Fish composition and assemblage structure in the estuarine mixing zone of a tropical estuary: comparisons between the main channel and an adjacent lagoon

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ORIGINAL ARTICLE

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Abstract
Spatial patterns of an estuarine habitat used by fish assemblages were determined for a protected adjacent lagoon and two areas of the main estuarine channel in a small tropical estuary. The tested hypotheses are that protected areas in estuarine zones support comparatively higher fish richness and abundance and have more small-sized fishes than the main channel. The lagoon and channel areas had distinct fish assemblage structures. Several abundant species (e.g. *Atherinella brasiliensis*, *Eugerres brasilianus*, *Geophagus brasiliensis*, *Achirus lineatus* and *Centropomus parallelus*) were of a smaller size in the lagoon compared with the estuarine channel and probably use the lagoon as nursery grounds. Moreover, some species (e.g. *Anchoa tricolor*, *Anchoa januaria*, *Gobionellus oceanicus* and *Poecilia vivipara*) were abundant and occurred only in the lagoon, whereas others (e.g. *Trinectes paulistanus*, *Ctenogobius shufeldti* and *Citharichthys arenaceus*) reached their highest abundance in the lagoon and were rarely found in the estuarine channel. Seasonal variation in the fish assemblage structure was not significant, which may be related to dominance of estuarine resident species. We found that the lagoon supported comparatively higher fish richness and abundance compared with the main estuarine channel because of the more sheltered and structured habitat. These results provide a better understanding of the role of adjacent habitats to fish assemblage and an improved basis for estuarine rehabilitation.

Key words: *Fish assemblages, estuaries, adjacent habitats, nursery, tidal lagoons*

Introduction

Estuaries consist of a complex mosaic of many distinctive habitat types and environmental features that combine to determine the fish assemblage structure (França et al. 2009; Fulford et al. 2011). Environmental habitat features in estuaries are largely dominated by temporal variability in temperature and salinity and spatial variability in dissolved oxygen concentration (Eby et al. 2005; Peterson et al. 2007). Physical features include structural components (e.g. vegetation, inanimate hard structures) that provide shelter from predation and nonstructural components (e.g. substrate type and bathymetry) that affect prey production (Manderson et al. 2003, 2004; Selleslagh et al. 2009). These features determine size-specific habitat use by fish species and relative abundances in different habitat types.

Estuarine channels are the most hydrodynamic part of an estuary because of the meeting of freshwater river flow and marine tides creating conditions of highly variable salinity and determining the habitat characteristics, such as substrate type, riparian vegetation and shelter. However, in areas adjacent to the main channel, the physical conditions are less severe, allowing the presence of macrophytes to flourish and that increases the habitat structural complexity (Sindilariu et al. 2006). Structural complexity can determine the success of some organisms in colonizing or using habitats by affecting resource availability and predation risk (Hixon & Menge 1991). Therefore, structurally complex habitats are expected to sustain higher densities of organisms and more diverse communities than structurally simple ones (Luckhurst & Luckhurst 1978; Diehl 1992; Humphries et al. 2011).

Some within-site variability in estuarine fauna appeared to be due to differences in vegetation, substrate type and current velocity between the channel and adjacent habitats (Keefer et al. 2008; Roach et al. 2009; Stevens et al. 2010). Protected areas, such as side lagoons, especially when permanently connected to the main channel, can act as important nursery grounds for fish species (Lehtinen et al. 1997; Grift et al. 2003, Lazzari et al. 2003). The use of shallow protected areas within estuaries by juvenile fishes has been attributed to the avoidance of predators (Paterson & Whitfield 2000) and strong currents (Beckley 1985; Strydom & Wooldridge 2005). Moreover, fish habitat choice changes with ontogeny (Burke et al. 2009; Manderson et al. 2002) and habitat bottlenecks have been identified, particularly for juvenile life stages (Bystrom et al. 1998; Ross 2003), during which variation in habitat quality can have a disproportional effect on population production and sustainability (Minello et al. 2003; Hickford & Schiel 2011).

The Mambucaba River, located on the coast of the state of Rio de Janeiro, Southeastern Brazil, has an estuarine mixing zone with a shallow lagoon permanently connected to the main channel. This lagoon has different levels of exposure to freshwater and tidal currents compared with the main channel. The type of substrate, extent of mangroves trees, grass and other margin cover change slightly between the main channel and the lagoon. Differences in fish assemblages across the longitudinal estuarine gradient (upper to lower estuary) were detected in a previous study in this estuary (Neves et al. 2011), which encompassed the whole estuarine zones but failed to examine in detail spatial fish distribution within each estuarine zone. As each zone has many distinctive habitat types, especially the mixing estuarine zone (middle estuary) that has the highest hydrodynamism, further studies on fish distribution within this part of the estuary are needed. The aim of this work was to compare the fish assemblage structure of the main channel with the adjacent lagoon. The tested hypotheses are that estuarine fish assemblages are likely to differ between these areas with the side lagoon supporting comparatively higher fish richness and abundance and higher number of small-sized species compared with the main channel. Revealing and incorporating information on distinctive estuarine habitat types on fish assemblages is a first step towards developing management strategies. Policies and restoration measures can benefit from these findings, since the uses of estuarine systems are increasing in tropical areas with corresponding losses of environmental quality.
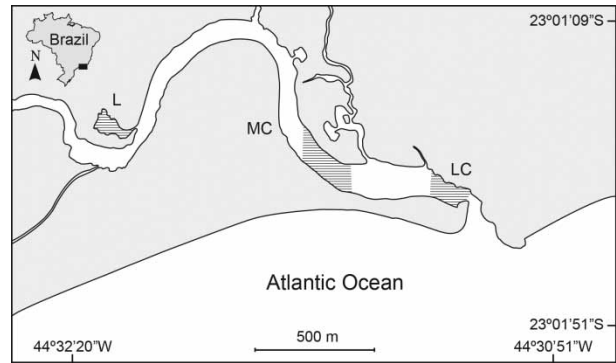

Figure 1. Map of the study area, Mambucaba estuary, with indication of the three estuarine areas. L, lagoon; MC, middle channel; LC, lower channel.

Material and methods

Study area

The Mambucaba River (23°01′37.30″S, 44°31′15.22″W), located on the coast of the State of Rio de Janeiro, southeastern Brazil, has a small open estuary (Figure 1). The study area covers the middle estuary, the most dynamic estuarine reaches where tide and river flows interact more intensively. The region has semi-diurnal tides, ranging from 0.1 m at neap tides to 1.3 m at the highest tides and is considered a micro-tidal estuary according to the McLusky & Elliott (2004) classification. The water circulation depends mainly on the tides and on a small freshwater input of about 13.8 $m^3 \cdot s^{-1}$ in the dry/winter season to 37.9 $m^3 \cdot s^{-1}$ in the wet/summer season (Francisco & Carvalho 2004). Average accumulated annual rainfall is 1770 mm, ranging from 180 mm in the dry/winter season (June–August) to approximately 750 mm in the wet/summer season (January–March). Temporal changes in rainfall and in river flow result in two seasons of comparatively low (winter) and high (summer) river influence and two intermediate seasons (spring and autumn).

The main channel of the middle estuary is approximately 120 m wide. Sandbanks divide the main water flow during low tide into two channels of approximately 3.5 m depth. The substrate is predominantly sandy with the margins surrounded by sparse mangrove cover at the lower reaches. A protected lagoon is connected to the main channel by a narrow channel of approximately 2 m width in the upper reaches. The lagoon has a depth of approximately 1.5 m with a predominantly muddy substrate and margins comprised of mangroves, ripraps and a small sandy beach. Part of the lagoon and the middle channel reaches are surrounded by mangrove, whereas the lower channel has a typical sandy beach as the main component of the

Table I. Physical characteristics of estuarine areas of the Mambucaba estuary.

