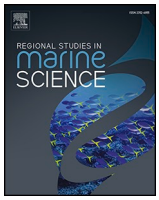
Regional Studies in Marine Science 93 (2026) 104706

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma



Spatial and seasonal drivers of fish fauna in estuaries from the Brazilian semiarid coast: Taxonomic and functional perspectives

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ARTICLE INFO

Keywords:
Community ecology
Estuarine fish
Estuarine guild
Northeastern Brazil
Trophic guild

ABSTRACT

Estuaries are spatiotemporally dynamic environments that structure biological communities in a complex manner. We investigated how the taxonomic and functional structures of the fish fauna in estuaries along the Brazilian semiarid coast (BSC) vary between estuarine zones and seasons. Standardized collection methods sampled fish in five estuaries of the BSC. Each species was categorized by trophic guild and estuarine use guild, and fish–estuary association score (FEAS). Non-metric multidimensional scaling (nMDS) analyzed species and trophic guild compositions according to zone and season. PERMANOVA tested differences among groups. Similarity percentage (SIMPER) analysis and the relative preference index (RPi) identified the species and trophic guilds that contributed most to group distinction (lower zone versus upper zone, and dry season versus rainy season). In total, 113 fish species were recorded. The most representative estuarine use guilds were marine migrants and estuarine. Among the nine trophic guilds, the most representative were detritivores, omnivores, opportunists, macrocarnivores, and zoobenthivores. Taxonomic (species composition) and functional (trophic guilds) approaches revealed both spatial and temporal differences. The functional approach using FEAS detected spatial variation of small magnitude and indicated temporal homogeneity. Thus, there is substantial taxonomic and functional heterogeneity considering approaches from species, estuarine use guilds, and trophic guilds.

1. Introduction

Estuaries are dynamic and productive ecosystems that serve as key spawning and nursery grounds for numerous fish species (Beck et al., 2001; Sales et al., 2018). Their ecological importance largely stems from their connectivity with adjacent habitats such as mangroves and seagrass meadows, which provide shelter, feeding opportunities, and enhanced survival for juvenile and adult fish (Barletta et al., 2005; Atwood et al., 2012; zu Ermgassen et al., 2025). Estuaries, as transitional systems between freshwater and marine environments, sustain complex ecological gradients driven by fluvial and tidal dynamics, which shape the spatial and temporal organization of fish assemblages (Whitfield,

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https://doi.org/10.1016/j.rsma.2025.104706
Received 22 August 2025; Received in revised form 18 October 2025; Accepted 9 December 2025
Available online 16 December 2025

1999; Blaber, 2000; Pichler et al., 2015). Thiel et al. (1995) reported that salinity is the best predictor of species richness in estuaries, whereas temperature is a better predictor of species abundance patterns. However, temperature is rarely a structuring factor in tropical areas, as it remains relatively stable throughout the year (Blaber, 2000; Araújo et al., 2002).

Estuarine ecosystems are often subdivided into longitudinal zones based on geomorphological characteristics and the influence of marine and freshwater inputs (Barletta et al., 2005; Day Jr. et al., 2013; Barletta et al., 2017). These zones experience highly dynamic environmental conditions, particularly regarding salinity—a key variable that structures fish communities in estuarine systems (Martino and Able, 2003; Selleslagh and Amara, 2008). The ecological requirements and physiological tolerance of species determine the zoning patterns observed within fish assemblages (Whitfield, 1999; Jaureguizar et al., 2003). While some fish species exhibit broad salinity tolerance and occur across all zones, others show clear spatial preferences (Neves et al., 2011). Seasonal hydrological changes also play a fundamental role in shaping the structure of estuarine fish communities (Akin et al., 2005; Lewis and Cook, 2023). Taxonomic patterns of estuarine fish assemblages largely reflect the presence of freshwater species capable of colonizing these environments during the rainy season, when salinity decreases, as well as by marine species that enter estuaries during the dry season, when salinity increases, or during specific ontogenetic stages, particularly the juvenile stage (Beck et al., 2001; Elliott et al., 2007; Sosa-López et al., 2007). Such spatiotemporal dynamics underlie the remarkable biodiversity of estuaries (Whitfield, 1999; Jaureguizar et al., 2003).

In addition to taxonomic approaches, the use of ecological guilds—particularly trophic and estuarine-use guilds—has gained prominence as a complementary tool for describing community

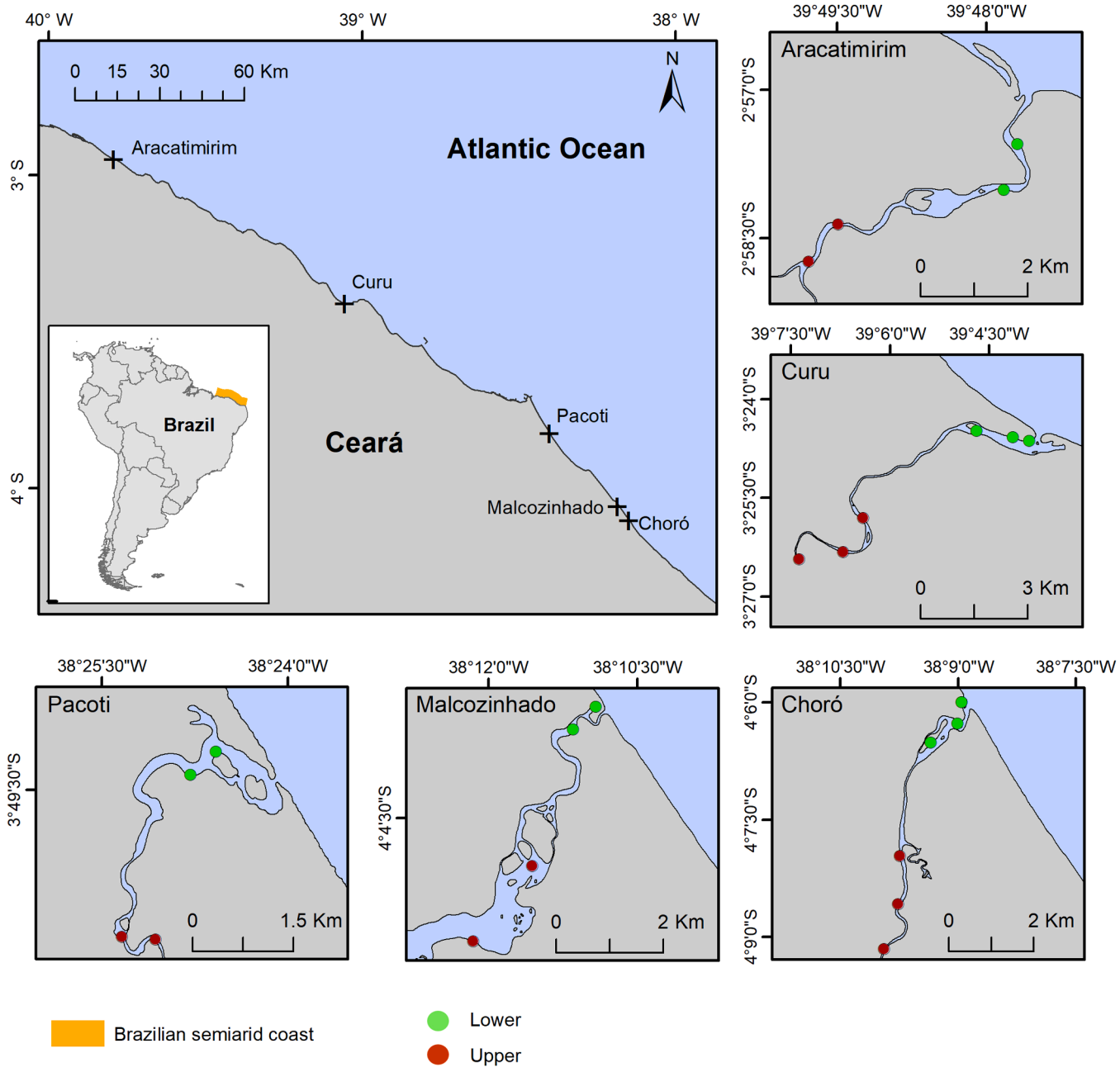

Fig. 1. Fish fauna sampling points in the lower and upper zones of the Aracatimirim, Choró, Curu, Malcozinhado, and Pacoti Estuaries, on the Brazilian semiarid coast.

structure and function (Harrison and Whitfield, 2008; Nicolas et al., 2010; Harrison and Whitfield, 2025). The combination of traditional taxonomy with a functional approach provides a more holistic understanding of the structure of biological communities (Franco et al., 2008). Functional classifications facilitate a more integrative understanding of ecological roles, enabling the identification of patterns in resource use and habitat association that may not be evident from species composition alone (Blaber, 2000; Blondel, 2003; Franco et al., 2008). Furthermore, functional metrics are increasingly recognized as valuable indicators of ecosystem health and resilience, supporting monitoring and management efforts in estuarine environments (Mathieson et al., 2000; Elliott et al., 2007). Despite the growing interest in functional approaches, few studies have evaluated how both taxonomic and functional compositions of fish assemblages vary across longitudinal estuarine zones and seasonal cycles, particularly along semiarid tropical coasts, where environmental fluctuations and estuarine productivity are highly variable (Tweedley et al., 2019; Soares et al., 2021).

