

Guild composition and habitat use by Tetraodontiformes (Teleostei, Acanthopterygii) in a south-western Atlantic tropical estuary

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Sampling of the demersal ichthyofauna of Guanabara Bay was conducted bimonthly for 2 years at 10 stations distributed along a hydrobiological gradient. A total of 16,081 Tetraodontiformes specimens were collected, representing 10 species distributed among Ostraciidae, Monacanthidae, Tetraodontidae and Diodontidae. Tetraodontiformes appear to be well adapted to hydrological variations and inhospitable conditions prompted by intense eutrophication. However, abiotic factors traditionally considered important in estuarine community structure play a secondary role in the distribution of Tetraodontiformes. The type of sediment appears to be the most important physical factor but acts only as an indicator of ecological domain. The low explanatory power of physicochemical variables, in addition to the relative stability of the bay's ichthyofauna, suggests an influence of biological parameters. The species exhibited wide variation in their use of Guanabara Bay and utilized it as a resting, feeding and growing area. Among the species captured, Stephanolepis hispidus, Lagocephalus laevigatus, Sphoeroides greeleyi, Sphoeroides testudineus, Sphoeroides tyleri, Chilomycterus reticulatus and Chilomycterus spinosus were categorized as marine estuarine opportunists, and Aluterus heudelotii and Aluterus schoepfii were classified as marine stragglers. Acanthostracion sp. could not be categorized. The boom of C. spinosus indicates an ecological imbalance and must be carefully investigated.

Keywords: Impacted ecosystem, estuarine fishes, functional groups, Tetraodontiformes, population biology, tropical estuaries, Guanabara Bay, south-western Atlantic, Brazil

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INTRODUCTION

Estuaries are sheltered, shallow and highly productive regions. Consequently, they represent resting areas for many organisms because of the limited presence of predators and an abundance of food (Blaber, 2000). These characteristics strongly attract human settlement, resulting in a wide range of impacts on these ecosystems and their fish fauna (Rosenfelder *et al.*, 2012; Silva-Júnior *et al.*, 2013). The importance of tropical estuaries has been increasingly recognized in the last 10 years, resulting in the development of studies of the biology and ecology of fishes (Blaber, 2013). However, few studies have examined the ecological aspects of Tetraodontiformes because this taxon is rarely among the most abundant fish taxa in these transition areas, even though Tetraodontiformes are often members of these tropical ecosystems.

Studies of Tetraodontiformes have focused on topics such as cytogenetics (Noletto *et al.*, 2012), phylogeny (Santini *et al.*, 2013; Matsuura, 2015), anatomy (Konstantinidis & Johnson, 2012), population biology (Denadai *et al.*, 2012) and fishing (Kawata, 2012). However, information about the

role of these fishes in estuarine function is scarce. The great morphological and physiological diversity of this order suggests that it might occupy numerous niches and contribute directly and indirectly to ecological processes in estuarine regions (Wootton, 1998).

In this work, we studied Guanabara Bay, an important tropical estuarine complex along the south Atlantic coast that is subject to increasing anthropogenic activity (Castro *et al.*, 2005; Silva-Júnior *et al.*, 2013). Despite the relevance of this tropical estuary, information about its ichthyofauna is deficient and mostly within the last decade (e.g. Rodrigues *et al.*, 2007; Andrade-Tubino *et al.*, 2009; Rosenfelder *et al.*, 2012; Silva-Júnior *et al.*, 2012, 2013; Mulato *et al.*, 2015), hindering the development of strategies for sustainable management as well as the settlement of fishing disputes and the drafting of more effective legislation (Jablonski *et al.*, 2006; Begot & Vianna, 2014). Preliminary data on the diversity of local estuarine fishes indicate that this ecosystem is very important for the breeding, feeding or growth of various populations of fish species (Castro *et al.*, 2005). Studies of structural changes in fish populations to complete knowledge gaps and enable the use of fish fauna to inform water body management are on-going (e.g. Silva Júnior *et al.*, 2013; Mulato *et al.*, 2015).

The aim of this study was to characterize the species of Tetraodontiformes in the tropical estuary of Guanabara Bay

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with respect to their use of the estuary. In addition, these species were categorized into functional groups. The study of community-based guilds enables a broader and more functional view of species as ecosystem components, which might function as an important tool in the environmental assessment of estuaries (Blaber & Barletta, 2007). The species that occur in the estuary were identified, spatial changes in richness and evenness were observed, and the spatio-temporal variation in abundance and its relationship with abiotic parameters were determined.

