From meso to hyperhaline: the importance of Neotropical coastal lagoons in supporting the functional fish diversity at regional scale

Ana Clara Sampaio Franco · Francisco Gerson Araújo ·
Alejandra Filippo Gonzalez Neves dos Santos · Magda Fernandes de Andrade-Tubino ·
Luciano Neves dos Santos

Abstract Shallow coastal habitats are ruled by fluctuating environmental conditions, which lead to shifts in fish communities. Functional groups of habitat use and trophic strategy were used to address the responses of fish composition and diversity, since comparisons of rich tropical systems are often complex through species-based approaches. We hypothesized that fish groups will have specific affinities in response to the prevailing environmental conditions, especially those reflecting the prevalence of oceanic or estuarine conditions, where guilds of habitat use would perform better as indicators. Despite the importance of other environmental factors (i.e. temperature and transparency), salinity was the key structuring factor irrespective of the coastal lagoon. Although harbouring the greatest biomass of piscivores, the harsh environmental conditions at Araruama lagoon were related to low diversity. A great number of indicator species, typically of marine affinity, was found at the Saquarema lagoon, probably due to the continuous and broad connection to the sea leading to the predominance of euhaline conditions. Despite the presence of non-native species (i.e. *Oreochromis niloticus*), the Maricá lagoon function as an important refuge for freshwater groups. Our results stressed the key role played by coastal lagoons of varied water conditions in supporting fish diversity at regional levels.

Keywords Coastal lagoon · Fish assemblage · Habitat affinity · Salinity · Trophic guild

A. C. S. Franco (✉) · L. N. dos Santos
Graduate Course in Neotropical Biodiversity,
Universidade Federal do Estado do Rio de Janeiro, Av.
Pasteur, 458 – R506A, Rio de Janeiro,
RJ 22290-240, Brazil
e-mail: anaclara306@gmail.com

F. G. Araújo · M. F. de Andrade-Tubino
Laboratório de Ecologia de Peixes, Universidade Federal
Rural do Rio de Janeiro, ICBS, Seropédica,
RJ 23871-970, Brazil

A. F. G. N. dos Santos
Laboratory of Applied Ecology, Universidade Federal
Fluminense (UFF), Rua Vital Brazil Filho, 64, Niterói,
RJ 24230-340, Brazil

Introduction

Transitional systems, such as estuaries and coastal lagoons, provide important ecosystem services, such as recreation, fisheries, gas regulation, and nutrient cycling (Potter et al., 2016). They are also essential

habitats for many fish species which use these systems as nursery, feeding, recruitment, and migrating areas between rivers and the sea (Elliott et al., 2007). However, their close relationship with the terrestrial ecosystem makes those coastal transitional systems extremely vulnerable to human impacts, such as water quality impairment, habitat destruction, silting, and overfishing (Elliott & Quintino, 2007; Blaber, 2013). The assessment of fish diversity and its relation to environmental conditions is key for the development of management strategies, especially when incorporating approaches based on functional groups, which could be more closely associated with the ecological functioning of those shallow coastal habitats (Whitfield & Elliott, 2002; Tweedley et al., 2017; Souza & Vianna, 2020).

The composition of fish assemblages in transitional systems is dictated by the combination of biotic and abiotic variables, particularly competition for space and food, and tolerance to diel and seasonal changes in salinity, turbidity, and temperature (Cyrus & Blaber, 1992; Barletta et al., 2005), which pose great physiological stress on these species (Elliott & Quintino, 2007). Coastal lagoons are examples of transitional habitats assembled by a mosaic of conditions, wherein depth, transparency, salinity, primary productivity, freshwater inflow, wind regime, solar radiation, and evaporation rates, operating both individually and synergistically, account as the major drivers (Vasconcelos et al., 2015; Teichert et al., 2017; Franco et al., 2019). These complex environmental conditions support species-rich assemblages, and their many functional groups may change with depth, temperature (Sosa-López et al., 2007), and particularly salinity, which have been considered as the major structuring force of fish communities in coastal lagoons (Camara et al., 2019; Franco et al., 2019). Salinity depends on the geomorphology of the ecosystem, precipitation-evaporation balance, and width and intermittency of the sea connection (Barletta et al., 2008; Becker et al., 2016). However, the magnitude and extent of variation of salt concentration are key for shaping the distribution and composition of fish assemblages, due to their potential for selecting species of specific osmoregulatory abilities and ontogenetic phases (Martino & Able, 2003; Telesh & Khlebovich, 2010; Moura et al., 2012).

The typical transitional characteristic of coastal lagoons allows for spatial gradients of salinity, which often range from low values nearby the sources of freshwater input to indeed seawater conditions near the connections to the sea (Knoppers, 1994; Barletta et al., 2005; Becker et al., 2016). Some coastal lagoons may also experience periodic or permanent hypersaline conditions (Cruz et al., 2018). These coastal shallow habitats are also marked by high primary productivity, which can influence fish diversity at local and regional levels (Connell & Orias, 1964; Dodson et al., 2010). This productivity–richness hypothesis together with varied salinity conditions promote patches of different environmental conditions which allows populations to persist, reducing extinction risk and thus supporting a higher diversity of niche specialists and groups with different levels of marine affinity (Willig et al., 2003; Tittensor et al., 2010; Vasconcelos et al., 2015). Fish assemblages in coastal lagoons may include resident species which are more adapted to broad variations in salinity, but also typically marine and freshwater species which enter transitional systems either as migrants or stragglers, as well as diadromous and amphidromous species (e.g., Elliott et al., 2007; Potter et al., 2015).

The persistent environmental fluctuation of transitional habitats poses great physiological stress on the species and groups that colonize these systems (Elliot & Quintino, 2007; Potter et al., 2016). Thus, these communities tend to be dominated by a fraction of the diversity of adjacent marine ecosystems (Martino & Able, 2003; Franco et al., 2019). Many ecological functions played by transitional systems for fish assemblages, such as breeding, recruitment, nursery, and food supply areas, are affected by fluctuations of environmental conditions (Vasconcelos et al., 2015). Despite the growing number of studies testing the relationship between richness and salinity in coastal lagoons (Sosa-López et al., 2007; Franco et al., 2019) and estuaries (Barletta et al., 2005; Barletta & Blaber, 2007), the influence of environmental variables on the composition of functional groups in these systems remains barely known.

In this sense, this study aimed to evaluate whether fish functional groups of three coastal lagoons along the coast of the Rio de Janeiro state (Brazil) are structured by the inherent environmental conditions of these systems, especially considering the trophic niche and level of habitat use as proxies of functional responses. We hypothesized that fish groups will have specific affinities in response to the prevailing

environmental conditions, especially those reflecting the prevalence of oceanic (more cold, saline and transparent waters) or estuarine (warmer, less saline and turbid waters) conditions. We expect that typically marine species (i.e. marine migrants and stragglers) will be related to water conditions closer to the sea (e.g.. Franco et al., 2019), while typically estuarine (e.g. residents/freshwater) species would thrive in estuarine conditions (e.g., Moura et al., 2012). Since guild composition might reflect environmental conditions through the selection of species according to their tolerance, we hypothesized that habitat use rather than trophic niche guilds would be better indicators of the functional fish diversity of Neotropical coastal lagoons. Thus, temperature, salinity, and transparency will act as the main drivers of the structure and composition of the fish groups. Although increased salinity was often related to greater species richness (Whitfield & Harrison, 2003), hyperhaline conditions might be harsh and less suitable for some species without the osmoregulatory ability to deal with the higher salinities (Elliot & Quintino, 2007; Whitfield et al., 2012; Henriques et al., 2017; Franco et al., 2019). The following questions will be also addressed: (i) will the differences among systems (Franco et al., 2019) influence the composition of functional groups related to trophic niche and the level of association with the estuary in the same way?; (ii) are there particular indicator species for each functional group at each system? The importance of our results for the preservation and management of coastal lagoons and their associated fish assemblages was also discussed.