Thus, we hypothesize that fish assemblages exhibit distinct taxonomic and functional structures depending on the estuarine zone and season in estuaries along the Brazilian semiarid coast (BSC). This study aimed to describe the spatial and seasonal variation of fish assemblages in estuaries along the BSC, with a focus on species composition, trophic guilds, and estuarine-use guilds (using the fish–estuary association scoring approach; Harrison and Whitfield, 2021). We seek to enhance our understanding of estuarine fish diversity and the ecological processes governing community dynamics in tropical estuarine ecosystems along the BSC.

2. Material and methods

2.1. Study area

The estuaries of the Aracatimirim, Choró, Curu, Malcozinhado, and Pacoti are part of the BSC (Fig. 1), a macro-geomorphological region on the northeast coast of Brazil between Ponta dos Mangues Secos in Maranhão State (western limit) and Cabo do Calcanhar in Rio Grande do Norte State (eastern limit) (Soares et al., 2021). BSC has estuaries prone to inverted hydrological regimes, characterized by limited freshwater contributions from continental drainage during part of the year (dry season, from July to December), which can result in higher salinity levels compared to the adjacent ocean (Potter et al., 2010; Largier, 2023). Additionally, river flows are, in part, regulated by reservoirs along their watersheds (Molisani et al., 2006). The region has a tropical climate with a dry summer (type 'As'), characterized by an average annual precipitation range of 1000–1300 mm, and moderate to low water deficiency. However, most of the watershed areas of the estuaries are in semiarid climate zones (type "BSh"), characterized by high water deficits (approximately 800 mm annually) (Alvares et al., 2014). The Intertropical Convergence Zone is responsible for establishing the rainy season in the region from February to May (Zanella, 2005). The BSC experiences semi-diurnal tides, ranging from 0.0 to 3.0 m, which are mesotidal according to McLusky and Elliott (2004).

2.2. Sampling

Fish sampling was conducted in each estuary (Aracatimirim: March, 2019; May, 2019; October, 2019; December, 2019; Choró and Curu: November, 2021; February, 2022; May, 2022; September, 2022; Malcozinhado: March, 2019; May, 2019; October, 2019; December, 2019; Pacoti: December, 2014; May, 2015; June, 2015; September, 2015), with two collections conducted during the dry season and two during the rainy season. Sampling at Choró and Curu included six points (three in the lower zone and three in the upper zone), whereas the remaining estuaries were sampled at four points (two per zone), covering the estuaries longitudinally (Fig. 1). The lower zone consisted of estuarine stretches with salinity values similar to the sea (35−37) more frequently over time; predominantly sandy and silty substrates; and generally wider estuarine widths. The upper zone, still under tidal influence, was characterized by freshwater during the rainy season; a predominance of silty and clayey substrates; and narrower channel widths.

Fish captures were standardized using a beach seine net (25 m × 2 m, mesh size 12 mm) and a cast net (3.5 m, mesh size 25 mm). Seine net tows targeted coastal areas up to 1.5 m deep, while cast net sampling was conducted at depths ranging from 1.0 to 3.5 m. Each tow covered approximately 200 m^2 ($A = D \times L$, where A is the area, D is the distance from shore [10 m], and L is the effective net length [20 m]), and each cast of the net sampled a circular area of 10 m^2 (πr^2). The number of individuals per species was divided by the number of seine tows and cast net throws, yielding densities expressed in individuals per square meter. Data from both devices were then compiled into standardized abundance units (individuals/100 m^2). All sampling occurred during neap tides, in daylight hours between the midpoint of ebb and flood tides. Specimens were anesthetized with clove oil and fixed in 10 % formalin, and after 48 h, preserved in 70 % alcohol. Collections were authorized by ICMBio/SISBio (Licenses #43014, 64269, 87874). Concurrently with fish sampling, salinity was measured at the water surface using a refractometer and classified as hyperhaline (≥40), euhaline (30–39), polyhaline (18–29), mesohaline (5–17), oligohaline (0.5–4), and limnetic (<0.5) (McLusky and Elliott, 2004).

2.3. Data compilation

Fish species were classified according to their use of the estuarine environment as marine stragglers (MS), marine migrants (MM), estuarine (ES), diadromous (DI), freshwater migrants (FM), and freshwater stragglers (FS) (Potter et al., 2015; Harrison and Whitfield, 2021). Species were assigned to trophic groups as detritivores (DT), herbivores (HV), planktivores (PL), insectivores (IN), zoobenthivores (ZB), omnivores (OV), opportunists (OP), macrocarnivores (MV), and piscivores (PV) (adapted from Elliott et al., 2007). Detritivores fish feed on detritus and microphytobenthos; herbivores consume macroalgae/macrophytes; planktivores predominantly consume phytoplankton and zooplankton; insectivores primarily feed on aquatic and terrestrial insects; zoobenthivores predominantly consume marine or estuarine benthic invertebrates; omnivores consume both plant material and benthic invertebrates or resources from different trophic levels, even if they do not include primary producers; macrocarnivores consume benthic macrofauna and fish in similar proportions; piscivores consume fish but may also consume other prey to a lesser extent; and opportunists have a broad diet that does not fit into the other categories (Elliott et al., 2007). Species were classified into these categories based on estuarine fish trophic literature and body size, as species may exhibit changes in trophic resource use depending on their ontogenetic stage.

2.4. Data analysis

Abundance data (density in individuals/100 m^2) were converted into dissimilarity matrices with the Bray-Curtis index for non-metric multidimensional scaling (nMDS) analyses, to examine spatial and seasonal variations in species and trophic guild composition. Multivariate Analysis of Variance Based on Distances and Permutations (PERMANOVA) determined whether the assemblage structure differs between estuarine zones (lower vs upper) and over time (dry vs rainy season). Finally, the Relative Preference index (RPi) (for species and trophic guilds) and analysis of similarity percentage (SIMPER) (for trophic guilds) identified the key species and trophic groups responsible for differentiating local assemblages across space and time.

Given SIMPER's limitations in detecting patterns in communities with a high proportion of rare species, we calculated an RPi for each species across estuarine zones and seasons. The index was defined as $(A_1 - A_2)/(A_1 + A_2)$, where A_1 and A_2 represent the species' abundances in the lower and upper zones, or during the dry and rainy seasons,

respectively. Values close to +1 indicate a strong preference for the lower zone (or dry season), while values close to −1 indicate a preference for the upper zone (or rainy season). We considered a species to have a preference when the index was $\geq |0.40|$, which represents at least 2.33 times higher abundance in one zone or season. RPi was also calculated to determine the preferences of trophic guilds across zones and seasons.

Based on the classification of species into estuarine habitat-use guilds (MS, MM, ES, DI, FM, FS), the fish estuary-association score (FEAS) database, provided by Harrison and Whitfield (2021), was used to compare estuarine zones and seasons. At each sampling point within the estuaries, an overall fish estuary-association score (S-FEAS) was computed. In this procedure, each species was assigned a FEAS value (Harrison and Whitfield, 2021), and a general index for each sampled point over time was calculated (S-FEAS) with abundance weighting. That is, the S-FEAS at each sampling point is the sum of all species' FEAS values multiplied by their respective relative abundances. Fish assemblages dominated by freshwater species will have S-FEAS values tending to 1.0, while assemblages dominated by typical marine species will have S-FEAS values tending to 5.0. Accordingly, we have 16 S-FEAS values for the Aracatimirim, Malcozinhado, and Pacoti Estuaries (four collections x four sampled points) and 24 values for the Choró and Curu Estuaries (four collections x six sampled points). S-FEAS values for sampled points within the same estuarine zone were compiled to compare means in space (Aracatimirim, Malcozinhado, and Pacoti: eight values in the lower zone and eight values in the upper zone; Choró and Curu: 12 ×12). The same was done for S-FEAS values for each season (Aracatimirim, Malcozinhado, and Pacoti: eight values in the dry season and eight in the rainy season; Choró and Curu: 12 ×12). Sample S-FEAS values were compared through a permutation *t*-test based on 1000 iterations. Each sampled point of the ichthyofauna was also associated with a salinity value and an S-FEAS value. ANOVA was used to compare mean S-FEAS values of each assemblage across salinity groups: hyperhaline, euhaline, polyhaline, mesohaline, oligohaline, and limnetic (McLusky and Elliott, 2004). All analyses were performed using R software (R Core Team, 2025).

