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Mangrove habitat use by fishes in Southeastern Brazil: are there temporal changes in the structure of the community?

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Abstract

We compared fish community structure in Guaratiba Mangrove, SE Brazil, among three seasons of the hydrological cycle [(i) spring, increasing temperature and rainfall, decreasing salinity; (ii) summer/early fall, high temperature and rainfall, intermediate salinity; (iii) late fall/winter, low temperature and rainfall, high salinity] and between the years 2002-2003 and 2008-2009. The aim was to test the hypothesis that the fish community structure changes seasonally, associated with seasonal changes in environmental conditions, and that changes occurred between the two yearly periods because of increased anthropogenic activities. The sampling protocol for the two surveys was identical. A total of 63 species was recorded, with 38 species occurring in 2002–2003, and 53 species in 2008–2009. The main changes in the mangrove's fish assemblage between 2002-2003 and 2008-2009 were (i) an increase in species richness, fish density and total biomass; and (ii) an increase in the zoobenthivorous species of gerreids Eucinostomus argenteus, Diapterus rhombeus and Ulaema lefroyi, and a decrease in the planktivorous clupeid Harengula clupeola. Other abundant species, such as the opportunistic atherinopsid. Atherinella brasiliensis, the detritivorous mullet Mugil liza and the zoobenthivorous pufferfish Sphoeroides testudineus did not differ in abundance between the two yearly periods. Ten species occurred only in 2002-2003, and 23 species only in 2008-2009, indicating significant changes in community structure over the 6-year period. Seasonal changes in community structure were more conspicuous in 2008-2009, when species abundance and richness were greatest. The highest fish abundance was recorded in spring and in summer/early fall, and the lowest in late fall/winter. The increased abundance and richness over time may be at least partially attributable to protection policies because of the effective implementation of a biological reserve in the area.

Introduction

Mangrove forests play a variety of roles for the associated fishes by providing feeding areas for some species or particular life stages, and refugia, nursery and/or spawning areas for others. However, these transition systems are subject to intense environmental pressures such as eutrophication, overfishing, building construction and other anthropogenic activities that lead to environmental degradation (Martinho *et al.* 2008). These ecosystems have been referred to as fish nurseries because they harbor high densities of juvenile stages (Parrish 1989; Dorenbosch *et al.* 2005; Adams *et al.* 2006). A nursery habitat is defined as a habitat that contributes a higher than average biomass to a spatially separated adult population compared with other juvenile habitats (Nagelkerken 2009;

Igulu et al. 2014). Sheaves et al. (2014) described 10 key components of nursery habitat value grouped into three types: (i) connectivity and population dynamics (includes connectivity, ontogenetic migration and seascape migration), (ii) ecological and ecophysiological factors (includes ecotone effects, ecophysiological factors, food/predation trade-offs and food webs) and (iii) resource dynamics (includes resource availability, ontogenetic diet shifts and allochthonous inputs). Although mangroves are often discussed in terms that imply that they function as a homogeneous unit (Beck et al. 2001; Sheridan & Hays 2003; Sheaves 2005), high spatial/temporal variability is a feature characteristic of the fishes in mangroves across broad geographic regions (Robertson & Duke 1990; Clynick & Chapman 2002; Raposa et al. 2003; Hindell & Jenkins 2004). Many of these species are of social and commercial importance, which represents a strong argument for the conservation of mangrove habitats (Griffin 1985; Lenaton & Potter 1987; Barletta et al. 2003, 2010).

The fish species that use mangroves habitats are mainly young-of-the-year, juveniles or small-sized species that are able to withstand the harsh conditions of the tidal channels. As mangroves are mainly semi-closed estuarine areas, periods of maximum nutrient loads in the system are associated with the highest fish productivity and seasonal changes in juvenile species have been associated with recruitment peaks (Gibson *et al.* 1993; Lazzari *et al.* 1999; Mariani 2001). Investigations of fish temporal distribution and the driving forces that determine distributional patterns in different time-scales are fundamental to understand changes in community composition and structure. This is crucial for understanding the dynamics of coastal ecosystem function and to help managers of resource conservation policies.

Intensification of anthropogenic activities has significantly changed community/species distribution patterns in mangrove forests, leading to changes in the richness and composition of assemblages across various temporal scales (Alongi 2002; Hindell & Jenkins 2004; Faunce & Serafy 2006). Various abiotic factors have been associated with seasonal changes in the structure of fish assemblages such as salinity and temperature, among others (Martino & Able 2003). These variables are widely recognized as important drivers of fish distribution in mangroves. Aguirre-León et al. (2014) found that salinity and temperature were the most important environmental variables determining fish community composition and distribution. Lorenz (1999), studying the impact of fluctuation in physico-chemical variables (i.e. salinity, water level and temperature) on the demersal mangrove fish community in Northeast Florida Bay, concluded that changes in water delivery could have altered the mangrove fish community,

thereby lowering prey availability for higher trophic levels. Igulu *et al.* (2014) reported the significant roles of water salinity, rainfall and tidal access as drivers of fish use of mangrove habitats. As fish assemblages are composed of diverse species, each with unique environmental tolerances, studies of changes in assemblage structure are desirable in order to investigate the responses of multiple species to environmental variability.

Guaratiba Mangrove (Biological and Archeological Reserve of Guaratiba, BARG) is an area protected by Brazilian law located in the inner Sepetiba Bay zone (Fig. 1) and managed by the Rio de Janeiro State Agency for Environment (INEA) since 1974. Nonetheless, there are several small villages with poor sewage treatment in areas nearby, which contributes to increased pollution and jeopardizes water quality (Barcellos *et al.* 1997; Copeland *et al.* 2003; Molisani *et al.* 2006; Cunha *et al.* 2009; Soares 2012).