Materials and methods

Study area

Three coastal lagoons located at the Rio de Janeiro state, southeastern Brazil were evaluated: Araruama (22° 53′ S and 42° 23′ W), Maricá (22° 56′ S and 42° 50′ W) and Saquarema (22° 55′ S and 42° 34′ W). These lagoons have permanent connections to the sea, but at different rates of seawater exchange and freshwater input, leading to different environmental characteristics, especially concerning salinity variations (Franco et al., 2019). The climate is equatorial with varying precipitation levels (greater at Maricá), according to the Köppen-Geiger climate classification

(Kottek et al., 2006). Regarded as the largest hyperhaline lagoon in Brazil, of average salinity ranging from 56 to 77 (Kjerfve & Schettini, 1996; Cruz et al., 2018), Araruama lagoon has an area of 210 km^2 and an average depth of 3 m, with a renewal time of 84 days for 50% of the water, according to Kjerfve (1994). Maricá lagoon has a surface area of 34.7 km^2 and predominantly mesohaline conditions, with an average salinity of 18. It has an intermediate residence time, requiring 27 days for 50% of water renewal in the inner zone, in contrast to 7 days for the outer zone (Kjerfve et al., 1990; Knoppers, 1994). Saquarema lagoon, the euhaline system, has an area of 21.2 km^2 and a mean salinity of 35 (Franco et al., 2019). It takes 23 days for renewing 50% of its waters in the inner zones, in comparison to only 6 days for outer zones (Knoppers, 1994).

Sampling

Fish sampling was carried out every 2 months in each of the three coastal lagoons between September 2017 and September 2018. All samples were performed in replicates ($N = 3$) during the day, between 0900 and 1700 h, at three beaches in each zone (inner, central and outer) of the lagoons. A beach seine net (20 m width × 1.5 m height; 7 mm mesh size; three replicates per beach) with a codend (5 mm mesh size) was positioned perpendicular to the coastline and dragged through 20-m hauling ropes parallel to the surface to sample a 400 m^2 area. Water temperature (°C), pH, conductivity (µS cm^{-1}) and salinity were measured during the samplings through a multi-parameter probe (Hannah HI 9626). Water transparency (%) was also appraised through a Secchi's disk.

The collected material was transferred to the laboratory where fishes were identified, according to Figueiredo & Menezes (1978, 1980, 2000) and Menezes & Figueiredo (1980, 1985), and weighted to a 0.01 g precision. Data on juveniles and fish larvae were excluded to avoid biases in our analyses and also in the classification of functional groups, since species traits may change ontogenetically. Species were classified into six trophic guilds, according to their preferential dietary items as available in the FishBase database (http://fishbase.org): piscivore, invertivorous, omnivorous, planktivorous, detritivorous, and herbivorous. We also further classified fish species into guilds of habitat use (i.e., degree of estuary

affinity) following the approach proposed by Elliott et al. (2007) and also through comparisons with previous studies performed in the region (Araújo et al., 2016, 2017): residents, marine stragglers, marine migrants, freshwater, and semi-anadromous species. This approach considers how fish species use the estuary, their requirements for estuarine resources, and also their interactions with adjacent areas (the open sea, coastal zones, and freshwater catchments; Elliott et al., 2007). The functional group's classification approach was used to allow for the assessment of differential relations of these fish groups with abiotic variables (especially salinity, temperature and transparency), given the differences among these functional groups regarding environmental uses and tolerances.

Statistical analyses

All statistical analyses were performed with the R statistical software version 4.0.0 (R Core Team, 2020). We used principal component analysis (PCA) to ordinate samples from the three coastal lagoons according to their water variables (centred and standardized data of temperature, pH, conductivity, salinity, and transparency) using function "rda" in the "vegan" package (Oksanen et al., 2016). We used the function "PCAsignificance" to estimate the number of significant axes based on the broken-stick criterion, as available in package "Biodiversity R" (Kindt, 2017). Redundancy analysis (RDA) was performed to test the relationship between water variables and the biomass of trophic guilds, and also with the abundance of the habitat use guilds ($\log_{10}$ transformed data for both matrixes), using function "rda". The axis significance was assessed through the "anova.cca" function in the "vegan" package (Oksanen et al., 2016). A distance-based permutational multivariable analysis of variance (PERMANOVA) was used to test for the relationship between functional guilds (trophic guilds as biomass and habitat-use guilds as abundance) and water variables (temperature, pH, salinity, and transparency). We tested for differences among systems (regarded as a random factor with three levels) with the "adonis" function as available in the "vegan" package. The multivariate PERMANOVA was performed based on Bray–Curtis dissimilarity measures and 1000 permutations of residuals (Anderson, 2008).

Species biomass was used to assess trophic guilds and species abundance for the habitat use guilds (as Sosa-López et al., 2005; Franco et al., 2016; Chaves et al., 2018) to avoid biases promoted by overly abundant, but with low biomass species, such as clupeids and engraulids, which have different estuary uses (e.g., marine stragglers and migrants) yet sharing the same trophic guild (i.e., planktivores). The biomass of trophic guilds and the abundance of habitat use guilds were compared among the lagoons through a PERMANOVA, using Euclidean distance as linkage function and 9999 permutations of raw data (Anderson, 2008). Significant differences were evaluated by a PERMANOVA pairwise posthoc comparisons test. We also used the indicator value method (IndVal; Dufrêne & Legendre, 1997) to detect which species could be used as an indicator of each trophic and habitat use guild on each of the three coastal lagoons. The indicator value of each species is based on specificity (the relative abundance of each species in each lagoon) and fidelity (the relative frequency of each species in each lagoon), which are incorporated in the formula: IndValij = Aij × Bij × 100, where: IndValij is the indicator value for the species i in lagoon j, Aij is the relative abundance of species i in lagoon j, and Bij is the relative frequency of species i in lagoon j. To test for the significance of the indicator value, the Monte Carlo test with 9999 permutations and a significance level of 95% was used. We further tested the biomass of trophic guilds and the abundance of habitat use guilds to compare the lagoons through a distance-based test for homogeneity of multivariate dispersion (PERMDISP) to check if there was any significant variation within the lagoons, using Euclidean distance as linkage function and 9999 permutations (Anderson, 2006).

Results

Environmental variables

The three coastal lagoons showed different environmental conditions which varied considerably within each system (Fig. 1; Table S1). Araruama lagoon was predominantly hyperhaline, where greater values of conductivity and temperature and intermediary conditions of transparency were recorded. On the other hand, the Maricá lagoon had the lowest salinity range
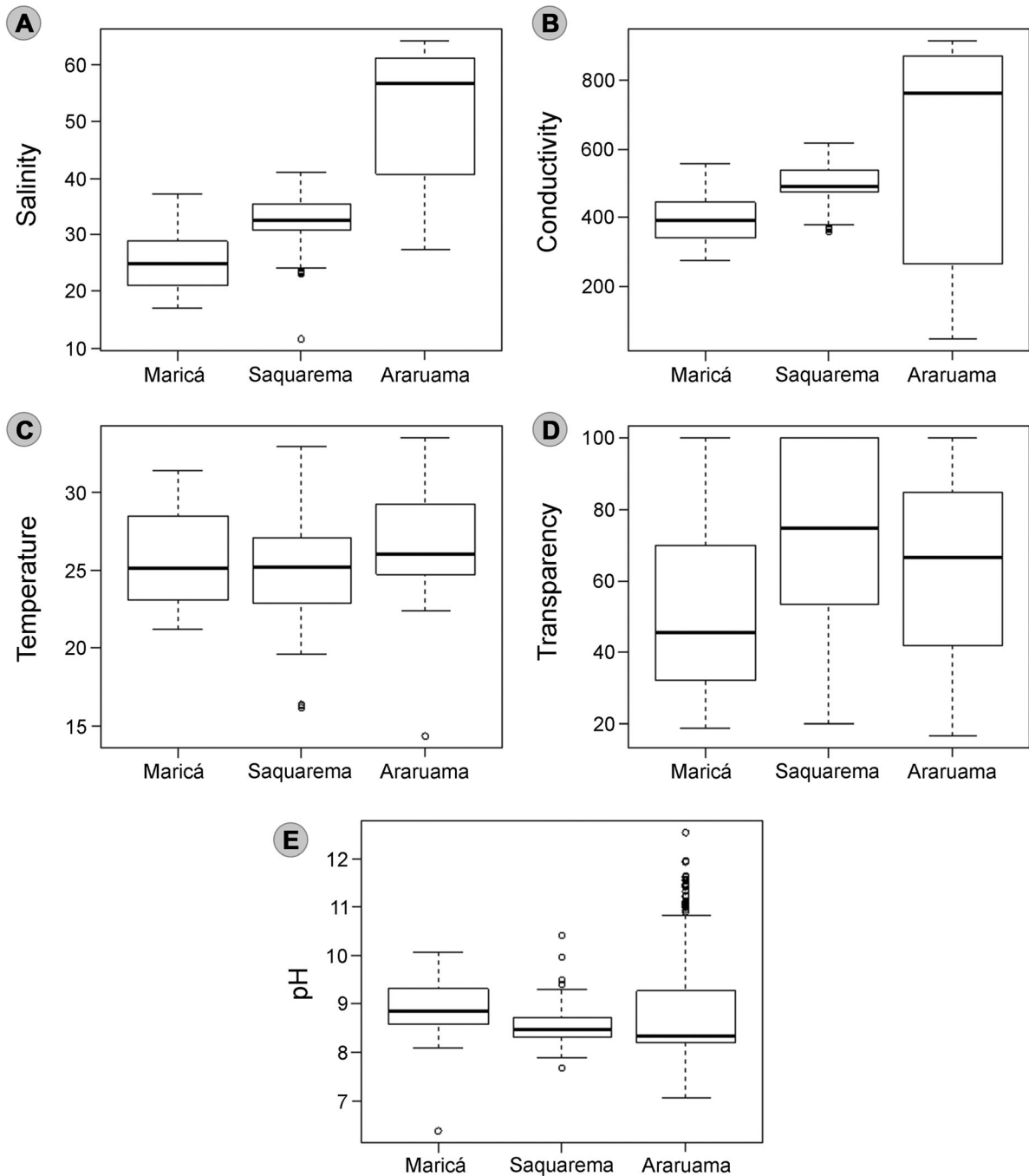
Fig. 1 Boxplot (median, box 25 and 75 percentile, whisker 10 and 90 percentile) of **A** salinity, **B** conductivity, **C** temperature, **D** transparency and **E** pH in the three Neotropical coastal lagoons