Sites	Distance to estuary mouth (m)	Substrate type and mixed deposits	Percentage of margin cover type (%)	Level of exposure to freshwater and tidal currents	Enclosure
Lagoon	2000	Muddy substrate with sparse submerged tree limbs and stumps	Mangrove (60%), ripraps (20%), sand beach (10%), grass (10%)	Highly sheltered	Partially enclosed (90% encircled by land)
Middle channel	500	Sandy with some muddy patches	Mangrove (70%), grass (30%)	Moderately exposed	Main channel
Lower channel	20	Sandy	Sand beach (90%), grass (10%)	Moderately to fully exposed	Main channel

landscape. Substrate type changes from muddy in the lagoon to sandy in the lower channel (Table I).

Comparisons of water conditions and fish assemblages were made between three estuarine sections (lagoon, middle channel and lower channel) to account for differences in river morphology (e.g. adjacent lagoon versus main channel) and in fish assemblages along the environmental gradient. The sampling surface area was 0.7 ha in the lagoon, 2.1 ha in the middle channel and 1.3 ha in the lower channel. Visual estimates of substrate type (sandy or muddy), habitat-associated vegetation (percentage of margin cover type) and hydrographic characteristics (level of exposure to freshwater and tidal currents) were recorded to characterize the habitat structure of the three areas.

Sampling methods

Sampling was conducted for two months in each season, from October 2007 to August 2008. We tried to allocate sampling effort proportional to the area of each zone. On each sampling occasion, two samples were collected inside the lagoon because of its comparatively smaller area, and three samples were collected in the middle and lower channels. Sixty-one samples, evenly distributed among the four seasons, were collected in three areas of middle Mambucaba Estuary: 21 in the lower channel, 24 in the middle channel and 16 in an adjacent lagoon. Some samplings were not conducted because of inclement weather. To minimize the confounding effects of variations in tidal stage and environmental conditions among each sampling period and to standardize the sampling regime, all sites were sampled at flooding tide during full or new moon because in such conditions the tidal gradient is better defined.

Fishes were collected with a seine net 40 m long, 5 m in height and 6 m at the cod end. The net has a mesh size of 10 mm at the wings, 5 mm at the centre, and 2.5 mm at the cod end. The net was set up with the help of a small boat and hauls were taken perpendicular to the shoreline at a standardized distance of 15 m. Each seine covered an area of approximately 450 m^2, according to the following equation: $A = D \times L$, where D is the distance from the margin (15 m) and L is the net length effectively used in the haul (30 m). All fishes were measured for total length (mm) and weighed to the nearest 0.1 g.

Environmental variables were measured on each sampling occasion immediately before the fishing procedure. Temperature, salinity and dissolved oxygen were determined using a multiprobe YSI 85. Turbidity was measured using a Policontrol model AP2000 turbidimeter. Depth was measured with a Speedtech model SM-5 digital sounder. Three measurements of each environmental variable were taken from water collected near to the bottom with a Van Dorn bottle. Three habitat descriptors (substrate, marginal plant cover and shelter) were examined to assign a habitat structure score (in this study, habitat structure refers to the substratum and structural attributes which have the potential to provide shelter and food for fish species). Each habitat descriptor was assigned a value from 1 to 3 representing its qualitative estimation. Two substrate-type categories (sandy and muddy) and the presence of mixed deposits (broken shells, tree limbs and stumps) were used to characterize the sites according to the substrate type and mixed deposits descriptor. For example, areas with bare sand substrate and no mixed deposits were assigned a value of 1, whereas other areas with a combination of muddy substrate with submerged tree limbs and stumps and broken shells were assigned a value of 3. A score of 2 was assigned to substrata of intermediate habitat complexity (e.g. few mixed deposits with a sandy or muddy substrate). Values for the marginal plant cover descriptor were attributed based on the dominant margin type (grass or mangrove) considering the degree of protection for fish. We considered the dominant habitat being that which covered more than 60% of the margins. The score of 1 was attributed to areas that had no structures standing above the substratum (as sandy beaches), a score of 2 was attributed to areas where grasses were the main cover structure of the margin while areas with

mangrove dominance scored 3. In relation to shelter, a score of 3 was attributed to areas highly sheltered from freshwater and tidal currents influences, value of 2 to areas moderately exposed and a value of 1 was attributed to fully exposed areas near to the estuary mouth as the lower channel. A total score was calculated by adding the scores of each of the three habitat descriptors to give an estimate of the overall degree of habitat structure of the sites, which ranged from 3 (lowest habitat structure) to 9 (highest habitat structure).

Data analysis

One-way analysis of variance ($P < 0.05$) was used to compare fish abundance, number of species and biomass and environmental variables among seasons for each area, and among areas for each season. An a-posteriori Tukey HSD test followed ANOVA procedures every time that the null hypothesis was rejected at $\alpha = 0.05$ (Zar 1999). All biotic and environmental data were previously log transformed using $\log_{10}(x+1)$, where x is the raw value, to address the assumptions of normality and homogeneity of variance of the parametric analyses. Species richness was calculated with the first order Jackknife estimators. This procedure was performed using the software PC-ORD for Windows (McCune & Mefford 1999). Total length (TL) and total weight (TW) data for the dominant species common to lagoon and channel areas were submitted to the nonparametric Kruskal–Wallis test to investigate possible spatial variations in the size of individuals. Whenever differences were detected, the Mann–Whitney test was applied to the data to quantify and establish those differences. Medians of total length (TL) of fish species were compared between areas using the Median χ^2-test. ANOVA and non-parametric tests were performed using STATISTICA 7.1.

Fish abundance data were log transformed and converted into a triangular matrix of similarities, using the Bray–Curtis similarity coefficient. Hierarchical agglomerative clustering with group-averaging linking and nonmetric multidimensional scaling (nMDS) was performed to investigate similarities among species (Clarke & Warwick 1994). We used a nonparametric permutation-based one-way analysis of similarity (ANOSIM) to test for differences in the fish assemblage structure among the estuarine areas (lower channel, middle channel and adjacent lagoon) and to compare assemblages among seasons within each area. The main species responsible for sample groupings and for the discrimination between specified groupings in these analyses were identified using the SIMPER routine

(Clarke 1993). These analyses were performed using the statistic package PRIMER version 5.2.4 (Plymouth Routines in Multivariate Ecological Research Package: Clarke & Warwick 1994).

Environmental influences on the dominant species of each zone were assessed with a Canonical Correspondence Analysis (CCA) on log-transformed [$\log_{10}(x+1)$] data (ter Braak 1986). Dominant species in a given area were those having a frequency of occurrence $> 30\%$ and total number of individuals accounting for $> 1\%$ of all fishes. The statistical significance of each environmental variable was assessed with a Monte Carlo permutation test, using 1000 sample permutations. The CCA was performed using CANOCO software for Windows, version 4.5.