Seasonal changes in environmental variables are a key feature in Guaratiba Mangrove, which is characterized by three hydro-climatic seasons (Fig. 2): (i) in the spring the area experiences variability in environmental variables, with strong southwestern winds bringing ocean currents into the bay, coinciding with the beginning of rainfall (wet period), and with increasing temperature and decreasing salinity; (ii) in summer/early fall, the highest temperature and rainfall occur, contributing to low salinity and relatively stable environmental conditions; and (iii) in late fall/winter, the environmental conditions are stable, characterized by decreased temperature and rainfall, high salinity, and consequently, a comparatively lower influence of continental drainage. This study aimed to compare whether the fish assemblage changed among seasons, and between two yearly periods with a time lag of 6 years (2002-2003 and 2008-2009). The hypothesis tested is that this mangrove community changes in richness and abundance over time, and that seasonal differences in community structure occur, associated with changes in environmental characteristics.

Material and Methods

Sampling and data analyses

The fish assemblages were sampled using a beach seine $(12 \times 2.5 \text{ m}; 5\text{-mm} \text{ mesh size})$. The net was fitted with 30-m hauling ropes and set perpendicular to the shoreline at approximately 1.5 m depth, and then hauled straight to the shore. Seine hauls were performed by two persons, one on each end of the rope, covering an extension of approximately 30 m; hauling lasted an average of 10 min. The distance seined and the time required for each haul was standardized, thus allowing comparison among



Fig. 1. Map of the study area with the sampled mangrove channel indicated (hatched area).

Fig. 2. Averaged monthly values for rainfall (in mm, line), temperature (°C, dark gray bars) and salinity (white bars) for the Sepetiba Bay area in 1999–2009. Sources: Meteorologic Station of Fundação Instituto de Geotécnica of Rio de Janeiro Municipality. http://www2.rio.rj.gov.br/georio/site/alerta/ alerta.htm Seasons: spring (November– December), summer/early fall (January–April); late fall/winter (May–September).

collections. The total sampled area was taken to be the distance that the net was laid offshore multiplied by the mean width of the haul, resulting in an effective fishing area of approximately 300 m^2 . Fish densities were converted to an effort of 100 m^2 to facilitate comparisons with other studies. Hauls were carried out at the sites, each separated by at least 200 m and no more than 500, taking care not to repeat coverage of the same area. All samplings were carried out during the day at low tide, and near to the full moon.

The Guaratiba Mangrove area (Fig. 1) was sampled monthly between November 2002 and August 2003, and

between November 2008 and September 2009. In each month, we carried out eight to 10 samplings at sites randomly chosen within the mangrove area, totaling 90 samples in 2002–2003 and 88 samples in 2008–2009. The annual seasons were defined as follows: spring (November and December), summer/early fall (January, February, March and April) and late fall/winter (May, June, July, August and September). These seasons characterize the changes in the environmental conditions of temperature, salinity and rainfall in the area (Fig. 2). This design resulted in 90 samples in 2002–2003 (18 in spring, 36 in summer–early fall; 36 in late fall–winter) and 88 samples in 2008–2009 (16 in spring, 32 in summer–early fall; 40 in late fall–winter). The sampling protocol for the two surveys was identical, using the same sampling technique,

the same collection periods and the same sampling area. Water temperature, dissolved oxygen and salinity were measured at every seine haul at approximately 0.5 m below water surface using a Horiba W-21 multiprobe. The rainfall data were obtained from the database at Meteorological Station of Foundation Institute Geotechnical of Rio de Janeiro Municipality. http://www.inmet.gov.br/html/clima.php#. Fish were fixed in 10% formalin, and after 48 h, preserved in 70% ethanol. All fishes were identified to the species level, counted, measured (total length in millimeters) and weighed (g). Fish vouchers were deposited in the Ichthyological Collection of the Universidade Federal Rural do Rio de Janeiro.

Statistical analyses

Species richness between the 2 years was compared for each season by using rarefaction of individuals. The individual-based rarefaction curves representing the means of repeated re-sampling of all pooled individuals (Gotelli & Colwell 2001) were computed by using EstimateS v. 7.5.2 (Colwell 2000). We also used the first- and second-order jack-knife estimator of species richness for each year and season. We followed this by square-root transforming our fish Catch per unit effort data to meet the assumptions of multivariate normality and to moderate the influence of extremes in species abundance. The transformed data were then used to create a Bray-Curtis dissimilarity matrix calculated for all pair-wise sample comparisons (Thorne et al. 1999). Next, we used a non-parametric permutation-based one-way analysis of similarity (ANO-SIM; Clarke 1993) to test for differences in the fish community structure among seasons and years, and nonmetric multidimensional scaling (nMDS) for ordination of the data and to detect eventual temporal patterns. ANOSIM is analogous to univariate analysis of variance (ANOVA), in that it tests for significant differences among groups. However, unlike ANOVA, ANOSIM is performed on a similarity matrix rather than the raw data; significance is based on comparisons of this matrix to random permutations of the matrix (Clarke & Warwick 1994), with the degree of dissimilarity associated with each factor being measured by an R statistic (comparable to the F statistic of ANOVA). The typical species responsible for similarity/dissimilarity among factors (years, seasons) were determined by a similarity percentage analysis (SIMPER; Clarke & Warwick 1994). The procedure also allowed us to quantify the average contribution that each species made to the overall measure of dissimilarity between years, within seasons and

between seasons within years. In order to accomplish these ends, the procedure uses the SD of the Bray–Curtis dissimilarity matrix, attributed to a species, for all species pairs and compares that with the average contribution of a species to the dissimilarity. These analyses were performed using the statistical packages PRIMER 6 v. 6.1.13 and PERMANOVA+ v. 1.0.3.