3. Results

3.1. Characterization of the ichthyofauna

In total, 113 fish species were collected, belonging to 50 families and 23 orders (Table A.1). Marine migrant species were the most numerous and had the highest abundance (61 species; 64.8 % of the total abundance), followed by the estuarine guild (18 species; 26.7 % of the total abundance) (Table A.1; Fig. A.1). Freshwater migrant species comprised six species (4.0 % total abundance), marine stragglers comprised 16 species (3.2 % total abundance), diadromous species comprised only two species (1.0 % total abundance), and freshwater stragglers comprised ten species (0.3 % total abundance) (Table A.1; Fig. A.1). Most of the species were macrocarnivores (43 species; 14.3 % total abundance), yet the most abundant trophic guild was detritivore (22.6 % total abundance, nine species), followed by omnivores with 20.1 % of the total abundance (21 species), and opportunists with 18.6 % of the total abundance even though they comprised only two species (Table A.1; Fig. A.1); zoobenthivores with 12.3 % of the total abundance (23 species), planktivores 11.5 % (nine species), piscivores 0.5 % (three species), herbivores 0.1 % (two species), and insectivores 0.01 % of the total abundance (one species) (Table A.1; Fig. A.1). Twenty-one species were the most abundant, with at least 1 % relative abundance (Fig. A.2), of which the majority are marine migrants (15), followed by estuarine species (four) and freshwater migrants (two) (Fig. A.2). However, regarding trophic guilds, there is a greater numerical balance, with two to four species in each trophic guild, except herbivore, insectivore, and piscivore that do not comprise the ranking of the most abundant (Fig. A.2).

3.2. Species and trophic guild composition in space and time

In general, 84 species occurred in the lower zone with a mean abundance of 24.75 individuals/100 m^2, while 87 species occurred in the upper zone with a mean abundance of 28.56 individuals/100 m^2. The dry season showed a total richness of 92 species and a mean abundance of 29.99 individuals/100 m^2, whereas the rainy season presented 93 species and 19.41 individuals/100 m^2. The estuaries exhibited differences in species and trophic guild composition, as well as between estuarine zones and seasons (Table 1; Fig. 2; Fig. A.3). There was also a significant interaction between estuarine zone and season on the composition of species and trophic guilds (Table 1; Fig. A.4; Fig. A.5).

Some families were more abundant in the lower zone: Acanthuridae (*Acanthurus bahianus*), Atherinopsidae (*Atherinella brasiliensis*), Cynoglossidae (*Symphurus tessellatus*), Dactylopteridae (*Dactylopterus volitans*), Echeneidae (*Echeneis naucrates*), Haemulidae (four of five species: *Conodon nobilis*, *Haemulon atlanticus*, *Haemulon parra*, and *Haemulopsis corvinaeformis*), Hemiramphidae (*Hyporhamphus unifasciatus*), Labridae (*Sparisoma radians*), Lutjanidae (*Lutjanus* spp., three of four species), Ophichthidae (*Myrichthys ocellatus*), Parallichthyidae (*Paralichthys brasiliensis*), Pomacentridae (*Abudefduf saxatilis*), Scombridae (*Scomberomorus cavalla*), Scorpaenidae (*Scorpaena plumieri*), Sphyraenidae (*Sphyraena barracuda* and *S. guachancho*), Syngnathidae (*Hippocampus reidi* and *Syngnathus pelagicus*), Synodontidae (*Synodus foetens*), and Triglidae (*Prionotus punctatus*). Carangidae had a greater number of species more abundant in the lower zone (*Oligoplites saurus*, *Selene vomer*, *Trachinotus carolinus*, *T. falcatus*), whereas *O. palometa* was more abundant in the upper zone, and *Caranx latus* was evenly distributed spatially. Dorosomatidae was also more abundant in the lower zone with *Harengula clupeola*, *Lile piquitinga*, and *Opisthonema oglinum*, whereas *Rhinosardinia amazonica* was more abundant in the upper zone (Fig. 3a).

Other families were more abundant in the upper zone: Achiridae (*Achirus* spp. and *Trinectes paulistanus*), Batrachoididae (*Batrachoides surinamensis*), Dasyatidae (*Hypanus guttatus*), Eleotridae (*Dormitator maculatus* and *Eleotris pisonis*), Elopidae (*Elops smithi*), Megalopidae (*Megalops atlanticus*), Oxudercidae (*Awaous tajasica*, *Ctenogobius* spp., *Evorthodus lyricus*, *Gobioides broussonnetii*, *Gobionellus* spp.), and Polynemidae (*Polydactylus virginicus*); along with, as expected, typical continental freshwater species from the families Acestrorhamphidae (*Astyanax bimaculatus* and *Moenkhausia costae*), Anostomidae (*Leporinus piau*), Auchenipteridae (*Pseudauchenipterus nodosus*), Callichthyidae (*Megalechis thoracata*), Cichlidae (*Astronotus ocellatus* and *Oreochromis niloticus*), Erythrinidae (*Hoplias malabaricus*), Poeciliidae (*Poecilia reticulata* and *P. vivipara*), Prochilodontidae (*Prochilodus brevis*), Serrasalmidae (*Serrasalmus rhombeus*), Synbranchidae (*Synbranchus marmoratus*), and Triportheidae (*Triportheus signatus*) were also more abundant in the upper zone (Fig. 3a).

Some families exhibited a more widespread distribution along the estuaries (such as Ephippidae (*Chaetodipterus faber*) and Gobiidae (*Bathygobius soporator*)), or with their species evenly distributed

Table 1
Effect of the estuary, estuarine zone, and season on species and trophic guild composition (ind/100 m^2). df: degrees of freedom, SS: sum of squares, R^2: determination coefficient, *F*: F-value, *p*: p-value. In bold, significant p-values.

Species composition	df	SS	R^2	*F*	*p*
Estuary	4	4.522	0.145	4.33	**0.001**
Zone (lower vs upper)	1	2.365	0.076	9.06	**0.001**
Season (dry vs rainy)	1	0.670	0.021	2.56	**0.007**
Zone:Season interaction	1	0.557	0.018	2.13	**0.013**
Residual	88	22.976	0.739		
Trophic guild composition	df	SS	R^2	*F*	*p*
Estuary	4	3.768	0.204	7.20	**0.001**
Zone (lower vs upper)	1	2.243	0.121	17.16	**0.001**
Season (dry vs rainy)	1	0.623	0.033	4.77	**0.001**
Zone:Season interaction	1	0.317	0.017	2.43	**0.045**
Residual	88	11.502	0.623		

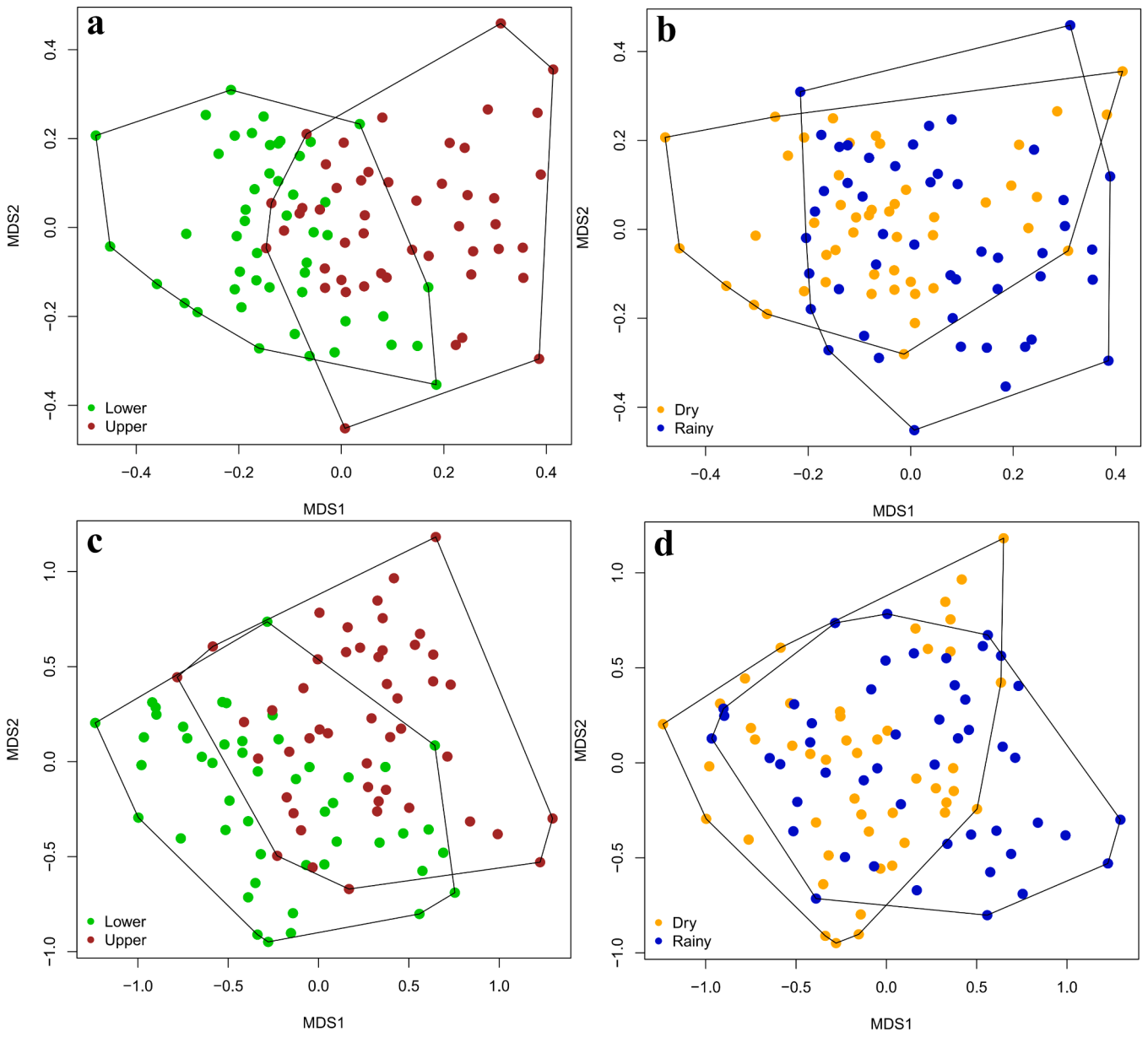

Fig. 2. nMDS comparing estuarine zones and seasons. Species composition (stress: 0.25): (a) lower zone vs upper zone, and (b) dry season vs rainy season. Trophic guild composition (stress: 0.22): (c) lower zone vs upper zone, and (d) dry season vs rainy season.