Results

Environmental variables

Water temperature varied from 20.9 to 29.3°C, with mean values ranging from 21.7°C in the lagoon during autumn to 28.6°C in the lower channel during spring (Table II). The only significant spatial difference occurred in autumn, with higher values in the channel areas than in the lagoon (ANOVA, $P < 0.05$). Significant seasonal changes ($P < 0.05$) in temperature were recorded for the three areas, with higher values during spring (means = 26.6–28.6°C) compared with the other seasons (means = 21.7–24.3°C). The three areas are typically mixohaline, with a mean salinity ranging from 0.2 to 26.2‰ in the lagoon and from 11.3 to 31.6‰ in channel areas. The two channel areas had comparatively higher salinity than the lagoon, except in spring. Significant seasonal changes in salinity were recorded only for the lagoon ($P < 0.05$), with the highest values in winter (mean = 26.2‰) and the lowest in summer (mean = 0.2) (Table II). In the middle channel salinity tended to increase from spring (mean = 11.3) to winter (mean = 31.6‰), whereas in the lower channel salinity means values were higher than 20‰ during all seasons. Turbidity values were significantly higher in the lagoon and middle channel (means = 1.7–15.3 NTU) compared to the lower channel (means = 0.02–1.9 NTU) during spring and autumn. Seasonally, the highest significant values ($P < 0.05$) were recorded in spring and summer (means = 10.1–15.7) and the lowest in autumn and winter (0.8–4.1 NTU) for the lagoon and the middle channel, whereas the lower channel had the highest values in summer (mean = 13.2 NTU) and the lowest in spring (mean = 0.02 NTU). Saturation of dissolved oxygen ranged from 52.6 to 102.8% in the lagoon, from 57 to 97.2% in the middle channel, and

Table II. Means (and SD) of environmental variables and *F*-values for among-seasons comparisons according to ANOVA for each estuarine area of the Mambucaba River estuary. Values having the same superscript letter were not significantly different within each area. Tukey comparisons among estuarine areas also indicated. L, lagoon; MC, middle channel; LC, lower channel. ns, non-significant at $\alpha =$ 0.05. *$P < 0.05$; **$P < 0.01$.

Seasons	Lagoon	Middle channel	Lower channel	*F*-Anova	Tukey comparisons
		Temperature (°C)			
Spring	26.6(0.9)[a]	27.1(2.1)[a]	28.6(0.5)[a]	ns	
Summer	23.6(0.2)[b]	24.3(1.6)[b]	24.3(1.6)[b]	ns	
Autumn	21.7(0.8)[b]	23.7(1.0)[a]	24.1(0.8)[a]	10.0**	MC, LC > L
Winter	23.2(1.0)[b]	23.6(1.1)[b]	23.6(1.0)[b]	ns	
F-ANOVA	25.8**	6.8**	12.8**		
		Salinity			
Spring	10.5(8.2)[ab]	11.3(9.6)[a]	26.8(0.6)[a]	ns	
Summer	0.2(0.0)[c]	13.0(13.4)[a]	23.3(1.5)[a]	12.7**	MC, LC > L
Autumn	2.4(2.8)[bc]	19.1(12.8)[a]	21.3(10.7)[a]	5.8*	MC, LC > L
Winter	26.2(2.2)[a]	31.6(1.6)[a]	29.4(1.2)[a]	12.2**	MC, LC > L
F-ANOVA	18.1**	ns	ns		
		Turbidity (NTU)			
Spring	10.1(1.8)[a]	15.3(5.3)[a]	0.02(0.0)[c]	116.4**	L, MC > LC
Summer	12.0(2.9)[a]	15.7(7.2)[a]	13.2(4.2)[a]	ns	
Autumn	4.1(1.9)[b]	1.7(0.8)[b]	1.9(0.7)[b]	6.3*	L, MC > LC
Winter	0.8(0.5)[b]	1.6(1.5)[b]	1.5(1.8)[bc]	ns	
F-ANOVA	39.9**	31.2**	27.4**		
		Dissolved oxygen (% saturation)			
Spring	80.3(15.8)[a]	77.8(17.4)[a]	82.5(2.7)[bc]	ns	
Summer	100.0(3.2)[a]	85.1(5.3)[a]	88.2(0.8)[ac]	19.0**	L > MC, LC
Autumn	78.4(11.5)[a]	78.6(10.1)[a]	86.4(5.0)[bc]	ns	
Winter	71.3(17.8)[a]	91.5(6.1)[a]	92.6(3.8)[a]	6.6**	MC, LC > L
F-ANOVA	ns	ns	6.0**		

from 78.4 to 98.1% in the lower channel. The lagoon had a higher saturation of dissolved oxygen (100%) than the channel areas (85.1–88.2%) during summer, but the lowest values during winter (71.3%). Seasonal changes were detected for the lower channel only, with significantly higher values in winter (mean = 96.2% saturation) and lower in spring (82.5% saturation) (Table II). The habitat structure score varied from 3 to 9 with mean values of 8.2 ± 0.7 SD in the lagoon, 6.3 ± 0.5 in the middle channel and 3.7 ± 0.9 in the lower channel.

Species composition

Fifty species belonging to 22 families and 32 genera were caught, yielding 7866 fish and 65,232 g in total weight for 61 samples (Table III). The number of recorded species was highest in the lagoon (36 species), decreasing in the middle channel (30 species) and having the lowest values in the lower channel (24 species). These values corresponded to about 65–80% of species richness estimated by the first Jackknife estimator for each estuarine area (lagoon, 45.4 species; middle channel, 46.3 species and lower channel, 31.5 species). The families with the highest number of individuals were Gerreidae (34% of the total number of fishes), Engraulidae (24.5%), Atherinopsidae (12.1%), Gobiidae (7.6%) and Achiridae (7.1%).

The mojarras *Eucinostomus melanopterus* (Bleeker, 1863), *Eucinostomus argenteus* Baird & Girard, 1855 and *Eugerres brasilianus* (Cuvier, 1830), the flatfishes *Trinectes paulistanus* (Miranda Ribeiro, 1915) and *Citharichthys arenaceus* Evermann & Marsh, 1900, the gobies *Ctenogobius shufeldti* (Jordan & Eigenmann, 1887) and *Gobionellus oceanicus* (Pallas, 1770), the common snook *Centropomus parallelus* Poey, 1860, the pearl cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824) and the silverside *Atherinella brasiliensis* (Quoy & Gaimard, 1825) were the dominant species in the lagoon. These species accounted for 58% of the total number of individuals collected. *Eucinostomus melanopterus*, *Eucinostomus argenteus*, *Eugerres brasilianus*, *A. brasiliensis*, *G. brasiliensis*, the common halfbeak *Hyporhamphus unifasciatus* (Ranzani, 1841), the timucu *Strongylura timucu* (Walbaum, 1792), and the flatfish *Achirus lineatus* (Linnaeus, 1758) were dominant in the middle channel and accounted for 96% of the total number of individuals. In the lower channel, *A. brasiliensis* was the only dominant species and accounted for 61% of the total number of individuals.

Fish abundance, biomass and species richness

The number of species was higher in the lagoon than in the two channel areas during all seasons (ANOVA,

Table III. Number of individuals (N), relative abundance (%), frequency of occurrence (FO) and mean size (TL, in mm) ±standard deviation (SD) for fish species in estuarine areas of the Mambucaba Estuary.