Logarithmic transformations $[\log 10(x + 1)]$ of fish abundance (number) data were performed to meet assumptions of normality and homoscedasticity and to reduce the bias of abundant species. Kolmogorov–Smirnov and Bartlett tests were then used to assess the data normality and homocedasticy assumptions, respectively, of parametric analyses of variance of biotic variables. As the assumptions of ANOVA were not met, we used a Kruskal–Wallis non-parametric test followed by a Mann– Whitney test to compare the biotic data between years and among seasons (P < 0.05). The Kruskal–Wallis test was used to compare number of species, number and biomass of individuals and densities of the most abundant species between years and among seasons. These analyses were performed using STATISTICA 7.1.

Results

Environmental variables

Temperature, salinity and dissolved oxygen were comparatively higher in 2002–2003 than in 2008–2009, whereas rainfall showed the opposite pattern, being higher in 2008–2009 compared with 2002–2003 (Table 1).

Average temperature was 26.1 °C in 2002–2003, and 24.6 °C in 2008–2009. In 2002–2003, average temperature rose from 26.1 °C in spring, peaked at 27.4 °C in summer/early fall, then decreased to 24.5 °C in late fall/winter (Table 1). A similar pattern of variation in average temperature was observed in 2008–2009, with an increase from 25.2 °C in spring to 26.3 °C in summer/early fall, and a decrease to 22.8 °C in late fall/winter.

Average salinity was 33.1 in 2002–2003, and 28.1 in 2008–2009. In both yearly periods, the highest salinities were recorded in late fall/winter (average = 34.1 in 2002–2003; 29.5 in 2008–2009) and the lowest in spring (31.7 in 2002–2003; 25.4 in 2008–2009).

Average dissolved oxygen was 5.7 mg·l⁻¹ in 2002–2003 and 3.7 mg·l⁻¹ in 2008–2009. In 2002–2003, the highest values were recorded in spring (average = 6.1 mg·l⁻¹) and the lowest in summer/early fall (5.3 mg·l⁻¹). In 2008–2009, the highest values were recorded in summer/ early fall (average = 4.4 mg·l⁻¹) and the lowest in late fall/winter (2.9 mg·l⁻¹).

Average rainfall was 99.6 mm in 2002–2003 and 97.4 mm in 2008–2009. The highest rainfall was observed

	spring			summer/early fall			late fall/winter		
	x±SE	range	n	x±SE	range	n	x±SE	range	n
temperature (°C	<u>(</u>)								
2002–2003	26.1 ± 0.4	23.4–30.0	21	27.4 ± 0.3	25.5-30.8	36	24.5 ± 0.3	22.8–26.5	28
2008–2009	25.2 ± 0.4	21.1-28.4	22	26.3 ± 0.4	21.6-30.5	32	22.8 ± 0.2	20.0-25.0	40
salinity									
2002–2003	31.7 ± 0.6	25.9–33.7	21	33.1 ± 0.2	29.7–34.4	36	34.1 ± 0.1	33.0–34.4	28
2008–2009	25.4 ± 0.8	20.5-32.5	22	28.1 ± 0.5	21.1-33.0	32	29.5 ± 0.4	25.7-34.1	40
dissolved oxyge	en (mg·l ^{−1})								
2002–2003	6.1 ± 0.2	3.9-7.1	21	5.3 ± 0.2	3.2-7.0	36	5.8 ± 0.2	4.1-8.8	28
2008–2009	3.9 ± 0.3	26.9	22	4.4 ± 0.3	1.4–9.3	32	2.9 ± 0.2	1.1–7.8	40
rainfall (mm)									
2002–2003	98 ± 3	94–102	18	153.0 ± 19.1	361–273	36	46.1 ± 4.4	17.2-85.0	36
2008–2009	132 ± 0.8	129–136	16	124.2 ± 6.8	69–168	32	61.8 ± -3.2	34–94	41

Table 1. Mean \pm standard error (x \pm SE) for environmental variables in Guaratiba Mangrove for each season during the two yearly periods examined in this study.

n = sample size.

in summer/early fall in both yearly periods (average = 153.0 mm in 2002–2003; 124.2 mm in 2007–2008) The driest season was late fall/winter (average = 46.1 mm in 2002–2003; 61.8 mm in 2008–2009).

Community structure

A total of 63 fish species and 14,731 individuals were recorded in the two yearly periods. In 2002-2003, 38 species and 4384 individuals were recorded, belonging to eight orders, 20 families and 25 genera. The families with the greatest numbers of species were Carangidae (five), Gerreidae (four), Tetraodontidae (four), Mugilidae (three) and Gobiidae (three). In 2008–2009, 53 species and 10,347 individuals were recorded in 10 orders, 24 families and 39 genera. The families with the greatest numbers of species were Carangidae (seven), Sciaenidae (five), Gerreidae (five) and Gobiidae (four). Thirty species were present in both yearly periods, 10 were present in 2002-2003 but absent in 2008-2009 and 23 were present in 2008-2009 but absent in 2002-2003 (Table 2). The most abundant species (those accounting for >1% of the total number of fishes) were Atherinella brasiliensis (64.7% of the total number of fishes), Mugil liza (17.3%), Harengula clupeola (6.7%), Eucinostomus argenteus (4.1%) and Poecilia vivipara (2.6%) in 2002-2003, and A. brasiliensis (54.2%), M. liza (17.8%), Ulaema lefroyi (8.6%), E. argenteus (6.8%). Sphoeroides testudineus (4.5%), Diapterus rhombeus (3.7%) and P. vivipara (1.1%) in 2007-2008. In relation to biomass, the species that accounted for >1% of the total weight in 2002-2003 were A. brasiliensis (64.8% of the total weight), M. liza (11.2%), H. clupeola (5.6%), P. vivipara (5.2%), E. argenteus (4.2%), Mugil curema (2.3%) and S. testudineus (1.5%), and in 2008–2009 were *A. brasiliensis* (55.7%), *S. testudineus* (11.7%), *E. argenteus* (9.2%), *M. liza* (7.2%), *D. rhombeus* (3.2%), *U. lefroyi* (2.3%), *Genidens* genidens (2.3%), *H. clupeola* (1.3%) and *P. vivipara* (1.1%).

