Spatial and temporal changes in the fish assemblage of a subtropical estuary in Brazil: environmental effects

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This work provides information about the fish assemblage structure along the estuarine gradient of Baía da Babitonga, south Brazil. The seasonal and spatial dynamics of fish and their relationship with physical – chemical variables were investigated. A total of 70,085 fish of 70 taxa were collected. Late larva and early juveniles of Engraulidae, Eucinostomus spp. and Mugil spp. dominated in abundance, representing 62% of all fish captured. Permutational multivariate analysis of variance identified distinct fish assemblages within the bay and during the year. The marine straggler species Harengula clupeola, Oligoplites saliens and Trachinotus carolinus and the estuarine migrant Anchoa tricolor were characteristic of the outer-most bay area, while the estuarine resident and migrant species Atherinella brasiliensis, Anchoa januaria, Sphoeroides greeleyi and Citharichthys spilopterus, and the marine migrant Diapterus rhombeus were characteristic of the inner portion of the estuary. The seasonal changes in community structure observed were mainly related to the greater abundance of T. carolinus in the warm/wet season, Micropogonias furnieri in the transition season and Oligoplites saliens in the cold/dry season. Depth, followed by salinity, explained the greater part of the variability in the abundance of dominant species and was found to be important in shaping the assemblages. Nevertheless, the amount of variation unexplained by the measured abiotic variables was relatively high (73%), suggesting the effect of additional regulatory factors. Many fish species use the shallow waters of the bay in transitory or permanent ways, and knowledge about their relationship with the environment is necessary for the success of conservation strategies for this ecosystem.

Keywords: Baía da Babitonga, estuaries, temporal variations, intertidal environment, fish community

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INTRODUCTION

Spatial and temporal changes in physical-chemical environmental characteristics strongly influence the structure of fish assemblages within estuarine ecosystems (Pessanha & Araújo, 2003), and other factors, such as predation and competition relationships, seem to act at a small scale (Kennish, 1990; Jung & Houde, 2003). In these environments, the fauna is highly dynamic due to interactions between speciesspecific physiological limitations and life strategies. The salinity, temperature, dissolved oxygen, turbidity and nutrient concentrations are the main abiotic factors controlling the abundance, distribution and composition of the fish communities in tropical and subtropical estuaries (Blaber, 2000; Rueda & Defeo, 2003). Thus, an investigation of the environmental affinities of species and of their distribution in space and time is a basic step toward conservation and sustainable use planning. This is especially relevant for Baía da Babitonga because the estuarine area and surrounding

Corresponding author: C.C. Vilar Email: cirovilar@nativa.org.br mangrove forests in this region have been assigned a highpriority status for conservation, and management measures, such as the establishment of a marine reserve, are currently being developed (MMA, 2007).

The role of environmental variables on the structure of fish assemblages in Brazilian estuaries is still poorly understood (Garcia *et al.*, 2001; Araújo *et al.*, 2002; Bouchereau & Chaves, 2003; Barletta *et al.*, 2005; Chagas *et al.*, 2006; Azevedo *et al.*, 2007). Published studies mainly deal with demersal species that live in deep areas (>3 m), leaving the environmental affinities of species that predominantly inhabit shallow water areas unclear. As elsewhere, logistical and financial constraints have traditionally impeded the determination of the environmental factors and interactions that most influence the distribution and structure patterns of Brazilian intertidal fish communities. Consequently, studies on fish assemblages in shallow water areas have minimized the spatial dimension in their analyses, obscuring patterns, variability scales and the interpretation of causal effects (Jung & Houde, 2003).

Baía da Babitonga is a subtropical estuary located near the southern extreme of the Brazilian zoogeographical province (*sensu* Briggs, 1995). It offers a particularly good opportunity for analysing the effects of environmental factors on species relative abundance and fish community structure in

the intertidal areas of the south-west Atlantic Ocean. Physically, its shore is dominated by low energy shallow water areas (< 1.5 m), with gradual spatial changes in environmental conditions along the bay main axis. In its inner zone, which is more influenced by continental discharge, salinity and transparency are relatively lower than in the outer zone, nearer the sea. The bay ichthyofauna consists of approximately 134 species, mainly marine and estuarine-dependents (IBAMA, 1998; Corrêa et al., 2006; Gerhardinger et al., 2006). Fishing pressure appears to have risen continuously since the 17th Century following the arrival of the Azoreans. In 1998, there were 33 landing areas, and 1089 registered fishermen obtained their livelihood or supported their income from artisanal fishing or tourism related to recreational fishing (IBAMA, 1998). Recently, signs of overfishing and environmental changes have been reported by most fishermen (Gerhardinger et al., 2006). Considering its capacity for exporting and dissolving nutrients, the bay is highly susceptible to contamination by organic and industrial waste. Among the impacts that have already been observed, nitrogen concentrations are currently much above normal due to anthropogenic enrichment (Mizerkowski, 2007).

This study provides information concerning the intertidal fish assemblage structure in Baía da Babitonga throughout its extension. The central aims are to test whether fish assemblage structure changes between the inner and outer sectors of the bay and among the seasons of the year, and to analyse the role of environmental characteristics in these changes. Additionally, this study aims to address the following questions: (1) what is the spatial and temporal similarity in species relative abundance and in composition?; (2) which of the measured environmental variables has the greatest influence on the assemblage structure?; and (3) how is the abundance of dominant species related to environmental variables?

MATERIALS AND METHODS

Study area

The Baía da Babitonga $(26^{\circ}02' - 26^{\circ}28'S; 48^{\circ}28' - 48^{\circ}50'W)$ is located in Santa Catarina State, south Brazil (Figure 1). It is divided into three main water bodies: the bay itself, which provides access to the Atlantic Ocean, and two divergent waterways located in its inner area, the Linguado Channel and Palmital River. The bay is an estuarine area of approximately 130 km², with an average depth of 6 m. The maximum depth is 28 m in the access channel to the international harbour of São Francisco do Sul, on its southern shore. The length of the bay is 20 km, and its width varies from 1.5 km at the inlet to the sea to 5 km in its inner portion. In addition to anthropized areas, its margins are covered by Atlantic Forest, mangroves (6200 ha) and salt marsh banks (mainly Spartina densiflora Brong.) along sandy beaches, rocky formations and extensive tidal flats. The bay sediment is mainly composed of sand varying from very coarse to very fine, but with the very fine type predominating. According to the Köppen-Geiger classification, the region has a humidsubtropical climate (Cfa) with year-round precipitation and a drier winter (Peel et al., 2007). The estuary is under a microtidal system with a semidiurnal regime and tide amplitude of 1.30 m. The main river into the bay, Palmital River, receives untreated domestic sewage and industrial waste from the city of Joinville (population 429,000).