MATERIALS AND METHODS

Guanabara Bay (Figure 1) is a shallow estuarine complex located on the south-western Atlantic Coast ($22^{\circ}24' - 22^{\circ}57'S$ $42^{\circ}33' - 43^{\circ}19'W$) in which 56% of the 381 km² water surface is less than 5 m deep but can reach up to 30 m in the central channel. The length of the bay measures 28 km, its greatest width is 27 km, and the mouth opening is 1.8 km. The volume of water, estimated at 2 billion cubic meters, is influenced by the rainfall in the region and the semi-diurnal tidal cycle, which has maximum amplitude of 1.4 m and results in a strong seasonal effect on water quality (Mayr *et al.*, 1989). The study area has a rainy season in summer (December through February) and is dry in the winter (July and August). Because of the size of the drainage basin, 4000 km², this seasonal weather pattern greatly influences local hydrological conditions. During the summer, vertical stratification of the water column occurs due to the dilution of surface waters, resulting in the formation of

thermoclines and haloclines. In the winter, the conditions become more homogeneous (Paranhos & Mayr, 1993). In addition, there is a hydrological gradient from the outer to the inner bay areas due to natural rainfall and tidal conditions as well as the discharge of domestic and industrial sewage (Valentin *et al.*, 1999).

Samples were taken every 2 weeks over 2 years (July 2005 to June 2007) from 10 points in the estuary using a vessel operating with bottom trawls. Each trawl lasted 30 min for a total of 240 h of fishing effort over the 48 campaigns (480 hauls). The net was 7 m long and 14 m wide at the mouth, with a mesh size of 18 mm and trawl doors of 23 kg each. The tows were conducted at a speed of approximately 1.5 km h⁻¹. The geographic coordinates of the beginning and end points of each trawl were obtained using a GPS device. The temperature, salinity, saturation and dissolved oxygen content on the surface and at the water bottom were measured using a multiparameter sonde. At the end of each drag, sediment samples were obtained with the aid of an Ekman bottom grab sampler for analysis of particle size distribution and organic matter content, as described by Suguio (1973). Rainfall data were acquired for the entire period of the study from a local weather station (C.P. Rio de Janeiro - Praça Mauá) and grouped into trimesters.

In the laboratory, the fish were identified and measured and weighed to accuracies of 0.1 cm and 0.1 g, respectively. The main references used for identifying the fish fauna were Fischer (1978), Figueiredo & Menezes (2000) and Leis (2006). Voucher specimens of each species were deposited in the ichthyological collection of the Museum of Zoology, University of São Paulo (MZUSP).

General analysis

For each species, the frequency of occurrence (FO%) per campaign and the index of relative importance (IRI) were calculated as absolute and percentage values (Pinkas *et al.*, 1971). The catch-per-unit-of-effort (CPUE) was obtained by dividing the sum of capture (number of specimens or total weight) by the sum of effort (hours trawling). A hierarchical cluster analysis was applied in Q mode to the CPUE data for each sampling station. The choice of the most appropriate grouping was based on the cophenetic correlation (minimum value >0.85), the stability of the clusters using the bootstrap method (100 replicates), and the biological coherence of the clusters.

All subsequent spatial analysis were calculated using the CPUE data and grouped into six areas as determined by the cluster analysis: BOT (station 4.2), NIT (station 4.1), CC (station 3.2), ME (stations 3.1, 5.1 and 5.2), AEL (stations 2.1 and 2.2) and AEO (stations 1.1 and 1.2). The diversity of the Tetraodontiformes in all six areas was compared graphically using their dominance-diversity curves (Magurran, 2004). To better understand the ecological components of these areas and identify possible overlaps in the distributions of key species, a correspondence analysis (CA) was applied to standardized, spatiotemporal CPUE data (N/trimester/area) after removing rare species (Legendre & Legendre, 1998). This analysis was performed excluding data for the extremely abundant species *Chilomycterus spinosus* (Linnaeus, 1758) to facilitate the detection of links between other species. Spatiotemporal correlations between abundances and environmental gradients in the bay were analysed using canonical