The number of individuals, number of species and biomass were significantly higher in 2008–2009 compared with 2002–2003 (P < 0.05). Moreover, a significantly higher number of individuals was recorded in spring and summer/ early fall compared with late fall/winter in both yearly periods, whereas the number of species was higher in spring and summer/early fall compared with late fall/winter in 2008–2009 only. Biomass was significantly higher in summer/early fall in 2002–2003 and in spring in 2008–2009 compared with the other seasons (Table 3 and Fig. 3).

The individual rarefaction curve for the 2008–2009 period lay well above the corresponding curve for the 2002–2003 period (Fig. 4). Moreover, the summer/early fall and late fall/winter curves lay above the spring curve in 2002–2003, while the summer/early fall and spring curves lay above the late fall/winter season in 2008–2009. The first- and second-order jack-knife estimators for the number of species were 48.9 and 54.8 for 2002–2003, and 71.8 and 83.6 for 2008–2009, respectively (Fig. 4).

Significant seasonal differences in assemblage structure were detected for each year, according to ANOSIM but with a comparatively low R-value (Table 4). Differences in assemblage structure among the seasons were more conspicuous in 2008–2009 (R Global = 0.30; P = 0.001) than in 2002–2003 (R Global = 0.21; P = 0.008). Significant dissimilarities were found between late fall/winter and the other two seasons, but no difference was found between spring and summer/early fall in 2002–2003. In 2008–2009, all seasons differed significantly from each

Table 2.	Mean number (\pm SE) of fish species in G	iuaratiba Mangrove in	n three seasons a	and two yearly	periods.	Trophic guilds als	o indicated.	The
significan	t highest number among the seasons for	yearly period are indi	cated in bold.					

	2002/03			2008/09					
species	Sp	Su/Fa	Fa/Wi	Sp	Su/Fa	Fa/Wi	size range (cm)	trophic guild ^a	
Atherinella brasiliensis (Quoy & Gaimard, 1825)	$\textbf{48.4} \pm \textbf{12.2}$	43.7 ± 7.6	19.4 ± 3.2	78.6 ± 21.7	72.0 ± 14.0	34.9 ± 7.0	1.3–14.5	OP6	
Mugil liza Valenciennes,	$\textbf{22.6}\pm\textbf{10.9}$	12.8 ± 5.0	1.1 ± 0.5	24.5 ± 12.8	$\textbf{35.5} \pm \textbf{20.1}$	2.5 ± 1.1	1.5–17.7	DE8	
Harengula clupeola (Cuvier, 1829)		$\textbf{4.8} \pm \textbf{3.2}$	1.7 ± 0.9	$\textbf{3.2} \pm \textbf{2.5}$	0.9 ± 0.5		1.5–8.6	PL2,6	
<i>Eucinostomus argenteus</i> Baird & Girard, 1855	1.6 ± 0.7	$\textbf{4.0} \pm \textbf{1.0}$	0.4 ± 0.2	0.5 ± 0.2	$\textbf{13.8} \pm \textbf{2.9}$	3.6 ± 0.7	1.0–12.6	BE1,2	
Poecilia vivipara Bloch & Schneider, 1801	0.6 ± 0.5	0.1 ± 0.1	$\textbf{3.0} \pm \textbf{1.9}$	0.5 ± 0.2	0.2 ± 0.1	2.9 ± 1.6	1.2–6.0	OP9	
Eucinostomus melanopterus (Bleeker, 1863)	0.1 ± 0.1	0.4 ± 0.2	0.7 ± 0.4	0.2 ± 0.1			2.3–6.7	BE	
Ctenogobius boleosoma (Jordan & Gilbert, 1882)	0.7 ± 0.3	0.4 ± 0.1		1.1 ± 0.3	0.7 ± 0.3	0.2 ± 0.1	1.7–5.1	BE9	
Sphoeroides testudineus (Linnaeus, 1758)	0.5 ± 0.1	0.2 ± 0.1	0.5 ± 0.2	$\textbf{24.9} \pm \textbf{10.2}$	0.9 ± 0.3	0.2 ± 0.1	1.3–19.8	ZB2,10	
Diapterus rhombeus (Cuvier, 1829)		0.4 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	$\textbf{7.7} \pm \textbf{3.1}$	0.6 ± 0.2	1.4–7.2	BE1,3	
Anchoa januaria (Steindachner, 1879)		0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.1			2.8–7.7	PL3,6	
Mugil curema Valenciennes 1836	0.1 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.1 ± 0.1		0.1 ± 0.1	15.4–16.6	DE8	
Anchoa tricolor (Spix & Agassiz, 1829)			0.4 ± 0.2				2.2–9.0	PL	
Mugil gaimardianus Desmarest, 1831	0.2 ± 0.1						5.5–12.0	DE	
Eucinostomus gula (Quov & Gaimard, 1824)	0.1 ± 0.1	0.2 ± 0.1		0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	1.0-8.3	HY10	
Citharichthys arenaceus Evermann & Marsh, 1900	0.2 ± 0.1	0.1 ± 0.1					1.7–8.0	ΗY	
<i>Trachinotus falcatus</i> (Linnaeus, 1758)	0.1 ± 0.1		0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	1.6–8.0	ΗY	
Hyporhamphus unifasciatus (Ranzani, 1841)		0.1 ± 0.1	0.1 ± 0.1				5.5–6.0	OM8	
<i>Sphoeroides greeleyi</i> Gilbert, 1900	0.1 ± 0.1		0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	3.5–9.8	BE9	
<i>Oligoplites saurus</i> (Bloch & Schneider, 1801)		0.2 ± 0.1	0.1 ± 0.1		3.0 ± 2.4	0.1 ± 0.1	1.8–7.4	PI	
Trachinotus carolinus (Linnaeus, 1766)		0.2 ± 0.1			0.2 ± 0.1	0.1 ± 0.1	5.1–11.1	ΗY	
Bairdiella ronchus (Cuvier, 1830)	0.2 ± 0.1				0.2 ± 0.1	0.1 ± 0.1	2.0-8.4	ΗY	
Ctenogobius shufeldti (Jordan & Eigenmann, 1887)	0.2 ± 0.1						3.0-4.0	BE5,9	
Strongylura timucu			0.2 ± 0.1	0.3 ± 0.1	0.08 ± 0.1	0.1 ± 0.1	1.1–34.7	PI	
Achirus lineatus (Linnaeus, 1758)	0.2 ± 0.1			0.2 ± 0.1	0.05 ± 0.04		1.8–6.3	BE2,10	

