collections were taken biannually in the years 2021 (winter), 2022 (summer and winter), and 2023 (summer). A total of 312 samples were taken (2 bays × 2 seasons × 2 years × 13 sites × 3 replicates). The sampling unit was defined as the sum of fish captured in the 3 replicates at each site, totaling 104 samples. Fish were anesthetized with benzocaine hydrochloride (50 mg × L^{-1}) immediately after capture and euthanized with ice. They were then fixed in 10 % formalin and preserved in 70 % ethanol after 48 h. Fish collection was conducted under the permission of the Chico Mendes Institute for Biodiversity Conservation (ICMBio#74672). All applicable international, national or institutional guildelines for the care and use of animals were followed, including Universidade Federal Rural do Rio de Janeiro, Brazil, Animal Care Protocol (CEUA # 11874).

The fish were also grouped into seven trophic guilds based on diet and feeding behavior, following Elliott et al. (2007) and additional literature (Froese and Pauly, 2021; Gomes-Gonçalves and Araújo, 2023) Piscivores, Planktivores, Benthivores, Hyperbenthivores, Herbivores, Opportunists, and Detritivores. However, analyses focused only on the three most representative trophic groups (Planktivores, Opportunists, and Benthivores), excluding rare and zero-inflated guilds.

2.3. Environmental, landscape, and anthropogenic variables

Environmental, landscape, and anthropogenic variables were either measured directly at sampling locations or obtained from existing databases using a combination of techniques. Environmental characteristics, including physical and chemical parameters of the water, such as temperature (°C), dissolved oxygen (mg/L), pH, electrical conductivity (mS/cm), and salinity, were measured with a Horiba U-52 G multisensor (Shanghai, China). Water transparency (meters) was assessed using a Secchi disk. Landscape variables such as depth (meters) were recorded using a SpeedTech SM-5 digital probe (Great Falls, USA), while beach width and length (km) were determined from satellite imagery available on Google Earth Pro. Equivalent bottom roughness (m) and water renewal rate (%) were obtained from hydrodynamic models provided by the SisBaHiA project (baiasdobrasil.coppe.ufrj.br). Anthropogenic disturbances, including population density and land use/cover, were assessed using the Human Footprint Index (Mu et al., 2022). The HFI is a spatial indicator that quantifies human impact on the environment by integrating multiple pressure variables, such as

Fig. 2. Aerial view of a trawl net being used on an insular sandy beach in Ilha Grande Bay for fish capture.

population density, land use, infrastructure, roads, and nighttime lights, which are standardized to a common scale and summed to generate a cumulative score (Allan et al., 2023; Sanderson, 2002). Higher values indicate greater human influence. To calculate the local human footprint, geographic coordinates of each sampling location were overlaid with raster layers (1 km^2 pixel resolution, reference year 2020). All geoprocessing tasks, such as layer overlay, reprojection, and data extraction, were conducted using the WGS 84 coordinate reference system in QGIS software (QGIS Development Team, 2024).

2.4. Data analysis

This study compares five community descriptors: fish assemblage structure, fish abundance (N), species richness (S), taxonomic distinctness (Δ+), and trophic guild composition (TG), in which fish species were grouped according to their feeding habits to allow comparisons across different bays (Ilha Grande *vs*. Sepetiba), seasons (winter *vs*. summer), and beach types (continental *vs*. insular). To determine whether fish community descriptors vary by bay, beach type, and season due to differing environmental features (H1), a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted using three fixed factors (bay, season, and beach type), with 9999 permutations and Type III partial sums of squares for p-value calculation. To reduce the influence of highly abundant species while preserving relative abundance information, the data were log-transformed (log (x+1)) as recommended by Borcard et al. (2011) and then converted into a Bray-Curtis dissimilarity matrix. For significant results ($p < 0.05$), pairwise comparisons were performed to identify differences between groups. Non-parametric tests were applied because the data did not follow a normal distribution, even after transformation. To identify the fish species that contributed most to within-group similarity among bays, seasons, and beach types, a multilevel pattern analysis (MPA) with the *multipatt* function from the *indicspecies* package (Cáceres and Legendre, 2009) was performed. Significant values were detected using the IndVal index, tested via permutation (Cáceres and Legendre, 2009).

To assess the relationship between fish assemblage composition, environmental factors, and sampling sites in Sepetiba and Ilha Grande Bays, a distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999; McArdle and Anderson, 2001) was performed. The response matrix consisted of species abundances per sampling site, which were square-root transformed to reduce the influence of dominant species. A Bray–Curtis dissimilarity matrix was then computed. Environmental and anthropogenic variables were standardized using z-scores to ensure comparability. Model and axis significance were tested via permutation ($n = 999$). The first two ordination axes were used to visualize sample distributions, species associations, and environmental gradients.