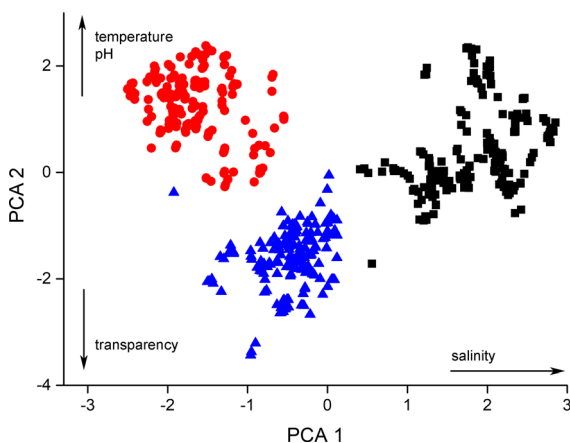(predominantly mesohaline conditions) and conductivity values. Saquarema lagoon was the most transparent and coldest system, and salinity was closer to the values found typically for sea (∼35%).

The principal component analysis (PCA) applied to the environmental variables had its first two axes jointly explaining 53.3% of the variance of abiotic variables. The first axis (eigenvalue = 2.40) split the
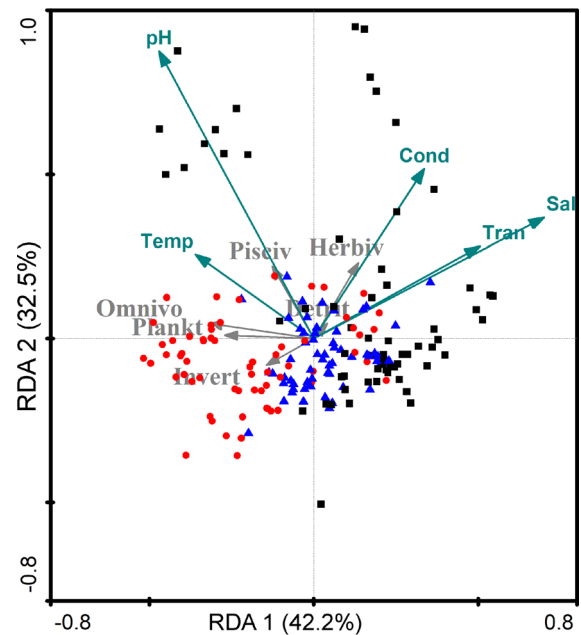
three systems based on their salinity values (Fig. 2). Araruama lagoon was confirmed as hypersaline, while Maricá had lower salinities. Axis 2 (eigenvalue = 1.87) separated the three systems based on temperature, pH and transparency. Saquarema lagoon had colder and more transparent waters, while Maricá and Araruama lagoons had warmer and more turbid conditions.

Functional fish groups

The redundancy analysis applied to test for the relationship between environmental variables and the trophic guilds identified salinity and pH as the main drivers of those relations, and temperature and transparency as of minor importance. The first RDA axis (42.2%; eigenvalue = 0.039; Fig. 3) split higher biomass of piscivores and herbivores at the Araruama lagoon. On the other hand, omnivores, planktivores, and invertivores had higher biomass at Maricá. The second RDA axis accounted for 32.5% of data variance (eigenvalue = 0.019) and separated some samples of the Araruama lagoon according to greater pH and conductivity values, showing that piscivores and herbivores were more associated with those samples. Samples from the Saquarema lagoon assumed an intermediate position between the other two coastal systems.
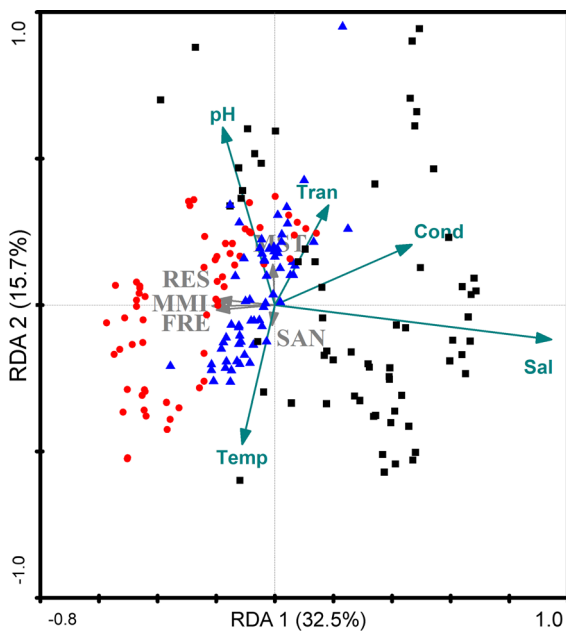

Fig. 3 Ordination diagram of the three coastal lagoons (●— Maricá; ▲—Saquarema; ■—Araruama) according to a redundancy analysis (RDA) of the relationship between environmental conditions and biomass of trophic guilds. All variables were centred and standardized

The redundancy analysis applied to test for the relationship between environmental variables and habitat use guilds retrieved salinity, temperature, and pH as the main drivers in selecting groups of habitat use. The first RDA axis (eigenvalue = 0.025; 32.5%; Fig. 4) showed that lower salinity was related to marine migrant, resident, and freshwater groups, which were recorded, mainly, for the Maricá system. Along the second RDA axis (eigenvalue = 0.005; 15.7%) marine stragglers were related to greater pH and transparency, and associated with some samples of the three systems, whereas the semianadromous group was associated with higher temperatures.

A distance-based PERMANOVA showed that the biomass of trophic guilds was influenced by salinity (adonis function: $F_{1, 197} = 14.03$; $P < 0.001$), temperature (adonis function: $F_{1, 197} = 4.77$; $P = 0.002$), and pH (adonis function: $F_{1, 197} = 3.14$; $P = 0.01$), but not by transparency. The patterns of abiotic variables influence over trophic guilds changed among systems (adonis function, $P < 0.05$). On the other hand, the abundance of habitat use guilds was influenced by temperature (adonis function: $F_{1, 197} = 2.67$;

Fig. 2 Ordination diagram of the three coastal lagoons (●— Maricá; ▲—Saquarema; ■—Araruama) according to a principal component analysis (PCA) of the physical and chemical water variables (temperature, pH, conductivity, salinity, and transparency). All variables were centred and standardized

Fig. 4 Ordination diagram of the three coastal lagoons (🔴 —Maricá; 🔺—Saquarema; ⬛—Araruama) according to a redundancy analysis (RDA) of the relationship between environmental conditions and abundance of habitat use guilds. All variables were centred and standardized

$P = 0.03$) and salinity (adonis function: $F_{1, 197} = 28.94$; $P < 0.001$), whereas all abiotic variables, except for pH, had different patterns among systems (adonis function, $P < 0.05$).