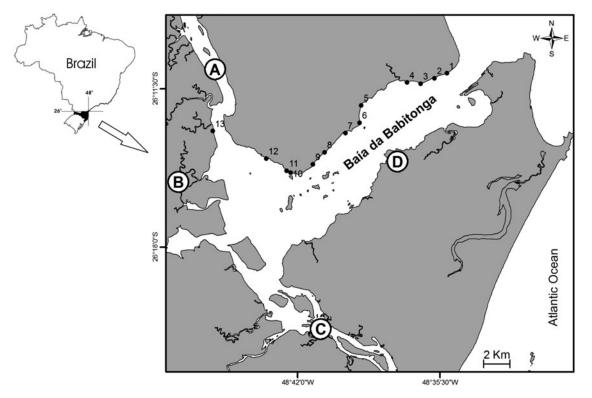


Fig. 1. Geographical location of Baía da Babitonga, showing adjacent water bodies (Palmital River (A) and Linguado Channel (C)), the city of Joinville (B), the international harbour of São Francisco do Sul (D) and the position of the thirteen sampling stations.

Data collection

Sampling was conducted during daylight hours on eight occasions (October and November 2007, January, February, April, May, July and August 2008) at thirteen stations distributed on the shoreline along a 21-km estuarine gradient. All thirteen stations were always sampled on the sample day. A beach seine net (15 m × 2 m; 2.5 mm mesh size) was hauled for 30 m parallel to the coastline at a maximum depth of 1.3 m. The unit effort is, thus, defined as one 30-m haul. Though it was strictly controlled to better standardize effort, the net aperture varied slightly between hauls (mean \pm SD: 12.6 \pm 1.5 m). However, no significant relationship between the number of captured individuals and the net aperture was found (linear regression: $r^2 = 0.04$, F = 1.12, P =0.301). At each sampling station, a single haul of approximately 376 m² was conducted, representing 0.004% of the bay area being sampled each day. This sampling protocol resulted in collection of 104 samples (1 haul \times 13 sampling stations \times 8 occasions). All fish caught were kept on ice and later frozen at the laboratory.

Salinity (refractometer), temperature (°C; mercury thermometer), pH (digital portable pH meter-206), transparency (cm; measured with a Secchi disc at a maximum distance of 50 m offshore) and depth (cm; measured with a ruler at the net extremity most distant from shore) were measured at each station on each occasion. Monthly rainfall data were obtained from the meteorological station of the Universidade da Região de Joinville (UNIVILLE), located near the estuary $(26^{\circ}15'19''S-48^{\circ}51'36''W;$ altitude 20 m).

Fish classification and enumeration

Captured individuals were identified to the lowest taxonomic level possible following Figueiredo & Menezes (1978, 1980, 2000) and Menezes & Figueiredo (1980, 1985), or by specialists, separated according to taxa and counted. Fish species were classified into the estuarine use functional guilds defined by Elliott et al. (2007): (i) marine migrants, species that spawn at sea and always enter estuaries in large numbers, particularly as juveniles; (ii) marine stragglers, species that spawn at sea and enter estuaries in low numbers, occurring most frequently in outer areas where the salinity is around 35; (iii) estuarine residents, species capable of completing their entire life cycle within the estuary environment; (iv) estuarine migrants, estuarine species in which the larval stages of their life cycles are completed outside the estuary, and/or are also represented by small marine or freshwater populations; and (v) freshwater migrants, freshwater species found regularly and in moderate numbers in estuaries whose distribution can extend beyond the oligohaline section of these systems. Species classification into functional guilds was based on the information provided by Chaves et al. (2000), Garcia & Vieira (2001) and Barletta et al. (2008). Fish nomenclature follows Eschmeyer (2008) and Figueiredo et al. (2010).

Late larvae and early juveniles from some abundant taxa (e.g. non-identified Engraulids, *Mugil* spp. Linnaeus 1758 and *Eucinostomus* spp. Baird & Girard, 1855) were not identified to species level due to the impossibility of recognizing diagnostic features in small individuals. Data from the collection of these taxa were not included in either the statistical analyses of the community structure or in the calculation of estuarine use ecological guilds (except *Mugil* spp. for guilds), because these species have different habitat preferences and life strategies (IBAMA, 1998; Corrêa *et al.*, 2006; Pessanha & Araújo, 2003). *Mugil* sp. refers to the undescribed species commonly known under the invalid name *Mugil gaimardianus* (Menezes *et al.*, 2003).

Statistical analyses

Seasonality was estimated from temperature and salinity data, and estuarine sectors were defined based on salinity data. In both cases, similarity matrices were used calculated from the Euclidean distance among samples (Q-mode; Legendre & Legendre, 1998). These matrices were submitted to cluster analysis to generate graphic representations and identify groups of occasions (e.g. seasons) and sampling stations (e.g. sectors). Differences in physical-chemical characteristics among seasons and sectors that were identified in the cluster analyses were tested by permutational multivariate analysis of variance (PERMANOVA), in which seasons and sectors were the factors. The Euclidean distance between samples computed from the environmental matrix was used in this analysis (Anderson et al., 2008). Non-parametric analysis of variance (np-ANOVA) was applied using the same distance data to individually test each environmental variable in relation to all factors included in the PERMANOVA. When the null hypothesis was rejected, comparisons of means among groups were made using a permutational Student's t-test (Anderson et al., 2008).

To verify whether the fish assemblage structure changed according to seasons and sectors, a bifactorial PERMANOVA was conducted on both the quantitative (abundance of each species per sample) and qualitative (presence/absence) data. The similarity matrices were built using the Bray–Curtis coefficient (quantitative) or Sorensen index (qualitative) (Anderson *et al.*, 2008). In all PERMANOVAs, np-ANOVAs and Student's *t*-tests, 5000 permutations were performed.

The similarities in species abundance and presence/absence among occasions and stations were analysed through cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA). The indices used to build the similarity matrices were the same as those used in the PERMANOVA. The species and their respective percentages of contribution to the mean similarity in the groups defined by the cluster analyses on abundance data were identified by similarity percentage analysis (SIMPER; Clarke & Warwick, 2001).

A canonical correspondence analysis (CCA) was used to assess the relationships between the most abundant fish species in the assemblage (>0.1% of total abundance) and the characteristics of the environment. In this type of analysis, a multiple linear regression is conducted between a matrix of species abundance in each sample (variable answers) and a matrix of environmental variable values (exploratory) (Legendre & Legendre, 1998). Only the environmental variables indicated by randomization Monte Carlo test to significantly and independently (P < 0.05 after 1000 runs) explain part of the variation in the biotic data were included in the model. The species *Anchoviella lepidentostole* (Fowler, 1911) was not included because it occurred in only one sample.