To determine how each environmental, landscape, and anthropogenic disturbance variable affects fish community descriptors (H2; response variables: N, S, Δ+, and TG), a full subset selection (FSS) approach and generalized additive mixed models (GAMMs) were employed. GAMMs apply smooth functions to model covariate effects, allowing flexible, non-parametric relationships between the response variable and covariates without requiring assumptions about the form of these relationships (Fisher et al., 2018; Wood, 2017). The FSS approach fits all possible variable combinations and calculates the AICc (Akaike Information Criterion corrected for small sample sizes) for each model (Akaike, 1998; Fisher et al., 2018). To prevent overfitting and facilitate interpretation, models were limited to two explanatory variables. To reduce collinearity, models containing variables with paired Spearman correlation coefficients exceeding 0.4 were excluded (Fig. S1, supplementary information), following recommendations for ecological regression and GAM-based analyses (Dormann et al., 2013; Zuur et al., 2010) as even low collinearity levels can lead to imprecise parameter estimates, reduced statistical power, and exclusion of significant predictors (Graham, 2003).

Sampling locations were included as random effects to enhance the inferential power of the models and account for overdispersion and correlation, including potential spatial autocorrelation, within the data (Harrison, 2014; Wood, 2006). The response variables were log(x+1) transformed and assigned to appropriate distributions: species richness was modeled using a Poisson distribution; taxonomic distinctness was modeled with a Gaussian distribution (with a log link); and other response variables were modeled with a Tweedie distribution. The Poisson distribution is suited for count data with randomly distributed (non-aggregated) events, while the Gaussian distribution with a log link is appropriate for data that approximates a normal distribution after log transformation. The Tweedie distribution is applied to data with many zeros and a combination of continuous and discrete positive values.

The importance of the variables was determined by summing the weight of all models that included each variable, and this was used to assess the relative importance of the predictor variables (Burnham and Anderson, 2002). Models were considered to have similar explanatory power if they were within two AICc units of the model with the lowest AICc, in which case the "best" models were selected based on the importance of the variables and model weight (Akaike, 1998). When there was no clearly defined "best" model, meaning models with an AICc difference of less than or equal to 2, models close to this threshold were included as candidate models. All statistical analyses were conducted using R and the packages FSSgam (version 1.11), gamm4 (version 0.2–6), and mgcv (version 1.8–40) (Fisher et al., 2018; R Core Team, 2022; Wood, 2006).

3. Results

3.1. Fish composition

A total of 58.894 individuals were recorded, spanning 69 species, 31 families, 18 orders and 13 suborders (Table S1). In terms of total abundance, the order Clupeiformes had the highest number of individuals, accounting for 73 % of the total, followed by Atheriniformes with 16.5 %. The most abundant species were *Anchoa januaria* (Steindachner, 1879) (N% = 33.2), *Anchoa lyolepis* (Evermann and Marsh, 1900) (N% = 31.6), *Atherinella brasiliensis* (Quoy and Gaimard, 1825) (N % = 16.5), and *Eucinostomus argenteus* (Baird and Girard, 1855) (N% = 6.2), together comprising over 87 % of all individuals captured in the study.

The species *Strongylura timucu* (Walbaum, 1792), *Dactyloscopus crossotus* Starks, 1913, *Sphoeroides testudineus* (Linnaeus, 1758), and *E. argenteus* were indicators (MPA; $p < 0.05$) of Ilha Grande Bay, while *Umbrina coroides* Cuvier, 1830, *Genidens genidens* (Cuvier, 1829), *Micropogonias furnieri* (Desmarest, 1823), *Stellifer stellifer* (Bloch, 1790), and the anchovies *Anchoa tricolor* (Spix and Agassiz, 1829), *A. januaria*, and *A. lyolepis* were indicators (MPA; $p < 0.05$) of Sepetiba Bay. Regarding beach types (continental vs. insular), six species were significantly associated with continental beaches (*A. januaria*, *A. lyolepis*, *M. furnieri*, *S. testudineus*, *Mugil liza* Valenciennes, 1836, and *Achirus lineatus* (Linnaeus, 1758)), while no species were indicators of insular beaches according to the MPA ($p > 0.05$). In relation to seasons, *Oligoplites saliens* (Bloch, 1793), *Oligoplites saurus* (Bloch and Schneider, 1801), and *Trachinotus falcatus* (Linnaeus, 1758) were associated with the summer, while another five species (*M. liza*, *D. crossotus*, *M. furnieri*, *Menticirrhus littoralis* (Holbrook, 1847), and *Sardinella brasiliensis* (Steindachner, 1879)) were associated with the winter season.

3.2. Descriptors of fish assemblage

The structure of the fish assemblage varied significantly ($p < 0.01$) across the fixed factors of bay, beach type, and season, with a significant interaction detected between bay and beach type, according to PERMANOVA (H1; Table S2).

Significant differences in abundance (N) and species richness (S) were found for beach types (Table S3), with continental beaches exhibiting higher abundances (mean ± s.d.; N = 1119 ± 537) and species richness (S = 7.4 ± 0.5) compared to insular beaches (N = 227 ± 45; S = 5.5 ± 0.3). For taxonomic distinctness, significant differences were observed only between seasons ($p = 0.04$), with the winter showing a mean of 76.8 ± 0.5, compared to 75.5 ± 0.5 in the summer (Table S3).