All the six trophic guilds were detected in all of the three coastal lagoons (Table S2). The biomass of omnivores was significantly lower in Saquarema lagoon (PERMANOVA; $F = 12.59$; $P = 0.0001$), where *Diplodus argenteus* (Valenciennes 1830) (Table 1, Fig. 5) was selected as indicator species. Planktivores were barely found in Araruama lagoon ($F = 8.21$; $P = 0.0004$). For Saquarema lagoon, the Atlantic anchoveta *Cetengraulis edentulus* (Cuvier 1829) and *Anchoa lyolepis* (Evermann & Marsh 1900) accounted for the indicator planktivorous species, while *Syngnathus scovelli* (Evermann & Kendall 1896) and *Brevoortia aurea* (Spix & Agassiz 1829) were retrieved as indicator planktivores in Maricá. Higher biomasses of herbivorous ($F = 5.58$; $P = 0.0003$) and piscivorous ($F = 2.42$; $P = 0.007$) groups were recorded in the Araruama system, and no indicator species was found for these groups, except for the piscivore *Strongylura marina* (Walbaum 1792)

in Saquarema lagoon. The biomasses of invertivorous and detritivorous groups did not differ among systems, but the invertivore *Albula vulpes* (Linnaeus 1758) was considered as indicator species in the Maricá lagoon.

The five guilds of habitat use were detected in all of the three lagoons, except for the semianadromous in Saquarema lagoon, but the patterns differed for each group and among systems (Fig. 6). The abundance of marine migrants was lowest in the Araruama lagoon and (PERMANOVA; $F = 8.28$; $P = 0.0002$), no difference was found for the other systems. Indicator species were also detected for Maricá (*Mugil curema* Valenciennes 1836; Table 3) and Saquarema (*Oligoplites saurus* (Bloch & Schneider 1801)) systems. Marine stragglers, on the other hand, were commonly found in mesohaline conditions at Maricá lagoon ($F = 8.37$; $P = 0.0001$), where *S. scovelli*, *A. lyolepis,* and *D. argenteus* accounted for the major indicator species. *Hyporhamphus unifasciatus* (Ranzani 1841) was the major indicator species of marine stragglers in the Araruama lagoon, while *B. aurea* for the Maricá lagoon. Although the abundance of the resident guild was not different among systems, *Bathygobius soporator* (Valenciennes 1837) was retrieved as the indicator species in the Araruama lagoon. The freshwater guild was much more abundant in the Maricá lagoon ($F = 4.08$; $P = 0.009$), where the introduced *Oreochromis niloticus* (Linnaeus 1758) was the single indicator species for this system. Finally, the semianadromous guild was represented by very few species, with no difference in abundance or indicator species among systems.

According to PERMDISP analyses, dispersion within each system varied significantly for omnivorous among all coastal lagoons ($F_{2, 195} = 14.6$; $P < 0.01$). The dispersions for the planktivore ($F_{2, 195} = 14.7$; $P < 0.01$), piscivore ($F_{2, 195} = 4.4$; $P = 0.04$) and herbivore ($F_{2, 195} = 18.6$; $P < 0.01$) species were significant within the Araruama lagoon. Dispersions within systems was marginally significant for detritivore and non-significant for invertivore. For the habitat use guild, PERMDISP revealed a significant dispersion within all coastal lagoons for semianadromous species ($F_{2, 195} = 3.6$; $P < 0.01$), whereas marine migrants had significant dispersion in Araruama ($F_{2, 195} = 20.6$; $P < 0.01$), and marine stragglers ($F_{2, 195} = 20.2$; $P < 0.01$) at Saquarema lagoons. Non-significant distribution patterns within

Table 1 Values of the Indicator Species (IndVal) Index of each fish species for each trophic and habitat use guild among the three Neotropical coastal lagoons

Variable 1 MAR 2 SAQ 3 ARA

Species	Trophic											
	Omnivore		Invertivore		Planktivore		Piscivore		Detritivore		Herbivore	
	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal
Abudefduf saxatilis	2	1.6										
Achirus lineatus												
Albula vulpes			2	**15.5****								
Anchoviella brevirostris					1	1.6						
Anchoa lyolepis					2	**10.2***						
Anchoa marinii					2	1.6						
Anchoa tricolor					2	**6***						
Archosargus probatocephalus			3	1.4								
Archosargus rhomboidalis			2	3.3								
Aspistor luniscutis												
Bathygobius soporator			2	3.6								
Brevoortia aurea					1	**10.8****						
Bryx dunckeri					1	1.6						
Caranx latus							1	4.5				
Caranx crysos							2	2.8				
Cetengraulis edentulus					2	**12.7****						
Centropomus parallelus							1	1.6				
Centropomus undecimalis							3	3				
Chaetodipterus faber			1	1.6								
Cosmocampus elucens					1	1.6						
Ctenogobius shufeldti			3	1.4								
Ctenogobius stigmaticus			3	1.4								
Cynoscion leiarchus							1	1.6				
Dactylopterus volitans			2	1.6								
Diapterus auratus			1	4.8								
Diplectrum formosum							2	1.6				
Diplodus argenteus	2	**9.5****										
Diplectrum radiale							2	1.6				
Dules auriga			2	4.8								
Eugerres brasilianus			1	1.6								
Eucinostomus gula	3	3.9										
Eucinostomus melanostomus	1	1.6										
Evoxymetopon taeniatus												
Geophagus brasiliensis									1	1.7		
Genidens genidens	1	1.6										
Haemulopsis corvinaeformis			3	2.8								
Hemiramphus brasiliensis											2	1.6
Hyporhamphus roberti											1	1.6
Hyporhamphus unifasciatus												
Kyphosus vaigiensis											2	1.6

Table 1 continued

Variable 1 MAR 2 SAQ 3 ARA

| Species | Trophic | | | | | | | | | | | |
| | Omnivore | | Invertivore | | Planktivore | | Piscivore | | Detritivore | | Herbivore | |
	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal
Lutjanus jocu			2	1.6								
Menticirrhus americanus			2	1.6								
Micropogonias furnieri												
Monacanthus ciliatus			2	1.6								
Mugil curema												
Odontesthes incisa	2	3.2										
Oligoplites saurus												
Oreochromis niloticus												
Paralichthys brasiliensis			3	1.4								
Paralichthys patagonicus			3	1.4								
Parablennius pilicornis	2	1.6										
Percophis brasiliensis			1	1.6								
Pomatomus saltatrix							2	4.8				
Prionotus punctatus			1	3.2								
Pseudupeneus maculatus			2	1.6								
Sardinella brasiliensis					2	**7***						
Scartella cristata											2	1.6
Scorpaena isthmensis			2	1.6								
Sphoeroides greeleyi												
Sphoeroides splengeri												
Sphoeroides testudineus			3	2.4								
Sphyraena tome							2	1.6				
Stephanolepis hispidus	2	1.6										
Strongylura marina							2	**9.5***				
Stellifer rastrifer												
Symphurus tessellatus			3	1.4								
Syngnathus folletti					1	1.6						
Synodus intermedius							2	1.6				
Syngnathus scovelli					2	**18.5***						
Trachinotus carolinus												
Trachinotus falcatus			3	1								
Trachinotus goodei			2	4.8								
Trachurus lathami			3	1.4								
Trichiurus lepturus							1	1.6				
Umbrina coroides			3	1.4								

