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RESEARCH ARTICLE

Spatial and seasonal fish assemblage dynamics in a heavily urbanized estuary affected by interbasin water transference (Northeast, Brazil)

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Abstract

Estuarine ecosystems exhibit substantial spatiotemporal variation in their environmental conditions, resulting in a dynamic fish assemblage. However, anthropogenic alterations in hydrological flow and nutrient concentrations can potentially modify the spatial and temporal structuring of the fish community. This study aimed to elucidate how the characteristics of fish assemblages vary in space and time in an estuary (Cocó River, Ceará State, Northeast Brazil) that experiences significant impacts stemming from untreated domestic effluent discharge and water transfer from other hydrographic basins. The fish assemblage exhibited low total species richness alongside a high number and biomass of freshwater species, including non-natives. A stable spatial structure across seasons was discerned, implying diminished connectivity between estuarine zones. Changes in the trophic structure of the ecosystem could be inferred from variations in trophic composition among different zones. The findings presented herein demonstrate the alterations that interbasin water transfer may induce in estuarine fish assemblages, with potential ramifications for ecosystem functioning.

Keywords Estuarine fish · Taxonomic composition · Functional composition · Diversity · Anthropogenic impacts

Introduction

Estuaries are dynamic coastal ecosystems, biotically and abiotically, located at the interface between marine and freshwater environments, primarily characterized by salinity gradients (Whitfield 2021). In estuarine systems, the ecocline results from the interaction between the intrusion of coastal waters and freshwater inputs (Attrill and Rundle 2002; Barletta et al. 2017). In the ecocline model, aquatic assemblages are structured along one or a few environmental drivers. Numerous studies have demonstrated the occurrence of this pattern in estuarine fish assemblages (Barletta et al. 2017; Chaves et al. 2018). Thus, salinity directly reflects the balance of this interaction; typically, estuaries exhibit a decreasing gradient of this variable with increasing distance from the sea. Fish assemblages are primarily structured spatially based on this salinity gradient, selecting species according to their osmotic tolerances (Barletta et al. 2005; Whitfield et al. 2012). According to classic models, freshwater species are expected to dominate the upstream sectors, while estuarine and marine species are more prevalent in areas closer to the sea (Potter et al. 2015). However, temporal variations in the spatial salinity gradient allow species to move between different areas, influencing the functioning and resilience of these ecosystems (Macedo et al. 2021, 2023).

However, estuaries are often subject to significant anthropogenic impact, with their natural dynamics frequently affected by various forms of pollution (Barletta and Lima 2019). Eutrophication, for instance, is one of the primary causes of declining water quality and can result from the discharge of effluents from domestic, industrial, or agricultural sources (Smith 2003; Malone and Newton 2020). Excess nutrients impact dissolved oxygen, turbidity, and primary productivity, leading to changes in estuarine biological

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assemblages and ecosystem characteristics (Powers et al. 2005; Jeppesen et al. 2018; De Lima et al. 2024). Water quality parameters (such as concentrations of dissolved oxygen, nitrite, nitrate, and phosphates) in estuaries also exhibit spatial structuring along their longitudinal axis (Costa et al. 2018; Duque et al. 2020). Upstream regions, where water residence time and proximity to pollution sources are greater, are more susceptible to lower water quality parameters and eutrophication (He et al. 2014). Conversely, the high rate of water renewal in downstream zones promotes more favorable water quality parameters (e.g., higher oxygen levels, lower turbidity) (Mourão et al. 2020). The gradients of salinity and water quality can interact, influencing the properties of the estuarine ecocline and acting as structuring factors for assemblages (Chaves et al. 2018; Duque et al. 2020). In addition to spatial variations, the continuous input of effluents into an aquatic system can contribute to the homogenization of the community over time (Cook et al. 2018).

The effects of environmental gradients on biodiversity can be investigated from various perspectives. The taxonomic approach considers species identity alone, whereas the functional approach considers species attributes, which are directly related to their ecological functions (Villéger et al. 2017). Thus, a functional dimension approach allows for inferences about how variations among species can translate into changes in ecosystem functioning (Mouillot et al. 2011). On the other hand, the taxonomic dimension is also important, as species richness in a community can positively affect its stability and functioning through functional redundancy and resilience to environmental disturbances (Loreau & Mazancourt 2013). Historically, the taxonomic approach has been more extensively explored than the functional facet (Villéger et al. 2017). Therefore, studies that jointly analyze both dimensions are essential for obtaining a holistic understanding of biodiversity patterns and how biodiversity contributes to ecosystem functioning (Villéger et al. 2010).

This study focuses on the Cocó estuary, located in Fortaleza city, the capital of the Ceará state in Northeastern Brazil, with a total population of 2.4 million inhabitants (IBGE 2022). Approximately 28% of the city's households are not connected to the sewage network (IBGE 2022), resulting in untreated domestic effluents being discharged directly into urban water bodies. The discharge of untreated domestic effluents has been identified as one of the main sources of pollution in the estuary (Schettini et al. 2017). In addition to the Cocó River basin, the city's water supply also relies on water from other basins, leading to the transfer of water from adjacent basins into the estuary (Schettini et al. 2017). This factor contributes to a positive freshwater budget in the estuary, resulting in a stable hyposaline profile, which is atypical for the region's pattern of seasonally hypersaline estuaries (de Freitas et al. 2015; Soares et al. 2021). The Cocó estuary is an important ecosystem for maintaining aquatic biodiversity (Gurgel-Lourenço et al. 2023b) despite urbanized location. Additionally, it provides numerous ecosystem services to society, ranging from recreational activities (Lima and Garcez 2017) to the provision of food resources through small-scale agriculture and artisanal fishing (SEMA 2024a).

Thus, the objective of this study was to assess how the characteristics of fish assemblages are structured across space and time in a highly urbanized estuary influenced by interbasin water transfer. We hypothesize that the anthropogenic impacts of the estuary leave a signature on the spatiotemporal patterns of the fish assemblage in two ways: (1) spatially, the interaction between nutrient discharge and hydrodynamics is expected to result in distinct structures across zones; (2) temporally, the continuous discharge of freshwater and effluents is likely to cause a homogenization of the fish assemblage. To this end, we tested the effects of different zones along the estuarine ecocline and seasonal variations on biomass, diversity indices, and the taxonomic and functional composition of the assemblage. These findings were then compared with the patterns reported in the literature for estuarine ecosystems along the semi-arid Brazilian coast.

Materials and methods

Study area

The Cocó River spans 48 km from its source to its mouth, forming a small coastal watershed of approximately 485 km^2 along with its tributaries, encompassing eight municipalities (SEMA 2024a). The basin is located in a hot sub-humid tropical climate area (IPECE 2024), with an average annual precipitation of 1340 mm, mostly concentrated between January and June (FUNCEME 2024). Historically, the Cocó River has experienced intermittent flow, but with the construction of reservoirs, its flow is now perennial, ranging from 3 to 6 m^3/s during the dry and rainy seasons, respectively (de Freitas et al. 2015; Molisani et al. 2006). The basin is critically important for the domestic and industrial water supply of the metropolitan area of Fortaleza. A significant portion of its lower course, located within the metropolitan area, lies within a fully protected conservation unit (Cocó State Park) (Fig. 1), which is the fourth largest natural park in an urban area in Latin America (SEMA 2024b).

Physicochemical parameters of the estuary's water, monitored at four points along the estuary from 2011 to 2019, indicate an environment characterized by low dissolved oxygen levels and high nutrient concentrations (SEMA 2024a). Trophic state indexes are computed with water quality data and are essential tools for classifying and quantifying the eutrophication level of aquatic ecosystems. Over this period,

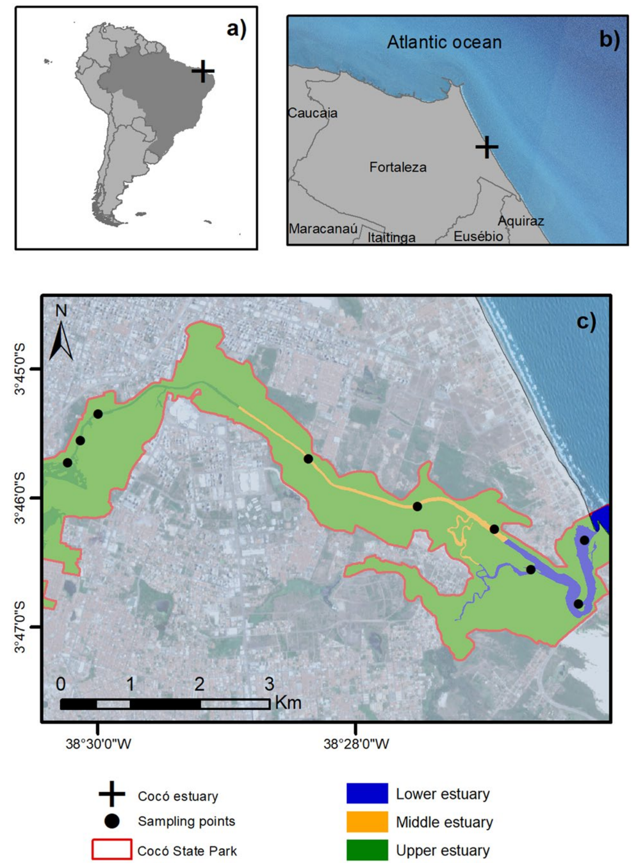

Fig. 1 **a**, **b** Location of the Cocó estuary (State of Ceará, northeastern Brazil), zones determined by this study, and ichthyofauna sampling points **c**