The abundance of benthivorous and planktivorous guilds displayed significant differences ($p < 0.05$) only with respect to beach type (Table S4), with higher values on continental beaches (Benthivore = 45.02 ± 20.2; Planktivore = 951.12 ± 541.4) compared to insular beaches (Benthivore = 37.6 ± 19.6; Planktivore = 25.03 ± 9.9) (Table S4). The opportunistic guild did not show significant differences for the fixed factors; however, a significant interaction was observed between bay and beach type ($p = 0.003$; Table S4). On insular beaches, no significant differences in the abundance of opportunists were detected between Sepetíba bay (102.46 ± 38.3) and Ilha Grande bay (108.4 ± 28.6) ($t = 1.07$; $p = 0.27$). However, on continental beaches, Ilha Grande showed a higher abundance of opportunists (101.3 ± 27.9) compared to Sepetiba (53.9 ± 23.3) ($t = 3.22$; $p = 0.003$).

3.3. Species-environment relationships

The dbRDA analysis revealed a clear separation between the samples from Sepetiba and Ilha Grande bays along the first axis (dbRDA1), which explained 41.1 % of the fitted variation (10.2 % of the total variation). The second axis (dbRDA2) explained 20 % of the fitted variation (5 % of the total variation), and did not show a clear separation between samples from the two bays (Fig. 3).

In Sepetiba Bay, species distribution was primarily influenced by beach length and the Human Footprint Index (HFI), favoring species such as *Micropogonias furnieri, Menticirrhus littoralis, Genidens genidens*, and *Anchoa januaria*, which clustered on the right side of the ordination. Coastline roughness also contributed to species distribution in this bay, particularly affecting *Trachinotus carolinus, Odontesthes saurus*, and *Anchoa tricolor*.

In contrast, Ilha Grande Bay was associated with higher values of salinity, temperature, water transparency, and dissolved oxygen (Table S5). These environmental conditions were linked to the occurrence of *Dactylopterus crossotus*, *Sphyraena timucu*, and *Anchoviella brasiliensis*, likely reflecting the bay's higher salinity and lower anthropogenic pressure. These samples and species were grouped on the left side of the ordination (Fig. 3).

3.4. Relationships between assemblage descriptors and environmental, landscape, and anthropogenic variables

The relative importance of environmental, landscape, and anthropogenic variables varied across different aspects of fish community structure (H2). Anthropogenic disturbance, represented by the Human Footprint Index (HFI), was the most influential variable, affecting multiple fish community descriptors (Table 1; Figs. 4 and 5). Fish abundance was positively influenced by HFI (VI, variable importance = 0.64) and negatively associated with beach length (VI = 0.41; Fig. 5). Species richness was also strongly positively influenced by HFI (VI = 0.99), while salinity showed a small positive effect (VI = 0.01) on richness, with increases at intermediate levels. Taxonomic distinctness was negatively influenced by depth (VI = 0.3), which was the only predictor consistently included in models for this community descriptor (Fig. 5). Other predictors had very weak and inconsistent effects on taxonomic distinctness, with the null model providing a comparatively better fit than most evaluated variables (Table 1; Fig. 5). This descriptor exhibited low R^2 and wAICc values, indicating limited explanatory power from the predictors used. Planktivorous were positively influenced by HFI (VI = 0.98) and substrate roughness (VI = 0.98), while opportunistic species were negatively associated with beach length (VI = 0.61) and showed

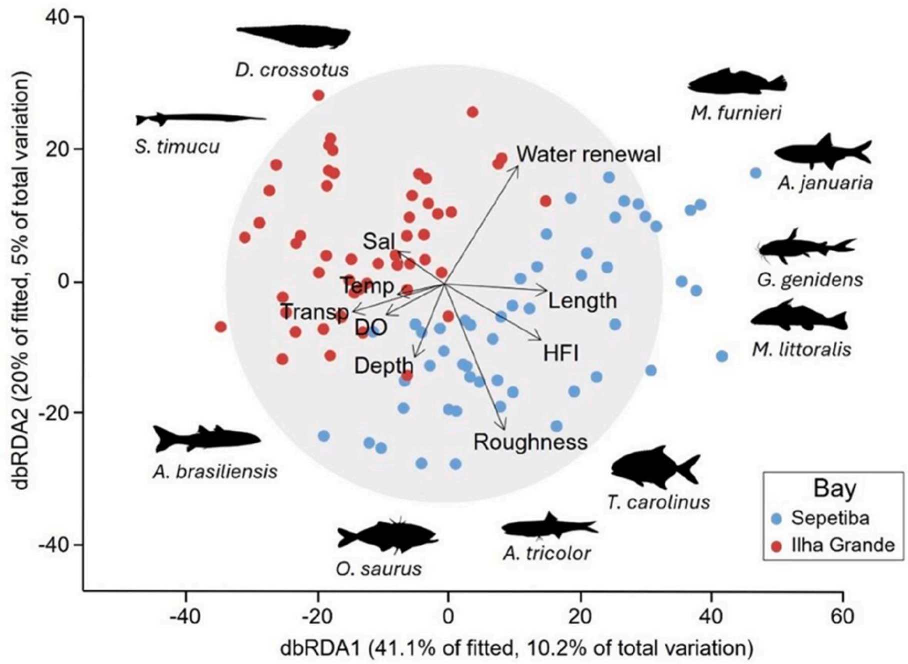

Fig. 3. Diagram of the ordination of the first two axes of the dbRDA analysis showing the fish community and environmental variables in Sepetíba and Ilha Grande bays. Sal, salinity; Temp, temperature; Transp, transparency; DO, dissolved oxygen.