Order/Family	Species	Lagoon N (%)	FO	Mean TL±SD (mm)	Middle channel N(%)	FO	Mean TL±SD (mm)	Lower channel N (%)	FO	Mean TL±SD (mm)
Clupeiformes										
Engraulidae	*Anchoa tricolor* (Spix & Agassiz, 1829)	1537(29.9)	6.3	42.0±8.7	–	–	–	–	–	–
	Anchoa januaria (Steindachner, 1879)	349(6.8)	25.0	62.4±10.0	–	–	–	–	–	–
	Anchoa lyolepis (Evermann & Marsh, 1900)	37(0.7)	18.8	56.0±10.0	–	–	–	1(0.1)	4.8	60.0
Siluriformes										
Ariidae	*Genidens genidens* (Curvier, 1829)	12(0.2)	12.5	83.0±32.3	1(0.1)	4.2	166.0	–	–	–
Mugiliformes										
Mugilidae	*Mugil* sp.	8(0.2)	18.8	29.0±2.0	–	–	–	3(0.4)	9.5	23.0±1.0
	Mugil liza Valenciennes, 1836	7(0.1)	6.3	139.1±236.6	1(0.1)	4.2	315.0	–	–	–
	Mugil curema Valenciennes, 1836	1(<0.1)	6.3	84.0	–	–	–	19(2.7)	23.8	108.5±57.5
Atheriniformes										
Atherinopsidae	*Atherinella brasiliensis* (Quoy & Gaimard, 1825)	87(1.7)	37.5	38.4±17.9	396(19.6)	62.5	83.7±40.6	466(65.6)	61.9	83.0±28.5
Beloniformes										
Hemiramphidae	*Hyporhamphus unifasciatus* (Ranzani, 1841)	1(<0.1)	6.3	240.0	368(18.2)	41.7	255.2±27.4	88(12.4)	23.8	230.3±27.7
	Hyporhamphus roberti (Valenciennes, 1847)	–	–	–	11(0.5)	8.3	184.3±15.7	–	–	–
Belonidae	*Strongylura timucu* (Walbaum, 1792)	24(0.5)	50.0	298.6±68.8	39(1.9)	45.8	344.2±90.7	11(1.6)	23.8	303.1±110.3
	Strongylura marina (Walbaum, 1792)	–	–	–	24(1.2)	8.3	276.3±39.7	1(0.1)	4.8	–
Syngnathiformes										
Syngnathidae	*Microphis lineatus* (Kaup, 1856)	2(<0.1)	12.5	113.0±31.1	–	–	–	1(0.1)	4.8	109.0
	Syngnathus folletti Herald, 1942	1(<0.1)	6.3	120.0	–	–	–	1(0.1)	4.8	–
Cyprinodontiformes										
Poeciliidae	*Poecilia vivipara* Bloch & Schneider, 1801	35(0.7)	31.3	28.7±5.1	–	–	–	–	–	–
Perciformes										
Centropomidae	*Centropomus parallelus* Poey, 1860	121(2.4)	62.5	68.4±33.6	1(0.1)	4.2	330.0	11(1.6)	14.3	177.1±26.1
	Centropomus undecimalis (Bloch, 1792)	1(<0.1)	6.3	345.0	–	–	–	–	–	–
Serranidae	*Acanthistius brasilianus* (Cuvier, 1828)	–	–	–	1(0.1)	4.2	40.0	–	–	–
Carangidae	*Caranx latus* Agassiz, 1831	4(0.1)	25	123.8±46.1	4(0.2)	12.5	131.0±28.6	42(5.9)	9.5	124.8±7.7
	Oligoplites saliens (Bloch, 1793)	–	–	–	–	–	–	2(0.3)	4.8	286.5±33.2
	Oligoplites saurus (Bloch & Schneider, 1801)	–	–	–	2(0.1)	8.3	41.0±1.4	4(0.6)	4.8	193.0±22.2
Gerreidae	*Eugerres brasilianus* (Cuvier, 1830)	1184(23.1)	100.0	61.6±22.2	105(5.2)	58.3	125.8±59.3	9(1.3)	19.1	46.6±43.2
	Eucinostomus melanopterus (Bleeker, 1863)	229(4.5)	68.8	58.1±14.9	463(22.9)	33.3	59.8±15.6	–	–	–
	Eucinostomus argenteus Baird & Girard, 1855	188(3.7)	87.5	76.6±26.5	496(24.5)	91.7	114.8±22.4	3(0.4)	4.8	115.0±29.1
	Eucinostomus gula (Quoy & Gaimard, 1824)	–	–	–	1(0.1)	4.2	146.0	–	–	–
Sparidae	*Archosargus probatocephalus* (Walbaum, 1792)	–	–	–	1(0.1)	4.2	203.0	–	–	–
Scianidae	*Micropogonias furnieri* (Desmarest, 1823)	4(0.1)	18.8	87.3±20.1	–	–	–	–	–	–
Cichlidae	*Geophagus brasiliensis* (Quoy & Gaimard, 1824)	102(2.0)	100.0	110.0±47.0	41(2.0)	50	163.4±22.2	–	–	–
	Oreochromis niloticus (Linnaeus, 1758)	4(0.1)	6.3	54.3±2.5	–	–	–	–	–	–
Eleotridae	*Eleotris pisonis* (Gmelin, 1789)	2(<0.1)	6.3	43.5±2.1	–	–	–	–	–	–
Gobiidae	*Ctenogobius shufeldti* (Jordan & Eigenmann, 1887)	270(5.3)	93.8	46.5±12.4	1(0.1)	4.2	51.0	2(0.3)	4.8	34.5±0.7
	Gobionellus oceanicus (Pallas, 1770)	250(4.9)	87.5	117.9±40.3	–	–	–	–	–	–
	Ctenogobius boleosoma (Jordan & Gilbert, 1882)	17(0.3)	43.8	43.1±4.3	1(0.1)	4.2	38.0	12(1.7)	19.1	39.7±8.1
	Evorthodus lyricus (Girard, 1858)	16(0.3)	50	59.8±6.3	1(0.1)	4.2	39.0	–	–	–
	Bathygobius soporator (Valenciennes, 1837)	4(0.1)	25	80.3±25.1	8(0.4)	12.5	200.3±95.2	10(1.4)	28.6	84.2±33.7
	Gobionellus stomatus Starks, 1913	4(0.1)	25	98.8±19.7	–	–	–	–	–	–
	Awaous tajasica (Lichtenstein, 1822)	1(<0.1)	6.3	79.0	–	–	–	–	–	–

Table III (*Continued*)

Order/Family / Species	Lagoon N (%)	FO	Mean TL±SD (mm)	Middle channel N(%)	FO	Mean TL±SD (mm)	Lower channel N (%)	FO	Mean TL±SD (mm)
Pleuronectiformes									
Achiridae									
Trinectes paulistanus (Miranda Ribeiro, 1915)	470(9.2)	100.0	44.8±13.2	1(0.1)	4.2	21.0	6(0.9)	14.3	38.5±5.3
Achirus lineatus (Linnaeus, 1758)	38(0.7)	87.5	53.3±10.6	35(1.7)	37.5	53.0±10.5	3(0.4)	14.3	91.3±15.0
Catathyridium garmani (Jordan, 1889)	–	–	–	–	–	–	2(0.3)	9.5	126.0±21.2
Cynoglossidae									
Symphurus tessellatus (Quoy & Gaimard, 1824)	–	–	–	1(0.1)	4.2	65.0	–	–	–
Paralichthyidae									
Citharichthys arenaceus Evermann & Marsh, 1900	88(1.7)	93.8	63.4±14.2	8(0.4)	8.3	56.1±10.1	4(0.6)	4.8	30.0±34.5
Citharichthys spilopterus Günther, 1862	29(0.6)	87.5	107.5±21.9	1(0.1)	4.2	111.0	–	–	–
Paralichthys orbignyanus (Valenciennes, 1839)	4(0.1)	18.8	79.8±16.5	–	–	–	–	–	–
Paralichthys brasiliensis (Ranzani, 1842)	2(0.1)	12.5	132.5±48.8	1(0.1)	4.2	151	–	–	–
Citharichthys macrops Dresel, 1885	–	–	–	6(0.3)	4.2	65.3±19.8	–	–	–
Tetraodontiformes									
Diodontidae									
Chilomycterus spinosus (Linnaeus, 1758)	–	–	–	1(0.1)	4.2	157.0	–	–	–
Tetraodontidae									
Sphoeroides greeleyi Gilbert, 1900	–	–	–	–	–	–	10(1.4)	19.1	88.4±78.8
Sphoeroides spengleri (Bloch, 1785)	–	–	–	–	–	–	1(0.1)	4.8	–
Sphoeroides testudineus (Linnaeus, 1758)	–	–	–	1(0.1)	4.2	61.0	–	–	–
	5133			2021			712		

$P<0.01$, Table IV). Significant seasonal changes ($P<0.01$) in the number of species were found for the lagoon, with the highest values in spring and summer (mean = 16 species) and lowest in autumn (mean = 11.3 species). In the lower channel, the highest values were recorded in winter (mean = 5.2 species) and the lowest in summer (mean = 1.8 species). The number of individuals was also higher in the lagoon compared with the channel areas, but departures from this pattern depended on season (Table IV). In spring, no significant difference was detected for the number of individuals because of high within-area variation. On the other hand, the number of individuals was higher in the lagoon compared with the lower channel in summer and compared with the middle and lower channel in autumn. In winter, a higher, significant number of individuals were found for the lagoon and the middle channel compared with the lower channel ($P<0.01$). No seasonal difference in the number of individuals was detected for any studied area. There was a considerable variability in the biomass estimates, especially in the middle channel. No seasonal differences were detected within each estuarine area. The biomass varied spatially, with higher values in the lagoon than in the lower channel during summer, and in the lagoon and in the middle channel compared with the lower channel in winter (Table IV).