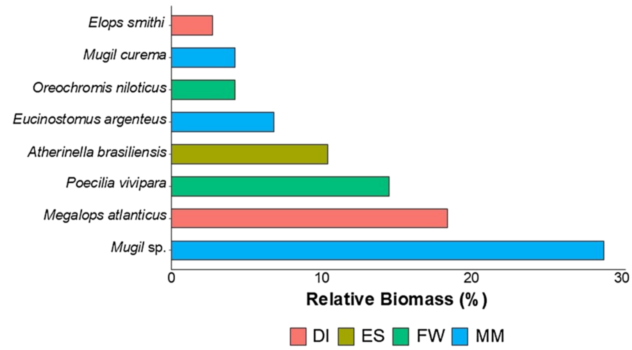

Fig. 2 Relative abundance of the species accounting for 90% of the total fish biomass sampled in this study from the Cocó estuary. DI: diadromous, *ES* estuarine, *FW* freshwater, *MM* marine migrant

the system exhibited high values of the Trophic State Index (TSI) (mean: 70.63 ± 6.51) and Trophic Index (TRIX) (mean: 8.32 ± 0.85) (Supplementary Information I). Accordingly, it was classified as hypertrophic (Carlson 1977) with a very high level of eutrophication and poor water quality (Vollenweider et al. 1998) according to both approaches. Additionally, there is a noticeable trend of increasing index values in locations situated further upstream in the system (Supplementary Information I – Fig. 2).

The longitudinal axis of an estuary can be divided into three compartments—the upper, middle, and lower zones—based on characteristics such as morphology and physicochemical variables (Barletta et al. 2017). Therefore, before the ichthyofauna sampling, reconnaissance campaigns were conducted to delineate the estuary into these distinct zones. The environmental characteristics assessed included substrate type, width, depth, associated vegetation, and water physical–chemical variables such as dissolved oxygen, salinity, and Secchi depth.

The lower zone encompassed sampling points closest to the estuary's mouth, characterized by predominantly sandy substrate, shallow depth (mean: 1.43 m, maximum: 2.32 m), the greatest river width (mean: 221.30 m ± 2.5), a predominance of *Rhizophora mangle* mangrove species, and the higher values of dissolved oxygen, salinity, and Secchi depth. The middle zone featured depths ranging from 1.5 m to 3.5 m, an average width of 39 m ± 3.5, predominantly clayey substrate, a dominance of *Avicennia germinans* mangrove species, and low levels of dissolved oxygen, salinity, and Secchi depth. The upper zone, located further upstream, had the narrowest channel width (29 m ± 2.5), the shallowest depths (0.5 to 2.0 m at low tide), riparian vegetation composed of bushes and medium-sized trees, dominance of aquatic macrophytes such as *Eichhornia crassipes* and *Panicum repens*, and freshwater salinity (Table 1). In each zone, three sampling points were selected, totaling nine points overall (Fig. 1c).

Sampling and laboratory procedures

Ichthyofauna sampling was conducted at three points within each estuarine zone, resulting in a total of nine sampling points. In total, six sampling events were carried out with a bimonthly frequency from July 2017 to May 2018, comprising three during the dry season (July to December) and three during the wet season (January to May) (Moura et al. 2015). Fish captures were performed using trawl nets (25 m long, 2 m high, with 12 mm mesh size between opposite knots), seines (3 m radius with 25 mm mesh size between opposite knots), and dip nets (1.31 m long, 0.93 m high).

Table 1 Mean and range values of physicochemical water variables measured in the lower, middle, and upper zones of the Cocó estuary

Zone	Dissolved oxygen (mg/l)	Salinity (ppt)	Secchi depth (cm)
Lower	6.0 (4.8–7.5)	14.8 (9–24)	110.5 (94–126)
Middle	2.6 (0.8–4.3)	1.8 (0–12)	50.0 (40–62)
Upper	2.1 (0.9–3.4)	0.0	45.6 (30–60)

In the lower and middle zones, trawl nets and seines were employed. In the upper zone, dip nets and seines were used because of the high abundance of aquatic macrophytes and riparian vegetation, which prevented the use of trawl nets. The total area sampled at each point was considered as the sum of the areas sampled per haul using the different fishing gear. All collections were carried out under the license of the environmental agency (Instituto Chico Mendes de Conservação da Biodiversidade/SISBio no. 57780). Collected individuals were killed with clove oil, stored on ice, measured for standard length (cm), weighed (g), fixed in 10% formalin, and preserved in 70% ethanol. Abundance was expressed as catch per unit effort (CPUE), calculated by dividing the biomass per species by the total area sampled at each point (g/m^2). Voucher specimens were deposited in the ichthyological collection of the Laboratory of Systematic and Evolutionary Ichthyology at the Federal University of Rio Grande do Norte (UFRN).

A set of 18 attributes (15 quantitative and three qualitative) was selected for the functional characterization of species. These attributes reflect characteristics related to species adaptations in the estuarine environment and the functional role each species performs in the ecosystem. The continuous attributes are related to feeding, locomotion, and habitat use and were derived from morphometric measurements of one to five individuals per species (Supplementary Information II), which were then combined into formulas (Supplementary Information III). The three qualitative attributes were Trophic Guild (Detri: detritivores, Plank: planktivores, Herb: herbivores, Invert: invertivores, Macro: macrocarnivores, Omniv: omnivores); Estuarine Guild (sensu Potter et al. 2015) (MS: marine stragglers, MM: marine migrants, ES: estuarine, DI: diadromous, FW: freshwater); and Presence of Adaptations for Survival in Hypoxic Environments: (hipox_1: with some adaptation; hipox_0: without adaptations). This information was compiled from FishBase (Froese and Pauly 2024) and specialized literature (Medeiros et al. 2017; Harrison and Whitfield 2021).

Data analysis

Non-metric multidimensional scaling (nMDS) was employed to assess spatial and seasonal patterns in taxonomic and functional composition. For the nMDS of taxonomic composition, a distance matrix was created using the Bray-Curtis index, based on species and abundance data per sampling point. For the nMDS of functional composition, a community weighted matrix (CWM) was used, which represents the mean attribute value for each sampled point (Lavorel et al. 2008). This matrix was derived from the intersection of species composition data per point and attribute data per species using the *functcomp* function from the FD package (Laliberté and Legendre 2010). From the CWM, a distance matrix was calculated using Euclidean distance and subsequently used to perform the nMDS.

The significance of the effects of zones and seasons on taxonomic and functional composition was investigated through a permutational analysis of variance (PERMANOVA) (Anderson 2017), using the *adonis* function from the vegan package (Dixon 2003). PERMANOVA tests were performed using the Bray-Curtis distance matrix for taxonomic composition and the Euclidean distance matrix for functional composition. Post-hoc PERMANOVA tests based on pairwise comparisons were employed, when necessary, to identify which zones differed from each other using the *pairwise.adonis* function (Martinez 2020). The *envfit* function from the vegan package was used to evaluate the relationship between functional attributes and the factors analyzed (zones and seasons).

Diversity indices (richness, Shannon-Wiener, and Simpson's dominance) were estimated using functions from the vegan package (Dixon 2003). To address the non-normality and heterogeneity of variances in the data, the univariate version of PERMANOVA from the vegan package (Dixon 2003) was used to investigate the effects of seasons and zones on diversity indices and CPUE. Post-hoc tests were employed as needed to identify differences in diversity indices among zones. All data analysis was performed using the R 4.4.0 software (R Core Team 2024).

Results

A total of 12,483 individuals from 46 fish species were collected, encompassing 26 families and 15 orders (Supplementary Information IV). The most represented families in terms of species number were: Gerreidae (five species), Lutjanidae (four species), Mugilidae (four species), Poeciliidae (three species), and Gobiidae (three species). The orders with the highest number of species were: Acanthuriformes (11 species), Carangiformes (7 species), Gobiiformes (five species), and Mugiliformes (4 species).