Before all analyses, the environmental variables were centred (mean = o) and standardized (SD = 1) to put them on the same scale, and the abundance data were transformed

in $\log_{10}(x + 1)$ to approximate the normal distribution and to minimize the dominant species effect (Legendre & Legendre, 1998).

RESULTS

Environmental parameters

The bay was dominated by marine water with a high salinity (mean and range: 27, 9-36), alkaline pH (7.8, 7.1-8.5), low transparency (90, 20-220 cm) and moderate temperature (22, 17-29°C).

The salinity and temperature constrained the sampling occasions to cluster into three seasons: a transition season (October and November 2007); a warm/wet season (January, February and April 2008); and a cold/dry season (May, July and August 2008) (Figure 2A). The environmental characteristics differed among seasons (PERMANOVA: $F_{2,98} =$ 20.8, P < 0.001), and, with the exception of depth, all characteristics differed individually (P < 0.05) among seasons. The

cold/dry season presented the lowest temperature (mean \pm SD: 19 \pm 1°C) and pH (7.7 \pm 0.1) and the highest salinity (32 \pm 3) and transparency (99 \pm 40 cm). Conversely, the highest temperatures (25 \pm 2°C) and pH (8 \pm 0.4) and the lowest salinity (23 \pm 6) and transparency (82 \pm 36 cm) occurred during the warm/wet season (Figure 3).

Two sectors were defined within the bay based on the salinity at sampling stations: an outer sector (Stations 1 to 6) and an inner sector (Stations 7 to 13) (Figure 2B). The innermost Station, 13, is highly influenced by continental drainage and, consequently, had lower salinity levels that separated it from all of the other sampling stations in the cluster analyses. However, due to its geographical proximity, it was considered to belong to the inner sector. Salinity, transparency and depth tended to decrease from the outer to the inner portion of the bay, while temperature showed the opposite trend. The pH presented no spatial pattern (Figure 3). The habitat characteristics differed between sectors (PERMANOVA: $F_{1,98} = 30.2$, P < 0.001). Individual analyses showed differences in salinity (mean \pm SD: 31 ± 4 outer sector; 24 ± 6 inner sector; P < 0.001), transparency (102 \pm 42 cm outer

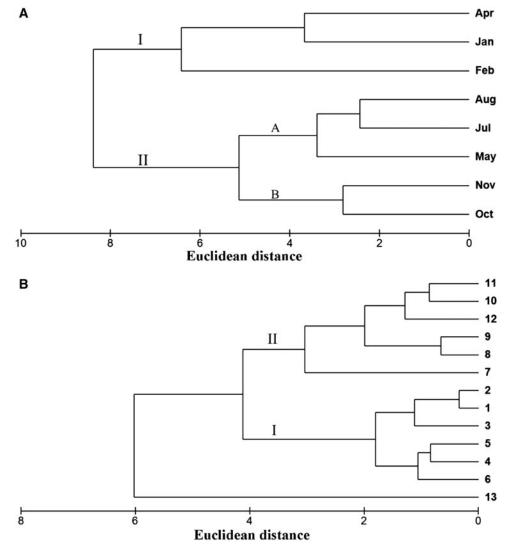


Fig. 2. Dendrograms based on mean monthly salinity and temperature values (A) for the eight sampling occasions and mean salinity values (B) at the thirteen sampling stations, using Euclidean distance. The groups defined were labelled as: (A) I, warm/wet season; II A, cold/dry season and II B, transition season; (B) I, outer sector and II, inner sector.

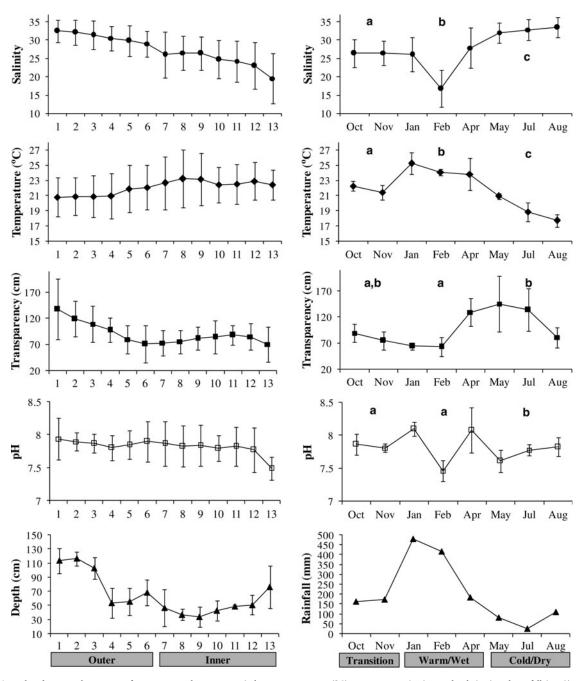


Fig. 3. Spatial and temporal variation of environmental parameters (salinity, temperature ($^{\circ}$ C), transparency (cm), pH, depth (cm) and rainfall (mm)) measured between October 2007 and August 2008 at thirteen stations along Baía da Babitonga. The values refer to mean \pm SD, except for rainfall (accumulated value for the month of sampling at the meteorological station). Seasons with the same letter are not significantly different from each other (permutational Student's pair-wise test).

sector; 79 ± 25 cm inner sector; P = 0.001), temperature $(21 \pm 3^{\circ}C \text{ outer sector}; 23 \pm 3^{\circ}C \text{ inner sector}; P < 0.001)$ and depth (85 ± 31 cm outer sector; 48 ± 20 cm inner sector; P < 0.001). The differences between the sectors were independent of seasonality (PERMANOVA: $F_{1,98} = 1.3$, P = 0.243), except for transparency (P = 0.050) and salinity (P = 0.021).

Fish assemblage composition

A total of 71,085 individuals from 70 taxa (65 species) distributed into 30 families were captured (Table 1). Late larvae and juveniles of Engraulidae, *Eucinostomus* spp. and *Mugil* spp. dominated the assemblage in abundance, comprising 62% of the total number of collected fish. Of the remaining, the 25 most abundant taxa represented over 36% of the total abundance and were further analysed in relation to the environmental variables.

Twenty-five taxa can be considered marine stragglers, 25 marine migrants, 12 estuarine residents, 5 estuarine migrants and 1 freshwater migrant (Table 1). Estuarine resident taxa were the most abundant (22.4% of total abundance), followed by marine migrants (19.7%), marine stragglers (4.9%), estuarine migrants (4.7%) and freshwater migrants (0.1%). Among

 Table 1. Mean catch per unit effort (CPUE) and percentage of occurrence (%) per sector and season for fish species collected in Baía da Babitonga.

 Ecological guilds are also indicated: MM, marine migrant; MS, marine straggler; E, estuarine; EM, estuarine migrant; FM, freshwater migrant. Codes used in the canonical correspondence analysis for the 25 most-abundant species are presented beside the species name.