Temporal and spatial patterns

Highly significant differences in fish assemblage structure were found among the three areas, according to ANOSIM (R global, 0.56; $P<0.001$). The highest differences were recorded between the lagoon and the two channel areas ($R>0.60$; $P<0.001$). The lowest R-value was found between middle and lower channel ($R=0.41$; $P<0.001$).

Cluster analysis showed that the lagoon and middle channel fell into one group (Figure 2), albeit at a relatively low similarity (34%), whereas samples from the lower channel formed a separate group, with a similarity to the others of 23.5%. The highest within-group similarity was recorded for the lagoon (57.7%) compared with the middle (45.1%) and lower (33.8%) channel. No strong pattern was observed for the seasons within each area (Figure 2). The wide scattering within the grouping comprised of middle and lower channel and high stress (0.18) in the nMDS plot indicated highly variable assemblages. In contrast, the lagoon samples were clustered together indicating a lesser within-group variability (Figure 3).

Trinectes paulistanus, *Eugerres brasilianus* and *Eucinostomus argenteus* had the highest contribution

Table IV. Means (and SD) of number of species, number of individuals and biomass and F-values for among-seasons comparisons according to ANOVA for each estuarine area of the Mambucaba River estuary. Values having the same superscript letter were not significantly different within each area. Tukey comparisons among estuarine areas also indicated. L, lagoon; MC, middle channel; LC, lower channel. ns, non-significant at $\alpha = 0.05$. * $P < 0.05$; ** $P < 0.01$.

Seasons	Lagoon	Middle channel	Lower channel	F-ANOVA	Tukey comparisons
			Number of species		
Spring	16.0(1.4)[a]	6.3(2.1)[a]	3.3(0.6)[ab]	42.0**	L > MC > LC
Summer	16.0(1.6)[a]	5.5(3.3)[a]	1.8(1.5)[b]	19.4**	L > MC > LC
Autumn	11.3(0.9)[b]	4.8(1.7)[a]	3.2(2.5)[ab]	12.7**	L > MC, LC
Winter	14.8(2.5)[a]	5.2(2.1)[a]	5.2(2.1)[a]	19.9**	L > MC, LC
F-ANOVA	8.0**	ns	3.3*		
			Number of individuals		
Spring	607(859)[a]	132(161)[a]	98(112)[a]	ns	
Summer	254(133)[a]	65(54)[a]	29(49)[a]	6.8**	L > LC
Autumn	159(87)[a]	32(23)[a]	13(11)[a]	10.5**	L > MC, LC
Winter	265(129)[a]	109(61)[a]	27(16)[a]	23.2**	L, MC > LC
F-ANOVA	ns	ns	ns		
			Biomass (g)		
Spring	1122(285)[a]	2299(3466)[a]	1168.4(1002)[a]	ns	
Summer	1188(599)[a]	628(518)[a]	241.9(484)[a]	5.5*	L > LC
Autumn	869(500)[a]	775(544)[a]	210.5(259)[a]	ns	
Winter	1224(489)[a]	2893(2465)[a]	304.7(357)[a]	8.8**	L, MC > LC
F-ANOVA	ns	ns	ns		

to the dissimilarity among the sites according to SIMPER. The highest within-group similarity was recorded for the lagoon (56.8%) and the lowest for the middle (35.5%) and lower channels (22.6%). The lagoon had a more diverse assemblage, with 11 species being characteristic of this area, according to SIMPER (Table V). *Eugerres brasilianus* and *Trinectes paulistanus* contributed with 17.1 and 16.9% to the within-group similarity, respectively. Typical species from middle channel were *E. argenteus* (46.3% of within-group similarity) and *Atherinella brasiliensis* (17.7%), whereas the lower channel had *A. brasiliensis* (69.6% of the within-group similarity) and *Hyporhamphus unifasciatus* (7.1%) as more characteristics species (Table V).
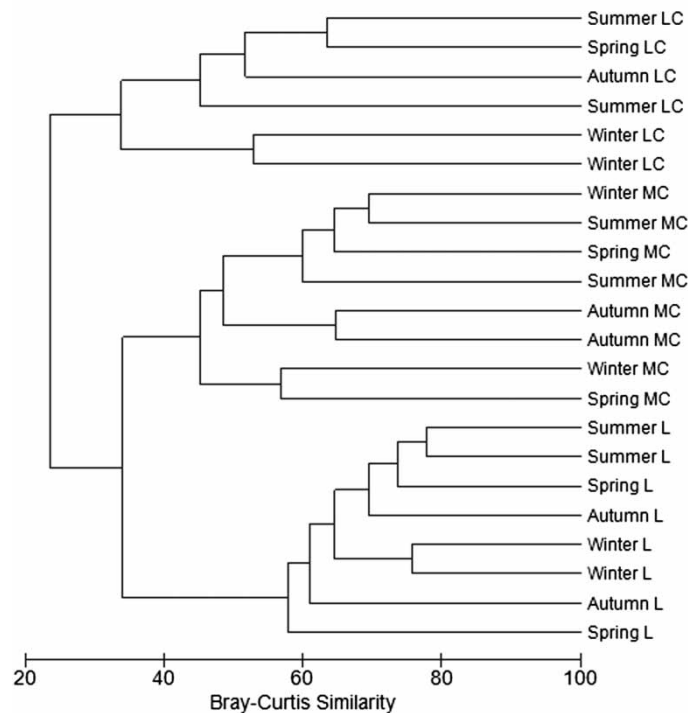

Figure 2. Cluster dendrogram of fish abundance data. L, lagoon; MC, middle channel and LC, lower channel.
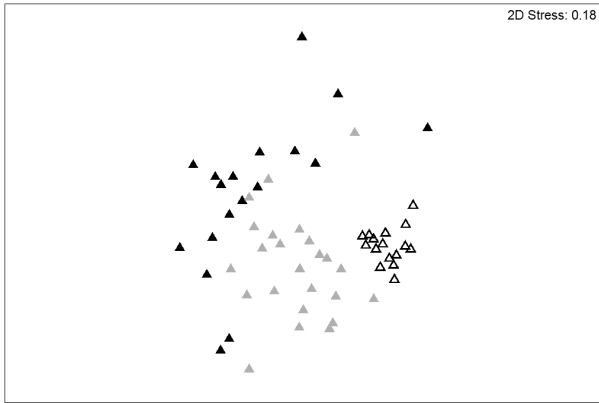
Figure 3. MDS ordination plot of the fish assemblages coded by estuarine areas. White triangles, lagoon; gray triangles, middle channel; black triangles, lower channel.