between the two estuarine zones. Gerreidae showed a distribution pattern in which *Eucinostomus* spp. were more abundant in the lower zone, while *Diapterus* spp. and *Eugerres brasilianus* favored the upper zone. A similar pattern was observed in Tetraodontidae, with *S. greeleyi* preferring the lower zone, *S. testudineus* exhibiting a more homogeneous distribution, and *Lagocephalus laevigatus* occurring predominantly in the upper zone. The Mugilidae exhibited spatial differentiation among species, with *M. rubrioculus* predominating in the lower zone, *M. liza* and *Mugil* sp. confined to the upper zone, and *M. curema* and *M. curvidens* displaying similar distributions across zones. In the Centropomidae family, *Centropomus undecimalis* was similarly distributed among the zones, while *C. parallelus* was more abundant in the upper zone. Within Cyclopsettidae, *Citharichthys spilopterus* and *Etropus crossotus* were similarly distributed across zones, whereas *Citharichthys arenaceus* was more abundant in the upper zone. Sciaenidae *Cynoscion leiarchus*, *Micropogonias furnieri*, *Stellifer naso*, and *S. punctatissimus* were more abundant in the upper zone; *Menticirrhus* spp. and *Larimus breviceps* were more abundant in the lower zone; and *Cynoscion acoupa* was similarly distributed. Engraulidae presented *Anchoviella brevirostris*, *A. lepidentostole*, *Anchoa januaria*, and *Cetengraulis edentulus* with more abundance in the upper zone; *Anchovia clupeoides* and *Anchoa hepsetus* with more abundance in the lower zone; and *Lycengraulis grossidens* was similarly distributed. Finally, in Ariidae, *Cathorops spixii* and *Sciades parkeri* exhibited a greater number of species with more abundance in the upper zone, whereas *Sciades herzbergii* and *S. proops* were similarly distributed among the zones (Fig. 3a).

Some families were more abundant during the dry season: Acanthuridae (*A. bahianus*), Anostomidae (*L. piau*), Cynoglossidae (*S. tessellatus*), Dactylopteridae (*D. volitans*), Dasyatidae (*H. guttatus*), Dorosomatidae (*H. clupeola*, *L. piquitinga*, *O. oglinum*, *R. amazonica*), Erythrinidae (*H. malabaricus*), Hemiramphidae (*H. unifasciatus*), Ophichthidae (*M. ocellatus*), Poeciliidae (*Poecilia* spp.), Pomacentridae (*A. saxatilis*), Scorpaenidae (*S. plumieri*), and Triglidae (*P. punctatus*). Engraulidae and Mugilidae also had most of their species more abundant during the dry season (Fig. 3b).

Families that were more abundant during the rainy season included

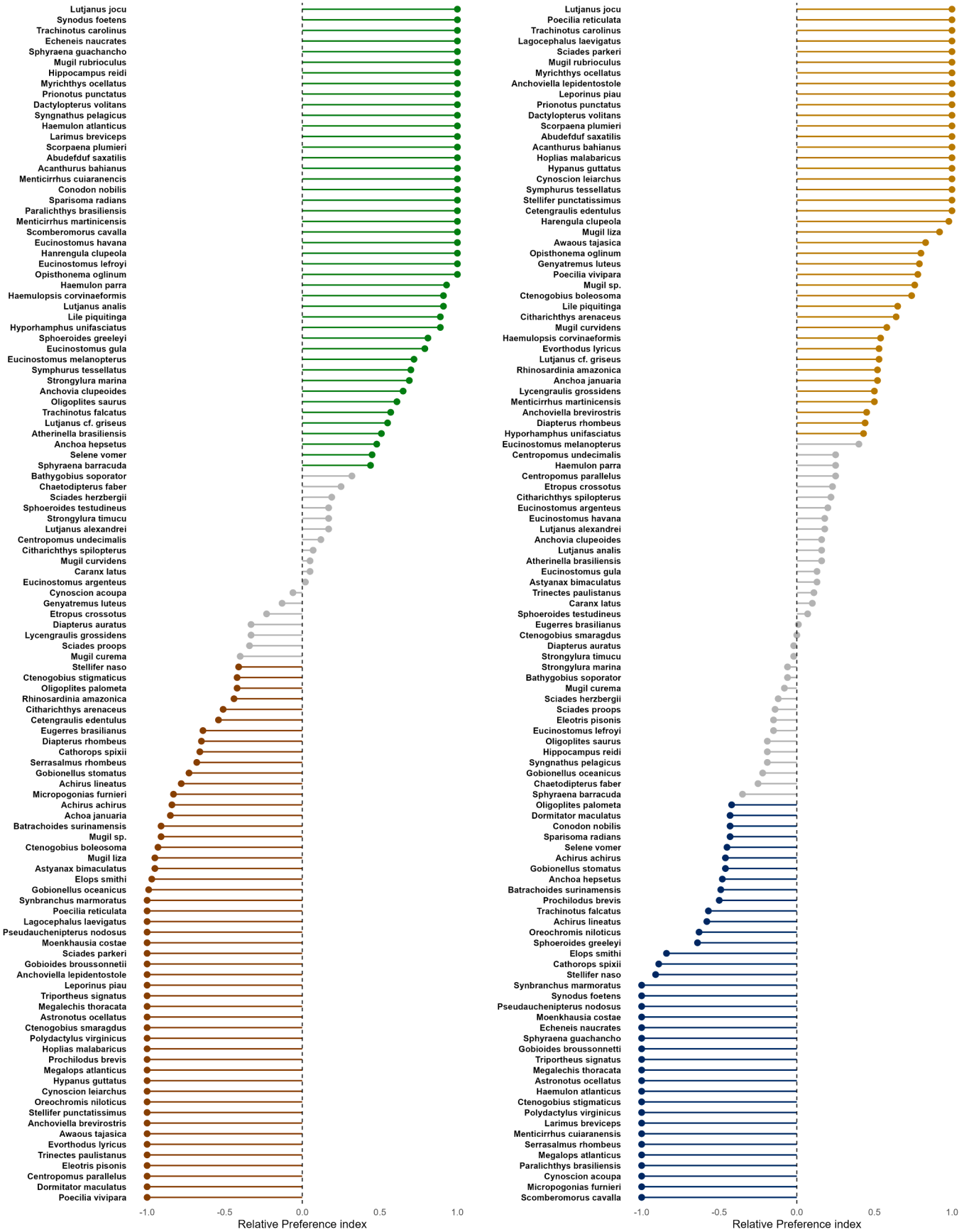

Fig. 3. Relative Preference index (RPi) showing fish species preferences for estuarine zones (a) (lower zone: green; upper zone: brown; no preference: gray) and seasons (b) (dry season: yellow; rainy season: blue; no preference: gray). RPi values can be found in Table A.2 and Table A.3.

Auchenipteridae (*P. nodosus*), Batrachoididae (*B. surinamensis*), Callichthyidae (*M. thoracata*), Cichlidae (*A. ocellatus*, *O. niloticus*), Echeneidae (*E. naucrates*), Elopidae (*E. smithi*), Megalopidae (*M. atlanticus*), Labridae (*S. radians*), Parallichthyidae (*P. brasiliensis*), Polynemidae (*P. virginicus*), Prochilodontidae (*P. brevis*), Scombridae (*S. cavalla*), Serrasalmidae (*S. rhombeus*), Synbranchidae (*S. marmoratus*), Synodontidae (*S. foetens*), and Triportheidae (*T. signatus*) (Fig. 3b). Some families exhibited a similar temporal occurrence in the estuaries: Atherinopsidae (*A. brasiliensis*), Belonidae (*Strongylura* spp.), Centropomidae (*Centropomus* spp.), Cyclopsettidae (*C. spilopterus* and *E. crossotus*), Ephippidae (*C. faber*), Gerreidae (*D. auratus*, *E. brasilianus*, and *Eucinostomus* spp.), Gobiidae (*B. soporator*), and Syngnathidae (*H. reidi*, *S. pelagicus*) (Fig. 3b).