Table 1
Best generalized additive mixed models (GAMMs) to predict fish abundance, species richness, taxonomic distinction, and abundance of selected trophic guilds in the bays of Sepetiba and Ilha Grande. Akaike information criterion corrected for small sample sizes (<2.0 ΔAICc); wAICc, AICc weight; edf: estimated degrees of freedom. The best models (<Δ AICc) are marked in bold.

Variable	Formula	R^2	edf	Δ AICc	wAICc
Abundance	**HFI + Length**	0.36	15.2	0.00	0.29
Richness	**HFI + Salinity**	0.36	11.2	0.00	0.43
Richness	**HFI + Length**	0.21	6.3	0.00	0.23
Taxonomic Dist.	**Depth**	0.28	10.4	0.00	0.09
Taxonomic Dist.	null	0.34	10.4	0.24	0.08
Taxonomic Dist.	Length + Roughness	0.24	9.7	0.54	0.07
Taxonomic Dist.	HFI + Water.ren.	0.33	13.0	1.09	0.05
Taxonomic Dist.	Water.renewal	0.35	12.8	1.11	0.05
Taxonomic Dist.	Depth + HFI	0.28	11.3	1.54	0.04
Taxonomic Dist.	Width	0.26	9.7	1.57	0.04
Taxonomic Dist.	Roughness + Width	0.22	8.8	1.75	0.04
Taxonomic Dist.	Depth + Length	0.29	11.7	1.79	0.04
Taxonomic Dist.	HFI	0.34	11.6	1.93	0.03
Taxonomic Dist.	Length	0.34	11.6	1.94	0.03
Taxonomic Dist.	Depth + Transp	0.26	10.6	1.23	0.05
Planktivore	**HFI + Roughness**	0.31	6.5	0.00	0.98
Opportunistic	**HFI + Length**	0.31	7.3	0.00	0.61
Opportunistic	HFI + Water.renewal	0.33	8.0	1.33	0.31
Benthivore	**Depth + Roughness**	0.08	4.1	0.00	0.38
Benthivore	Depth	0.07	3.0	1.93	0.14

increases at intermediate levels of disturbance (VI = 0.97). Benthivorous species were negatively associated with depth (VI = 0.86) and substrate roughness (VI = 0.47) (Table 1; Figs. 4 and 5).

4. Discussion

In this study, we compared the fish assemblages and three of their descriptors, along with trophic group composition, between two large tropical bays in the southern region of Rio de Janeiro. The comparison also encompassed different beach types within each system (continental and insular) across two seasons. The first hypothesis (H1) was that the distinct environmental configurations of each habitat, shaped by factors such as bay morphology, degree of oceanic exposure, freshwater input, and anthropogenic pressures, would differentially influence fish assemblage structure, biodiversity descriptors, and trophic organization. This hypothesis is grounded in the understanding that environmental heterogeneity plays a central role in structuring fish communities, particularly in dynamic coastal systems. Variations in habitats are known to affect fish occurrence, abundance, and functional roles, thereby leading to spatial differences in community metrics across regions and habitat types.

We also aimed to advance the understanding of species–environment relationships by identifying and quantifying the influence of environmental predictors on fish composition and assemblage descriptors (abundance, richness, taxonomic distinctness, and trophic groups). In this context, the second hypothesis (H2) proposed that environmental variables exert distinct and measurable effects on these descriptors. This is based on the premise that fish communities respond to environmental gradients in a multidimensional way, with some descriptors (e.g., richness or taxonomic distinctness) being more sensitive to specific factors such as physical and chemical variables, while others (e.g., trophic group composition) may be more closely associated with productivity, or structural complexity. Understanding these relationships is key to identifying the main drivers of spatial and temporal variability in fish assemblages in tropical coastal systems.

4.1. Fish community

Baía de Sepetiba (BS) and Baía da Ilha Grande (BIG) differ markedly in their environmental and anthropogenic conditions. BS is more enclosed, receives greater continental drainage, and is heavily influenced by urban and industrial activities (Castelo et al., 2021; Copeland et al., 2003; Fonseca et al., 2013). Over the past 40 years, BS has undergone increased deposition of fine sediments, largely due to urban expansion and industrialization (Pereira et al., 2024), resulting in higher nutrient and pollutant inputs. This is reflected in elevated concentrations of suspended particulate matter (SPM), chlorophyll-a and high pH levels, classifying BS as mesotrophic according to the TRIX index (Oliveira, 2022). In contrast, BIG is more open, better connected to the ocean, and experiences lower anthropogenic pressure (Miranda, 2024;