No seasonal difference in the structure of the fish assemblage was found for the middle estuary ($P >$ 0.05) with low R-values from ANOSIM (-0.03 to 0.09) for all season comparisons. Low within-group mean similarities were recorded for each season with summer (32.2% mean similarity) having the highest values, and autumn the lowest (20.1% mean similarity). *Eucinostomus argenteus*, *Eugerres brasilianus*, *Atherinella brasiliensis* and *Achirus lineatus* were the species that contributed more to within-group similarity and occurred throughout the year in most samples.

Table V. Discriminating species of each estuarine area determined by SIMPER analysis. The highest contributions for each area are in bold.

	Lagoon (56.8)	Middle channel (35.5)	Lower channel (22.6)
Average similarity (%)	Contribution (%)		
Eugerres brasilianus	**17.1**	11.1	2.3
Trinectes paulistanus	**16.9**		
Ctenogobius shufeldti	10.8		
Geophagus brasiliensis	9.1	5.2	
Eucinostomus argenteus	8.1	**46.3**	
Gobionellus oceanicus	7.9		
Citharichthys arenaceus	6.1		
Eucinostomus melanopterus	5.4		
Citharichthys spilopterus	4.8		
Achirus lineatus	4.1		
Centropomus parallelus	3.6		
Atherinella brasiliensis		17.7	**69.6**
Hyporhamphus unifasciatus		7.3	7.1
Bathygobius soporator			5.8
Strongylura timucu		5.4	3.6
Mugil curema			3.4

Environmental influences on fish assemblage

The first two axes from canonical correspondence analysis accounted for 84.5% of the cumulative percentage of variance for the environmental-species relationship (Figure 4), with the Monte Carlo analysis revealing that habitat structure contributed
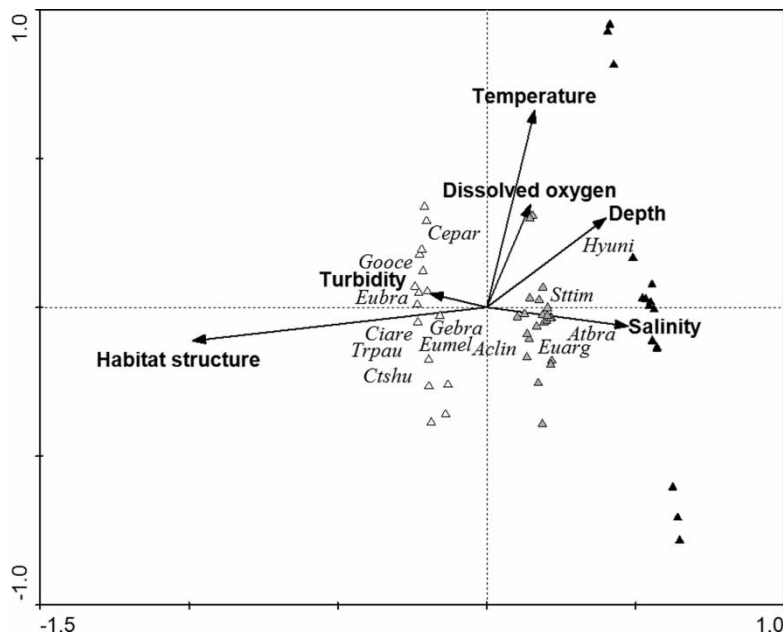

Figure 4. Ordination diagram from canonical correspondence analysis on fish abundance and environmental variables with samples coded by the estuarine areas. White triangles, lagoon; gray triangles, middle channel; black triangles, lower channel. Species code: *Gebra, Geophagus brasiliensis*; *Eubra, Eugerres brasilianus*; *Atbra, Atherinella brasiliensis*; *Eumel, Eucinostomus melanopterus*; *Euarg, Eucinostomus argenteus*; *Trpau, Trinectes paulistanus*; *Sttim, Strongylura timucu*; *Hyuni, Hyporranphus unifasciatus*; *Ctshu, Ctenogobius shufeldti*; *Gooce, Gobionellus oceanicus*; *Cepar, Centropomus parallelus*; *Aclin, Achirus lineatus*; *Ciare, Citharrichthys arenaceus*.
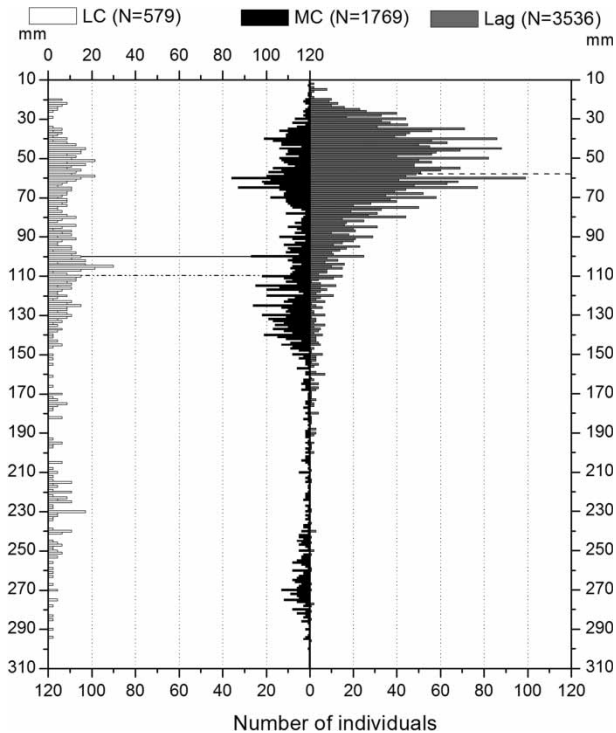
Figure 5. Comparison of the total length–frequency distribution of all measured fish in the lagoon (grey bars), middle channel (black bars) and lower channel (white bars). The medians were indicated by dash, dash-dot and solid lines for the lagoon, middle channel and lower channel, respectively. The top *x*-axis indicates the number of individuals of the lower channel.

most to species distribution. Samples representing the lagoon, middle channel and lower channel were separated along the first axis. Axis 1 was negatively correlated with habitat structure and turbidity, and positively correlated with salinity, depth and, to a lesser extent, with temperature and dissolved oxygen. Axis 2 was positively correlated with temperature, dissolved oxygen and depth.

Trinectes paulistanus, Citharichthys arenaceus, Ctenogobius shufeldti, Gobionellus oceanicus, Eugerres brasilianus, Geophagus brasiliensis and *Eucinostomus melanopterus* were associated with high habitat structure and high turbidity of the lagoon. Conversely, *Atherinella brasiliensis, Eucinostomus argenteus, Strongylura timucu* and *Hyporhamphus unifasciatus* were associated with the opposite conditions of the middle and lower channel that had high salinity and depth (Figure 4).

Size structure

Fish size differed among the three areas ($P < 0.001$; $\chi^2 = 674.3$) according to the Median test. The lagoon had individuals of smaller size (median = 58 mm TL) compared with the middle (median = 110 mm TL) and lower channel (median = 100 mm TL) (Figure 5). Total length and total weight data showed that some of the dominant species (*Eucinostomus argenteus, Centropomus parallelus, Atherinella brasiliensis* and *Geophagus brasiliensis*) were smaller in the lagoon compared with the channel areas according to the Kruskal–Wallis test (Table VI). *Eugerres brasilianus* followed the same trend, although a few individuals (9) recorded in the lower channel were of a similar size to those from the lagoon (Tables III and VI). On the other hand, *Achirus lineatus* did not differ significantly in size among the three areas.

Table VI. Results of the Kruskal–Wallis test (H) for the comparison of total length (TL, mm) and total weight (TW, g) median of selected species among the three areas of Mambucaba river estuary. The medians and quartiles for total length and total weight also shown. Values having the same superscript letter were not significantly different according to Mann–Whitney test. ⋆ $P < 0.05$; ⋆⋆ $P < 0.01$.