Table 2. Continued

	2002/03			2008/09				
species	Sp	Su/Fa	Fa/Wi	Sp	Su/Fa	Fa/Wi	size range (cm)	trophic guild ^a
Prionotus punctatus	0.1 ± 0.1					0.1 ± 0.1	3.9–7.8	HY2
(Bloch, 1793) Synodus foetens			0.2 ± 0.1	0.1 ± 0.1		0.2 ± 0.1	5.3–12.8	PI1
Lagocephalus lagocephalus lagocephalus (Linnaeus, 1758)		0.1 ± 0.1	0.1 ± 0.1				3.7–5.1	BE
<i>Citharichthys spilopterus</i> Günther, 1862	0.1 ± 0.1		0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.08	0.2 ± 0.1	1.8–14.7	HY 2,7
<i>Symphurus tessellatus</i> (Quoy & Gaimard, 1824)		0.1 ± 0.1	0.1 ± 0.1		0.01 ± 0.01		2.6–12.2	HY2,7
Chilomycterus spinosus spinosus (Linnaeus, 1758)	0.2 ± 0.1					0.1 ± 0.1	1.2–9.8	BE
Chaetodipterus faber (Broussonet, 1782)		0.1 ± 0.1		0.1 ± 0.1	0.05 ± 0.02		2.7–4.4	BE8
Gobionellus stomatus Starks, 1913		0.1 ± 0.1					2.9–2.9	BE
Oligoplites palometa (Cuvier, 1832)		0.1 ± 0.1		0.2 ± 0.1	0.33 ± 0.11	0.4 ± 0.1	2.1–9.0	PI1
Oligoplites saliens (Bloch, 1793)		0.1 ± 0.1					3.1–5.0	PI
Hemiramphus brasiliensis (Linnaeus, 1758)			0.1 ± 0.1	0.2 ± 0.1			12.5–19.4	HE8
Lagocephalus laevigatus (Linnaeus, 1766)			0.1 ± 0.1	0.2 ± 0.1		0.2 ± 0.1	4.0-8.2	BE
Monacanthus ciliatus (Mitchill, 1818)			0.1 ± 0.1			0.1 ± 0.1	2.5–2.5	BE
Strongylura marina (Walbaum, 1792)			0.1 ± 0.1				2.1-7.0	PI
<i>Ulaema lefroyi</i> (Goode, 1874)				3.6 ± 2.7	$\textbf{28.1} \pm \textbf{7.9}$	0.3 ± 0.1	1–8.9	BE
Brevoortia aurea (Spix & Agassiz, 1829)				0.8 ± 0.6			5.4–8.1	PL
Genidens genidens (Cuvier, 1829)				0.5 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	5.1–13	OP2
Ctenogobius stigmaticus (Poev. 1860)				0.6 ± 0.4	0.2 ± 0.1		2.4–5.5	BE
Micropogonias furnieri (Desmarest 1823)				0.2 ± 0.1	0.2 ± 0.1	0.25 ± 0.1	2.3–17	BE1,2
Elops saurus Linnaeus, 1766				0.1 ± 0.1	0.1 ± 0.1		1.3–25.2	PI
Anchoviella brevirostris (Günther, 1868)				0.2 ± 0.1			2.5–2.8	PL
Sardinella brasiliensis					0.1 ± 0.1		5.2–7.0	PL
Citharichthys macrops				0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	2.7–6.0	ΗY
Centropomus parallelus				0.2 ± 0.1			2.7–5.0	PI9
<i>Etropus crossotus</i> Jordan & Gilbert, 1882				0.1 ± 0.1			1.1–9.1	HY2