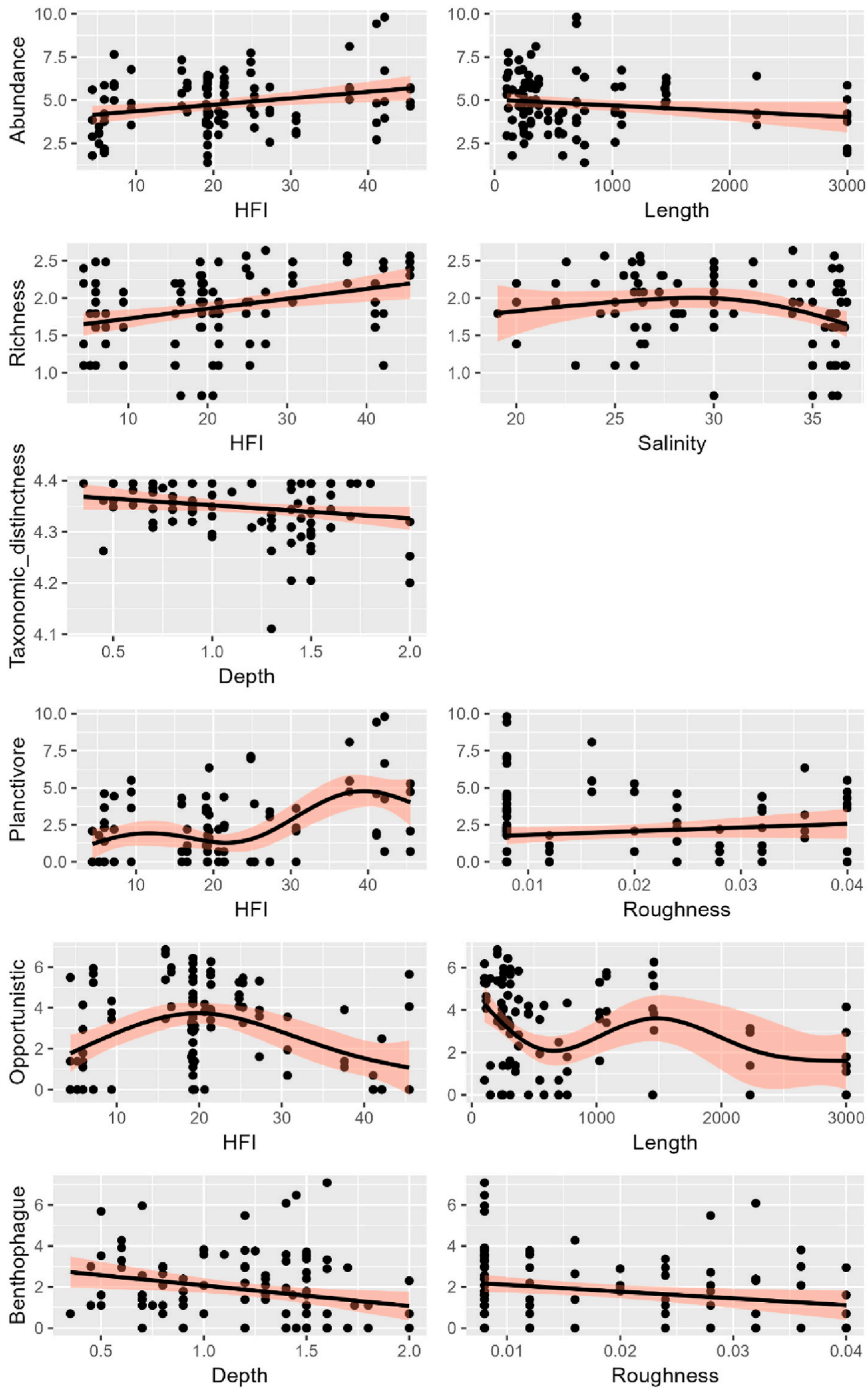

Fig. 4. Residual plots of the best generalized additive mixed models (GAMM) for structural and functional descriptors of fish assemblages in Sepetíba and Ilha Grande bays.

Oliveira, 2022; Pereira et al., 2024). It is oligotrophic, with lower nutrient levels, SPM, chlorophyll-a, and dissolved oxygen (Miranda, 2024). These contrasting environmental and anthropogenic conditions shape the ecological dynamics and fish assemblages observed in each bay. This study recorded a rich ichthyofauna comprising 69 species, dominated by Clupeiformes, particularly *Anchoa januaria* and *Anchoa lyolepis*, which play key ecological roles as prey in coastal food webs (Loebens et al., 2025; Nascimento et al., 2021). Significant differences in community descriptors were observed across bays, beach types (continental vs. insular), and seasons, supporting H1 that environmental and anthropogenic conditions differentially influence fish assemblages.