Eight species comprised 90% of the total biomass (Fig. 2). All were typically brackish species except for the freshwater species *Poecilia vivipara* and *Oreochromis niloticus*. Species richness was highest in the lower zone (37 species), followed by the middle zone (16 species) and the upper zone (10 species). A considerable portion of species richness was found exclusively in the lower zone (68%), which also had the highest number of exclusive species (25). The only species present in all three zones was *P. vivipara*. Four non-native fish species were recorded: *Poecilia sphenops* and *O. niloticus* in the middle and upper zones, respectively, and *Betta splendens* and *Poecilia reticulata*, both in the upper zone.

Most of the total abundance was marine migrants (34.2%), followed by estuarine species (22.9%), freshwater species (21.6%), diadromous species (21.2%), and marine stragglers (0.1%). The lower zone exhibited the highest abundance of marine migrants, followed by estuarine species (Fig. 3), and recorded the exclusive presence of marine stragglers (0.2% of the abundance in this zone). Diadromous species were more prevalent in the middle (34.4%) and upper zones (26.8%). Freshwater species showed an increase in relative abundance from mouth to upstream: lower zone (1.4%), middle zone (26.8%), and upper zone (45.7%).

The taxonomic composition of the fish assemblage in the Cocó estuary exhibited a clear spatial structure according to the previously defined zones (Fig. 4a; Table 2). Pairwise comparisons between zones revealed distinct assemblages among the three zones (Table 3). However, no seasonal variation was detected (Table 2). Although PERMANOVA identified an interaction between zone and season (Table 2), post-hoc tests for zones and seasons did not reveal significant differences (Table 4). The functional composition of the fish assemblage also displayed significant spatial structure (Table 2), primarily along the first axis of the NMDS (Fig. 4b), but was similar over time (Table 2). Pairwise comparisons between zones indicated differences between the lower zone and the others (Table 3).

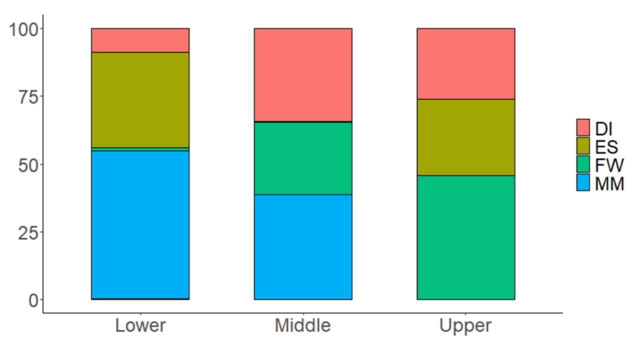

Fig. 3 Relative biomass distribution of fish guilds, based on estuarine use, across the three zones in the Cocó estuary. *DI* diadromous, *ES* estuarine, *FW* freshwater, *MM* marine migrant, *MS* marine straggler

Table 2 Results of PERMANOVA for comparing the taxonomic and functional composition of fish in the Cocó estuary (State of Ceará, Brazil), between zones and seasons

Composition	Factors	df	SS	F	p
Taxonomic	Zone	2	2.415	2.916	**0.001**
	Season	1	0.478	1.155	0.219
	Zone:season	2	1.074	1.297	**0.042**
	Residual	36	14.910		
Functional	Zone	2	199.128	4.037	**0.001**
	Season	1	15.896	0.645	0.783
	Zone:season	2	45.220	0.917	0.548
	Residual	36	887.756		

df Degrees of freedom, *SS* sum of squares, *F* F-value, *p* *p*-value

The visual assessment of the functional structure of the fish assemblage in space, along the first axis of the NMDS, was confirmed by ANOVA ($F = 17.78$, $p < 0.05$). The *envfit* function applied to the first axis revealed two sets of attributes correlated with different zones. Since our results did not detect significant differences in functional composition between the middle and upper zones (Table 3), these zones were pooled together in graphical representation (Fig. 5). The lower zone showed a significant correlation with marine migrant and marine straggler species, as well as with herbivores, macrocarnivores, and planktivores. This zone also exhibited associations with higher values for the following morphological attributes: caudal peduncle traction (Cpt), caudal aspect (CFar), oral cavity shape (Osh), body transverse shape (Bsh), and body mass (logM). In contrast, the middle and upper zones were more strongly correlated with freshwater species, omnivores, species adapted to hypoxic

Fig. 4 NMDS of the taxonomic composition **a** and functional composition **b** of the fish assemblage in the Cocó estuary

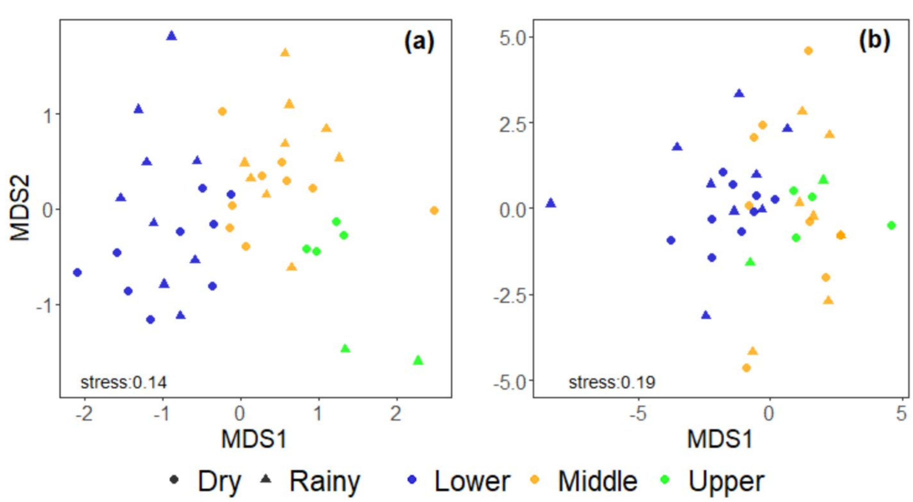

Table 3 Results of the PERMANOVA post-hoc pairwise comparisons for the taxonomic and functional composition of fish in the Cocó estuary (State of Ceará, Brazil), between zones

Composition	Comparisons	df	SS	F	p adj
Taxonomic	Lower vs middle	1	1.328	3.102	**0.003**
	Lower vs upper	1	1.133	2.607	**0.003**
	Middle vs upper	1	1.102	2.753	**0.003**
Functional	Lower vs middle	1	156.934	6.289	**0.003**
	Lower vs upper	1	87.295	3.762	**0.003**
	Middle vs upper	1	25.779	1.053	1

df degrees of freedom, *SS* dum of squares, *F* F-value, *p adj p*-value with Bonferroni correction

Table 4 Results of the PERMANOVA post-hoc pairwise comparisons for the interaction between seasons for the fish in the Cocó estuary (State of Ceará, Brazil)

Comparisons	SS	F	p adj
(Lower) dry vs rainy	0.549	1.235	1
(Middle) dry vs rainy	0.329	0.801	1
(Upper) dry vs rainy	0.675	2.197	1

SS sum of squares, *F* F-value, *p adj p*-value with Bonferroni correction

conditions, and a higher body cross-sectional area index (Bsf).

The factors zone and season were significant in explaining the differences in diversity values observed, but no interaction between these two factors was detected (Table 5). The mean richness in the lower zone was significantly different from that in the other two zones (Table 6; Fig. 6a). No significant difference in richness was found between the middle and upper zones. The Shannon-Wiener index was higher in both the lower and upper zones, with no significant difference between them (Table 6; Fig. 6b). Conversely, Simpson's dominance index was higher in the middle zone (Fig. 6c). No significant difference in this index was observed between the lower and upper zones (Table 6). Regarding seasons, richness and Shannon-Wiener index were higher during the dry period, while Simpson's dominance was higher during the wet period (Fig. 6d–f).

CPUE values were highest in the upper zone (3.89 g/m$^2 \pm 3.94$), followed by the lower zone (1.86 g/m$^2 \pm 1.87$) and the middle zone (1.29 g/m$^2 \pm 2.30$). Regarding the seasons, CPUE was greater during the dry season (2.69 g/m$^2 \pm 3.11$) compared to the wet season (1.03 g/m$^2 \pm 1.15$) (Fig. 7). However, PERMANOVA indicated significant differences only between seasons ($F = 4.16$, $p = 0.04$). Differences between zones and the interaction between zones and seasons were not significant (zone: $F = 2.71$, $p = 0.07$; zone:season: $F = 0.51$, $p = 0.57$).