Table 2. Continued

	2002/03			2008/09					
species	Sp	Su/Fa	Fa/Wi	Sp	Su/Fa	Fa/Wi	size range (cm)	trophic guild ^a	
Ophioscion punctatissimus Meek & Hildebrand, 1925					0.2 ± 0.1		1.5–1.7	BE	
Catathyridium garmani (Jordan, 1889)					0.2 ± 0.1		3.2-4.0	BE	
Gobiosoma hemigymnum (Eigenmann & Eigenmann, 1888)				0.1 ± 0.1			11.1	BE	
Carangoides bartholomaei (Cuvier, 1833)				0.1 ± 0.1			4.7	PI	
Symphurus plagusia (Bloch & Schneider, 1801)				0.1 ± 0.1			7.5	BE	
Caranx latus Agassiz, 1831				0.1 ± 0.1			7.1	PI1	
<i>Syngnathus folletti</i> Herald, 1942				0.1 ± 0.1			9.8	PL	
Scorpaena isthmensis Meek & Hildebrand, 1928				0.1 ± 0.1			8.2	PI	
<i>Caranx lugubris</i> Poey, 186					0.1 ± 0.1		4.9	PI	
<i>Larimus breviceps</i> Cuvier, 1830					0.1 ± 0.1		2.8	ΗY	
Centropomus undecimalis (Bloch 1792)					0.1 ± 0.1		19.2	PI	
Menticirrhus americanus					0.1 ± 0.1		6.1	BE2	
(Chabanaud, 1928)					0.1 ± 0.1		6.4	BE	
Ctenogobius smaragdus (Valenciennes, 1837)						0.1 ± 0.1	4.8-4.8	BE	
Number of individuals Number of species	$\begin{array}{c} \textbf{75.2} \pm \textbf{16.2} \\ 4.6 \pm 0.5 \end{array}$	68.0 ± 9.3 5.2 ± 0.3	$\begin{array}{c} 28.0 \pm 5.2 \\ 4.1 \pm 0.4 \end{array}$	$\begin{array}{r} \textbf{140.9}\pm\textbf{35.4}\\ \textbf{7.5}\pm\textbf{0.7}\end{array}$	$\begin{array}{r} \textbf{155.0} \pm \textbf{35.6} \\ \textbf{8.3} \pm \textbf{0.4} \end{array}$	$\begin{array}{c} 43.5\pm7.2\\ 5.7\pm0.3\end{array}$			

Seasons: Sp = spring; Su/Fa = summer/early fall; Fa/Wi = late fall/winter.

Trophic guilds (according to Elliott *et al.* 2007): PL = planktivorous; DE = detritivorous; OV = omnivorous; HR = herbivorous; PI = piscivorous; BE = benthophagous; HY = hyperbenthophagous; ZB = zoobenthivorous, OP = opportunistic.

^aReferences: 1, Pessanha & Araújo (2014); 2, Guedes et al. (2014); 3, Sergipense et al. (1999); 4, Froese & Pauly (2014); 5, Zanlorenzi & Chaves (2011); 6, Chaves & Vendel (2008); 7, Guedes et al. (2004); 8, Vasconcelos Filho et al. (2009); 9, Corréa & Uieda (2007); 10, Vasconcelos Filho et al. (2010).

other (R > 0.25). Samples from late fall/winter are located mainly on the lower-right side of the diagram, while those from the spring and summer/early fall are located on the upper-left part of the diagram in both yearly periods according to nMDS (Fig. 5). Samples from the spring and summer/early fall tended to overlap. The average similarity was high (>50%) for all seasons in both years.

The SIMPER analysis revealed the species that most contributed to the within-group similarity in each season and yearly period. The opportunist Brazilian silversides, *A. brasiliensis*, was the most abundant species and made the biggest contribution to within-group average similarity during all seasons in both yearly periods. *Mugil liza*, a detritivorous species contributed most to within-group average similarity in spring and in summer/early fall in both yearly periods. The gerreids, all benthophagous species, tended to be identified as discriminant species in 2008–2009 those that have the highest contribution to within-group average similarity. *Eucinostomus argenteus*

	2002–2003 (1) × 2008 –2009 (2)		2002–2003 Sp×Su/Fa×	Fa/Wi	2008–2009 Sp×Su/Fa×Fa/Wi	
	Н	U	Н	U	Н	U
number of species	30.6**	2 > 1	n.s.	_	16.6**	Sp–Su/Fa>Fa/Wi
number of individuals	6.01**	2 > 1	23.4**	Sp–Su/Fa>Fa/Wi	20.5**	Sp–Su/Fa>Fa/Wi
biomass (g)	22.6**	2 > 1	9.6**	Su/Fa>Sp_Fa/Wi	6.5*	Sp>Fa/Wi
Atherinella brasiliensis	n.s	_	16.5**	Sp–Su/Fa>Fa/Wi	n.s.	_
Mugil liza	n.s.	_	26.4**	Sp–Su/Fa>Fa/Wi	6.9**	Sp–Su/Fa>Fa/Wi
Eucinostomus argenteus	10.5**	2 > 1	21.7**	Sp–Su/Fa>Fa/Wi	45.7**	Su/Fa–Fa/Wi>Sp
Diapterus rhombeus	13.0**	2 > 1	12.4**	Su/Fa–Fa/Wi>Sp	31.7**	Su/Fa>Fa/Wi– Sp
Ulaema lefroyi	68.7**	2 > 1	n.s.	_	43.7**	Sp–Su/Fa>Fa/Wi
Sphoeroides testudineus	n.s.	_	21.4**	Sp–Fa/Wi>Su/Fa	47.3**	Sp>Su/Fa–Fa/Wi
Harengula clupeola	3.6*	1 > 2	n.s.	_	9.9**	Sp–Su/Fa>Fa/Wi

Table 3. Comparisons for the number of individuals, number of species, biomass and densities of dominant species between the two yearly periods and among the three seasons for each yearly period, according to Kruskal–Wallis (*H*) and Mann–Whitney tests (*U*) for pair-wise significant differences.

Seasons: Sp = spring; Su/Fa = summer/early fall; Fa/Wi = late fall/winter.

*P < 0.05; **P < 0.01; n.s., not significant.

contributed most to within-group average similarity in summer/early fall during both yearly periods, in spring in 2002–2003 and in late fall/winter in 2008–2009. Other important species that contributed to average similarity were the zoobenthivorous puffer fish *S. testudineus* in spring and the benthophagous *U. lefroyi* in spring and summer/early fall during 2008–2009 (Table 5).