The dbRDA reveals that fish assemblages are strongly structured by contrasting environmental and anthropogenic conditions between the two bays. As transition systems, estuaries connect marine and freshwater ecosystems, and persistent environmental fluctuations impose considerable physiological demands on the species that use these habitats (Elliott and Quintino, 2007). Fish communities in estuaries include estuarine resident species, as well as marine and freshwater species that

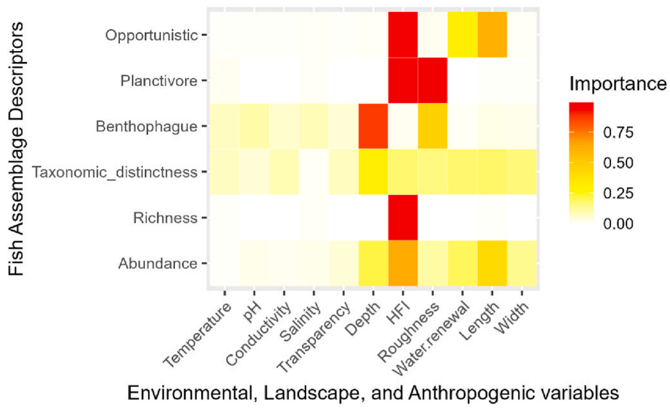

Fig. 5. Heat map showing the variable importance (VI) among the predictor variables included in the generalized additive mixed models analyses of complete subsets of fish assemblages.

enter estuaries as migrants or visitors (Elliott et al., 2007; Vasconcelos et al., 2015; Whitfield, 2020b). While *Atherinella brasiliensis* was abundant in both, Ilha Grande, characterized by higher salinity, temperature, transparency, and lower human impact (Teixeira-Neves et al., 2016), supports marine and disturbance-sensitive species such as *Dactylopterus crossotus*, *Sphyraena timucu*, *Anchoviella brasiliensis*, *Eucinostomus argenteus*, and *Strongylura timucu*. In contrast, Sepetiba Bay, which is more urbanized and characterized by higher water renewal, greater shoreline roughness, and a higher Human Footprint Index, favors tolerant, opportunistic estuarine species such as *Menticirrhus littoralis*, *Genidens genidens*, *Anchoa januaria*, and *Trachinotus carolinus*. The dominance of anchovies (*Anchoa spp.*), carangids (*Oligoplites saurus*, *T. carolinus*), and stress-tolerant species such as *Umbrina coroides* and *Micropogonias furnieri* in Sepetiba further reflects nutrient enrichment and habitat alteration (Araújo et al., 2016; Gomes-Gonçalves and Araújo, 2023). Collectively, these patterns highlight how geomorphological and environmental gradients, coupled with human pressures, shape tropical coastal fish communities, reinforcing our initial hypothesis (H1) and underscoring the need for context-specific conservation strategies (Villéger et al., 2010; Whitfield, 2021). This interpretation is strengthened by the indicator species analysis, which consistently associates marine taxa with Ilha Grande Bay and tolerant estuarine taxa with Sepetiba. Providing robust guidance for bay-specific management and conservation.

The structure of the fish community also varied across beach types (continental vs. insular), with a significant interaction between bay and beach type, underscoring the complex influence of local environmental conditions. Beaches on islands far from the continental margin likely experience different conditions, resulting in fish assemblages that differ from those on the mainland coast (Pereira et al., 2015). Thus, the position of sandy beaches in coastal systems can play an important role in shaping fish communities, given the environmental, ecological, and connectivity differences between these habitats. This pattern is supported by the indicator species analysis, which identified six species significantly associated with continental beaches (*A. januaria, A. lyolepis, M. furnieri, S. testudineus, Mugil liza,* and *Achirus lineatus*), while no species were indicators of insular beaches (MPA, $p > 0.05$). Together, these findings highlight the ecological distinctiveness of continental beaches and reinforce the importance of considering beach type in conservation and management strategies.

The structure of the fish assemblage also varied across seasons (winter vs. summer). This result is corroborated by the indicator species analysis: *Oligoplites saliens*, *Oligoplites saurus*, and *Trachinotus falcatus* were associated with the summer, while *M. liza*, *D. crossotus*, *M. furnieri*, *Menticirrhus littoralis*, and *Sardinella brasiliensis* were associated with the winter. Thus, seasonal changes driven by different levels of precipitation shaped the dynamics of fish assemblages between winter and summer periods. This effect is primarily attributed to the strong correlation between precipitation and several abiotic parameters, particularly salinity, which significantly influences coastal assemblages and can restrict the presence or entry of various species (Moustaka et al., 2025; Silva et al., 2021b; Souto-Vieira et al., 2023). These findings underscore the central role of seasonal variability in structuring coastal fish communities and reinforce the importance of incorporating climatic drivers into ecological assessments and management.

4.2. *Community descriptors*

Fish abundance and richness were higher on continental beaches, not differing between bays and seasons. This pattern likely reflects differences in habitat connectivity and nutrient input. Continental beaches are generally more connected to estuarine and riverine systems, enhancing nutrient availability and ecological linkage, which supports greater fish diversity. In contrast, insular beaches, being more isolated and dependent on oceanic processes, may limit resource input and dispersal, although they can support specialized or endemic species adapted to stable, oligotrophic conditions (Mattos et al., 2023). These results highlight how habitat position within coastal systems shapes fish diversity and emphasize the need to account for continental–insular contrasts in biodiversity assessments and management.