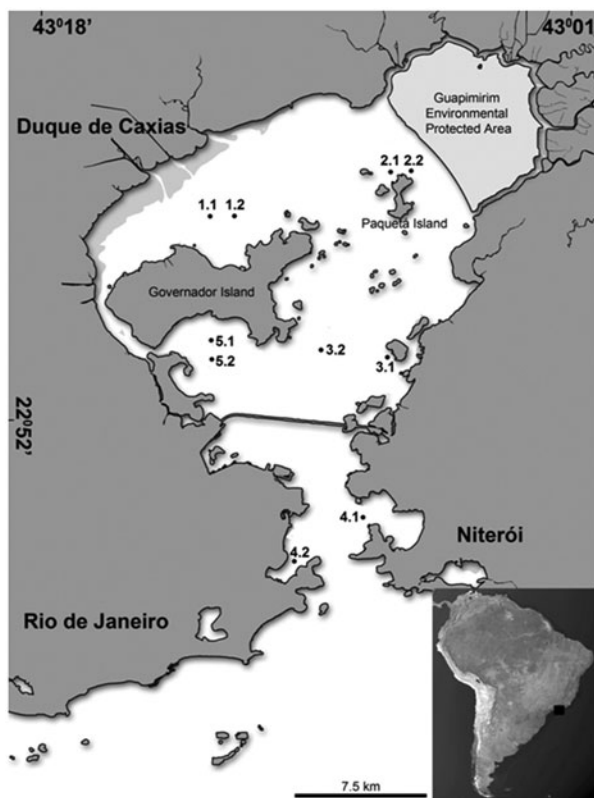


Fig. 1. The estuary of Guanabara Bay ($22^{\circ}24' - 22^{\circ}57'S$ $42^{\circ}33' - 43^{\circ}19'W$); the locations of all 10 sampling stations are indicated.

correspondence analysis (CCA) (Legendre & Legendre, 1998). The abundance matrix was composed of the number of individuals of the six most abundant species. Rare species were removed from this analysis to minimize deviations.

Population analysis

The population aspects of the most representative species in the tropical estuary were investigated to clarify issues identified in the general analysis. Rare species were not included in this analysis due to a lack of data. The monthly samples were organized by trimesters to increase the sampling period and help visualize seasonal differences. The seasonal variation in abundance was assessed using CPUE data, the number of individuals and weight per hour of trawling, grouped into trimesters. When possible, the structure of the catch was outlined by the frequency distribution by size class per trimester. The difference between the 2 years of sampling was tested using the Kolmogorov–Smirnov test to compare the frequency distributions (Siegel, 1956). For very small samples, seasonal analysis was not performed, and the data were grouped into a single histogram representing the entire sampling period. All histograms were drawn with the aid of the Sturges algorithm (Sturges, 1926) to determine the number and amplitude of the size classes. The same procedure was applied to data grouped by area to denote the spatial distribution of abundance and the size range of the Tetraodontiformes.

The range of environmental parameters occupied by the six major species was calculated using the weighted average and the coefficient of variation (CV) of the abiotic factors recorded at the time of the catch (Zar, 1999). The relative proportion of each size fraction of the sediment was also calculated (Folk's texture classification). Seldom-selected classes of sediments (i.e. silty sand, sandy silt) were grouped into a single class denoted 'Mixed'.

The classification of each species into functional guilds based on their use of the estuary considered all the results obtained in the analysis above along with information from the scientific literature. To this end, the classification and recommendations proposed by Elliott *et al.* (2007) were followed.

RESULTS

Spatiotemporal distribution of species

Ten species of Tetraodontiformes distributed in four families were identified: *Aluterus heudelotii* Hollard, 1855 – MZUSP 94704; *Aluterus schoepfii* (Walbaum, 1792) – MZUSP 94705, 94706, 94707; *Stephanolepis hispidus* (Linnaeus, 1766) – MZUSP 94704; *Acanthostracion* sp. – MZUSP 94708; *Lagocephalus laevigatus* (Linnaeus, 1766) – MZUSP 94714; *Sphoeroides greeleyi* Gilbert, 1900 – MZUSP 94715; *Sphoeroides testudineus* (Linnaeus, 1758) – MZUSP 94713; *Sphoeroides tyleri* Shipp, 1972 – MZUSP 94716; *Chilomycterus reticulatus* (Linnaeus, 1758) – MZUSP 94712; and *Chilomycterus spinosus* (Linnaeus, 1758) – MZUSP 94710, 94711. The pufferfish *C. spinosus* was the dominant species, with an IRI value greater than 95% (Table 1).

Six areas were of particular interest with respect to the numerical abundance of Tetraodontiformes (Figure 2 and

Table 2). Of the lower estuary stations, 4.1, 4.2 and 3.2 were very distinct from each other and could not be grouped; therefore, these stations were treated as independent areas: Botafogo inlet – BOT (station 4.2), Niterói Coast – NIT (station 4.1), and Central Channel – CC (station 3.2). By contrast, stations 3.1, 5.1 and 5.2 formed a cohesive group in the middle estuary (ME). The upper estuary was divided into two areas: one to the east (AEL) incorporating stations 2.1 and 2.2 and another to the west (AEO) comprising stations 1.1 and 1.2.