Dominant species

Densities of *A. brasiliensis*, *M. liza* and *Sphoeroides testudineus* did not differ significantly between years (P > 0.05; Table 3). By contrast, densities of *E. argenteus*, *Diapterus rhombeus* and *U. lefroyi* were significantly higher (P < 0.05) in 2008–2009, whereas *H. clupeola* was significantly higher in 2002–2003.

In 2002–2003, densities of *A. brasiliensis*, *M. liza* and *E. argenteus* were significantly higher (P < 0.01) in spring and summer/early fall, *D. rhombeus* in summer/early fall and late fall/winter, while *S. testudineus* had the lowest densities in summer/early fall.

In 2008–2009, A. brasiliensis did not change abundance among seasons (P > 0.05), whereas densities of M. liza, H. clupeola and U. lefroyi were significantly higher in spring and in summer/early fall, E. argenteus in summer/ early fall and in late fall/winter, D. rhombeus in summer/ early fall and S. testudineus in spring (Table 3 and Fig. 6).

Discussion

Our data indicate that changes in fish assemblage structure in Guaratiba Mangrove occurred between 2002–2003 and 2008–2009, with increases in abundance and richness in the latter period, suggesting improved conditions of increases in the abundance of dominant species common in both yearly periods, such as the resident A. brasiliensis, and the marine migrants M. liza and E. argenteus. Low abundance species that were recorded only occasionally in the samples did not contribute to the differences in fish densities between the two yearly periods, although they did contribute to the increases in richness in the latter period. Moreover, we recorded significant species replacement in these low abundance species between the two yearly periods. Of the total of 63 recorded species in this study, 10 species (16% of the total number of species) were exclusively recorded in 2002-2003 and 23 (40%) were recorded only in 2008–2009. The mangrove habitat connection with the inner part of Sepetiba Bay and with the adjacent marine coastal area is made possible through the channels that enable permanent hydrological connection. This may favor species turnover in the study area. The presence of mangroves in close proximity to other habitats has been indicated as an important factor affecting fish assemblages (Dorenbosch et al. 2007; Unsworth et al. 2008; Nagelkerken 2009). In Guaratiba Mangrove, the dynamism of tidal flooding pulses exposing both extensive sandbanks and the mangrove forest is probably the key feature structuring the fish community. However, no studies have yet investigated connectivity between Guaratiba Mangrove and other habitats.

this habitat for fish species. These changes were due to

Some species are highly abundant in mangroves, such as the Brazilian silversides *A. brasiliensis*, the most abundant fish species in Guaratiba Mangrove. The affinity of *A. brasiliensis* for the highly structured habitats in Guaratiba Mangrove was reported by Neves *et al.* (2006), who found a high contribution of this species to the local ichthyofauna (57.9% of the total number; 54.8% of the



Fig. 3. Means +1 SE (vertical lines) of the number of fish species, individuals and biomass (g) in three seasons. Sp, spring; Su/Fa, summer/ early fall; Fa/Wi, late fall/winter; black bars, 2002–2003; white bars, 2008–2009.

total weight). In beaches of Sepetiba Bay that lack mangroves, Pessanha & Araújo (2003) found a relatively lower contribution of this species to the icththyofauna (1.8% of the total number; 5.6% of the total weight), which reinforces the view that the mangrove habitat is a very suitable area for A. brasiliensis. This species inhabits other habitats such as estuaries and coastal lagoons in Southeastern Brazil (Andreata et al. 1990a,b; Araújo et al. 1997). Andreata et al. (1990a) reported A. brasiliensis as the most abundant fish species, contributing to 41.7% of the total number of fishes in the Marapendi Lagoon, and 31.4% of the total number of fishes in Rodrigo de Freitas Lagoon (Andreata et al. 1997), two coastal systems in Rio de Janeiro State. According to Neves et al. (2006), A. brasiliensis is an abundant resident species of Guaratiba Mangrove but occurs at comparatively lower abundances



Fig. 4. Individual-based rarefaction curves for species richness by seasons and yearly periods. SP, spring; SU/FA, summer/early fall; FA/ WI, late fall/winter.

Table 4. R-statistics of one-way analysis of similarity comparisons of the fish community among seasons for each yearly period.

Seasons	2002–2003	2008–2009
R Global	0.21**	0.30**
spring × summer/early fall	0.07n.s.	0.35**
spring × late fall/winter	0.22**	0.38**

**P < 0.01; n.s. = not significant.

in other nearby habitats. Pessanha & Araújo (2003) found the highest abundance of this species in the sandy beaches of Sepetiba Bay close to Guaratiba Mangrove, an indication that the mangrove 'exports' *A. brasiliensis* to sandy beaches nearby and that there is connectivity between these two types of habitat.

Many fish species found in mangroves rearing grounds during their early life history, with the adult life stage occurring in marine waters (Blaber & Milton 1990; Chong 2005). Many fish species enter estuaries as postlarvae and juveniles after spending the larval stage in offshore waters where the adults spawn (Bell *et al.* 1984; Little *et al.* 1988; Sarpedonti & Chong 2008). One point of uncertainty is



Axis 1

Fig. 5. Ordination diagram from non-metric multidimensional scaling analyses on fish assemblage abundance for each yearly period with samples coded by seasons. Black circles, spring; white circle, summer/ early fall; asterisks, late fall/winter.

that not all mangroves are equally valuable as nursery habitat; even within one geographic area, not all mangroves have the same density of juvenile fish relative to the surrounding habitats or to each other (Huxham *et al.* 2004; Chittaro *et al.* 2005). Guaratiba Mangrove seems to be used in different ways by different species: *M. liza* and some gerreid species mainly occur as seasonal marine migrants, *A. brasiliensis* is present as a resident species and a large number of species occasionally frequent the mangrove in low numbers.