Discussion

Consistent with the initial hypotheses, our results confirm the presence of a spatial structure in the fish assemblage, characterized by distinct zones along the estuarine gradient and accompanied by temporal homogenization. The Cocó estuary exhibited a clear spatial pattern in its fish fauna from a taxonomic perspective, with distinct richness and composition across the different estuarine zones. From a functional perspective, there was homogenization in fish community

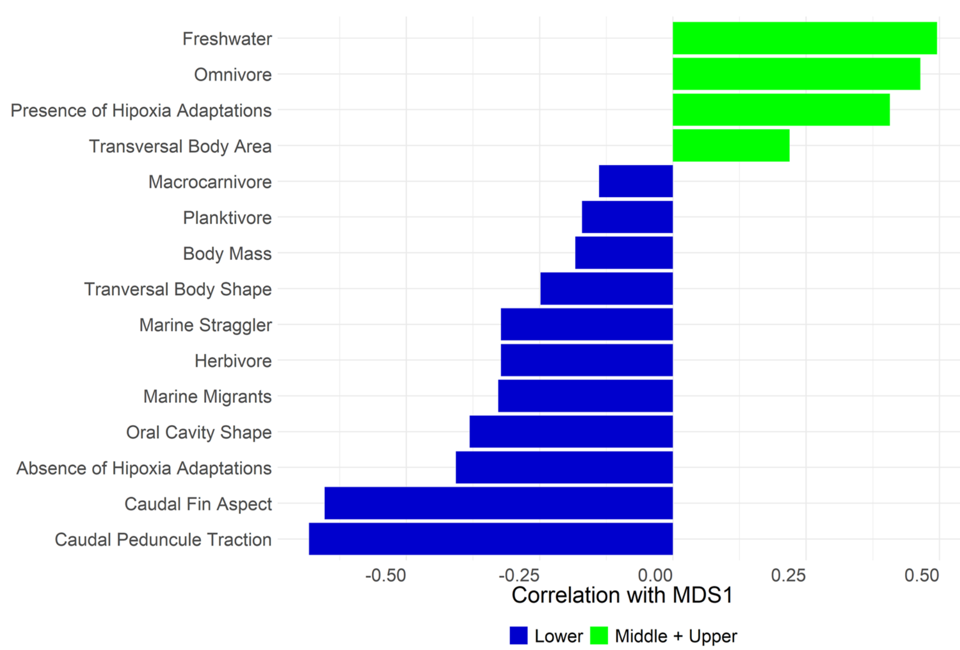

Fig. 5 Correlations between the attributes of fish assemblages in the Cocó estuary and the values of the first NMDS axis. Blue: attributes related to the lower zone. Green: attributes related to the midlle and upper zones

Table 5 Results of PERMANOVA to assess the effect of the factors zone and season on the diversity indices of the fish fauna in the Cocó estuary

	Factor	df	SS	F	p
Richness	Zone	2	219.778	14.179	**< 0.001**
	Season	1	35.551	4.587	**0.039**
	Zone:season	2	6.171	0.398	0.674
	Residuals	36	279.000		
Shannon-Wiener	Zone	2	7.165	20.066	**< 0.001**
	Season	1	2.364	13.238	**0.001**
	Zone:season	2	0.243	0.680	0.513
	Residuals	36	6.428		
Simpson	Zone	2	1.516	16.774	**< 0.001**
	Season	1	0.554	12.255	**0.001**
	Zone:season	2	0.018	0.199	0.820
	Residuals	36	1.627		

df Degrees of freedom, *SS* sum of Squares, *F* F-value, *p p*-value

Table 6 Results of PERMANOVA post-hoc pairwise comparisons of diversity indices between zones in the Cocó estuary fish fauna

	Pairwise comparisons	SS	F	P_{adj}
Richness	Lower vs middle	1.172	14.262	**0.003**
	Lower vs upper	0.294	5.203	**0.033**
	Middle vs upper	0.208	2.711	0.279
Shannon-Wiener	Lower vs middle	6.904	29.562	**0.003**
	Lower vs upper	0.204	0.666	1.000
	Middle vs upper	1.979	12.793	**0.012**
Simpson	Lower vs middle	1.377	24.545	**0.006**
	Lower vs upper	0.004	0.066	1.000
	Middle vs upper	0.584	12.158	**0.018**

SS sum of squares, *F* F-value, *p adj p*-value with Bonferroni correction

composition within the middle and upper zones. This result can be attributed to the lower salinity and shorter water residence time in these zones, which favored the presence of freshwater species and those tolerant to hypoxia. The characteristics of the fish assemblage in the estuary revealed by this study can be directly linked to alterations in the ecosystem due to the influence of a major urban center. The interbasin water transfer through effluent discharge to which the system is subjected modifies a range of physico-chemical characteristics of the water as well as the regular seasonal patterns of estuarine environmental conditions (Barroso et al. 2016; Schettini et al. 2017). These impacts appear to shape both the spatial and temporal patterns of fish diversity, with effects that may also influence the functioning and resilience of the ecosystem.

Distinct features of the fish assemblage

In the semi-arid coastal region of Brazil, high salinity values and seasonal occurrences of hypersalinity are natural factors that limit the presence of freshwater species in estuaries (Gurgel-Lourenço et al. 2023a, b). The fish fauna of the Cocó estuary exhibits characteristics that set it apart from the regional pattern. The continuous influx of freshwater through interbasin water transfer promotes a higher proportion of freshwater species, a proportion considered atypical, especially for regions with low precipitation (Whitfield 2015). The relatively low species richness recorded in this study (46), compared to other estuaries in the semi-arid coastal region of Brazil (between 71 and 95 species) (Gurgel-Lourenço et al. 2023b), can be explained by several factors.

First, there is evidence of a positive relationship between salinity and estuarine fish richness (Vergès et al. 2022; Gurgel-Lourenço et al. 2023a). This correlation is expected since most of the species pooled in estuarine assemblages are of marine origin (Whitfield et al. 2012), which is much more speciose than the freshwater fauna of the region (Lima

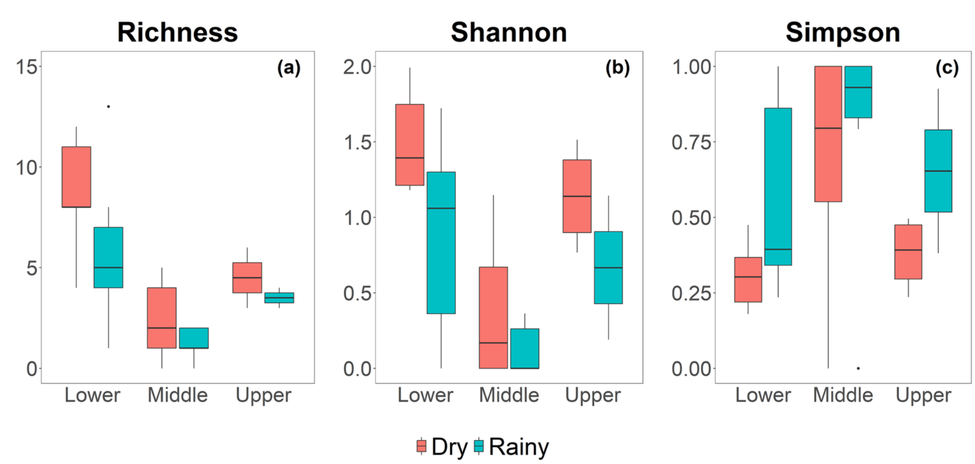

Fig. 6 Richness **a**, Shannon diversity **b** and Simpson dominance index **c** values by zone and season for the Cocó estuary fish assemblage

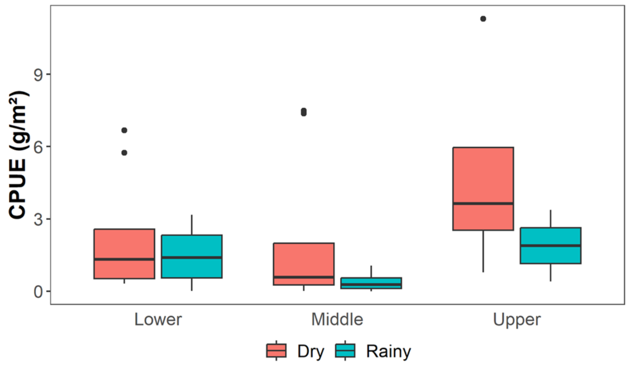

Fig. 7 Capture per unit effort (CPUE, g/m^2) across zones and seasons for the Cocó estuary fish assemblage

et al. 2017; Rosa et al. 2023). Therefore, the increased influx of freshwater into the estuary through interbasin water transfer results in a loss of habitat suitability for marine species. Additionally, another factor contributing to the uniqueness of this assemblage is the high volume of effluents received by the system (Schettini et al. 2017), which decreases water quality (Silva et al. 2004; Barroso et al. 2016; Schettini et al. 2017) and also likely contributes to the lower species richness in the estuary. High concentrations of nitrate and phosphate in the water are associated with anthropogenic activities such as wastewater runoff (Camargo and Alonso 2006) and are negatively correlated with fish richness (Duque et al. 2020). These two factors have shaped an assemblage with species exhibiting traits related to freshwater affinity and tolerance to low oxygen levels, particularly evident in the fish fauna of the middle and upper zones.