Table 1 continued

Variable 1 MAR 2 SAQ 3 ARA										
Species	Habitat use									
	Marine migrant		Marine straggler		Resident		Freshwater		Semianadromous	
	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal
Abudefduf saxatilis			2	1.6						
Achirus lineatus					3	4.9				
Albula vulpes	2	**13.8****								
Anchoviella brevirostris					1	1.6				
Anchoa lyolepis			2	**12****						
Anchoa marinii			2	1.6						
Anchoa tricolor	2	4.6								
Archosargus probatocephalus			3	1.4						
Archosargus rhomboidalis			1	4.3						
Aspistor luniscutis									3	2.8
Bathygobius soporator					2	**7.6***				
Brevoortia aurea			1	**10.7****						
Bryx dunckeri	1	1.6								
Caranx latus			1	3.8						
Caranx crysos			2	3						
Cetengraulis edentulus	2	**12.7****								
Centropomus parallelus	1	1.6								
Centropomus undecimalis	3	2.4								
Chaetodipterus faber			1	1.6						
Cosmocampus elucens			1	1.6						
Ctenogobius shufeldti					3	1.4				
Ctenogobius stigmaticus					3	1.4				
Cynoscion leiarchus			1	1.6						
Dactylopterus volitans			2	1.6						
Diapterus auratus					1	3.2				
Diplectrum formosum			2	1.6						
Diplodus argenteus			2	**9.5****						
Diplectrum radiale			2	1.6						
Dules auriga			2	4.8						
Eugerres brasilianus			1	1.6						
Eucinostomus gula			1	2.2						
Eucinostomus melanostomus					1	1.6				
Evoxymetopon taeniatus	2	1.6								
Geophagus brasiliensis							1	1.6		
Genidens genidens									1	1.6
Haemulopsis corvinaeformis	3	2.8								
Hemiramphus brasiliensis			2	1.6						
Hyporhamphus roberti			1	1.6						
Hyporhamphus unifasciatus			3	**20.8****						
Kyphosus vaigiensis			1	2.4						
Lutjanus jocu			2	1.6						

Table 1 continued

| Variable 1 MAR 2 SAQ 3 ARA										
Species	Habitat use									
	Marine migrant		Marine straggler		Resident		Freshwater		Semianadromous	
	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal	CL	IndVal
Menticirrhus americanus	2	1.6								
Micropogonias furnieri	2	**15.6****								
Monacanthus ciliatus			2	1.6						
Mugil curema	1	**13.3***								
Odontesthes incisa					2	3.2				
Oligoplites saurus	2	**37.5****								
Oreochromis niloticus							1	**6.3***		
Paralichthys brasiliensis			3	1.4						
Paralichthys patagonicus			3	1.4						
Parablennius pilicornis					2	1.6				
Percophis brasiliensis			1	1.6						
Pomatomus saltatrix			2	4.8						
Prionotus punctatus			1	3.2						
Pseudupeneus maculatus			2	1.6						
Sardinella brasiliensis										
Scartella cristata					2	1.6				
Scorpaena isthmensis			2	1.6						
Sphoeroides greeleyi	2	**30.2****								
Sphoeroides splengeri	2	6								
Sphoeroides testudineus					3	2.1				
Sphyraena tome	2	1.6								
Stephanolepis hispidus			2	1.6						
Strongylura marina	2	**9.5****								
Stellifer rastrifer	3	2.8								
Symphurus tessellatus	3	1.4								
Syngnathus folletti			1	1.6						
Synodus intermedius			2	1.6						
Syngnathus scovelli			2	**12.6***						
Trachinotus carolinus			3	1.7						
Trachinotus falcatus			1	0.8						
Trachinotus goodei			2	4.8						
Trachurus lathami			3	1.4						
Trichiurus lepturus	1	1.6								
Umbrina coroides			3	1.4						

CL coastal lagoon, *1* Maricá, *2* Saquarema, *3* Araruama

Bold numbers represent the significant values; *P* < 0.05; **P* < 0.005
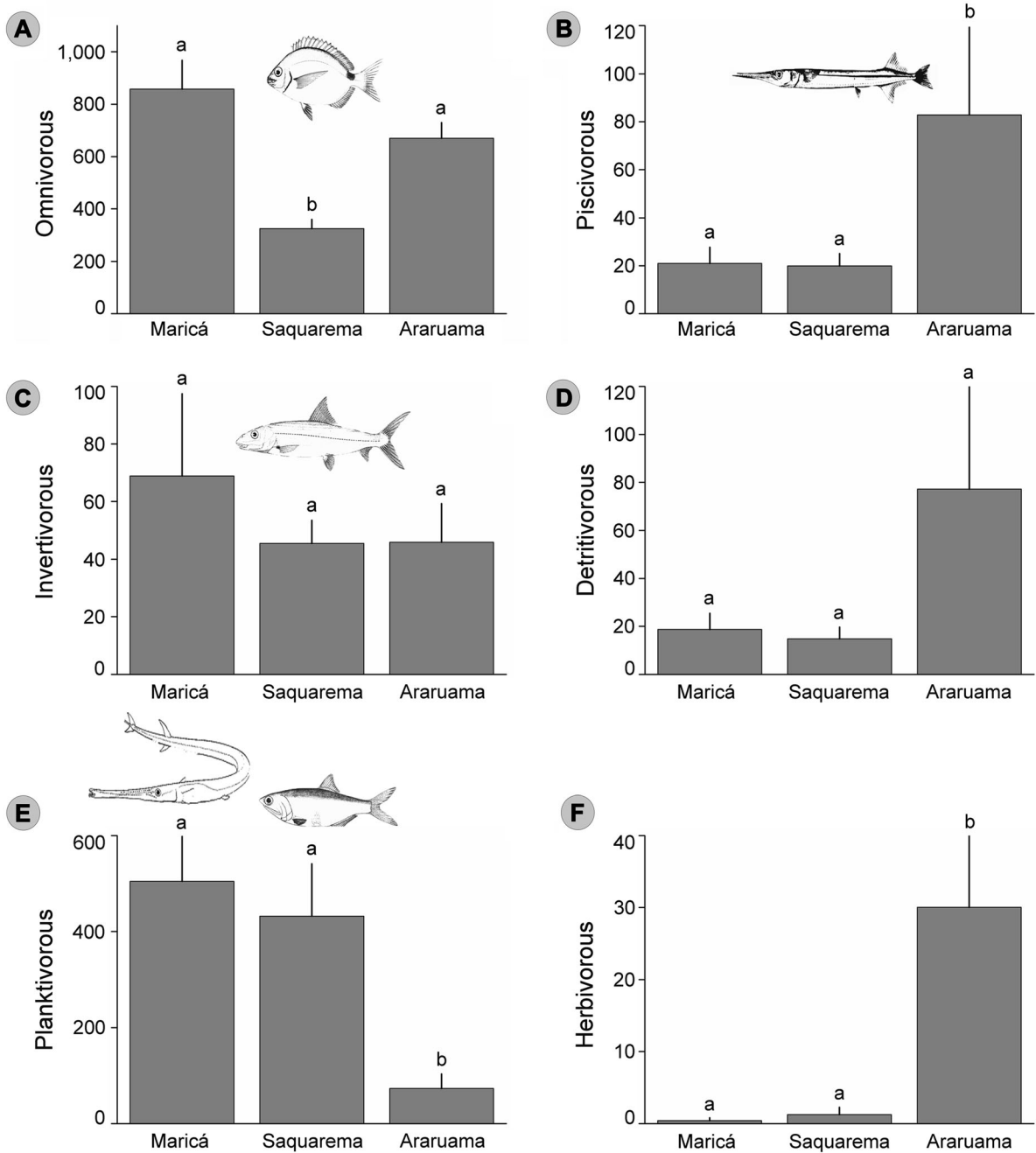
Fig. 5 Mean biomass (lines are standard errors) of the six trophic guilds recorded for the three coastal lagoons: **A** omnivores, **B** piscivores, **C** invertivores, **D** detritivores, **E** planktivores, and **F** herbivores. Different letters indicate significant differences among lagoons, according to the permutational analysis of variance (PERMANOVA). Fish drawings represent the indicator species of each lagoon, according to an IndVal analysis
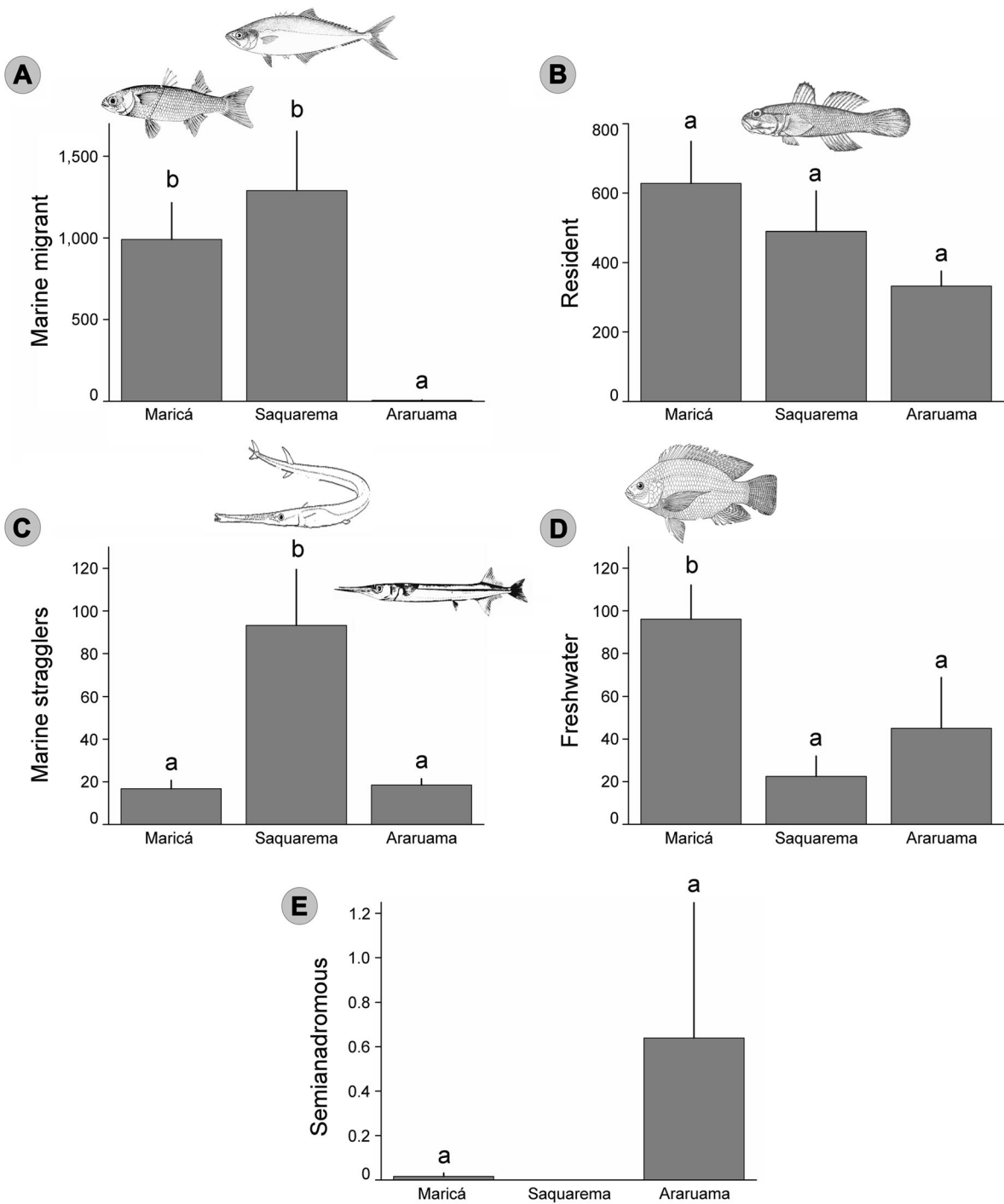
Fig. 6 Mean abundance (lines are standard errors) of the five guilds of habitat-use recorded for the three coastal lagoons: **A** marine migrants, **B** marine stragglers, **C** semianadromous, **D** resident, and **E** freshwater. Different letters indicate significant differences among lagoons, according to a permutational analysis of variance (PERMANOVA). Fish drawings represent the indicator species of each lagoon, according to the IndVal analysis