The six areas established by the hierarchical analysis (Figure 2) exhibited distinct ecological patterns, but the strong dominance of *C. spinosus* was evident in all areas (Table 2). BOT was the only station in which evenness was slightly higher and was also the richest in number of species. The other areas of the lower estuary (NIT and CC) were notably less diverse. The average estuary (ME) exhibited a high degree of species richness (seven species) but strong *C. spinosus* dominance, in contrast to BOT. The separation of the upper estuary into two areas by cluster analysis was corroborated by the dissimilar ecological patterns between AEL and AEO, in which the eastern region exhibited the lowest evenness but twice the number of species compared with the western region, which had only three taxa.

Correspondence analysis considered both spatial and temporal components of the samples. The removal of *C. spinosus* from the analysis did not change the significance of the axes; explicability was greater than 80% in both cases (Table 3). We chose not to include the third axis, which would have increased the explicability beyond 90%, due to its low eigenvalue and the difficulty of interpreting ordination in three dimensions.

The high abundance of *C. spinosus* greatly influenced the correspondence analysis (Figure 3). The dominance of this species in most of the samples is evident in concentrated points in the lower left corner of the graph, particularly those corresponding to samples from the AEL, AEO, ME and NIT areas. Areas in which *C. spinosus* was less abundant

Table 1. Absolute frequency (N), total weight (TW), frequency of occurrence (FO) and index of relative importance (IRI), of Tetraodontiformes, in Guanabara Bay between July 2005 and June 2007.

Species	N	%	TW (g)	FO (%)	IRI	%
Monacanthidae	252	1.6	11,456.2	91.7	2.5	1.3
<i>Aluterus heudelotii</i>	2	0.0	38.8	4.2	0.0	0.0
<i>Aluterus schoepfii</i>	3	0.0	17.3	6.3	0.0	0.0
<i>Stephanolepis hispidus</i>	247	1.5	11,400.1	91.7	2.5	1.3
Ostraciidae	1	0.0	2.2	2.1	0.0	0.0
<i>Acanthostracion</i> sp.	1	0.0	2.2	2.1	0.0	0.0
Tetraodontidae	990	6.2	20,836.8	100.0	7.1	3.6
<i>Lagocephalus laevigatus</i>	353	2.2	7311.0	85.4	2.5	1.3
<i>Sphoeroides greeleyi</i>	525	3.3	8169.4	95.8	3.9	2.0
<i>Sphoeroides testudineus</i>	51	0.3	4782.0	50.0	0.4	0.2
<i>Sphoeroides tyleri</i>	61	0.4	574.4	60.4	0.3	0.1
Diodontidae	14,838	92.3	935,220.1	100.0	188.9	95.2
<i>Chilomycterus reticulatus</i>	1	0.0	412.1	2.1	0.0	0.0
<i>Chilomycterus spinosus</i>	14,837	92.3	934,808.0	100.0	188.9	95.2
Total	16,081	100.0	961,575.3		198.5	100.0

Table 2. Relative frequency and sampling effort of Tetraodontiformes, by area in Guanabara Bay, between July 2005 and June 2007.

Species	BOT	NIT	CC	ME	AEL	AEO	N total
<i>Acanthostracion</i> sp.	0.00						1
<i>Aluterus heudelotii</i>		0.00					2
<i>Aluterus schoepfi</i>	0.00	0.00					3
<i>Chilomycterus reticulatus</i>				0.00			1
<i>Chilomycterus spinosus</i>	0.46	0.89	0.72	0.95	0.98	0.92	14,837
<i>Lagocephalus laevigatus</i>	0.01	0.00	0.08	0.02	0.01	0.08	353
<i>Sphoeroides greeleyi</i>	0.38	0.02	0.10	0.01	0.00		525
<i>Sphoeroides testudineus</i>	0.00			0.00	0.00		49
<i>Sphoeroides tyleri</i>	0.02		0.03	0.00	0.00		61
<i>Stephanolepis hispidus</i>	0.12	0.08	0.07	0.00	0.01	0.01	247
N total	855	780	199	11,452	2126	667	16,079
Effort (trawling hours)	24.35	23.78	24.03	71.75	47.92	48.03	239.86

included BOT and CC; in addition, *C. spinosus* was less abundant than *L. laevigatus* in the spring of the second year and summer of the first year in AEO. In BOT, an alternation in the abundance of *S. greeleyi*, *S. tyleri* and *S. hispidus* was observed throughout the seasons, although with no distinct seasonal pattern. The disparity between the two sampling years is evident by the distance between points in different years that were associated with the same areas and seasons.