Species such as *P. vivipara* and *O. niloticus* are among those with the highest biomass representation in the assemblage. These species are typically freshwater, but since they originate from evolutionary lineages that were originally marine, they are classified as physiologically secondary or peripheral and can tolerate moderate salinity levels (Myers 1949; Franco et al. 2024). In addition to their freshwater affinity, these species also possess adaptations for surviving in hypoxic conditions. Species of the genus *Poecilia* can utilize surface oxygen (Kramer and Mehegan 1981), and *O. niloticus* can reduce its metabolism in oxygen-poor environments (Bergstedt et al. 2021).

Another notable feature of this assemblage was the significant abundance of *Megalops atlanticus* recorded, which was the second most biomass-representative species. The presence and high abundance of this species have not been reported in other estuaries in the region (Gurgel-Lourenço et al. 2023a, b). Although of marine origin, juveniles of this species have a strong affinity for freshwater environments (Kurth et al. 2019; Navarro-Martinez et al. 2020). Additionally, they possess a swim bladder with four rows of highly vascularized tissue that allows atmospheric oxygen uptake, aiding their survival in hypoxic conditions (Geiger et al. 2000). These two characteristics enable this species to thrive in the environment of the Cocó estuary, characterized by low salinity and water quality. Currently assessed as 'vulnerable' globally by the International Union for Conservation of Nature (IUCN) (Adams et al. 2019) and nationally by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio 2018), its presence in an ecosystem like the Cocó estuary suggests a conservation paradox, where, counterintuitively, more anthropogenically impacted conditions seem to benefit an endangered species.

The fish assemblage of the Cocó estuary records the highest number of non-native species among estuarine ecosystems on the semi-arid coast of Brazil (Gurgel-Lourenço et al. 2023b). This study provides a detailed spatial breakdown of the occurrence of these species, which were recorded primarily in the middle and upper zones. In addition to the greater number of non-native species, they are also notably abundant: *O. niloticus* is among the eight species that account for 90% of the total biomass captured. The lower salinity and poor water quality in these zones seem to favor the presence of non-native species, all of which are freshwater species with adaptations to hypoxic environments (Kramer and Mehegan 1981; Mendez-Sanchez and Burggren 2017; Bergstedt et al. 2021). Another characteristic of the non-native species recorded is trophic plasticity (de Carvalho et al. 2019; Ganassin et al. 2020; Tesfahun and Alebachew 2023), recognized as a determining attribute in colonization success (Bernery et al. 2024) and adaptation to degraded environments (Wootton 2017). The observed pattern suggests a synergistic interaction between different anthropogenic vectors (Comte et al. 2021): the high urbanization of the region increases the pressure from non-native species propagules, while interbasin water transfer, through the influx of freshwater with high nutrient concentrations, creates less favorable conditions for native fish species.

Effects of anthropogenic impacts on assemblage dynamics

No differences in taxonomic composition were detected when comparing the dry and rainy seasons. Thus, the results indicate the presence of a spatial structure in the assemblage that remained stable throughout the entire evaluated seasonal cycle. Interbasin water transfer creates stable environmental conditions across the different zones throughout the year due to the continuous influx of effluents (Schettini et al. 2017). Salinity is the primary factor that structures patterns of fish diversity in estuaries across space and time (Barletta et al. 2005). The Cocó estuary consistently maintained a positive salinity profile throughout the sampling period. Therefore, the maintenance of the same salinity gradient pattern may explain the temporal stability of the spatial structure of the assemblage. Another contributing factor to this result is the constant discharge of effluents with high nutrient concentrations into the system. There is evidence that assemblages subjected to eutrophication exhibit a high degree of temporal homogenization in their composition (Cook et al. 2018).

Distinct composition among different sections of the ecosystem is commonly found in estuaries (Barletta and Lima 2019). Variation in environmental characteristics across space generates different sectors within the ecocline and acts as a filter that selects different sets of species based on their affinities and tolerances (Barletta et al. 2017). However, the position of the ecocline sectors shifts along the longitudinal axis of the estuary according to precipitation patterns (Barletta et al. 2008). Estuarine fish assemblages respond to these changes and undergo seasonal rearrangements (da Silva et al. 2021; Souto-Vieira et al. 2023). During the dry season, greater intrusion of saline waters commonly favors the occurrence of marine stragglers, particularly in the lower zones of the estuary (Potter et al. 2015). On the other hand, during the rainy season, marine species tend to occur closer to the mouth in zones with higher salinity values (Potter et al. 2015). These patterns of natural variability are crucial for structuring and maintaining estuarine fish biodiversity, supporting the presence of species with different environmental preferences within the same ecosystem.

A spatial structure in the assemblage without changes over time may indicate limited connectivity between different zones of the estuary. Species movement between different zones is quite restricted in the Cocó estuary. Only one species (*Poecilia vivipara*) occurs throughout the entire estuary, and the number of species found exclusively in just one of the three zones is relatively high. Variation in species occurrence patterns over time is a key factor for the functioning and resilience of estuarine ecosystems (Silva et al. 2023). Species movement is responsible for the transport of biomass between different zones and contributes to organic matter cycling in the system (Deegan 1993; Arantes et al. 2019). Moreover, movement between different parts of the estuary is essential for some species to access different habitats and resources throughout their ontogeny (Jaureguizar et al. 2004; Dantas et al. 2010; Ramos et al. 2016), maximizing their growth and survival conditions (Gillanders 2005; Dingle and Drake 2007).

Similar to the taxonomic composition, the diversity indices of the fish assemblage also showed significant differences between the zones. Species richness was higher in the lower zone due to its greater proximity to the marine species pool and more favorable environmental conditions (Vergès et al. 2022). The closer proximity to the sea in this zone results in shorter water residence times, contributing to higher salinity values and better water quality parameters. Conversely, the middle zone exhibited the lowest Shannon-Wiener diversity values and the highest Simpson's dominance. In this zone, environmental conditions may be more stressful because of reduced water quality resulting from longer residence times and increased freshwater influence. Consequently, these two factors likely act together as a strong environmental filter, diminishing the diversity values of the fish assemblage in this part of the estuary.

The Cocó estuary has a smaller area of direct marine influence compared to other systems along the semi-arid coast of Brazil (Gurgel-Lourenço et al. 2023a). Although environmental factors are widely recognized as the primary determinants of estuarine fish assemblage structure, biotic interactions should not be dismissed as irrelevant (Whitfield 1999). A smaller area with suitable conditions for marine species can affect coexistence processes based on spatial niche segregation (Hofer et al. 2004) among species of this group. Evidence suggests that similar species within the same family exhibit spatial distribution patterns that reflect resource partitioning, such as in Gerreidae (Araújo et al. 2016; Silva et al. 2016) and Gobiidae (Shi et al. 2014). With less available area for these species to establish themselves, those with competitive advantages may dominate the assemblage and potentially lead to the local extinction of others, thereby reducing the overall diversity of the ecosystem (Tilman 1994; Chesson 2000). For instance, species commonly found in other estuaries along the semi-arid coast of Brazil were not recorded in the Cocó, such as *Gobionellus* spp., *Rhinosardinia amazonica*, *Oligoplites* spp., *Haemulopsis corvinaeformis*, Sciaenidae, and others (Gurgel-Lourenço et al. 2023a, b).

From a functional composition perspective, the middle and upper zones did not show significant differences between between each other, suggesting a similar ecosystem functioning (Villéger et al. 2017) and some degree of functional redundancy (Naeem 1998). The primary attributes associated with these zones were freshwater guilds, omnivory, and adaptations to hypoxia. This combination of attributes allows species to persist despite the local environmental conditions. Indeed, the greater distance from the sea in these zones impedes the penetration of salinity. Additionally, the closer proximity to wastewater discharge sources and the longer water residence time contribute to poorer water quality parameters in these zones.