Family/taxa (code)	Sectors				Seasons						Ecological
	Outer		Inner		Transition		Warm		Cold		guilds
	CPUE	%	CPUE	%	CPUE	%	CPUE	%	CPUE	%	
Achiridae											
Achirus lineatus			0.05	3.57			0.05	2.56	0.03	2.56	Е
Ariidae											
Genidens barbus	0.42	6.25	0.21	3.57	0.15	7.69	0.72	7.69			MM
Genidens genidens (G gen)	2.21	6.25	2.75	8.93	0.08	7.69	6.62	15.38			MM
Atherinopsidae											
Atherinella brasiliensis (A bra)	55.08	60.42	117.14	89.29	208.73	76.92	88.41	84.62	8.44	66.67	Е
Odontesthes bonariensis (O bon)	1.13	14.58	0.54	10.71	0.77	11.54	1.62	23.08	0.03	2.56	FM
Belonidae											207
Strongylura marina	0.27	14.58	0.20	14.29	0.38	19.23	0.28	17.95	0.08	7.69	MM
Strongylura sp. (S sp.)	1.29	14.58	0.36	17.86	1.54	19.23	1.08	30.77			MM
Carangidae							0.00	- ()		(MC
Caranx hippos Chloroscombrus chrysurus	0.00		0.07	7.14	0.04	2 8 -	0.08	7.69	0.03	2.56	MS MS
<i>,</i>	0.23	4.17	0.04	3.57	0.04	3.85	0.31	7.69			MS MM
Oligoplites palometa (O pal)	2.02	4.17	0.18	5.36	0.15	- 60	2.74	12.82	16.01	10.80	MM
Oligoplites saliens (O sal) Oligoplites saurus (O sau)	30.38 1.48	29.17 12.50	2.71 0.05	17.86 1.79	0.15 0.04	7.69 3.85	24.87 1.87	43.59 15.38	16.31	12.82	MM MM
Selene vomer	0.04	4.17	0.05	3.57	0.04	3.05 11.54	1.0/	13.30	0.03	2.56	MM
Trachinotus carolinus (T car)	8.92	4.1/ 52.08	0.07	3.93	7.58	46.15	4.49	30.77	2.54	15.38	MS
Trachinotus falcatus (T fal)	5.42	29.17	0.11	5.36	0.12	7.69	5.23	33.33	1.51	5.13	MS
Centropomidae).42	29.17	0.11).90	0.12	/.09).23	33.33	1.91	J.1 J	1010
Centropomus undecimalis			0.04	3.57			0.05	5.13			EM
Clupeidae			0.04	5.57			0.0)).15			2211
Harengula clupeola (H clu)	43.96	22.92	2.89	12.50	0.92	3.85	56.05	33.33	1.59	10.26	MS
Opisthonema oglinum	0.46	2.08	,			510 9	0.56	2.56			MS
Sardinella brasiliensis	1.00	4.17	0.29	1.79			1.62	5.13	0.03	2.56	MS
Cynoglossidae											
Symphurus tesselatus	0.02	2.08	0.41	14.29	0.54	15.38	0.23	10.26	0.03	2.56	MM
Dactylopteridae											
Dactylopterus volitans			0.02	1.79					0.03	2.56	MS
Diodontidae											
Chilomycterus spinosus	0.08	8.33	0.07	7.14	0.04	3.85	0.05	5.13	0.13	12.82	Е
Engraulidae											
Anchoa januaria (A jan)	7.71	27.08	106.75	42.86	2.65	23.08	159.95	66.67	1.05	12.82	Е
Anchoa tricolor (A tri)	28.56	25.00	11.96	26.79	0.04	3.85	46.21	25.64	6.10	41.03	EM
Anchoviella lepidentostole			3.48	1.79			5.00	2.56			Е
Cetengraulis edentulus (C ede)	2.08	12.50	0.96	14.29			1.51	20.51	2.44	15.38	MM
Lycengraulis grossidens (L gro)	2.02	54.17	0.84	55.36	0.96	46.15	0.26	89.74	2.79	25.64	MM
Not identified (n.i.)	61.42	25.00	330.05	26.79	100.15	38.46	458.64	7.69	24.10	35.90	
Ephippidae						_					
Chaetodipterus faber	0.25	16.67	0.09	3.57	0.04	3.85	0.38	20.51	0.03	2.56	MS
Fistulariidae					0	0			0		P
Fistularia petimba			0.09	3.57	0.08	3.85			0.08	2.56	Е
Gerreidae				96			. (.		0.00	(MM
Diapterus rhombeus (D rho)	0.04	2.08	2.07	17.86			2.64	25.64	0.38	2.56	MM
Eucinostomus argenteus (E arg)	0.25	8.33	1.93	25.00		<u> </u>	3.00	41.03	0.08	5.13	MM
Eucinostomus gula Eucinostomus melanopterus	0.02	2.08 2.08	0.02	1.79	0.04	3.85	0.03	2.56	0.05	2.56	MM MS
Eucinostomus meunopierus Eucinostomus spp.	0.02 236.50		0.75	14.29	0.04	3.85	1.03	17.95	0.05	2.50 12.82	1015
Gobiidae	230.50	31.25	23.57	32.14			324.36	71.79	0.56	12.02	
Bathygobius soporator	0.02	2.08	0.18	16.07	0.04	3.85	0.18	15.38	0.08	7.69	MM
Ctenogobius boleosoma	0.02	2.08	0.18	21.43	0.04	5.05	0.18	23.08	0.38	10.26	MM
Ctenogobius stigmaticus	0.02	2.00	0.93	1.79			0.9/	23.00	0.38	2.56	E
Gobionellus oceanicus			0.48	1.79			0.03	2.56	0.09	2.30	E
Gobionellus stomatus			0.02	1.79			0.05	2.90	0.03	2.56	E
Microgobius meeki			0.02	3.57			0.05	5.13	0.05	2.90	MS
Haemulidae			5107	5.57			5.05	<i>.</i> ,			
Pomadasys corvinaeformis (P cor)	10.98	18.75	0.66	7.14			14.33	30.77	0.13	2.56	MM