systems were found for freshwater and resident species.

Discussion

Our findings confirmed environmental differences among coastal lagoons influencing the composition of trophic and habitat use groups of fish species, and salinity was the key structuring factor. To a lesser extent, temperature and transparency were also important drivers of functional groups, especially to separate groups under the meso and euhaline conditions, but also influencing variation within systems. The hyperhaline conditions found at the Araruama lagoon selected a most singular guild composition, yet with low diversity, which was probably selected by the harsh environmental conditions that constraint the ability of some species to thrive in this system. On the other hand, systems with a higher level of connection to the adjacent sea (i.e., Saquarema and Maricá lagoons) selected a greater amount of indicator species from both functional groups, agreeing with other studies performed in estuarine ecosystems, that indicates a greater diversity promoted by the colonization of species with marine salinity preference (Whitfield et al., 2012; Vasconcelos et al., 2015; Henriques et al., 2017).

Analysing fish communities by using an approach based on functional groups (i.e., functions that species perform in a given ecosystem regardless of its taxonomy) along with abiotic constraints allow depicting a more realistic scenario of the composition, structure and spatial distribution of assemblages (Mouillot et al., 2013). The trait-environment relationship also allows for predictions of species responses to a changing environment, which can be used for the delimitation of conservation strategies (Violle et al., 2014). Considering that estuaries are under considerable threat for human activities in their surroundings, it is extremely important to investigate how functional groups are structured by environmental conditions, yet this information is still lacking for aquatic ecosystems (Brind'Amour et al., 2011; Bender et al., 2013; Henriques et al., 2017; Franco et al., 2019). Our study showed a strong influence of salinity, but also temperature and transparency, as drivers of the composition and structure of functional groups of three coastal lagoons at the coast of Rio de Janeiro.

These findings agree with global patterns of functional composition of fish assemblages in estuarine ecosystems (see Whitfield et al., 2012; Henriques et al., 2017), but also with studies performed from a local perspective (e.g., Chaves et al., 2018; Franco et al., 2019), which can provide further information on specific determinants of groups occurrence.

The role of salinity in structuring fish assemblages have been largely described worldwide, such as in community assessments in estuarine systems (Barletta et al., 2005; Whitfield et al., 2012; Chaves et al., 2018), fossil records in transitional systems (Hudson, 1963, 1980), and also as a tool for classification of estuarine biota (Elliott & Whitfield, 2011). Herein we demonstrate that this role is not only played on richness and abundance patterns, but also through the selection and structuring of guilds of trophic niche and habitat use. The environmental conditions in a coastal lagoon are given by a balance between saltwater and freshwater intrusions (McLusky, 1989) and evaporation rates, which demands individuals to adapt to these conditions according to their osmoregulatory abilities. However, the distribution of fishes is further related to other factors, but especially temperature gradients, also found as a driver of functional groups in our study, which can influence species osmoregulation at extreme temperature (both low or high temperatures; Blaber, 1973; Whitfield & Blaber, 1976), metabolic rates (influencing trophic guilds distribution; Gillooly et al., 2001; Floeter et al., 2005), and, indirectly, through primary productivity (Henriques et al., 2017). Salinity is such an influential force over both individuals, species and functional groups that can restructure trophic and assemblage dynamics within an ecosystem, thus species can be used as indicators of the spatial heterogeneity of the habitats (Whitfield et al., 2012). Considering climate change scenarios which are predicted to reflect into marinization and sea level rises (Chaalali et al., 2013; Pawluck et al., 2021), it can be expected that estuaries may also change, thus the knowledge on species vulnerability to salinity conditions is even more important to subsidize conservation strategies.