These findings differ from those of Pereira et al. (2015), who reported higher richness and abundance on an insular beach in Baía de Sepetiba, likely due to lower anthropogenic pressure and its function as a nursery area. In this study, higher values observed on continental beaches, despite greater human impact, suggest that local environmental features such as nutrient enrichment and habitat heterogeneity may offset stressors and promote conditions under which generalist and opportunistic fish species thrive due to their adaptability and ability to exploit altered environments (Elliott et al., 2007; Teichert et al., 2018; Whitfield, 2021). The patterns can be interpreted within the framework of the Intermediate Disturbance Hypothesis, which predicts increased species richness and abundance under intermediate levels of disturbance due to the successful establishment of stress-tolerant generalist and opportunistic species (Connell, 1978). This contrast underscores the context-dependent nature of ecological interactions influencing fish assemblages and highlights the need for site-specific management strategies that account for both habitat type and environmental conditions.

Taxonomic distinctness did not differ significantly between bay or beach types, although slight seasonal variation was observed, with higher values in the winter. Taxonomic distinctness measures the relatedness of species in a community rather than species number, defined as the path length along the taxonomic hierarchy for each species pair (Clarke and Warwick, 1998, 1999; Leonard et al., 2006). Results indicate that winter exhibits greater taxonomic diversity in the ichthyofauna than summer, likely due to the influence of salinity and temperature on the structure and distribution of fish assemblages (Andrade-Tubino et al., 2008; Araújo et al., 2018). During the winter, lower rainfall reduces the salinity gradient, allowing greater permanence or entry of marine species, resulting in more phylogenetically distinct assemblages. Three species, represented by two genera, were associated with summer, whereas five species, each representing a different genus, were associated with winter. Therefore, communities in which species are distributed across many genera exhibit higher taxonomic and phylogenetic diversity, consistent with the present findings.

4.3. *Trophic groups*

Continental beaches were more favorable to planktivores and, to a lesser extent, benthic feeders, with these patterns driven primarily by spatial differences between bays and beach types rather than by seasonal variation. The higher availability of organic matter and nutrients derived from riverine and terrestrial runoff likely enhances phytoplankton and zooplankton production, while also supporting a richer benthic community, thereby increasing food availability for these trophic guilds (Elliott et al., 2007; Whitfield, 2020b). This resource base helps explain the greater abundance of planktivorous and benthivorous species in continental beaches.

Although Andrade-Tubino et al. (2020) reported benthic feeders as the dominant trophic group on continental beaches, the present results indicate stronger contribution from planktivorous and benthivorous species, suggesting regional or system-specific responses to environmental gradients. Furthermore, the strong association between planktivores and the Human Footprint Index (HFI) indicates that anthropogenic nutrient inputs play an important role in structuring this guild. Overall, trophic guilds patterns varied mainly between bays and beach types, with seasonal effects acting as a secondary modulating factor. These results highlight the dominant role of spatial heterogeneity, environmental gradients, and human pressure in shaping fish community structure, with important implications for ecosystem-based management.

4.4. Relationships between assemblage descriptors and environmental, landscape, and anthropogenic variables

This study examined how environmental, landscape, and anthropogenic variables shape fish community descriptors across two large coastal bays in Rio de Janeiro. We found that the relative importance of these variables varied across habitats and descriptors, supporting hypothesis H2. The Human Footprint Index (HFI) was the strongest predictor of both fish abundance and species richness, particularly in the Sepetiba Bay. This positive correlation may reflect nutrient enrichment from domestic and industrial sewage, which increases organic loads, stimulates primary productivity and favors tolerant species. Although anthropogenic activities often cause environmental degradation and biodiversity loss (Barletta and Lima, 2019; Brandão et al., 2025; Fiori et al., 2022), in some cases they can create conditions that enhance fish richness and abundance. Nutrients inputs (e.g., nitrogen and phosphorus) may boost primary productivity supporting fish population such as and the planktivorous guild, which showed a direct association with HFI (Miró et al., 2020; Nodo et al., 2023). Nonetheless, excessive eutrophication threatens trophic structures and oxygen availability. In this context, tidal exchange in these bays helps disperse nutrient loads and maintain ecological balance (Defeo et al., 2009; Selleslagh et al., 2013). However, long-term urbanization and sedimentation, particularly in the Sepetiba Bay, have intensified anthropogenic stressors, underscoring the need for adaptive management.

The presence of ports, marinas, piers, and other coastal structures can create microhabitats that some fish species use for shelter and feeding. Opportunistic fish showed higher abundances at intermediate HFI values, where disturbances are sufficient to suppress sensitive species but still allow adaptable and resilient ones to thrive. In such environments, food resources remain available in adequate quantities, and nutrient inputs can enhance primary productivity, benefitting planktivorous fish closely associated with HFI. Likewise, artificial structures increase habitat heterogeneity, supporting species such as *Atherinella brasiliensis*. These findings are consistent with the intermediate disturbance hypothesis, which predicts that resilient species dominate under moderate impact levels (Moi et al., 2020; Nodo et al., 2023).