Analyzing the functional attributes related to species' diets allows for inferences about differences in ecosystem functioning along the longitudinal gradient of the estuary. A higher diversity of trophic guilds (macrocarnivores, herbivores, planktivores) was associated with the lower zone, while the contribution of omnivores was greater in the middle and upper zones. Omnivorous species are better suited to surviving in eutrophicated environments (Ritterbusch et al. 2022). Dietary plasticity enables adaptation to different trophic positions based on resource availability (Wootton

2017). Nutrient enrichment has the potential to alter estuarine productivity and influence higher trophic levels, thereby affecting the trophic organization of fish assemblages (Warry et al. 2016; Horka et al. 2023). These differences in the trophic composition of the fish assemblage indicate variations in the functioning of the trophic web throughout the ecosystem. The lower diversity of trophic guilds in the upstream zones of the estuary suggests a more simplified trophic web, which may also influence ecosystem characteristics such as resistance and resilience (O'Gorman et al. 2012).

Seasonal differences in fish assemblage biomass did not follow the patterns commonly described in the literature. Generally, higher biomass values for estuarine fish are observed during the rainy season (Blaber and Barletta 2016) because of the increased nutrient concentrations brought by continental freshwater inputs, which boost ecosystem productivity (Saeck et al. 2013). Thus, an increased availability of resources would attract a greater abundance of marine-origin fish to the estuary (Vergès et al. 2022). However, the seasonal dynamics of nutrients can be altered in anthropogenically influenced estuaries (Statham 2012; Guenther et al. 2015). In the Cocó estuary, higher concentrations of nutrients and chlorophyll-a were found during the dry period (Barroso et al. 2016). This pattern occurred because of the dilution of sewage discharge points caused by freshwater influx during the rainy season (Eyre and Ferguson 2006; Barroso et al. 2016). Other factors contributing to the lower estuarine fish biomass during the rainy season may include reduced oxygen and salinity levels recorded during this period (Barroso et al. 2016). Thus, the higher biomass during the dry season deviates from the typical patterns observed in other estuarine ecosystems and seems to be directly related to anthropogenic interference in the system.

While this study provides valuable insights into the dynamics of estuarine fish assemblages under anthropogenic conditions, certain limitations must be acknowledged. The number of sampling locations was relatively small ($n = 9$); however, it is important to consider the regional natural characteristics, marked by low-inflow and short estuarine systems (Schettini et al. 2017; Soares et al. 2021). Our data collection was limited to a single year of sampling and can be interpreted as a temporal snapshot. A deeper understanding of seasonal patterns in fish assemblages could be achieved through multi-year datasets. This would require establishing a long-term monitoring program for fish assemblages and water quality. Continuous monitoring would be crucial for detecting and understanding emerging impacts on biodiversity, particularly in an urbanized ecosystem such as the one studied here (Gangloff et al. 2016; Rosso et al. 2023). Despite these constraints, this study contributes to the growing body of literature highlighting anthropogenic impacts on estuarine fish assemblages globally. As such, the findings presented here also serve as a microcosm for addressing similar challenges in other regions.

Conclusion

This study highlights the changes that interbasin water transfer can induce in estuarine fish assemblages. Compared to other estuaries in the same region of Brazil's semi-arid coast, the Cocó estuary exhibits distinctive ichthyofaunal characteristics due to the impacts of increased freshwater input and deteriorated water quality resulting from this intervention. The greater presence of freshwater fish species and species adapted to hypoxia, including non-native ones, is directly related to these impacts. The lack of seasonal variability in the fish assemblage indicates a loss of the natural dynamics of the system, essential for biodiversity generation mechanisms. The results suggest that fundamental factors for ecosystem functioning, such as biomass flow between different areas and trophic structure, may be altered because of interbasin water transfer.

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Data availability All data on the fish assemblage and the functional attributes of the species that support the findings of this study are included in the Supplementary Information files.

Declarations

Conflict of interest The authors declare no competing interests.

References

Adams AK, Guindon K, Horodysky T, et al (2019) *Megalops atlanticus*. The IUCN Red List of Threatened Species 2019

Anderson MJ (2017) Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online. John Wiley Sons Ltd, NY, pp 1–15

Arantes CC, Fitzgerald DB, Hoeinghaus DJ, Winemiller KO (2019) Impacts of hydroelectric dams on fishes and fisheries in tropical rivers through the lens of functional traits. Curr Opin Environ Sustain 37:28–40. https://doi.org/10.1016/j.cosust.2019.04.009

Attrill MJ, Rundle SD (2002) Ecotone or Ecocline: Ecological Boundaries in Estuaries. Estuar Coast Shelf Sci 55:929–936. https://doi.org/10.1006/ecss.2002.1036

Barletta M, Lima ARA (2019) Systematic Review of Fish Ecology and Anthropogenic Impacts in South American Estuaries: Setting Priorities for Ecosystem Conservation. Front Mar Sci 6:237. https://doi.org/10.3389/fmars.2019.00237

Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G (2005) The role of salinity in structuring the fish assemblages in a tropical estuary. J Fish Biol 66:45–72. https://doi.org/10.1111/j.0022-1112.2005.00582.x

Barletta M, Amaral CS, Corrêa MFM et al (2008) Factors affecting seasonal variations in demersal fish assemblages at an ecocline in a tropical–subtropical estuary. J Fish Biol 73:1314–1336. https://doi.org/10.1111/j.1095-8649.2008.02005.x

Barletta M, Lima ARA, Costa MF, Dantas DV (2017) Estuarine Ecoclines and the Associated Fauna: Ecological Information as the Basis for Ecosystem Conservation. In: Finkl CW, Makowski C (eds) Coastal Wetlands: Alteration and Remediation. Springer International Publishing, Cham, pp 479–512

Bergstedt JH, Pfalzgraff T, Skov PV (2021) Hypoxia tolerance and metabolic coping strategies in *Oreochromis niloticus*. Comp Biochem Physiol A Mol Integr Physiol 257:110956. https://doi.org/10.1016/j.cbpa.2021.110956

Bernery C, Bellard C, Courchamp F et al (2024) A global analysis of the introduction pathways and characteristics associated with non-native fish species introduction, establishment, and impacts. Ecol Process 13:22. https://doi.org/10.1186/s13717-024-00495-8

Blaber SJM, Barletta M (2016) A review of estuarine fish research in South America: what has been achieved and what is the future for sustainability and conservation? J Fish Biol 89:537–568. https://doi.org/10.1111/jfb.12875

Camargo JA, Alonso Á (2006) Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: A global assessment. Environ Int 32:831–849. https://doi.org/10.1016/j.envint.2006.05.002

Carlson RE (1977) A trophic state index for lakes. Limnol Oceanogr 22:361–369. https://doi.org/10.4319/lo.1977.22.2.0361

Chaves MCNR, Franco ACS, Seixas LB et al (2018) Testing the ecocline concept for fish assemblages along the marine-estuarine gradient in a highly-eutrophic estuary (Guanabara Bay, Brazil). Estuar Coast Shelf Sci 211:118–126. https://doi.org/10.1016/j.ecss.2018.02.004

Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annu Rev Ecol Syst 31:343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Comte L, Grantham T, Ruhi A (2021) Human stabilization of river flows is linked with fish invasions across the USA. Glob Ecol Biogeogr 30:725–737. https://doi.org/10.1111/geb.13258

Cook SC, Housley L, Back JA, King RS (2018) Freshwater eutrophication drives sharp reductions in temporal beta diversity. Ecology 99:47–56. https://doi.org/10.1002/ecy.2069

Costa CR, Costa MF, Dantas DV, Barletta M (2018) Interannual and Seasonal Variations in Estuarine Water Quality. Front Mar Sci 5:301. https://doi.org/10.3389/fmars.2018.00301

da Silva VEL, Dolbeth M, Fabré NN (2021) Assessing tropical coastal dynamics across habitats and seasons through different dimensions of fish diversity. Mar Environ Res 171:105458. https://doi.org/10.1016/j.marenvres.2021.105458

Dantas DV, Barletta M, Costa MF et al (2010) Movement patterns of catfishes (Ariidae) in a tropical semi-arid estuary. J Fish Biol 76:2540–2557. https://doi.org/10.1111/j.1095-8649.2010.02646.x

de Barroso H, S, Becker H, Melo VMM, (2016) Influence of river discharge on phytoplankton structure and nutrient concentrations in four tropical semiarid estuaries. Braz J Oceanogr 64:37–48. https://doi.org/10.1590/S1679-87592016101406401

de Araújo ALF, Dantas RP, Pessanha ALM (2016) Feeding ecology of three juvenile mojarras (Gerreidae) in a tropical estuary of northeastern Brazil. Neotrop Ichthyol 14:e150039. https://doi.org/10.1590/1982-0224-20150039

de Carvalho DR, Flecker AS, Alves CBM et al (2019) Trophic responses to aquatic pollution of native and exotic livebearer fishes. Sci Total Environ 681:503–515. https://doi.org/10.1016/j.scitotenv.2019.05.092

de Freitas PP, Menezes MOB, Schettini CAF (2015) Hydrodynamics and particulate suspended matter transport in a shallow and highly urbanized estuary: the Cocó estuary, Fortaleza, Brazil. Braz J Geophys 33:579–590

de Medeiros APM, de Xavier JH, A, Rosa IM de L, et al (2017) Diet and trophic organization of the fish assemblage from the Mamanguape River Estuary, Brazil. Lat Am J Aquat Res 45:879–890. https://doi.org/10.3856/vol45-issue5-fulltext-2