Continued

Family/taxa (code)	Sectors				Seasons						Ecological
	Outer		Inner		Transition		Warm		Cold		guilds
	CPUE	%	CPUE	%	CPUE	%	CPUE	%	CPUE	%	
Hemiramphidae											
Hyporhamphus unifasciatus	0.10	6.25	0.39	8.93	0.73	15.38	0.15	5.13	0.05	5.13	EM
Monacanthidae											
Monacanthus ciliatus	0.02	2.08					0.03	2.56			MS
Mugilidae											
Mugil curema	0.21	6.25	0.27	10.71	0.31	3.85	0.44	20.51			MM
Mugil sp. (M sp.)	0.60	16.67	0.93	17.86			1.49	35.90	0.59	10.26	MM
Mugil spp.	137.08	66.67	60.93	51.79	12.19	65.38	239.10	76.92	8.97	35.90	MM
Ophichthidae											
Myrophis punctatus	0.08	6.25			0.04	3.85	0.05	2.56	0.03	2.56	Е
Paralichthyidae											
Citharichthys arenaceus	0.33	8.33			0.12	7.69			0.33	5.13	MS
<i>Citharichthys spilopterus</i> (C spi)	0.29	16.67	1.68	53.57	0.88	30.77	1.56	53.85	0.62	23.08	Е
Etropus crossotus	0.52	27.08	0.63	17.86	0.38	15.38	1.15	35.90	0.13	12.82	MS
Paralichthys orbignyanus	0.04	4.17	•	,			0.03	2.56	0.03	2.56	MM
Polynemidae		. ,								-	
Polydactylus virginicus	0.13	6.25			0.04	3.85	0.13	5.13			MM
Pomatomidae	5					5		<i>y y</i>			
Pomatomus saltatrix (P sal)	1.42	8.33							1.74	10.26	MS
Sciaenidae									91		
Cynoscion leiarchus	0.02	2.08	0.07	3.57			0.10	5.13	0.03	2.56	MS
Menticirrhus americanus	0.27	10.42	0.29	10.71	0.19	11.54	0.59	17.95	0.03	2.56	ММ
Menticirrhus littoralis (M lit)	3.08	20.83	0.05	3.57			0.87	10.26	3.00	20.51	MS
Micropogonias furnieri (M fur)	0.79	16.67	2.27	25.00	5.23	46.15	0.21	7.69	0.54	17.95	MM
Stellifer rastrifer (S ras)	7.46	10.42	0.14	1.79	1.58	15.38	8.33	5.13		-/-//	MM
Serranidae	7.40	10172	0114		1.)0	1).90	0.99).15			
Diplectrum radiale	0.02	2.08							0.03	2.56	MS
Mycteroperca sp.	0.02	2.08	0.04	3.57	0.12	11.54			0.03	2.90	MS
Syngnathidae	0.02	2.00	0.04	3.)/	0.12	11.)4					1010
Cosmocampus elucens	0.06	4.17	0.07	5.36					0.18	12.82	MS
Syngnathus folletti	0.00	22.92	0.07	7.14	0.38	15.38	0.21	15.38	0.13	12.82	E
Syngnathus pelagicus	0.40	22.92	0.07	/.14	0.30	15.50	0.21	15.30	0.05	2.56	MS
Synodontidae	0.04	2.00							0.05	2.90	1413
Synodus foetens	0.27	12.50	0.05	1.79	0.15	11.54	0.31	10.26			MS
Tetraodontidae	0.2/	12.90	0.05	1./9	0.15	11.54	0.31	10.20			1015
Lagocephalus laevigatus	0.04	4.1-	0.02	1 70	0.08	7.69	0.00	0.56			MS
Sphoeroides greeleyi (S gre)	0.04	4.17	0.02 16.77	1.79 98.21	6.77	7.69 69.23	0.03	2.56	12.05	74.26	EM
Sphoeroides testudineus (S tes)	4.75 1.00	47.92	2.02	98.21 60.71			13.36 2.26	79.49	-	74.36	EM
	1.00	29.17	2.02	00./1	0.73	38.46	2.20	61.54	1.38	35.90	LIVI
Triglidae	·		0.1-		0.0 <i>i</i>	2 8 -	0.00		0.10	- 60	MS
Prionotus punctatus	0.04	4.17	0.11	7.14	0.04	3.85	0.08	5.13	0.10	7.69	1015
Uranoscopidae		0				_ /					MC
Astroscopus y-graecum	0.13	8.33			0.15	7.69	0.03	2.56	0.03	2.56	MS

Table 1. Continued

the estuarine fish, the most abundant species were *Atherinella* brasiliensis (Quoy & Gaimard, 1825) (12.9%) and *Anchoa* januaria (Steindachner, 1879) (8.9%). Mugil spp. (14%) had the greater contribution among the marine migrants, *Harengula clupeola* (Curvier, 1829) (3.2%) among the marine stragglers and *Anchoa tricolor* (Spix & Agassiz, 1829) (2.8%) and *Sphoeroides greeleyi* Gilbert, 1900 (1.6%) among the estuarine migrants. *Odontesthes bonariensis* (Valenciennes, 1835) was the only representative of the freshwater fauna, corresponding to only 0.1% of the total abundance.

Spatial and seasonal changes

Significant differences in assemblage structure were found among the bay sectors (PERMANOVA using relative abundance: $F_{1,98} = 10.0$, P < 0.001; PERMANOVA using presence/absence: $F_{1,98} = 10.5$, P < 0.001). These differences were independent of seasonality in both quantitative (PERMANOVA: $F_{2,98} = 1.3$, P = 0.102) and qualitative (PERMANOVA: $F_{2,98} = 1.2$, P = 0.243) analyses. The thirteen sampling stations clustered into three groups connected with 53 and 63% of similarity for abundance and presence/ absence, respectively. Overall, the stations clustered according to an estuarine gradient in which central stations (4–9, group II) separated the outer-most (1-3, group I) from the innermost (10-13, group III) stations (Figure 4A, B). The SIMPER analysis computed a 62% mean similarity among the stations of group I, with the greater contributions coming from the marine stragglers H. clupeola and Trachinotus carolinus (Linnaeus, 1766), the marine migrant Oligoplites saliens (Bloch, 1793) and from the estuarine

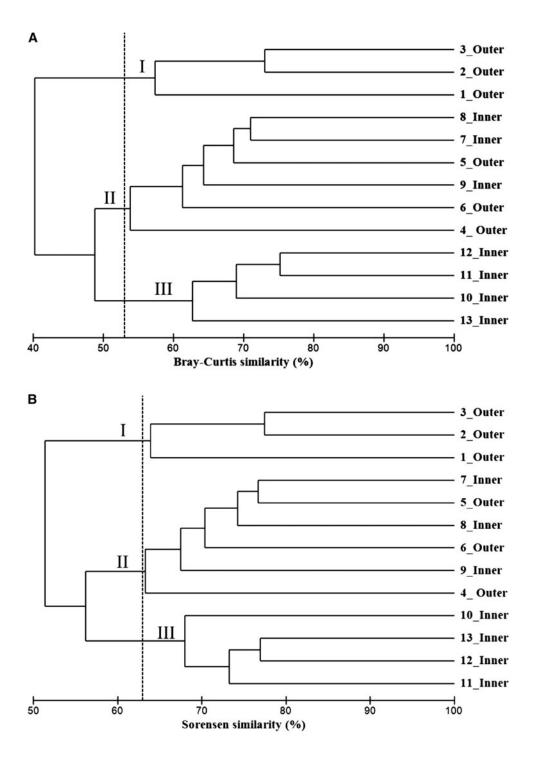


Fig. 4. Dendrograms based on the abundance (A) and presence/absence (B) of fish species collected at thirteen stations in Baía da Babitonga. Each object corresponds to the sampling station (1 to 13) and sector (inner; outer) where the samples were collected.

migrant *A. tricolor*. Stations from group II were linked with 60.9% of the mean similarity, with the greater contributions coming from the estuarine-resident *A. brasiliensis* and *A. januaria*, and the estuarine migrant *S. greeleyi*. In group III, the mean similarity among the stations was 66.8%, with the species most important for the individualization of this group being the same as those of group II, reinforced by the estuarine resident *Citharichthys spilopterus* Gunther, 1862

and the marine migrant *Diapterus rhombeus* (Curvier, 1829) (Table 2).