Regarding trophic guild composition, only detritivores, opportunists, and macrocarnivores showed significant differences between zones according to SIMPER and RPi, with detritivores and macrocarnivores more abundant in the upper zone, whereas opportunists were more abundant in the lower zone (Table 2). RPi also showed differences between zones for planktivores, herbivores, and piscivores (greater abundance in the lower zone), and insectivores (upper zone, represented solely by freshwater straggler *M. costae*) (Table 2). Omnivores were also more abundant in the upper zone, but without a significant difference (Table 2). Omnivores indeed preferred the upper zone during the dry season; however, their abundances were similar between zones during the rainy season (Fig. 4). Zoobenthivores exhibited similar abundances between zones (Table 2), but their abundances varied between zones depending on the season (Fig. 4).

Omnivores and planktivores were significantly more abundant during the dry season according to SIMPER and/or RPi (Table 2). However, omnivores showed greater abundance during the dry season in the upper zone while similar abundances in the lower zone (Fig. 4). Detritivores were also more abundant in the dry season (RPi) but showed higher abundance during the dry season in the upper zone, while their abundances in the lower zone were similar (Table 2; Fig. 4). Opportunists showed more abundance during dry season, but without significant difference or preference (Table 2; Fig. 4). Zoobenthivores exhibited similar abundances between the seasons (Table 2), however, showed different abundances depending on the estuarine zone (Fig. 4). Macrocarnivores were more abundant in the rainy season, but without a significant difference or preference (Table 2), and showed higher abundance during the rainy season in the upper zone, while similar abundances in the lower zone (Fig. 4). Regarding the other guilds, piscivores and herbivores exhibited similar abundances between the seasons (Table 2), but piscivores vary their preferences depending on the zone (Fig. 4); and insectivores were exclusive to the rainy season (Table 2).

3.3. S-FEAS in space and time

As expected, most marine stragglers were more abundant in the lower zone and during the dry season. In contrast, diadromous, freshwater migrants, and freshwater stragglers preferred the upper zone and tended to occur mainly during the rainy season (Table A.1). Most estuarine species showed a higher association with the upper zone. However, roughly half of them exhibited no clear seasonal pattern (Table A.1). Finally, marine migrants were broadly distributed across zones and seasons (Table A.1).

The estuarine zones exhibited a significant difference in the assemblage fish estuary association index (S-FEAS) (Fig. 5a); the lower zone ranged from 2.99 to 4.39 (3.73 ± 0.26), while the upper zone ranged from 3.15 to 4.01 (3.58 ± 0.24). It is noteworthy that only the Malcozinhado Estuary showed a significant difference between the estuarine zones when comparing the zones of each estuary individually (Fig. A.6). Overall, spatial differences are greater than seasonal ones when analyzing each zone and each season separately (Table A.6). S-FEAS values did not differ between seasons (dry season: 3.67 ± 0.29; rainy season: 3.64 ± 0.23) (Fig. 5b), even when comparing the seasons of each estuary and each zone separately (Fig. A.7, Table A.6).

There was a difference in the S-FEAS values between stretches of higher salinities (hyperhaline and euhaline) and the freshwater stretches (limnetic) (Fig. 5c). S-FEAS in hyperhaline and euhaline ranged from 3.30 to 4.39 (3.83 ± 0.28) and 3.15–4.35 (3.74 ± 0.24), respectively. S-FEAS values decreased progressively, with polyhaline ranging from 2.99 to 3.96 (3.62 ± 0.24) and mesohaline from 3.20 to 3.89 (3.58 ± 0.27), while limnetic stretches ranged from 3.16 to 3.90 (3.52 ± 0.22). Only one oligohaline point was recorded (S-FEAS = 3.71).

Salinity dynamics varied among the estuaries across both space and time. Aracatimirim exhibited freshwater homogeneity during the rainy season and saline homogeneity during the dry season, but no specific pattern was evident in S-FEAS values (Table A.7). Choró Estuary lacked coherence between the seasons and salinity gradients, showing a negative gradient in part during the dry season and in part during the rainy season until it presented freshwater along its entire length in May (rainy season) and a positive saline gradient in September (dry season) (Table A.7). Curu Estuary also demonstrated temporal incoherence between the seasons and salinity gradients, with a positive saline gradient

Table 2
SIMPER results for trophic guilds in each estuarine zone (lower/upper) and season (dry/rainy). Cumsum indicates the ordered cumulative contribution. Bold p-values denote significant differences between groups (α = 0.05). Bold RPi values indicate preferences for zone and season (RPi ≥ |0.40|).

	Average abundance (individuals/100 m²)					
Trophic guild	Lower zone	Upper zone	Cumsum	*p*-value	RPi	Preference
Detritivore (DT)	2.08	19.44	0.223	**0.001**	**-0.80**	Upper zone
Opportunist (OP)	13.90	3.75	0.426	**0.03**	**0.57**	Lower zone
Omnivore (OV)	7.87	11.29	0.595	0.23	-0.18	-
Macrocarnivore (MV)	3.84	9.72	0.737	**0.01**	**-0.43**	Upper zone
Planktivore (PL)	8.44	2.47	0.871	0.09	**0.54**	Lower zone
Zoobenthivore (ZB)	6.74	4.98	0.991	0.93	0.15	-
Piscivore (PV)	0.38	0.09	0.999	0.91	**0.62**	Lower zone
Herbivore (HV)	0.05	-	0.999	0.90	**1.00**	Lower zone
Insectivore (IN)	-	0.005	1.000	0.14	**-1.00**	Upper zone
	Dry season	Rainy season				
Opportunist (OP)	11.03	6.62	0.206	0.08	0.25	-
Detritivore (DT)	15.22	6.31	0.408	0.43	**0.41**	Dry season
Omnivore (OV)	12.30	6.86	0.584	**0.04**	0.28	-
Planktivore (PL)	8.74	2.17	0.732	**0.001**	**0.60**	Dry season
Macrocarnivore (MV)	4.56	9.00	0.870	1.00	-0.32	-
Zoobenthivore (ZB)	5.43	6.30	0.991	1.00	-0.07	-
Piscivore (PV)	0.17	0.31	0.999	0.99	-0.29	-
Herbivore (HV)	0.024	0.026	0.999	0.97	-0.04	-
Insectivore (IN)	-	0.005	1.000	0.99	**-1.00**	Rainy season

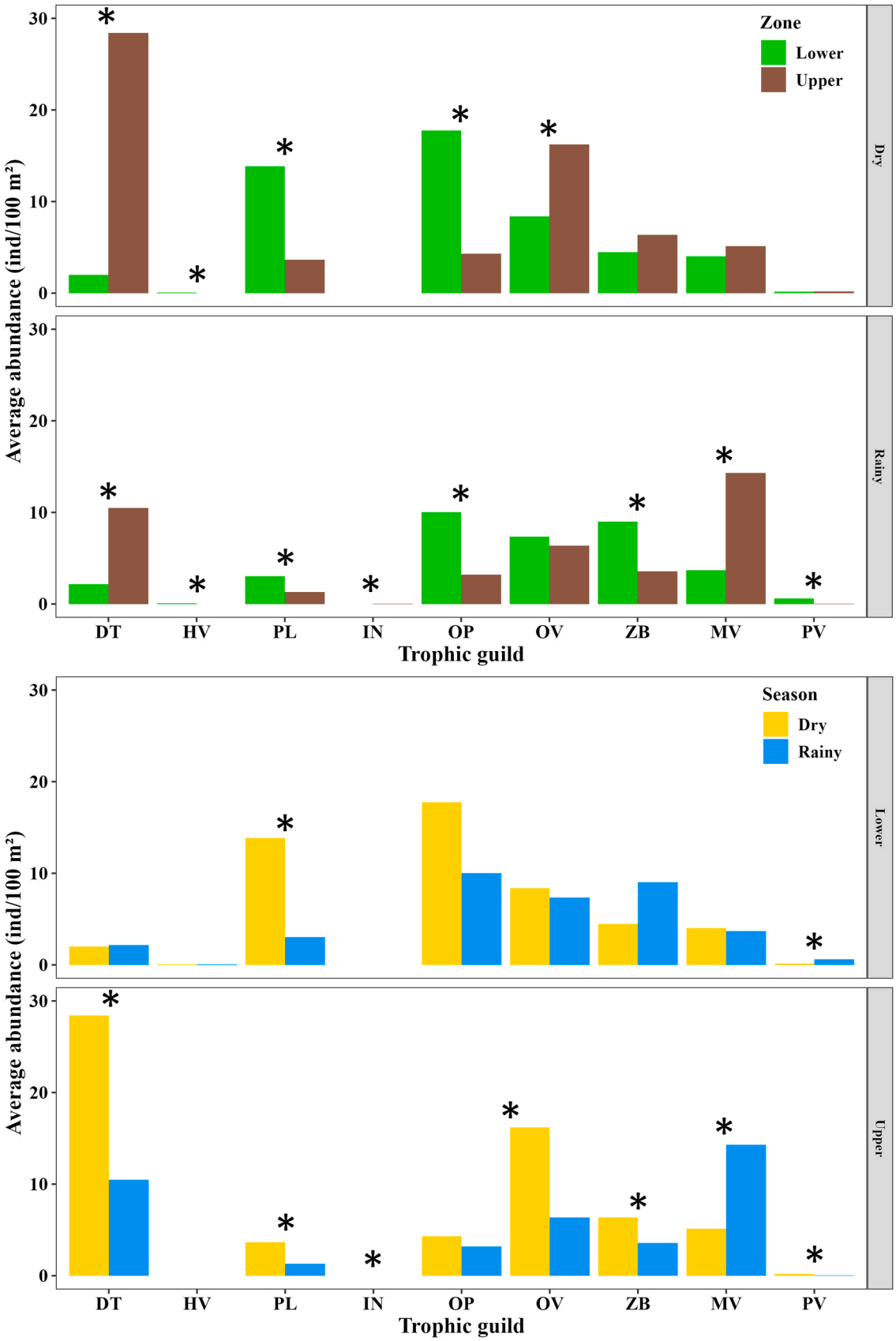

Fig. 4. S-FEAS between (a) zones (lower x upper: z = 2.86; p = 0.007), (b) seasons (dry x rainy: z = 0.67; p = 0.485), and (c) salinity categories (hyperhaline: 40 or greater, euhaline: 30–39, polyhaline: 18–29, mesohaline: 5–17, oligohaline: 0.5–4, limnetic: zero salinity; F = 4.04; p = 0.002, superscript letters indicate pairwise differences considering α = 0.05).