The mojarras *E. argenteus* and *Diapterus rhombeus*, and the clupeid *H. clupeola*, which are common in Sepetiba Bay (Araújo & Santos 1999; Pessanha & Araújo 2003, 2014), also rank among the most abundant species in Guaratiba Mangrove. These mojarras are dominant in

Table 5. Species that most contributed to within-group average similarity according to similarity percentages analyses.

snecies	2002–2	2003		2008–2009				
average similarity (%)	Sp 57.59	Su/Fa 59.57	Fa/Wi 56.25	Sp 50.41	Su/Fa 58.95	Fa/Wi 55.26		
Atherinella brasiliensis	35.7	46.2	52.1	29.4	21.3	38.7		
Mugil liza Eucinostomus argenteus	12.8 5.6	2.8 7.5		3.1	4.1 15.0	2.1 9.8		
Sphoeroides testudineus				11.7				
Ulaema lefroyi Diapterus rhombeus				5.1	12.5 3.4			

Seasons: Sp = spring; Su/Fa = summer/early fall; Fa/Wi = late fall/winter.

the Sepetiba Bay mudflats, where they have developed ontogenetic dietary shifts in order to avoid intra- and inter-specific competition (Pessanha & Araújo 2014). Conversely, other abundant species in Sepetiba Bay, such as the white croaker, *Micropogonias furnieri* (Costa & Araújo 2003), and the anchovies *Anchoa januaria* and *Anchoa tricolor* (Araújo *et al.* 2008) were present at low abundance or rare in Guaratiba Mangrove, suggesting that the mangrove is not an appropriate habitat for early life stages of these species. By contrast, the pompano *Trachinotus carolinus* uses both habitats, the mangrove, a wellstructured system, and the oceanic beaches, which have little physical structure and great wave dynamism (Pessanha & Araújo 2003).

We detected a remarkable seasonal change in the use of Guaratiba Mangrove by the fish assemblage, with the highest abundance of individuals and greatest species richness in summer and the lowest levels of both of these factors in winter. Peaks of rainfall in summer associated with high temperatures seem to favor entrance of fishes into the mangrove. By contrast, decreasing temperatures, high salinity and a comparatively lesser influence of continental drainage in the late fall/winter seem to be environmental conditions that are less suitable for fish species in this mangrove. Moreover, seasonal changes in fish structure were better defined in 2008-2009, when greater numbers of individuals and species of fish were using the mangrove area. Seasonality in the occurrence of fish species depends upon many factors, among them the timing of the peak of spawning, and variations in the currents and tides that transport eggs and larvae, environmental constraints and the suitability of rearing grounds (McFarland 1963; Ross et al. 1987; Gibson et al. 1993; Potter et al. 2001). Seasonal changes in fish abundance in mangroves have been reported elsewhere, with peaks in the



Fig. 6. Means +1 SE (vertical lines) of the number of fish and biomass (g) of dominant species in three seasons and two yearly periods in Guaratiba Mangrove. Sp, spring; Su/Fa, summer/early fall; Fa/Wi, late fall/ winter; black bars, 2002–2003; white bars, 2008–2009.

rainy season and troughs in the dry season (Rooker & Dennis 1991; Barletta *et al.* 2003; Lugendo *et al.* 2007) and the present study has confirmed this pattern for Guaratiba Mangrove.

The abundant *M. liza* and *A. brasiliensis* had consistent seasonal changes in abundance during the two yearly periods examined, peaking in spring/summer. *Mugil liza* seems to be a marine migrant that visits the mangrove in periods of high temperature and rainfall. According to Albieri & Araújo (2010), adult individuals of *M. liza* have a short spawning period in coastal waters near to Sepetiba bay, between May and August. Silva & Araújo (2000) reported recruitment of young-of-the-year into the bay from May to October. It is therefore reasonable to suppose that *M. liza* recruits in Guaratiba Mangrove between spring and early fall when this species reaches peaks of abundance in the area. Moreover, the state of Rio de Janeiro has the largest artisanal mullet fisheries in Southeastern Brazil (IBAMA 2007) and Guaratiba Mangrove is therefore likely to make an important contribution to these fisheries.

We found remarkable increases in the number of species and in fish abundance in 2008–2009 compared with 2002–2003. This may indicate an improvement of the suitability of Guaratiba Mangrove for ichthyofauna. Environmental conditions did not change remarkably between the two periods, with the latter period having higher dissolved oxygen, slightly lower temperatures and more even rainfall across the months. The reasons for the increased number of fish species and abundance in the latter period are unknown. The comparatively higher rainfall and wider seasonal variation in temperature and salinity in 2008–2009 compared with 2002–2003 may have contributed to enhancing these dimensions of the niche and attracted a large number of species to the mangrove but this speculation needs to be confirmed by further studies. Enhancement of the niche dimensions that a given ecosystem contains has long been thought to be a major driver of species diversity. Ooi & Chong (2011), studying fish larvae, reported that salinity appeared to be the most significant factor influencing the distribution and abundance of most larval fish, mainly those of the mugilid, sciaenid and cynoglossid families, which generally preferred more saline waters. By contrast, Lugendo et al. (2007) suggested that mangroves are not suitable habitats for juvenile fish during the rainy season, probably due to physiological stress caused by reduced salinity and high turbidity, which is not in accordance with our findings. Increased species abundance and richness in the last studied period could be at least partially attributable to protection policies in the area, as the mangrove is a Biological Reserve of State of Rio de Janeiro. Although the biological reserve was created in 1974 by the law n° 7.549 of 20 November 1974, its area was finally delimited, including the mangrove, only at the end of 2002 through the law n° 32.365 of 10 December 2002. This may have influenced the increased number of fish species from 2002-2003 to 2008-2009. However, further studies on the causes of these changes need to be performed to understand better the dynamics of this mangrove and its role in the functioning of the coastal ecosystem.

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