Seasonal changes in the fish assemblage structure were detected based on abundance (PERMANOVA: $F_{2,98} = 5.5$, P < 0.001) and presence/absence data (PERMANOVA: $F_{2,98} = 6.3$, P < 0.001). In the paired tests, all stations differed from each other (P < 0.001) for both quantitative and qualitative data. The eight sampling occasions (months) clustered into

 Table 2. Percentage of contribution of the six most important species identified by the similarity percentage analysis as responsible for the similarity within the groups of sampling stations and sampling occasions defined by the cluster analysis.

Species	Sites		Months			
	I	II	III	I	II	III
Harengula clupeola	10.2					
Anchoa tricolor	9.9		5.6	5.4		
Oligoplites saliens	8.9	7.7				13.8
Trachinotus carolinus	8.9	5.3		7.1	9.4	
Anchoa januaria	7.7	10.2	12.2	5.5	7.2	
Trachinotus falcatus	7.2					
Sphoeroides greeleyi		11.7	10.7	9.8	10.4	12.3
Atherinella brasiliensis		11.3	14.2	10.5	11.2	11.1
Citharichthys spilopterus			6.2			
Diapterus rhombeus			6.6			
Sphoeroides testudineus		5.1		5.9		6.6
Stellifer rastrifer					7.0	
Micropogonias furnieri					9.3	
Menticirrhus littoralis						7.7
Lycengraulis grossidens						7.4
Mean similarity	62.5	60.9	66.8	54.9	66.9	69.8

three groups of 52% or greater similarity in species relative abundance. The warm/wet season months (January, February and April) and the first cold/dry season month (May) defined group I. The cold/dry months presenting the lowest temperatures and the highest salinity (July and August) were segregated into group III. The transitional months (October and November) aggregated into group II (Figure 5A). These seasonal changes were well supported by the SIMPER analysis. A mean similarity of 54.9% was found among group I months, 66.9% among group II months and 69.8% among group III months. In all three groups, the estuarine-resident A. brasiliensis and estuarine-migrant S. greeleyi, which were common to abundant year-round, were among the three most important species contributing to within-group similarity. The other species are T. carolinus for the warm/wet season (group I), T. carolinus and Micropogonias furnieri (Desmarest, 1823) for the transition season (group II) and O. saliens for the cold/dry season (group III) (Table 2). With respect to the qualitative data (presence/absence), the last transition month (November), all warm/wet months and the first cold/dry month (May) were united in a single group (group I), presenting 62% similarity. The remaining two cold/dry months were separated from the rest, presenting 73% similarity between them (group II), and October remained isolated (Figure 5B).

Species – environment relationships

After the Monte Carlo randomization test, the CCA evidenced significant associations between environmental characteristics (depth, salinity, transparency and temperature) and the abundance of 25 taxa (P = 0.001). However, only 20.7% of the variation in species abundance was explained by the four selected axes. Species distribution was unrelated to the pH (P = 0.282), and this factor was, therefore, not included in the analysis. The first CCA axis explained 9.2% of the variation in species abundance and was positively correlated with depth and salinity. Axis 2 explained 7.1% and was strongly correlated to

temperature (negatively) and transparency (positively). Axes 3 and 4 presented lower contributions to the variability explained by the analysis (Table 3).

Sectors were clearly distributed along the first axis, with outer sector samples on the positive side and those of the inner sector on the negative side. Seasons were distributed along the second axis, with transition and cold/dry samples on the positive side and the samples from warm/wet season on the negative side (Figure 6).

Species were distributed throughout the plane defined by axes 1 and 2 according to their affinities to the abiotic parameters included in the analysis. Thus, the species that showed a low or variable association with those parameters are located close to axes origins, while species having a stronger relationship with one or the other parameter are located farther from the origins. Pomatomus saltatrix (Linnaeus, 1766) and Menticirrhus littoralis (Holbrook, 1847) were strongly associated with high transparency, high salinity, high depth and low temperature (i.e. outer stations and cold/dry season; upper right quadrant of Figure 6). On the other hand, D. rhombeus and Genidens genidens (Cuvier, 1829) were typical of low transparency, low salinity, low to medium depth and high temperature samples (i.e. inner stations and warm/wet season; lower left quadrant of Figure 6). Oligoplites saurus (Bloch & Schneider, 1801) and Trachinotus falcatus (Linnaeus, 1758) were strongly associated with higher depths (i.e. outer stations; lower right quadrant), while Cathorops spixii (Agassiz, 1829), Sphoeroides testudineus (Linnaeus, 1758), S. greelyi and M. furnieri were weakly associated with lower depths (i.e. inner stations; upper left quadrant of Figure 6).

DISCUSSION

Salinity and depth exhibited a strong gradient along the estuary, generated by freshwater, sediment and organic matter influx into the inner portion of the bay. In addition, the protection of the bay against the predominant swells (from the south-east quadrant), together with the low tide amplitude, favours the formation of extensive tidal flats near the mouth of small perennial rivers, especially in the inner bay area. The temperature varied according to the depth and proximity to the ocean, being lower in the deeper outer stations and higher in the shallower inner ones. The salinity gradient was most pronounced during the warm/wet season. The observed seasonal patterns for physical-chemical features of the water follow the rainfall regime of the region, with higher levels of precipitation in summer (January, February and March) and lower levels in winter (July, August and September) (Mizerkowski, 2007).