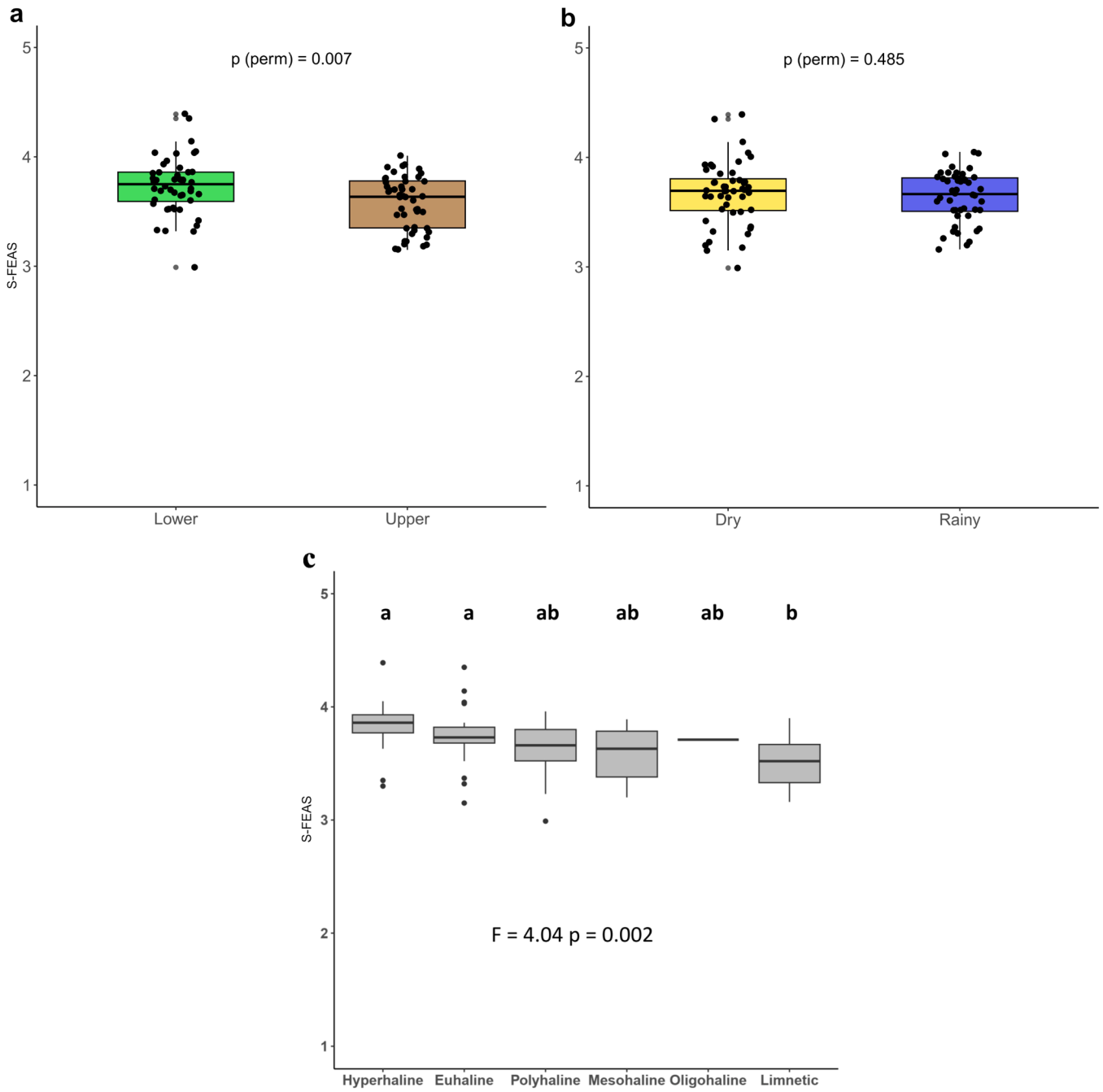

Fig. 5. Average abundances (ind/100 m^2) of trophic guilds for each estuarine zone by season (above) and for each season by estuarine zone (below). Detritivores (DT), herbivores (HV), planktivores (PL), insectivores (IN), opportunists (OP), omnivores (OV), zoobenthivores (ZB), macrocarnivores (MV), piscivores (PV). (*) significant difference in SIMPER ($p < 0.05$) and/or a high Relative Preference index (Table A.4, Table A.5).

in November (dry season) and February (rainy season); it then showed freshwater homogeneity in May (rainy season) and a positive gradient still in September (dry season) (Table A.7). Malcozinhado and Pacoti Estuaries were more consistent between salinity gradients and seasons. The Malcozinhado Estuary exhibited a positive salinity gradient during the rainy season, homogeneous salinity in October (dry season), and a negative gradient in December (also during the dry season). However, the S-FEAS values were not as divergent over time (Table A.7). Pacoti Estuary showed a negative gradient in November (dry season), followed by a positive gradient in May (rainy season) and saline homogeneity in June (late rainy season) and September (dry season) (Table A.7).

4. Discussion

The estuaries of the BSC exhibit spatiotemporal variation in the taxonomic and functional compositions of the ichthyofauna. The number of species and the diversity of functional groups contribute to the complex dynamics of habitat occupation in response to environmental variability. About 85 % and 70 % of species exhibited preferences for a particular zone or season, respectively. Marine migrant and estuarine species dominate the BSC estuaries, representing roughly 90 % of the total abundance, while marine stragglers, diadromous, and freshwater species exhibit clear spatial segregation. Regarding trophic aspects, generalist species (opportunists, omnivores, and macrocarnivores) accounted for 53 % of total abundance in BSC estuaries, yet all trophic

guilds showed distinct spatiotemporal segregation. In addition, the association of ichthyofauna with the estuary (FEAS approach) was consistently intermediate/high throughout the year, ranging from approximately 3.00–4.40. The main feature lies in the relative difference in the S-FEAS between the estuarine zones, while seasonal differences are minimal. Overall, substantial taxonomic and functional heterogeneity was evident when considering species, estuarine use guilds, and trophic guilds.

S-FEAS values demonstrated significant differences between the estuarine zones (with a mean difference of 0.15; values in the lower zone were higher than in the upper zone), although the magnitude of this difference was not substantial compared to other estuaries (Harrison and Whitfield, 2021; for instance, Casamance Estuary showed a difference of 0.30). The lower zone presented slightly higher values, which may be related to the predominance of marine species and the negligible presence of freshwater species. However, when comparing the zones for each estuary individually, only the Malcozinhado River displayed a significant spatial difference (3.64 lower vs 3.32 upper, mean difference of 0.32). This indicates the functional homogenization of the estuaries of the BSC regarding the use of the estuarine environment by the ichthyofauna. Whether this process is inherent to the region or has been intensified by climate change remains to be determined, especially following a recent prolonged drought that increased functional redundancy due to greater richness of marine-origin species (Gurgel-Lourenço et al., 2023). On the one hand, spatial comparisons in the Casamance Estuary spanned over 150 km (Kantoussan et al., 2012; Harrison and Whitfield, 2021), whereas the BSC estuaries evaluated extended less than 10 km, reflecting their much smaller size. Conversely, Belarmino et al. (2021) observed decreased abundances of *Atherinella brasiliensis* in southern Brazil, resulting from reductions in seagrass meadows associated with El Niño events. Excessive precipitation negatively affects these vegetations, which provide essential substrates for silverside spawning. In the BSC, the effect of El Niño is the opposite, promoting below-average precipitation, which, in theory, would favor seagrass meadows and, consequently, silversides. *Atherinella brasiliensis* was the most abundant species in the estuaries of the BSC, potentially exemplifying one environmental factor shaping the assemblage based on this single-species case.