Among the environmental variables, salinity was a key variable influencing fish richness. Richness peaked around salinity values of 30, which provide stable and productive conditions for marine species. In Baía de Ilha Grande, surface salinity ranged from 27 to 37, while in Baía de Sepetiba it ranged from 22.9 to 34.3 (Oliveira, 2022). These patterns reflect river inflows in specific areas and strong marine influence, which maintains salinity near oceanic levels across much of both bays. Semi-enclosed estuarine systems typically display salinity gradients decreasing from the ocean toward inner areas, driven mainly by continental inputs. Salinity is a key structuring factor of fish assemblages in tropical coastal bays and can serve as a proxy for the alternating influence of estuarine and oceanic waters (Franco and Santos, 2018). Different salinity ranges shape communities according to osmotic regulation strategies, separating freshwater and marine species (Barletta et al., 2008; Getz and Eckert, 2023). Franco et al. (2018) also showed that a euhaline lagoon, with salinity close to marine conditions, supported higher fish richness than hyperhaline and mesohaline lagoons. In this study, the high richness observed is likely related to the predominance of salinities close to marine conditions in both bays.

Beach morphology also shaped community structure. Depth was inversely associated with taxonomic distinctness, while benthic feeders were negatively related to both depth and substrate roughness. These patterns reflect independent responses of different aspects of the fish community to environmental gradient. Reduced light penetration, lower nutrient availability, and diminished benthic prey abundance occur in deeper waters (Borland et al., 2017; Rubin et al., 2024). The lower density and diversity of benthic invertebrates, the main food source for benthic fish, further limit their presence in deeper environments (Howe and Simenstad, 2011; Rubin et al., 2024). Specifically, lower taxonomic distinctness in deeper areas may result from a reduction in habitat heterogeneity and decreased environmental complexity, which can limit the presence of rare or specialized species (Clarke and Warwick, 2001). Similarly, the lower abundance of benthic feeders in deeper and smoother habitats likely reflects reduced light penetration, lower nutrient availability, and diminished benthic prey density, which constrain their feeding opportunities. Together, these findings highlight the ecological importance of shallow, structurally complex, and nutrient-rich zones for maintaining both functional diversity (through benthivorous guilds) and evolutionary diversity (through taxonomic distinctness), while clarifying that the two response variables are not causally linked.

Beach length showed a more complex relationship with fish assemblage descriptors. Although larger beaches can provide greater microhabitat diversity, we observed reduced abundance, particularly of opportunistic fish. Beach morphology is in dynamic equilibrium with wave action, sediment size, tidal variation, river inputs, and the presence of rocky outcrops (Castelle and Masselink, 2023). These factors strongly influence beach ecology, including habitat use by fish. Along the studied coast, promontories and rocky escarpments—formed by the Serra do Mar reaching the shoreline—shape a rugged coastline (Muehe and Valentini, 1998; Silva et al., 2019). Fish assemblages near these rocky promontories tend to be highly abundant and diverse (Mosman et al., 2024). Thus, the lower richness observed on longer beaches may reflect the tendency of juvenile fish to concentrate near rocky edges, reducing diversity across the remaining sandy habitat. Higher roughness was positively associated with planktivores but negatively with benthic fish, reflecting their contrasting feeding strategies and sensitivities to turbulence. Increased roughness can concentrate plankton, creating favorable feeding conditions for planktivores, whereas it may hinder benthic fish by reducing access to prey and lowering foraging efficiency. Fish distribution in marine landscapes is strongly shaped by substrate composition and habitat complexity. Estuarine seascapes, in particular, provide diverse terrains that serve as critical foraging, refuge, and spawning habitats (Bradley et al., 2017; Henderson et al., 2019). Borland et al. (2022) further showed that fish abundance and diversity were generally higher in areas of lower roughness. Together, these findings highlight the dual role of beach roughness: enhancing conditions for planktivores while constraining benthic feeders.

5. Conclusions

This study highlights the critical role of environmental variables and landscape configuration in shaping fish communities in two large tropical bays on the Brazilian coast. Community structure varied between bays, beach types, and seasons, driven by distinct sets of interacting environmental factors. These results support hypothesis H1 and underscore the need for a multidimensional approach to assess biodiversity patterns across coastal habitats. Among the physical, chemical, and landscape drivers, the Human Footprint Index (HFI), salinity, beach depth, and width emerged as key predictors of fish abundance, richness, and trophic structure. These findings also confirm that anthropogenic impacts, interacting with local conditions, influence fish assemblages in complex and spatially variable ways, supporting hypothesis H2. By advancing understanding of fish–environment relationships in tropical coastal systems, this study provides a basis for biodiversity management under accelerating environmental change.

CRediT authorship contribution statement

Wagner Uehara: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Gustavo Henrique Soares Guedes:** Writing – review & editing, Investigation, Formal analysis. **Marcia Cristina Costa de Azevedo:** Writing – review & editing, Visualization, Supervision, Investigation, Conceptualization. **Victória de Jesus Souza:** Writing – original draft, Visualization, Formal analysis. **Francisco Gerson Araújo:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109683.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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