Species	Attribute	*H*	Median (1st–3rd quartiles)		
			Lagoon	Middle channel	Lower channel
Atherinella brasiliensis	TL	116.2⋆⋆	30(26–46)[b]	78(45–122)[a]	83(57–105)[a]
	TW	122.5⋆⋆	0.13(0.1–0.5)[b]	2.9(0.5–10.2)[a]	3.4(1.1–6.9)[a]
Eucinostomus argenteus	TL	209.9⋆⋆	90(47–114)[b]	116(100–133)[a]	115(110–120)[a]
	TW	211.3⋆⋆	13.8(4.8–15.0)[b]	15.8(9.5–25.7)[ac]	17.1(8.3–29.0)[bc]
Eugerres brasilianus	TL	117.1⋆⋆	23(22–70)[b]	119(119–158)[a]	62(62–78)[b]
	TW	144.9⋆⋆	1.2(0.1–4.1)[b]	19.5(4.4–50.7)[a]	2.5(0.8–5.1)[b]
Geophagus brasiliensis	TL	43.2⋆⋆	115(84–143)[b]	162(143–179)[a]	
	TW	42.8⋆⋆	22.8(8.2–45.8)[b]	69.4(49.6–90.2)[a]	
Eucinostomus melanopterus	TL	5.66⋆	60(55–65)[a]	55(55–67)[b]	
	TW	3.9⋆	2.0(1.4–2.5)[a]	1.5(0.9–2.7)[b]	
Achirus lineatus	TL	ns	56.5(47–62)	51(46–59)	99(74–101)
	TW	ns	2.54(1.95–3.84)	2.6(1.9–4.2)	16.0(7.4–20.2)
Trinectes paulistanus	TL	ns	42(36–54)	21	39.5(29–43)
	TW	ns	1.3(0.72–2.70)	0.07	0.94(0.34–0.72)
Centropomus parallelus	TL	30.8⋆⋆	60.0(44–90)[b]	330	175(130–220)[a]
	TW	29.9⋆⋆	1.6(0.7–6.2)[b]	319.4	38.1(28.6–45.2)[a]

Most of the dominant species exhibited size-specific habitat use across the estuarine areas (Figure 6). The smallest (<70 mm TL) *E. argenteus* individuals were almost exclusively collected in the lagoon, whereas the largest (>125 mm TL) individuals were found almost exclusively in the main channel areas. Individuals of *E. brasilianus* smaller than 130 mm TL were found in the lagoon and middle channel areas, although the largest (>150 mm TL) were exclusively collected in the middle channel. *Eucinostomus melanopterus* had sizes ranging from 40 to 140 mm TL in the lagoon and middle channel, with modes of 50 mm in lagoon and 70 mm in the middle channel.

Atherinella brasiliensis had mode of 30 mm TL in the lagoon, whereas the largest (>90 mm TL) individuals were exclusively collected in the two main channel areas. *Geophagus brasiliensis* had sizes ranging from 20 to 220 mm TL in the lagoon and 140 to 230 mm TL in the middle channel, with the individuals smaller than 140 mm TL found only in the lagoon. *Achirus lineatus* had a size range of 30–70 mm TL in the lagoon, 40–90 mm TL in the middle channel and only few individuals (80–110 mm TL) were recorded in the lower channel. *Trinectes paulistanus* had sizes ranging from 20 to 90 mm TL in the lagoon with a small number of individuals occurring in the channel areas. The smaller (<130 mm TL) *Centropomus parallelus* individuals were exclusively collected in the lagoon, with individuals larger than 150 mm TL being collected mainly in the lower channel (Figure 6).

Discussion

The estuarine channel and the adjacent lagoon of the Mambucaba River played different roles for fish assemblages because of different habitat and hydrological conditions. The lagoon had comparatively higher fish richness and abundance with smaller fish size, whereas the two channels areas had comparatively lower number of fish species with relatively larger size, reflecting a differentiated use of the area. Some dominant species found in the lagoon (e.g. *Trinectes paulistanus*, *Ctenogobius shufeldti*, *Citharichthys arenaceus*, *Centropomus parallelus*) were rarely collected in the two main channel areas, whereas other species were abundant in the lagoon and in the middle channel (*Eucinostomus argenteus*, *Eucinostomus melanopterus*, *Eugerres brasilianus*). Despite the difference in the sample size among the three areas, the sampling design seems to be appropriate to assess spatial patterns. This is confirmed, for example, by the highest richness and abundance found in the lagoon that had the lowest sampling size.
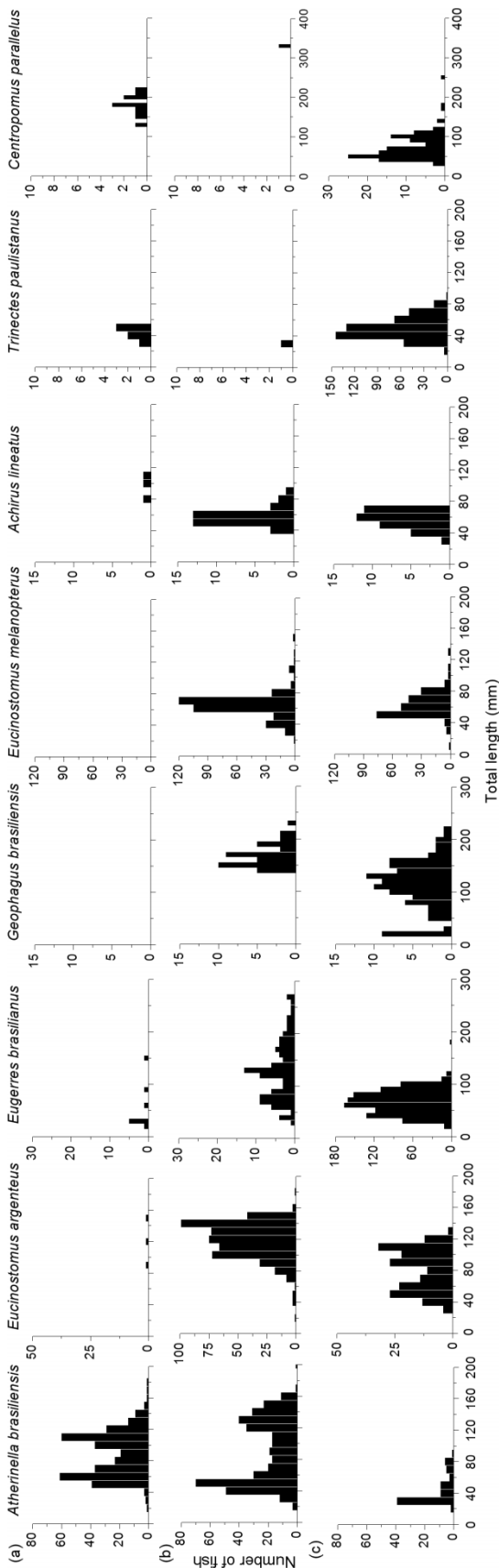

Figure 6. Length–frequency distributions for dominant species in the lower channel (a), middle channel (b) and lagoon (c) of the Mambucaba estuary.