Temporally, there were no differences regarding the association with the environment by the ichthyofauna (S-FEAS mean difference of 0.03, with values slightly higher in the dry season than in the rainy season). This similarity between the seasons suggests that, despite seasonal variations in species composition and trophic guilds, this functional aspect of the estuarine communities of the BSC remains relatively stable over time. Even in individual comparisons, no BSC estuary exhibited temporal differences, contrasting with the Mhlanga Estuary in South Africa, which showed pronounced seasonal variation: winter (dry season) had an S-FEAS of 3.41, whereas spring (rainy season) had 2.67, representing a difference of 0.74 (Harrison and Whitfield, 2021). The seasonal similarity in S-FEAS values within the BSC may stem from the hydrodynamic complexity of these systems, which is influenced by both seasonality and local factors such as riverine input and evaporation (Molisani et al., 2006). Moreover, freshwater retention in watershed reservoirs likely causes each estuary to exhibit unique dynamics, both annually and interannually, depending on reservoir storage levels and the timing of freshwater releases, as determined by water resource management in each basin. At the beginning of the rainy season, freshwater inflows are often insufficient to reduce estuarine salinity. This phenomenon is particularly evident when typical dry-season salinity gradients persist during the rainy season, as observed in the negative gradient of the Choró Estuary and the high salinity homogeneity of the Curu Estuary. However, even when accounting for these inconsistencies between the seasons and the salinity gradient, the difference between the seasons increased to only 0.06 (3.67 dry vs 3.61 rainy).

The zero-salinity homogeneity observed in some estuaries during the rainy season may indicate the strong freshwater influence during these periods, which likely directly affects the composition of fish communities (Lewis and Cook, 2023). We observed a clear relationship between salinity and S-FEAS at the sampling point level; higher-salinity categories exhibited distinct values compared to freshwater stretches. Hyperhaline and euhaline stretches presented higher average S-FEAS values, while polyhaline and mesohaline stretches showed intermediate averages, and limnetic stretches exhibited the lowest average S-FEAS. However, many S-FEAS values were shared or overlapped across almost all salinity types. Furthermore, S-FEAS values were consistently above 3.00, even in freshwater, highlighting the dominance of estuarine and marine species in these estuaries (Harrison and Whitfield, 2021).

The shallow-water estuarine fauna typically comprises numerous marine species and relatively few freshwater taxa (Garcia and Vieira, 2001; Jung and Houde, 2003; Spach et al., 2004; Barletta and Blaber, 2007; Paiva et al., 2008; Pichler et al., 2015; Whitfield, 2015; Bot Neto et al., 2023). In Australian estuaries, which also exhibit relatively uniform salinity, fish biomass is dominated by marine species, whereas in Amazonian estuaries with higher freshwater runoff, the assemblages of typically estuarine species dominate (Barletta and Blaber, 2007; Giarrizzo and Krumme, 2008). Resident estuarine species represented only 18 species (26.7 % total abundance) in BSC, of which only four were among the most abundant. The resident estuarine fish species in the BSC belong predominantly to marine-origin families and potentially complete their entire life cycle within the estuarine environment (Potter et al., 2015). Although estuarine species, such as *A. brasiliensis*, *G. oceanicus*, *C. boleosoma*, and *A. achirus*, were highly abundant and dominant in the BSC, marine migrants were more abundant overall, particularly in terms of species richness (61 species). In general, species capable of completing their entire life cycles within estuaries represent a small percentage compared to migratory species that frequent them (Day Jr. et al., 2013; Potter et al., 2015). This lower representativity, when compared to marine migrant species, is similar to patterns observed in estuaries from Brazil and other regions of the world (Mathieson et al., 2000; Lamberth and Turpie, 2003; Lobry et al., 2003; Franco et al., 2008; Neves et al., 2008; Paiva et al., 2009; Selleslagh et al., 2009; Nicolas et al., 2010; Hoeinghaus et al., 2011; Solari et al., 2015). Marine migrant species typify the estuarine ichthyofauna, with representatives from the genera *Mugil*, *Centropomus*, *Diapterus*, *Eucinostomus*, *Lutjanus*, *Sphoeroides*, and others. These taxa are primarily found in estuarine environments during their juvenile stages, utilizing nursery and growth areas, and are mostly considered of commercial or subsistence importance for artisanal fisheries (Blaber, 1997; Manson et al., 2005; Aburto-Oropeza et al., 2008; Basílio and Garcez, 2014; Botero et al., 2023). This finding supports the essential role of BSC estuaries as transitional areas between marine and continental environments, supporting a diversity of coastal species that depend on these habitats at various stages of their life cycles, particularly in tropical regions where estuaries serve as feeding, reproduction, and recruitment areas (Sales et al., 2018; Whitfield et al., 2024).

No diadromous, freshwater migrant, or freshwater straggler species showed a preference for the lower estuarine zone. Only a few specimens occurred, as reflected in the low abundances of freshwater migrant and freshwater straggler species. Most freshwater fish species, concentrated in the upper zone and restricted to low-salinity areas (Elliott et al., 2007; Potter et al., 2015), were constrained by elevated salinity throughout much of the length of BSC estuaries for most of the year. The scarcity of freshwater species can be explained by the high salinity in estuaries with predominant marine influence, among other factors that contribute to a lower proportion of freshwater species, such as greater predation pressure from piscivorous fishes and birds, and loss of connectivity due to reservoirs (Whitfield, 2015). Nevertheless, the variation in salinity in the BSC estuaries during the rainy season appeared to be a determining factor for the occurrence of freshwater species such as *A. ocellatus*, *M. costae*, *M. thoracata*, *O. niloticus*, *P. brevis*, *S. rhombeus*, *S. marmoratus*, and *T. signatus*. Although some freshwater species, such as

H. malabaricus and *L. piau*, were more abundant during the dry season, they occurred in freshwater stretches.

Salinity is a key environmental variable in estuaries (Barletta et al., 2005, 2008; Barletta and Blaber, 2007; Selleslagh et al., 2009; Vilar et al., 2011) that influences the taxonomic structure along the longitudinal profile of the BSC estuaries. Differences in species compositions between estuarine zones have been reported for tropical estuaries (Barletta et al., 2005; Paiva et al., 2008; Lima et al., 2020; Bot Neto et al., 2023), commonly showing higher species richness in the lower zone, coinciding with the upstream decrease in salinity (Thiel et al., 1995; Whitfield, 1999; Araújo et al., 2002; Akin et al., 2003; Martino and Able, 2003; Vega-Cendejas and de Santillana, 2004; Hackradt et al., 2011; Neves et al., 2011; Mourão et al., 2015). However, the species richness and abundance in the lower zone were similar to those in the upper zone in the BSC estuaries, but about 85 % of the species exhibited a spatial preference. This pattern indicates spatial homogenization in richness and abundance, coupled with compositional heterogeneity between estuarine zones. The BSC estuaries exhibited diverse salinity regimes, ranging from moderate to high salinity, as well as entirely freshwater conditions. In smaller estuaries with limited continental freshwater input, it is expected to be substantially modified by hypersaline areas, leading to gradient inversion (Potter et al., 2010; Largier, 2023), as observed in most BSC estuaries. This is evidence of the inland intrusion of marine waters, a result of the semiarid region's climatic dynamics, with prolonged periods of low rainfall, in addition to the retention of freshwater in upstream reservoirs, a process known in other estuaries influenced by similar climates (Lima et al., 2020; Bot Neto et al., 2023). During the rainy season, river flow dilutes salinity, allowing freshwater species to enter estuarine areas, while marine stragglers leave offshore waters in search of stable salinity conditions (Garcia and Vieira, 2001; Elliott et al., 2007; Potter et al., 2015). In the BSC estuaries, the greatest salinity changes occurred in the upper zone, due to concentrated rainfall, unlike what typically happens in positive estuaries, where the upper zone always presents fresh water (Neves et al., 2011; Passos et al., 2013). Nonetheless, these changes did not significantly affect variation in species richness, despite differences in mean abundance, with approximately 70 % of species exhibiting a seasonal preference.

Resident estuarine species and many marine migrant species capable of tolerating salinity fluctuations (Blaber, 2000) were generally evenly distributed between the zones in the BSC estuaries, such as Ariidae, Engraulidae, Sciaenidae, and Tetraodontidae. For example, Gerreidae was both dominant and consistently present across all three zones of the Formoso Estuary (Paiva et al., 2008), as well as in the BSC. However, many species contributed to the differentiation of the ichthyofauna between zones. For instance, most species of the Dorosomatidae family were more abundant in the lower zone, while Oxudercidae occurred in greater abundance in the upper zone. According to Martino and Able (2003), large-scale patterns (10 km) in fish assemblage structure are primarily the result of responses to environmental gradients, whereas smaller-scale patterns (1 km) seem to be driven more by habitat selection, competition, and predator avoidance strategies.

The trophic ecology of fish in estuaries is highly diverse, with all trophic levels represented (Paiva et al., 2008; Whitfield et al., 2024; Harrison and Whitfield, 2025). The number of trophic groups found in the BSC estuaries was similar to that reported for other estuaries (Passos et al., 2013; Harrison and Whitfield, 2025). Zoobenthivores and piscivores dominated in estuaries in southern Brazil (Passos et al., 2013), while zoobenthivores were predominant in worldwide estuaries (Krumme et al., 2004; Paiva et al., 2008; Whitfield et al., 2024; Harrison and Whitfield, 2025). However, the most representative group in the present study was detritivores, followed by omnivores, opportunists, and macrocarnivores. Zoobenthivores ranked only fifth in abundance. The contribution of omnivores, opportunists, and macrocarnivores, together comprising about 53 % abundance, shows the importance of these trophic guilds in structuring the BSC estuarine communities and that more generalist trophic guilds benefit, which could indicate that the estuaries of the BSC are environmentally challenging.