De Lima LG, Araújo FG, Macário BS, Pessanha ALM (2024) Larval fish assemblages in selected Brazilian estuaries: Species-environment relationships under different anthropogenic influences. Mar Pollut Bull 198:115858. https://doi.org/10.1016/j.marpolbul.2023.115858

Deegan LA (1993) Nutrient and Energy Transport between Estuaries and Coastal Marine Ecosystems by Fish Migration. Can J Fish Aquat Sci 50:74–79. https://doi.org/10.1139/f93-009

Dingle H, Drake VA (2007) What Is Migration? Bioscience 57:113–121. https://doi.org/10.1641/B570206

Dixon P (2003) VEGAN, a package of R functions for community ecology. J Veg Sci 14:927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x

Duque G, Gamboa-García DE, Molina A, Cogua P (2020) Effect of water quality variation on fish assemblages in an anthropogenically impacted tropical estuary, Colombian Pacific. Environ Sci Pollut Res 27:25740–25753. https://doi.org/10.1007/s11356-020-08971-2

Eyre BD, Ferguson AJP (2006) Impact of a flood event on benthic and pelagic coupling in a sub-tropical east Australian estuary (Brunswick). Estuar Coast Shelf Sci 66:111–122. https://doi.org/10.1016/j.ecss.2005.08.008

Franco ACS, Azevedo-Santos VM, de Nogueira MAM, P, et al (2024) Tilapia venturing into high-salinity environments: A cause for concern? Aquat Ecol 58:47–55. https://doi.org/10.1007/s10452-023-10069-z

Froese R, Pauly D (2024) FishBase. www.fishbase.org. Accessed 10 May 2024

Ganassin MJM, Frota A, Muniz CM et al (2020) Urbanisation affects the diet and feeding selectivity of the invasive guppy *Poecilia reticulata*. Ecol Freshw Fish 29:252–265. https://doi.org/10.1111/eff.12511

Gangloff MM, Edgar GJ, Wilson B (2016) Imperilled species in aquatic ecosystems: emerging threats, management and future prognoses. Aquat Conserv Mar Freshwat Ecosyst 26:858–871. https://doi.org/10.1002/aqc.2707

Geiger SP, Torres JJ, Crabtree RE (2000) Air Breathing and Gill Ventilation Frequencies in Juvenile Tarpon, *Megalops atlanticus*: Responses to Changes in Dissolved Oxygen, Temperature, Hydrogen Sulfide, and PH. Environ Biol Fishes 59:181–190. https://doi.org/10.1023/A:1007640132059

Gillanders BM (2005) Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuar Coast Shelf Sci 64:47–57. https://doi.org/10.1016/j.ecss.2005.02.005

Guenther M, Araújo M, Flores-Montes M et al (2015) Eutrophication effects on phytoplankton size-fractioned biomass and production at a tropical estuary. Mar Pollut Bull 91:537–547. https://doi.org/10.1016/j.marpolbul.2014.09.048

Gurgel-Lourenço RC, Rodrigues-Filho CAS, Pinto LM, Sánchez-Botero JI (2023a) Prolonged drought influences the taxonomic and functional structure of fish assemblages in estuaries along the Brazilian semiarid coast. Hydrobiologia 850:4443–4466. https://doi.org/10.1007/s10750-022-05059-5

Gurgel-Lourenço RC, Silva LDM, Mesquita Pinto L et al (2023b) Fish fauna from the estuaries of Ceará state, Brazil: a checklist in support of conservation of the Brazilian semiarid coast. Check List. https://doi.org/10.15560/19.1.63

Harrison TD, Whitfield AK (2021) A global assessment of fish estuary associations: A numerical approach to assessing estuary-associated fish functional guilds. Fish Fish 22:874–898. https://doi.org/10.1111/faf.12558

He B, Dai M, Zhai W et al (2014) Hypoxia in the upper reaches of the Pearl River Estuary and its maintenance mechanisms: A synthesis based on multiple year observations during 2000–2008. Mar Chem 167:13–24. https://doi.org/10.1016/j.marchem.2014.07.003

Hofer U, Bersier L-F, Borcard D (2004) Relating niche and spatial overlap at the community level. Oikos 106:366–376. https://doi.org/10.1111/j.0030-1299.2004.12786.x

Horka P, Musilova Z, Holubova K et al (2023) Anthropogenic nutrient loading affects both individual species and the trophic structure of river fish communities. Front Ecol Evol 10:1076451. https://doi.org/10.3389/fevo.2022.1076451

IBGE (2022) Censo Brasileiro de 2022. https://censo2022.ibge.gov.br/panorama/ . Accessed 10 Jul 2024

ICMBio (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Brasília - DF

IPECE (2024) Ceará em Mapas Interativos. https://www.ipece.ce.gov.br/ceara-em-mapas-interativos/. Accessed 10 Jul 2024

Jaureguizar AJ, Menni R, Guerrero R, Lasta C (2004) Environmental factors structuring fish communities of the Río de la Plata estuary. Fish Res 66:195–211. https://doi.org/10.1016/S0165-7836(03)00200-5

Jeppesen R, Rodriguez M, Rinde J et al (2018) Effects of Hypoxia on Fish Survival and Oyster Growth in a Highly Eutrophic Estuary. Estuar Coast 41:89–98. https://doi.org/10.1007/s12237-016-0169-y

Kramer DL, Mehegan JP (1981) Aquatic surface respiration, an adaptive response to hypoxia in the guppy, *Poecilia reticulata* (Pisces, Poeciliidae). Environ Biol Fish 6:299–313. https://doi.org/10.1007/BF00005759

Kurth BN, Peebles EB, Stallings CD (2019) Atlantic Tarpon (*Megalops atlanticus*) exhibit upper estuarine habitat dependence followed by foraging system fidelity after ontogenetic habitat shifts. Estuar Coast Shelf Sci 225:106248. https://doi.org/10.1016/j.ecss.2019.106248

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Lavorel S, Grigulis K, McIntyre S et al (2008) Assessing functional diversity in the field – methodology matters! Funct Ecol 22:134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x

Lima SMD, Garcez DS (2017) Áreas verdes públicas urbanas e sua relação com a melhoria da qualidade de vida: um estudo de caso em um Parque Ecológico Urbano na cidade de Fortaleza (Ceará, Brasil). Rev Bras Ciênc Ambient. https://doi.org/10.5327/Z2176-947820170126

Lima SMQ, Ramos TPA, da Silva MJ, de Souza RR (2017) Diversity, Distribution, and Conservation of the Caatinga Fishes: Advances and Challenges. In: da Silva JMC, Leal IR, Tabarelli M (eds) Caatinga: The Largest Tropical Dry Forest Region in South America. Springer International Publishing, Cham, pp 97–131

Loreau M, Mazancourt C (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16:106–115. https://doi.org/10.1111/ele.12073

Macedo MM, Angelini R, da Silva VictorEL, Fabré NN, (2021) Trophic structure of coastal meta-ecosystems in the tropical Southwestern Atlantic. Estuar Coast Shelf Sci 263:107654. https://doi.org/10.1016/j.ecss.2021.107654

Macedo M, Fabré NN, Da Silva VEL et al (2023) Influence of the river flow pulse on the maturity, resilience, and sustainability of tropical coastal ecosystems. Mar Environ Res 183:105806. https://doi.org/10.1016/j.marenvres.2022.105806

Malone TC, Newton A (2020) The globalization of cultural eutrophication in the coastal ocean: causes and consequences. Front Mar Sci. https://doi.org/10.3389/fmars.2020.00670

Martinez PA (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis

Mendez-Sanchez JF, Burggren WW (2017) Cardiorespiratory physiological phenotypic plasticity in developing air-breathing anabantid fishes (Betta splendens and Trichopodus trichopterus). Physiol Rep. https://doi.org/10.14814/phy2.13359