The shallow-water fish faunas of Baía da Babitonga and Lagoa dos Patos, south of Brazil (Garcia & Vieira, 2001), Chesapeake bay, USA (Jung & Houde, 2003) and Embley estuary, Australia (Barletta & Blaber, 2007) share a number of features, such as a large number of marine species and an absence or scarcity of freshwater taxa. In fact, the dominance (in richness) of assemblages by marine species seems to be a general feature of the tropical and temperate estuaries of the western Atlantic (Vieira & Musick, 1993). Overall, the species adapted to complete their life cycles within tropical and temperate estuaries actually represent a small percentage compared to the marine stragglers and migrant taxa, which

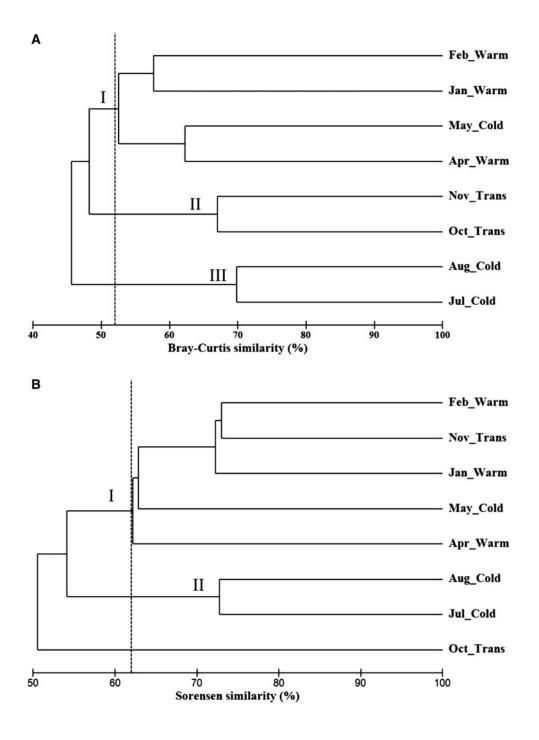


Fig. 5. Dendrograms based on the abundance (A) and presence/absence (B) of fish species collected on eight occasions in Baía da Babitonga. Each object corresponds to the month and season (transition; warm/wet; cold/dry) of the year in which the samples were collected.

use them seasonally (Day *et al.*, 1989). However, although marine species dominated the fish estuarine assemblage composition, estuarine fish were numerically more abundant in both Baía da Babitonga and Lagoa dos Patos (Garcia & Vieira, 2001). In the Embley estuary, Australia, where salinity is relatively uniform, fish biomass is dominated by marine species, whereas in areas influenced by freshwater influxes from Amazonian rivers in northern Brazil, the assemblages are dominated in biomass by estuarine species (Barletta & Blaber, 2007; Giarrizzo & Krumme, 2008). The distribution and abundance of ecological guilds within estuaries are determined primarily by the hydrological features and by the habitat availability found at each location (Barletta & Blaber, 2007), and the scarcity and/or low abundance of freshwater species can be explained by the relatively high salinity level in marine-dominated estuaries.

Variation in species abundance and composition occurred across the bay in association with environmental characteristics, suggesting that these observations may be related to species-specific environmental preferences and habitat use strategies. The fish fauna of the outer sector, which is under a stronger marine influence, exhibited a greater abundance

 Table 3. Results of the canonical correspondence analysis (CCA) performed between environmental variables and the 25 most-abundant fish species of Baía de Babitonga.

CCA summary	Axis						
	1	2	3	4			
Eigenvalues	0.30	5 0.236	6 0.096	6 0.051			
Species – environmental variables correlations	0.84	0.87	0.64	0.50			
% of variance explained (species data) Accumulated variance (%)	9.22	7.12	2.89	1.55			
of species data	9.22	16.30	19.20	20.70			
of species-environmental variables	42.69	75.66	89.04	96.22			
Correlations of environmental variables							
Temperature	-0.23	-0.60	0.25	0.24			
Salinity	0.58	0.40	-0.31	0.09			
Transparency	0.43	0.58	0.33	0.03			
Depth	0.73	-0.24	0.02	-0.18			

of juveniles of marine migrant species (e.g. *Oligoplites saliens*, *Oligoplites saurus* and *Pomadasys corvinaeformis* (Steindachner, 1868)) and marine stragglers (e.g. *Trachinotus carolinus*, *Trachinotus falcatus*, *Menticirrhus*

littoralis and Harengula clupeola). The estuarine residents and migrant species (e.g. Anchoa januaria, Atherinella brasiliensis, Sphoeroides greeleyi and Citharichthys spilopterus), and the marine migrant Diapterus rhombeus which tolerate low salinity levels dominated in the inner estuary. Another few abundant species that were not identified as important in the characterization of each sector by the SIMPER analysis also contributed to the differentiation of the fauna. For example, the marine species Pomatomus saltatrix, Opisthonema oglinum (Lesueur, 1818), Paralichthys orbignyanus (Valenciennes, 1839) and Citharichthys arenaceus Evermann & Marsh, 1900 were found exclusively in the outer sector, while gobies were more abundant or only found in the inner bay. Despite small seasonal changes in species spatial distribution, the sectors defined according to salinity corresponded satisfactorily to the ichthyofauna distribution within the bay.

Evidence for the spatial and temporal partitioning of estuaries among abundant fish species that are either transitory or resident in these ecosystems have been provided for both shallow (Pessanha *et al.*, 2003) and deeper areas (Chagas *et al.*, 2006). In Baía da Babitonga, seasonality was more pronounced in relation to species abundance than to ichthyofauna composition (presence/absence). In qualitative terms,

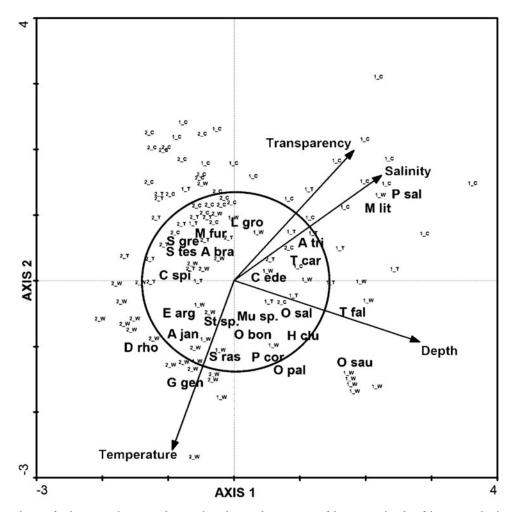


Fig. 6. Ordination diagram for the canonical correspondence analysis showing the association of the 25 most abundant fish species with selected environmental variables (represented by vectors). Species names are codified according to Table 1. Samples are codified according to sector (1, outer; 2, inner) and seasons (T, transition; W, warm/wet; C, cold/dry). Species inside the circle showed a low association with environmental parameters, while species having a stronger relationship with a particular parameter are located outside the circle.

seasonal differentiation resulted from the occurrence of a few species restricted to the warm/wet season months (e.g. Oligoplites palometa (Cuvier, 1833) and D. rhombeus) or the cold/dry season months (e.g. P. saltatrix and Cosmocampus elucens (Poey, 1868)). The occurrence of some species extended from the last transition season month (November) throughout the warm/wet season months (e.g. Mugil curema Valenciennes, 1836, Lagocephalus laevigatus (Linnaeus, 1766) and Chloroscombrus chrysurus (Linnaeus, 1766)). Other species occurred from this summer period to the first cold/dry season month (May) (e.g. Achirus lineatus (Linnaeus, 1758), Caranx hippos (Linnaeus, 1766), Sardinella brasiliensis (Steindachner, 1789), Ctenogobius boleosoma (Jordan & Gilbert, 1882) and P. corvinaeformis), contributing to the similarity among seasons found in the assemblage composition.