Differences in species composition between estuarine zones may be associated with substrate distribution (Reis-Filho and Santos, 2014), which may have an indirect link to trophic ecology (Whitfield et al., 2024; Harrison and Whitfield, 2025). For example, certain detritivores that tolerate hypoxia are common in muddy substrates with lower dissolved oxygen levels (Aguilar et al., 2018; Reis-Filho et al., 2014). Indeed, detritivores were more abundant in the upper zone of the BSC estuaries. The abundance of detritivores in the upper zone may indicate that these regions offer greater availability of organic matter, a source of detritus originating from the mangrove and river inflow, as well as the longer water residence time during the dry season (Yuan et al., 2007; Atwood et al., 2012). Estuaries are well-known for their conspicuous detritus-based food webs, which influence the dominance of fish groups that exploit these resources (Day Jr. et al., 2013; Whitfield et al., 2024). In fact, detritivores were the most abundant trophic guild in the BSC estuaries, with many species being exclusive to the upper zone. Estuaries experiencing extreme hypersalinity tend to favor detritivorous fishes (Tweedley et al., 2019), and this guild is comparatively more abundant in arid-region estuaries than in those of other bioregions (Harrison and Whitfield, 2025). These conditions may become more frequent in the BSC under future climate change scenarios associated with rising temperatures (Tweedley et al., 2019; Soares et al., 2021).

High abundance of macrocarnivores in the upper zone, especially during the rainy season, may be directly related to their foraging strategy or prey abundance, utilizing turbid environments as a refuge (Hetch and van der Lingen, 1992; Lunt and Smee, 2014), since, in addition to piscivores, macrocarnivores include a substantial quantity of fish in their diet. On the other hand, planktivores were more abundant in the lower zone and during the dry season, likely associated with greater light penetration and, consequently, better visual detection for capturing prey in the water column (Utne-Palm, 2002). These trophic patterns reflect the complex ecological dynamics of estuaries, where resource availability and predation pressure vary according to species' feeding strategies, as well as the zone and season.

The high abundance of opportunists reflects the dietary plasticity of these species, which can exploit a wide range of food resources in variable environments, such as estuaries (Elliott et al., 2007; Whitfield et al., 2024). However, they were significantly more abundant in the lower zone, whereas omnivores exhibited similar abundances across zones. Therefore, opportunists and omnivores, with more plastic feeding strategies, are less likely to experience food scarcity compared to other trophic guilds, which likely confer advantages reflected in their abundances. Another food resource frequently utilized by estuarine fish is benthic macrofauna, consumed to a considerable extent by macrocarnivores. Notably, all these guilds feed on benthic fauna to varying degrees, consuming organisms typically present in estuaries (Day Jr. et al., 2013), including zoobenthivores, whose diets reflect benthic prey availability. According to Blaber (2000), zoobenthivorous fish are common in all types of substrates in estuaries. Indeed, zoobenthivorous fish exhibited similar abundances across the estuarine zones of the BSC, however, varying with higher abundances in the lower zone during the rainy season and in the upper zone during the dry season, likely following the dynamics of benthic invertebrates, which generally die or move away from the upper zone during periods of increased freshwater inflow (Quan et al., 2025). The fact that omnivores (20.1 % abundance) and zoobenthivores (12.3 %) also displayed relative representation reinforces the idea that estuaries provide high availability of different food resources (Whitfield et al., 2024).

Other less abundant trophic guilds in the BSC estuaries were piscivores, herbivores, and insectivores. Piscivores included only *Strongylura marina*, *S. timucu*, and *Scomberomorus cavalla*, while herbivores comprised only *A. bahianus* and *S. radians*, and insectivores included only *M. costae*. The small number of herbivorous and insectivorous species is common in estuaries (Franco et al., 2008; Ferreira et al., 2019; Harrison and Whitfield, 2025). However, piscivores tend to be more

abundant (Franco et al., 2008; Whitfield, 2015; Ferreira et al., 2019; Whitfield et al., 2024; Harrison and Whitfield, 2025). Thus, the question arises as to why the piscivores were less abundant in the BSC estuaries, and future studies should investigate this question. However, the classification of some species as macrocarnivorous, based on their juvenile size, may have underestimated the true piscivorous identity of some species. Moreover, among all recorded species, only one belonged to Elasmobranchii, typically top predators. Browne and Lutz (2010) and Ecoutin et al. (2010) found that anthropogenic disturbances result in the loss of top predators. The low representativeness of the number of species in this group may be a current characteristic of the ichthyofauna in the small estuarine environments of northeastern Brazil. Basílio et al. (2008) and Basílio et al. (2009) documented a higher representativity of some fish predators like sharks, rays, Epinephelidae, Grammistidae, and Serranidae in the Curu Estuary. It is likely that these groups currently lack suitable local estuarine habitats for feeding or nursery grounds due to coastal environmental changes such as siltation, sediment transport, etc., which have emerged over the last few decades, or the likely overfishing in the coastal environment to which they are subject (Morais and Pinheiro, 2011; Quintela-Falcão et al., 2011; Soares et al., 2021).

Finally, there were differences in species composition and trophic guilds among the estuaries. Sheaves (2016) investigated potential variation among estuarine ecosystems at smaller scales using a theoretical model that incorporates unpredictable factors. One key factor is the influence of ocean currents on the colonization of fish larvae, which depends on the distance between estuarine mouths and coastal spawning areas. In contrast, intrinsic factors within the estuaries may have a greater influence on species that spawn locally, such as physical variables affecting reproduction, predation pressure, and other factors that similarly affect species spawning outside the estuary (Sheaves, 2016). In this study, however, our focus was on investigating general spatial and temporal patterns in the BSC estuaries. Future research should explore differences among individual BSC estuarine systems.

In conclusion, the composition of fish species, their trophic guilds, and estuarine use guilds exhibits spatial variation between the lower and upper zones in the estuaries of the BSC, reflecting substantial taxonomic and functional heterogeneity. Temporally, there were differences in species composition and trophic guilds between the dry and rainy seasons; however, the ichthyofauna exhibited no significant functional differences in estuarine use between seasons. A clear relationship exists between salinity and the association of ichthyofauna with estuaries, as higher-salinity areas differed from freshwater stretches. Nevertheless, S-FEAS values never fell below 3.00, indicating the persistent dominance of estuarine and marine species in these estuaries. This study contributes to filling the knowledge gap regarding the spatial and temporal distribution of fish assemblages and functional groups in small estuaries of the BSC. It provides ecological insights into the ichthyofauna dynamics in estuaries influenced by the Brazilian semi-arid climate, while also highlighting questions for future research on the patterns and processes governing these assemblages. Overall, the results highlight the importance of estuaries as environments that support a wide diversity of species and trophic guilds, whose distribution depends on both spatial (estuarine gradients) and seasonal factors. These findings underscore the need for targeted conservation strategies in these ecosystems, given their critical role in maintaining coastal biodiversity.

Research Data

The datasets supporting the conclusions of this study are not publicly available to allow ongoing and future research by the authors' group. Public release at this stage could compromise the integrity and originality of forthcoming studies

Author contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by Ronaldo César Gurgel-Lourenço, Leonardo Mesquita Pinto, Danielle Sequeira Garcez, and Jorge Iván Sánchez-Botero. Data analyses were performed by Ronaldo César Gurgel-Lourenço, Leonardo Mesquita Pinto, and Carlos Alberto de Sousa Rodrigues-Filho. The first draft of the manuscript was written by Ronaldo César Gurgel-Lourenço, and all authors commented on previous versions. All authors read and approved the final manuscript.

CRediT authorship contribution statement

Ronaldo César Gurgel-Lourenço: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Leonardo Mesquita Pinto:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Carlos Alberto de Sousa Rodrigues-Filho:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Danielle Sequeira Garcez:** Writing – review & editing, Validation, Funding acquisition, Conceptualization. **Jorge Iván Sánchez-Botero:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Ethics approval

All procedures performed in the study were approved by 43014, 64269, and 87874 authorizations from the Chico Mendes Institute for Biodiversity Conservation (SISBio/ICMBio, Ministry of Environment, Brazil).

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.

Acknowledgments

The authors would like to thank the Federal University of Ceará (UFC). We are grateful to past and current members of the LEAC for collecting and analyzing samples. Funding information: Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support through the MCTI/CNPq Program (Grant 28/2018, 423628/2018–6 and Grant 63/2022, 409354/2022–8) for the field and scholarship support to Ronaldo César Gurgel-Lourenço and Leonardo Mesquita Pinto. We are grateful for the support of the National Institute of Science & Technology of Materials Transfer at the Continent-Ocean Interface (INCT-TMCOcean), based at UFC.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104706.

Data availability

The data used for this research are available in the Supplementary Material attached to the manuscript.

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