Estuaries are highly dynamic ecosystems that connect marine and freshwater ecosystems, which naturally impose strong environmental variations upon fish assemblages (Whitfield et al., 2012). Therefore, fish assemblages in those systems are composed of species with different salinity affinities which can

be separated into functional groups (see Elliott et al., 2007; Potter et al., 2015). These groups include typically marine species, freshwater, and estuarine brackish species which enter estuaries either as migrants or stragglers, as well as migratory species (Elliott et al., 2007; Potter et al., 2015). Marine species are usually the dominants in fish assemblages in estuaries worldwide (Elliott et al., 2007; Whitfield et al., 2012; Henriques et al., 2017) and their contribution is directly related to the hydrological connectivity among the estuary and the marine ecosystem. This connection acts as an ecological corridor that links the systems and facilitates the migration of marine species in both ways (James et al., 2007). Moreover, higher sea-estuary connectivity was also positively related to increased species richness and turnover by previous studies (Henriques et al., 2016; Chaves et al., 2018). Our findings indicated greater abundance and number of indicator species in systems with higher connections to the sea (e.g., Saquarema and Maricá), especially of typically marine functional groups at the euhaline system. On the other hand, lower diversity and also a low abundance of marine species was detected at hyperhaline conditions (i.e., Araruama lagoon) where freshwater and marine species are expected to decrease, while more brackish tolerant guilds (e.g., residents and semianadromous) may thrive (Whitfield et al., 2012; Henriques et al., 2017). Besides, the great diversity of freshwater fish species at the Neotropical region may lead to an expectation of a greater contribution of the freshwater guild inside coastal lagoons, as have been found by previous studies (Garcia et al., 2003; Moura et al., 2012). Even though this pattern was not clear in our findings, since the importance of the freshwater guild may vary along the estuary and could be greater at upper stretches of the system, near the river discharge, further studies focusing on comparing different zones of the estuary may help to elucidate those patterns.

The global analyses performed by Henriques et al. (2017) found a positive association between high sea-estuary connectivity and species of carnivore and planktivore diets, and a negative relation to species of herbivore, detritivore and omnivore diets. They also related hyperhaline conditions with omnivore species. However, our findings indicated lower contributions of piscivores and herbivores, and greater contributions of planktivores at higher sea-estuary connectivity levels found at the Maricá and Saquarema lagoons,

where the piscivore *Strongylura marina* was an indicator species at the latter. On the other hand, the Araruama lagoon had a greater contribution of piscivores, herbivores, and omnivores, but this pattern was not related to any specific species. These findings suggest that the structure of trophic guilds may be highly influenced by local factors, such as abiotic conditions and resource availability, rather than global patterns or the degree of connection to the sea, and can be further variable within estuaries (present study). It is also important to highlight that tropical fish species usually exhibit considerable trophic plasticity and feeding opportunism (Cruz et al., 2018) which can be influential on the observed patterns. In this sense, further studies focusing on disentangling within and between variations of functional guilds, which also incorporates other descriptors (e.g., data on stomach contents, and food resource availability) should elucidate those patterns.

Our study indicated a significant variability within and between the three Neotropical lagoons, suggesting that spatial and/or seasonal effects on the environmental and biotic variables should be further investigated. Besides, although not addressed in this study, we are aware that coastal lagoons are very sensitive to human impacts, due to their vulnerable location between the sea and the mainland and their shallow depths. These systems are subject to numerous human impacts, such as aquaculture, touristic activities, and fishing. In this sense, the patterns described herein cannot be disassociated from the possible human impacts on the studied systems, especially for the omnivorous and planktivorous group that are more tolerant to organic loads and eutrophication processes, and for resident and marine migrant species which are highly susceptible to habitat degradation, due to their dependence of lagoons for spawning, feeding and nursery grounds (Elliott et al., 2007; Franco et al., 2009). Although further studies incorporating human impacts descriptors, especially those related to pollution and fishing activities, are recommended, our results confirmed the importance of protecting coastal lagoons of varied environmental conditions, particularly concerning salt concentrations, to preserve the functional diversity of Neotropical fish assemblages.

Author contributions ACSF, LNdS, and FGA contributed to the study conception and design. Material preparation and data

Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This research was conducted under SISBIO Collection of Species Permit Number 10707 issued by ICMBio, Brazilian Environmental Agency.

References

Anderson, M. J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253.

Anderson, M.J, 2008. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Araújo, F. G., M. C. C. Azevedo & A. P. P. Guedes, 2016. Interdecadal changes in fish communities of a tropical bay in southeastern Brazil. Regional Studies in Marine Science 3: 107–118.

Araújo, F. G., S. M. Pinto, L. M. Neves & M. C. C. Azevedo, 2017. Inter-annual changes in fish communities of a tropical bay in southeastern Brazil: what can be inferred from anthropogenic activities? Marine Pollution Bulletin 114: 102–113.

Barletta, M., & S. J. M. Blaber, 2007. Comparison of fish assemblages and guilds in tropical habitats of the Embley (Indo-West Pacific) and Caeté (Western Atlantic) Estuaries. Bulletin of Marine Science 80: 647–680.

Barletta, M., A. Barletta-Bergan, U. Saint-Paul, & G. Hubold, 2005. The role of salinity in structuring the fish assemblages in a tropical estuary. Journal of Fish Biology 66: 45–72.

Barletta, M., C. S. Amaral, M. F. M. Correa, F. Guebert, D. V. Dantas, L. Lorenzi & U. Saint-Paul, 2008. Factors affecting seasonal variations in demersal fish assemblages

at an ecocline in a tropical-subtropical estuary. Journal of Fish Biology 73: 1314–1336.

Becker, A., A. K. Whitfield, P. D. Cowley, V. J. Cole & M. D. Taylor, 2016. Tidal amplitude and fish abundance in the mouth region of a small estuary. Journal of Fish Biology 89: 1851–1856.

Bender, M. G., M. R. Pie, E. L. Rezende, D. Mouillot, & S. R. Floeter, 2013. Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages. Global Ecology and Biogeography 22: 1173–1182.

Blaber, S. J. M., 1973. Temperature and salinity tolerance of juvenile Rhabdosargus holubi (Steindachner) (Teleostei: Sparidae). Journal of Fish Biology 5: 593–599.

Blaber, S. J. M., 2013. Fishes and fisheries in tropical estuaries: the last 10 years. Estuarine Coastal and Shelf Science 135: 57–65.

Brind'Amour, A., D. Boisclair, S. Dray, & P. Legendre, 2011. Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. Ecological Applications 21: 363–377.

Camara, E. M., M. C. C. Azevedo, T. P. Franco & F. G. Araújo, 2019. Hierarchical partitioning of fish diversity and scale-dependent environmental effects in tropical coastal ecosystems. Marine Environmental Research 148: 26–38.

Chaalali, A., G. Beaugrand, P. Boët & B. Sautour, 2013. Climate-caused abrupt shifts in a European macrotidal estuary. Estuaries and Coasts 36: 1193–1205.

Chaves, M. C. N. R., A. C. S. Franco, L. B. Seixas, L. R. Cruz & L. N. Santos, 2018. Testing the ecocline concept for fish assemblages along the marine-estuarine gradient in a highly-eutrophic estuary (Guanabara Bay, Brazil). Estuarine, Coastal and Shelf Science 211: 118–126.

Connell, J. & E. Orias, 1964. The ecological regulation of species diversity. American Naturalist 98: 399–414.

Cruz, L. R., L. N. Santos & A. F. G. N. Santos, 2018. Changes of fish trophic guilds in Araruama Lagoon, Brazil: what can be inferred about functioning and structure of hypersaline lagoons? Estuarine, Coastal and Shelf Science 211: 90–99.

Cyrus, D. P. & S. J. M. Blaber, 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Estuarine, Coastal and Shelf Science 35: 545–563.

Dodson, S. I., S. E. Arnott & K. L. Cottingham, 2010. The relationship in lake communities between primary productivity and species richness. Ecology 81: 2662–2679.

Dufrêne, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible assymetrical approach. Ecological Monographs 67: 345–366.

Elliot, M. & V. Quintino, 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Marine Pollution Bulletin 54: 640–645.

Elliott, M. & A. K. Whitfield, 2011. Challenging paradigms in estuarine ecology and management. Estuarine, Coastal and Shelf Science 94: 306–314.

Elliott, M., A. K. Whitfield, I. C. Potter, S. J. M. Blaber, D. P. Cyrus, F. G. Nordlie & T. D. Harrison, 2007. The guild approach to categorizing estuarine fish. Fish and Fisheries 8: 241–268.

Figueiredo, L. L. & N. A. Menezes, 1978. Manual de peixes marinhos do sudeste do Brasil. II Teleostei. Museu de Zoologia de São Paulo, São Paulo.

Figueiredo, L. L. & N. A. Menezes, 1980. Manual de peixes marinhos do sudeste do Brasil. III Teleostei. Museu de Zoologia de São Paulo, São Paulo.

Figueiredo, L. L. & N. A. Menezes, 2000. Manual de peixes marinhos do sudeste do Brasil. VI Teleostei. Museu de Zoologia de São Paulo, São Paulo.

Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddack & M. H. Horn, 2005. Geographical gradient of marine herbivorous fishes: patterns and processes. Marine Biology 147: 1435–1447.

Franco, A., P. Torricelli & P. Franzoi, 2009. A habitat-specific fish-based approach to assess the ecological status of Mediterranean coastal lagoons. Marine Pollution Bulletin 58: 1704–1717.

Franco, A. C. S., M. C. N. Chaves, M. P. B. Castel-Branco & L. N. Santos, 2016. Responses of fish assemblages of sandy beaches to different anthropogenic and hydrodynamic influences. Journal of Fish Biology 89: 921–938.

Franco, T. P., L. M. Neves & F. G. Araújo, 2019. Better with more or less salt? The association of fish assemblages in coastal lagoons with different salinity ranges. Hydrobiologia 828: 83–100.

Garcia, A. M., M. B. Raseira, J. P. Vieira, K. O. Winemiller & A. M. Grimm, 2003. Spatiotemporal variation in shallow-water freshwater fish distribution and abundance in a large subtropical coastal lagoon. Environmental Biology of Fishes 68: 215–228.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage & E. L. Charnov, 2001. Effects of size and temperature on metabolic rate. Science 293: 2248–2251.

Henriques, S., P. Cardoso, I. Cardoso, M. Laborde, H. N. Cabral & R. P. Vasconcelos, 2016. Processes underpinning fish species composition patterns in estuarine ecosystems worldwide. Journal of Biogeography 44: 627–639.

Henriques, S., F. Guilhaumon, S. Villéger, S. Amoroso, S. França, S. Pasquad, H. N. Cabral, & R. P. Vasconcelos, 2017. Biogeographical region and environmental conditions drive functional traits of estuarine fish assemblages worldwide. Fish & Fisheries 18: 752–771.

Hudson, J. D., 1963. The recognition of salinity controlled mollusc assemblages in the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. Palaeontology 6: 318–326.

Hudson, J. D., 1980. Aspects of brackish-water facies from the Jurassic of north-west Scotland. Proceedings of Geologists' Association 91: 99–105.

James, N. C., P. D. Cowley, A. K. Whitfield, & S. J. Lamberth, 2007. Fish communities in temporarily open/closed estuaries from the warm-and cool-temperate regions of South Africa: a review. Reviews in Fish Biology and Fisheries 17: 565–580.

Kindt, R., 2017. Package "BiodiversityR" for Community ecology and suitability analysis. R package version 2.8–0. https://cran.r-project.org/web/packages/BiodiversityR/BiodiversityR.pdf Accessed Oct 2020.

Kjerfve, B, 1994. Coastal lagoon processes. In Kjerfve, B. (ed.), Elsevier Oceanography Series, Vol. 60. Elsevier, Amsterdam: 243–286.

Kjerfve, B. & C. A. F. Schettini, 1996. Hydrology and salt balance in a large, hypersaline coastal lagoon: Lagoa de Araruama, Brazil. Estuarine, Coastal and Shelf Science 42: 701–725.

Kjerfve, B., B. Knoppers, P. F. Moreira & B. Turcq, 1990. Hydrological regimes in Lagoa de Guarapina, a shallow Brazilian coastal lagoon. Acta Limnologica Brasiliensia 3: 291–317.

Knoppers, B., 1994. Aquatic primary production in coastal lagoons. In Kjerfve, B. (ed.), Coastal Lagoon Processes. Elsevier Oceanography Series. Elsevier, Amsterdam: 243–286.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, & F. Rubel, 2006. World Map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15: 259–263.

Martino, E. J., K. W. Able, 2003. Fish assemblages across the marine to low salinity transition zone of a temperate estuary. Estuarine, Coastal and Shelf Science 56: 969–987.

McLusky, D. S, 1989. The estuarine ecosystem. Springer, Dordrecht: 216.

Menezes, N. A. & L. L. Figueiredo, 1980. Manual de peixes marinhos do sudeste do Brasil. IV Teleostei. Museu de Zoologia de São Paulo, São Paulo.

Menezes, N. A. & L. L. Figueiredo, 1985. Manual de peixes marinhos do sudeste do Brasil. V Teleostei. Museu de Zoologia de São Paulo, São Paulo.

Moura, P. M., J. P. Vieira & A. M. Garcia, 2012. Fish abundance and species richness across an estuarine–freshwater ecosystem in the Neotropics. Hydrobiologia 696: 107-122.

Mouillot, D., N. A. Graham, S. Villeger, N. W. Mason & D. R. Bellwood, 2013. A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution 28: 167–177.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, & H. Wagner, 2016. vegan: Community Ecology Package. R package version 2.4–1. https://CRAN.R-project.org/package=vegan Accessed Oct 2020.

Pawluck, M., M. Fujiwara & F. Martinez-Andrade, 2021. Climate effects on fish diversity in the subtropical bays of Texas. Estuarine, Coastal and Shelf Science 249: 107–121.

Potter, I. C., J. R. Tweedley, M. Elliott & A. K. Whitfield, 2015. The ways in which fish use estuaries: a refinementand expansion of the guild approach. Fish and Fisheries 16: 230–239.

Potter, I. C., R. M. Warwick, N. G. Hall & J. R. Tweedley, 2016. The physico-chemical characteristics, biota and fisheries of estuaries. In: Craig, J. F. (ed.) Freshwater Fisheries Ecology. Wiley, New York: 920.

R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sosa-López, A., D. Mouillot, T. Do Chi & J. Ramos-Miranda, 2005. Ecological indicators based on fish biomass distribution along trophic levels: an application to the Terminos coastal lagoon, Mexico. ICES Journal of Marine Science 62: 453–458.

Sosa-López, A., D. Mouillot, J. Ramos-Miranda, D. Flores-Hernandez & T. D. Chi, 2007. Fish species richness

decreases with salinity in tropical coastal lagoons. Journal of Biogeography 34: 52–61.

Souza, G. B. G., M. Vianna, 2020. Fish-base indices for assessing ecological quality and biotic integrity in transitional waters: a systematic review. Ecological Indicators 109: 106665.

Teichert, N., S. Pasquaud, A. Borja, G. Chust, A. Uriarte & M. Lepage, 2017. Living under stressful conditions: fish life history strategies across environmental gradients in estuaries. Estuarine, Coastal and Shelf Science 188: 18–26.

Telesh, I. V. & V. V. Khlebovich, 2010. Principal processes within the estuarine salinity gradient: a review. Marine Pollution Bulletin 61: 149–155.

Tittensor, D. P., C. Mora, W. Jetz, H. K. Lotze, D. Ricard, E. V. Berghe & B. Worm, 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466: 1098–1101.

Tweedley, J. R., R. M. Warwick, C. S. Hallett & I. C. Potter, 2017. Fish-based indicators of estuarine condition that do not require reference data. Estuarine, Coastal and Shelf Science 101: 209–220.

Vasconcelos, R. P., S. Henriques, S. França, S. Pasquaud, I. Cardoso, M. Laborde & H. N. Cabral, 2015. Global patterns and predictors of fish species richness in estuaries. Journal of Animal Ecology 84: 1331–1341.

Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist & J. Kattge, 2014. The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences of the United States of America 111: 13690–13696.

Whitfield, A. K. & S. J. M. Blaber, 1976. The effects of temperature and salinity on *Tilapia rendalli* Boulenger 1896. Journal of Fish Biology 9: 99–104.

Whitfield, A. K. & M. Elliott, 2002. Fishes as indicators of environmental and ecological changes within estuaries – a review of progress and some suggestions for the future. Journal of Fish Biology 61(Suppl. A): 229–250.

Whitfield, A. K. & T. D. Harrison, 2003. River flow and fish abundance in a South African estuary. Journal of Fish Biology 62: 1467–1472.

Whitfield, A. K., M. Elliot, A. Basset, S. J. M. Blaber & R. J. West, 2012. Paradigms in estuarine ecology – A review of the Remane diagram with a suggested revised model for estuaries. Estuarine, Coastal and Shelf Science 97: 78–90.

Willig, M. R., D. M. Kaufman & R. D. Stevens, 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annual Review of Ecology, Evolution, and Systematics 34: 273–309.