Asynchronic peaks in the dominant species abundance were responsible for the seasonal changes seen in the assemblage structure. The results of the present study are consistent with information widely reported about the ichthyofauna of shallow areas (Pessanha & Araújo, 2003; Nanami & Endo, 2007; Araujo et al., 2008), i.e. that seasonal changes in species relative abundance result from variation in reproduction periods and in subsequent recruitment because most of the captured individuals in these environments are at the juvenile stage. The use of shallow areas by young-of-the-year is related to the increase in growth promoted by high food abundance and the decrease in mortality due to lower predation (Whitfield, 1999; Layman, 2000). In Baía da Babitonga, as elsewhere, some species use shallow waters only at the beginning of their life and migrate towards deeper areas after the juvenile phase (e.g. H. clupeola and Mugil spp.; Pessanha & Araújo, 2003), contributing to the seasonal dynamics of the ichthyofauna. However, although the assemblage structure changed seasonally according to the abundance peaks of species (e.g. O. saliens, M. littoralis and Lycengraulis grossidens (Agassiz, 1829) in the cold/dry season; Micropogonias furnieri and Stellifer rastrifer (Jordan, 1889) in the transition season), it was dominated by the estuarine taxa A. brasiliensis and S. greeleyi throughout the year. Adaptive features, such as extended spawning periods (Schultz et al., 2002; Favaro et al., 2003) and tolerance to environmental variation, seem to contribute to the extensive distribution and high abundance of these species.

Although shallow areas may be considered safer (Whitfield, 1999), the abundance of most species was positively correlated with depth, which was the factor responsible for the higher explicative power for the assemblage structuring. Based on these results, we can hypothesize that the benefits offered by shallowness, which are widely accepted (Whitfield, 1999; Layman, 2000), can be outweighed by higher risks in very low water levels, making the fish avoid these environments. Chagas et al. (2006) reported that depth effects on the fish assemblage of Baía de Vitória, south-east of Brazil, may be caused by a series of factors that include hydrostatic pressure and the reduction of predation risk through access to vertical dimensions. Additionally, we suggest that fish species distribution in the shallowest areas is influenced by more extreme temperature, greater risk of predation by aerial visually-oriented predators (i.e. birds), greater susceptibility to wave stress and an increased possibility of getting trapped when the tide retreats. Species especially correlated with shallow areas, such as Sphoeroides testudineus and S. greeleyi are, hypothetically, protected by their tetraodontoxins (Matsumura, 1995). This would make them less susceptible to predation, thus facilitating their occupation of a niche released by other taxa.

Salinity played an important role in structuring the fish assemblage of Baía da Babitonga, similar to previous findings (Pessanha et al., 2003; Barletta et al., 2008). The gradient present was sufficient to affect species relative abundance and locally determine the assemblage composition, even, in the absence of a proper liminic zone. Opportunistic euryhaline marine species have a lower ability to osmoregulate at low salinity, which does not allow them to penetrate deeper into estuaries (Rueda & Defeo, 2003). Thus, there is probably a physiological barrier to the occupation of the inner bay by typical marine species such as T. carolinus and P. saltatrix. In addition, many species present preferences for distinct salinity levels during their ontogenetic development (Marshall & Elliott, 1998). For example, the late larva and early juveniles of Eucinostomus spp. were more abundant in the outer sector, whereas congeneric individuals at late juvenile stages predominated in the inner sector of the estuary, which is a pattern previously described for Baía de Sepetiba, Rio de Janeiro (Araújo & Santos, 1999). Contrarily to marine taxa, estuarine species are not adapted to high salinity conditions (Whitfield, 1999). Atherinella brasiliensis, a species typical of estuarine systems in south and south-east Brazil (Ramos & Vieira, 2001; Pessanha et al. 2003), was extremely abundant between salinities of 20 and 29 and was little represented at stations having lower or higher values.

The CCA results showed a secondary contribution of transparency and temperature in species distribution. Protection from visually oriented predators and increases in food availability are the two main factors contributing to the importance of turbidity for small, juvenile or small-sized adult fish (Cyrus & Blaber, 1992; Whitfield, 1999). However, Johnston et al. (2007) could not find any evidence that turbidity influenced species distribution in four tropical estuaries and, thus, stated that support to validate these theories is still inconclusive. Temperature was negatively correlated with transparency and salinity, mainly because of the increase in pluviosity during the warm/wet season. Thus, while salinity and depth (and possibly other factors, such as sediment type) may be the main factors spatially structuring the assemblages, temperature seems to have effects on the temporal scale (Marshall & Elliott, 1998; Rueda, 2001). Migration, reproduction and recruitment processes are directly related to seasonal variations in temperature (and photoperiod). Such processes are the dominant factors influencing the temporal distribution of fish in the Humber estuary, England (Marshall & Elliott, 1998) and, most probably, in Baía da Babitonga.

As has been suggested for estuaries in general (Whitfield, 1999), the physical environmental characteristics (in decreasing order of importance: depth, salinity, transparency and temperature) predominantly influence the spatiotemporal distribution of species in Baía da Babitonga. However, the amount of variation unexplained by the abiotic variables included in the CCA model was high (73%). This is a common situation and, for example, only 39.3% of the assemblage variation was explained in Baía de Sepetiba, south-east of Brazil (Pessanha *et al.*, 2003) and 18.4% in the Humber estuary, UK (Marshall & Elliott, 1998). Many other biotic and abiotic factors, such as substratum type (Rueda, 2001), pollution (Whitfield & Elliott, 2002), habitat availability

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(Barletta & Blaber, 2007), bay margin usage (Tong, 2001), competition, predator – prey interactions and food availability (Kennish, 1990), may concomitantly exert some control over species distributions.

Some of the complex and poorly understood relationships between the fish species that live in estuarine shallow areas in south Brazil and the environment have been clarified, such as the small-scale depth effect and salinity preferences, although the influence of many other factors that may regulate distribution and abundance remain to be investigated. We suggest that further research aimed at analysing the relationships existing between species and environmental characteristics should attempt to better isolate these variables during sampling, to avoid the confounding effects of multicollinearity (see Mac Nally, 2000).

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