Availability of large areas of complex habitat, particularly mangrove forest, is an important reason why fish use tropical estuaries as nursery areas (Johnston & Sheaves 2007; Wang et al. 2009). Mangroves provide shelter and increased surface area for accumulation of food (Laegdsgaard & Johnson 2001). Sindilariu et al. (2006) found higher fish density in adjacent lagoons (mean density $= 31$ individuals m^{-2}) in the lower Danube River compared with the main channel (mean density $=$ 5.6 individuals m^{-2}) and attributed those areas as nursery grounds because of the presence of macrophytes that enhance habitat complexity. The protected adjacent lagoon in the Mambucaba Estuary and the nearby mangrove that encompasses part of the middle channel are favourable habitats for the ichthyofauna. However, during the ebb tides, a large area of the mangrove is not available for fish species, when the lack of habitat structure may result in the absence of shelter. Therefore, the highest abundance and richness of fish species in the lagoon compared with the channel areas suggests that this protected and structured area with permanent connection with the estuarine channel has a particular ecological value in this estuarine system.

Substrate heterogeneity and water flow seem to be among the main characteristics influencing habitat selection by fish species. The more sheltered area in the protected lagoon, with low turbulence and predominant muddy substrate and the estuarine channel, with more hydrodynamism and sandy substrate, influence fish assemblages in different ways. Areas of reduced water flow usually have silty sediments (Wood & Armitage 1997) with high organic matter (Rhoads & Young 1970) that will favourably affect the occurrence of benthic invertebrates (Rhoads & Young 1970; Day et al. 1989) and consequently attract fish species (Szedlmayer & Able 1996). Moreover, the high structural complexity usually supports higher organism density, provides enhanced refuge and food availability and facilitates higher growth rate (Orth & van Montfrans 1990; Beck et al. 2001; Fonseca et al. 2006). Species from the families Gobiidae, Centropomidae and Paralichthyidae occurred mainly in the lagoon, suggesting that habitat characteristics strongly influence their distribution in the estuary.

The geomorphology and associated habitat differences between channel and lagoon areas, more than the environmental variables, seem to be the main factors structuring fish assemblages in Mambucaba estuary. Although the salinity gradient is stronger during flooding tides, the oligohaline conditions predominate during ebb tides in all three areas and the estuarine fish community of the mixture estuarine zone seems to be adapted to this kind of diel variation in environmental variables. Most of the species that were more abundant in the lagoon and main channel are estuarine residents (*sensu* Elliott et al. 2007), completing their life cycle in the estuary. These species from the families Gerreidae, Achiridae, Gobiidae, Hemiramphidae and Atherinidae are recognized as tolerant of changes in salinity in many estuaries (Blaber 2000; Araújo & Costa 2001; Barletta et al. 2005; Contente et al. 2011). The lagoon, with more vegetated margins and calm waters contrasting with more dynamism and lesser habitat structure of the main channel, seems to attract more fish, with salinity being a secondary factor dictating fish distribution.

Canonical correspondence analysis revealed that habitat structure, depth and salinity explained most of the observed variation in assemblage structure at the relatively small-scale of this study. Habitat structure and depth effects appeared to be influential in discriminating the fish assemblage structure from the highly structured habitat of the lagoon to the less-structured habitat of the lower channel. Although a salinity gradient exists, the relatively large vector representing habitat heterogeneity indicates its importance in shaping assemblage structure across the areas. Patterns in the structure of estuarine fish assemblages at smaller scale (1 km) appear to be the result of habitat associations that are most likely driven by habitat selection, competition and/or predator avoidance strategies (Martino & Able 2003). Conversely, salinity is the most influential variable to large-scale (10 km) fish assemblage structure across the whole estuarine gradient (upper to lower estuary) (Wagner & Austin 1999; Neves et al. 2011).

The higher within-group average similarity of fish assemblage in the lagoon compared with the channel areas reinforces the expectation that protected lagoons shelter a more stable fish assemblage compared with the main channel where conditions are more dynamic. Monteiro-Neto et al. (2008) reported that high constancy in the occurrence of fish species in a Brazilian coastal lagoon is associated with its permanent connection with the sea and with the sheltered area that enables high biological productivity.

The middle channel had more habitat structure and more fish abundance and richness compared to the lower channel. Enlargement of the middle channel, decreasing influence of river flow and tides and the presence of mangrove nearby contribute to increased habitat complexity, which is associated with the occurrence of some constant and abundant species (e.g. *Eugerres brasilianus*, *Eucinostomus melanopterus*, *Eucinostomus argenteus*, *H. unifasciatus*). On the other hand, the lower channel, with lower

habitat structure and sandy substrate, low turbidity and higher tide influence may be associated with low within-group average similarity recorded by SIMPER. Only *A. brasiliensis* was frequent (60% of frequency of occurrence) and abundant (65.6% of the total number of fishes) in this estuarine area.

Size-specific changes across the estuarine areas were most clearly defined for the species *Eucinostomus argenteus*, *Centropomus parallelus* and *Geophagus brasiliensis* that had the smallest individuals registered in the lagoon. The lagoon also seems to be a suitable habitat for small-sized species (e.g. *Ctenogobius shufeldti* and *Gobionellus oceanicus*), which were dominant in the lagoon and rarely found in the two channel areas. These observations might be an indication of the important role that this habitat plays for fish recruitment and for the maintenance of some small-sized species in this mixing estuarine zone. These findings are in line with observations from temperate rivers, where connected lagoons function as major nurseries for fish (Grift et al. 2003; Sindilariu et al. 2006). However, few studies have demonstrated differences in fish size distribution between an adjacent lagoon and main channel areas in an estuarine zone.

Marginal lagoons and artificial secondary channels have been built as mechanisms to help the system re-establish lateral connectivity and to create areas with more stable conditions and resources as a way to mitigate the effects of margin degradation and previous channelization (van den Brink et al. 1996; Buijse et al. 2002). Although these steps are necessary, care must be taken not to prioritize such measures over the preservation of natural riparian vegetation such as mangroves and marshes. Several river recovery projects are based on increasing the interaction between river and floodplains and include re-opening or creating artificial secondary channels or marginal lagoons (Buijse et al. 2002). Our findings corroborate the adequacy of such measures since we demonstrated that a protected lagoon permanently connected to the estuarine channel played an important role as nursery areas and supported abundant fish populations, especially small-sized species.

Seasonal changes in salinity in estuaries are main predictors of fish movements toward the inner and outer estuaries (Whitfield & Kok 1992; Valesini et al. 1997). During the wet season, floods decrease estuarine salinity and enable freshwater species to visit the estuarine areas while marine stragglers leave the area to search for more stable salinity levels (Garcia & Vieira 2001). In spite of wide changes in salinity in the mixture zone of the Mambucaba estuary between the summer/wet season (lagoon = 0.2; middle channel = 13; lower channel = 23.3)

and the winter/dry season (lagoon = 26.2; middle channel = 31.6; lower channel = 29.4), such differences were not related to seasonal changes in the fish community parameters (number of species, number of individuals and biomass) that did not change between summer and winter, except for the number of species in the lower channel. In this estuary, the lack of seasonal change in fish assemblages can be related to the resident species (e.g. *Eucinostomus argenteus*, *Eugerres brasilianus*, *Atherinella brasiliensis* and *Achirus lineatus*), which are dominant, have long recruitment seasons and tolerate a broad range of environmental conditions. In tropical estuaries, seasonality in species communities is less apparent (Day et al. 1989; Laroche et al. 1997) and sometimes masked by large variances in catch data (Robertson & Duke 1990).

Overall, the mixing zone of the Mambucaba Estuary was characterized by wide changes in environmental variables and habitat variability. We found that fish species use different parts of the estuarine area and that the habitat structure is the major factor determining spatial patterns. The river geomorphology (main channel versus lagoon) seems to influence habitat selection by estuarine species structuring the fish assemblages at small spatial scale. Although changes in fish size, richness and abundance were found between the estuarine areas, further studies on the importance of marginal lagoons and main channel areas to the fish assemblage are required. A sampling design that encompasses different estuaries and between-year variations should be implemented to corroborate this study's findings.

Acknowledgements

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