Molina A, Duque G, Cogua P (2020) Influences of environmental conditions in the fish assemblage structure of a tropical estuary. Mar Biodivers 50:5. https://doi.org/10.1007/s12526-019-01023-0

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLoS ONE 6:e17476. https://doi.org/10.1371/journal.pone.0017476

Moura ÍJM, Santos DFD, Pinheiro FGDM, Oliveira CJD (2015) Caracterização dos períodos seco e chuvoso da cidade de Fortaleza-CE. Ciênc E Nat 37:3–7. https://doi.org/10.5902/2179460X16206

Mourão FV, De Sousa ACSR, Da Luz Mendes RM et al (2020) Water quality and eutrophication in the Curuçá estuary in northern Brazil. Reg Stud Mar Sci 39:101450. https://doi.org/10.1016/j.rsma.2020.101450

Myers GS (1949) Salt-Tolerance of Fresh-Water Fish Groups in Relation to Zoogeographical Problems. Bijdr Tot Dierkd 28:315–322. https://doi.org/10.1163/26660644-02801038

Naeem S (1998) Species Redundancy and Ecosystem Reliability. Conserv Biol 12:39–45. https://doi.org/10.1111/j.1523-1739.1998.96379.x

Navarro-Martinez ZM, Angulo-Valdés J, Garcia-Córdova L, Adams A (2020) Habitat characterization of juvenile atlantic tarpon (Megalops atlanticus) in Isle of Youth, Cuba. Gulf Caribb Res. https://doi.org/10.18785/gcr.3101.08

O'Gorman EJ, Fitch JE, Crowe TP (2012) Multiple anthropogenic stressors and the structural properties of food webs. Ecology 93:441–448. https://doi.org/10.1890/11-0982.1

Potter IC, Tweedley JR, Elliott M, Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. Fish Fish 16:230–239. https://doi.org/10.1111/faf.12050

Powers SP, Peterson CH, Christian RR et al (2005) Effects of eutrophication on bottom habitat and prey resources of demersal fishes. Mar Ecol Prog Ser 302:233–243. https://doi.org/10.3354/meps302233

R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Ramos J, a. A, Barletta M, Dantas DV, Costa MF, (2016) Seasonal and spatial ontogenetic movements of Gerreidae in a Brazilian tropical estuarine ecocline and its application for nursery habitat conservation. J Fish Biol 89:696–712. https://doi.org/10.1111/jfb.12872

Ritterbusch D, Blabolil P, Breine J et al (2022) European fish-based assessment reveals high diversity of systems for determining ecological status of lakes. Sci Total Environ 802:149620. https://doi.org/10.1016/j.scitotenv.2021.149620

Rodrigues BN, Molina Junior VE, Canteras FB (2023) Green Infrastructure as a solution to mitigate the effects of climate change in a coastal area of social vulnerability in Fortaleza (Brazil). Environ Adv 13:100398. https://doi.org/10.1016/j.envadv.2023.100398

Rosa RS, Medeiros APM, Felinto A et al (2023) Marine teleost fishes of the northeastern Brazilian coast: 166 years of compiled data. Syst Biodivers 21:2228314. https://doi.org/10.1080/14772000.2023.2228314

Rosso JJ, Langerhans RB, Avigliano E (2023) Editorial: Fish as sentinels of urbanization impacts in aquatic ecosystems. Front environ sci 11:1190398. https://doi.org/10.3389/fenvs.2023.1190398

Saeck EA, O'Brien KR, Weber TR, Burford MA (2013) Changes to chronic nitrogen loading from sewage discharges modify standing stocks of coastal phytoplankton. Mar Pollut Bull 71:159–167. https://doi.org/10.1016/j.marpolbul.2013.03.020

Schettini CAF, Valle-Levinson A, Truccolo EC (2017) Circulation and transport in short, low-inflow estuaries under anthropogenic stresses. Reg Stud Mar Sci 10:52–64. https://doi.org/10.1016/j.rsma.2017.01.004

SEMA (2024a) Plano de Manejo do Parque Estadual do Cocó. https://www.sema.ce.gov.br/wp-content/uploads/sites/36/2021/03/PMPC_01.pdf. Accessed 10 Jul 2024

SEMA (2024b) Parque Estadual do Cocó. https://www.sema.ce.gov.br/gestao-de-ucs/unidades-de-conservacao-de-protecao-integral/parques/parque-estadual-do-coco_/. Accessed 10 Jul 2024

Shi YR, Chao M, Quan WM, Shen XQ (2014) Spatial and seasonal variations in fish assemblages of the Yangtze River estuary. J Appl Ichthyol 30:844–852. https://doi.org/10.1111/jai.12448

Silva AIM, Vieira RHSF, Menezes FGR et al (2004) Bacteria of fecal origin in mangrove oysters (*Crassostrea rhizophorae*) in the Cocó River estuary, Ceará State, Brazil. Braz J Microbiol 35:126–130. https://doi.org/10.1590/S1517-83822004000100021

Silva RS, Carvalho KD, Pessanha ALM (2016) Distribution and feeding ecology of three juvenile mojarras in a hypersaline tropical estuary in Northeastern Brazil. Mar Ecol 37:1266–1281. https://doi.org/10.1111/maec.12316

Silva ACB, De Barros MSF, Da Silva VEL et al (2023) Composition and distribution of fish assemblages in a tropical river–estuarine continuum. Hydrobiologia 850:4467–4477. https://doi.org/10.1007/s10750-023-05172-z

Smith VH (2003) Eutrophication of freshwater and coastal marine ecosystems a global problem. Environ Sci Pollut Res 10:126–139. https://doi.org/10.1065/espr2002.12.142

Soares MO, Campos CC, Carneiro PBM et al (2021) Challenges and perspectives for the Brazilian semi-arid coast under global environmental changes. Perspect Ecol Conserv 19:267–278. https://doi.org/10.1016/j.pecon.2021.06.001

Souto-Vieira D, da Silva VEL, Fabré NN (2023) Seasonal rearrangements in the use of coastal habitat mosaics by tropical fishes create a cyclic functional trajectory. Reg Stud Mar Sci 67:103225. https://doi.org/10.1016/j.rsma.2023.103225

Statham PJ (2012) Nutrients in estuaries — An overview and the potential impacts of climate change. Sci Total Environ 434:213–227. https://doi.org/10.1016/j.scitotenv.2011.09.088

Tesfahun A, Alebachew S (2023) Food and feeding habits of the Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) from Ribb reservoir, Lake Tana sub-basin. Ethiopia Cogent Food Agric 9:2212457. https://doi.org/10.1080/23311932.2023.2212457

Tilman D (1994) Competition and Biodiversity in Spatially Structured Habitats. Ecology 75:2–16. https://doi.org/10.2307/1939377

Vergès LHMC, Contente RF, Marion C et al (2022) Relationship between fish assemblage structure and predictors related to estuarine productivity in shallow habitats of a Neotropical estuary. Neotrop Ichthyol 20:1–20. https://doi.org/10.1590/1982-0224-2022-0006

Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522. https://doi.org/10.1890/09-1310.1

Villéger S, Brosse S, Mouchet M et al (2017) Functional ecology of fish: current approaches and future challenges. Aquat Sci 79:783–801. https://doi.org/10.1007/s00027-017-0546-z

Vollenweider RA, Giovanardi F, Montanari G, Rinaldi A (1998) Characterization of the trophic conditions of marine coastal waters with special reference to the NW Adriatic Sea: proposal for a trophic scale, turbidity and generalized water quality index. Environmetrics 9:329–357

Warry FY, Reich P, Cook PLM et al (2016) Nitrogen loads influence trophic organization of estuarine fish assemblages. Funct Ecol 30:1723–1733. https://doi.org/10.1111/1365-2435.12647

Whitfield AK (1999) Ichthyofaunal assemblages in estuaries: A South African case study. Rev Fish Biol Fish 9:151–186. https://doi.org/10.1023/A:1008994405375

Whitfield AK (2015) Why are there so few freshwater fish species in most estuaries? J Fish Biol 86:1227–1250. https://doi.org/10.1111/jfb.12641

Whitfield AK (2021) Estuaries – how challenging are these constantly changing aquatic environments for associated fish species? Environ Biol Fish 104:517–528. https://doi.org/10.1007/s10641-021-01085-9

Whitfield AK, Elliott M, Basset A et al (2012) Paradigms in estuarine ecology – A review of the Remane diagram with a suggested revised model for estuaries. Estuar Coast Shelf Sci 97:78–90. https://doi.org/10.1016/j.ecss.2011.11.026

Wootton KL (2017) Omnivory and stability in freshwater habitats: Does theory match reality? Freshw Biol 62:821–832. https://doi.org/10.1111/fwb.12908

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