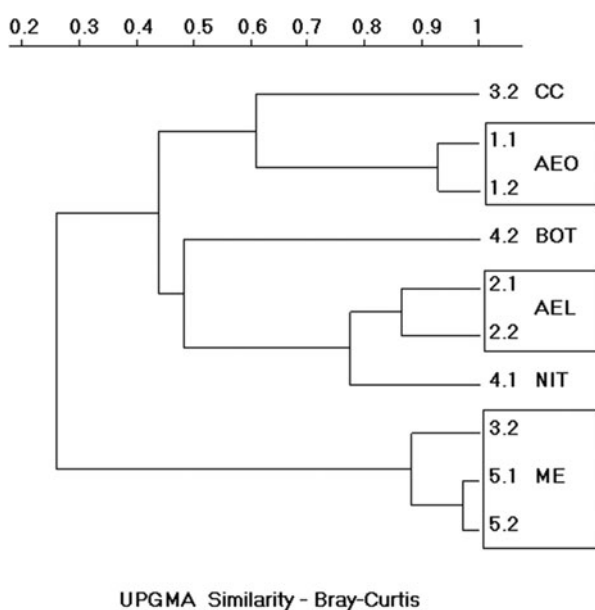
Removal of the *C. spinosus* data enhanced the spatial segregation between the other species (Figure 4). There was a gradient in species composition along the main axis (F1) of the outermost stations (BOT and NIT) from the left side of the figure to the innermost stations (AEL and AEO) on the right side that passed through the central regions of the tropical estuary (ME and CC) at the centre of the graph. The lower estuary stations were characterized by a higher contribution of *S. hispidus* and *S. greeleyi* throughout the study period. However, the second axis shows a clear distinction between BOT and NIT. *Sphoeroides greeleyi* was associated with the first, while *S. hispidus* favoured the latter. Furthermore, *S. hispidus* mainly appeared during the

summer and autumn seasons, whereas *S. greeleyi* and *S. tyleri* were predominant during the winter and spring. The ME and CC stations appeared as transition areas between the upper and lower estuaries with greater participation of *S. tyleri*, *S. testudineus* and *L. laevigatus*. The latter contributes to the samples from the upper estuary (AEL and AEO).

Based on the length of the CCA vectors, the abiotic variables that influenced the structure of the Tetraodontiformes assembly were medium sand, percentage of organic matter (OM%) and silt (Figure 5), emphasizing the importance of the sediment for these demersal fish. Medium sand exhibited a strong positive association with depth, OD, and fine sand with silt and a negative association with OM%. These parameters all exhibited a higher correlation with axis 1. Therefore, this axis separated fish populations depending on their sediment preference. The second axis separated the species based on hydrological factors, such as salinity, temperature, and percentage of carbonates, but with lower explicability. The only species clearly positioned on the ordination axis, *L. laevigatus*, had a tendency to occupy areas with lower salinity. Close to the origin of the vectors, *C. spinosus* was the only species to display no preference for environmental conditions, in agreement with its dominance in all areas of the bay. By contrast, the preference of *S. greeleyi* and *S. hispidus* for the lower estuary was confirmed by their strong association with sand with low organic matter content, high DO and low temperature. The other two *Sphoeroides* species displayed greater tolerance to higher temperatures and OM% but remained in intermediate areas.

Table 3. Eigenvalue, variance and cumulative variance of the eigenvectors generated by correspondence analysis of the spatiotemporal CPUE-n data, for Tetraodontiformes, in Guanabara Bay, between July 2005 and June 2007.

	F1	F2	F3	F4	F5
CA with <i>Chilomycterus spinosus</i>					
Eigenvalue	0.447	0.113	0.066	0.058	0.010
Variance %	64.461	16.226	9.543	8.353	1.417
Cumulative variance %	64.461	80.687	90.230	98.583	100.000
CA without <i>Chilomycterus spinosus</i>					
Eigenvalue	0.526	0.329	0.118	0.053	-
Variance %	51.269	32.056	11.483	5.192	-
Cumulative variance %	51.269	83.325	94.808	100.000	-

**Fig. 2.** Hierarchical analysis of the CPUE-n data by area for Tetraodontiformes caught in Guanabara Bay between July 2005 and June 2007 (cophenetic correlation = 0.8029).

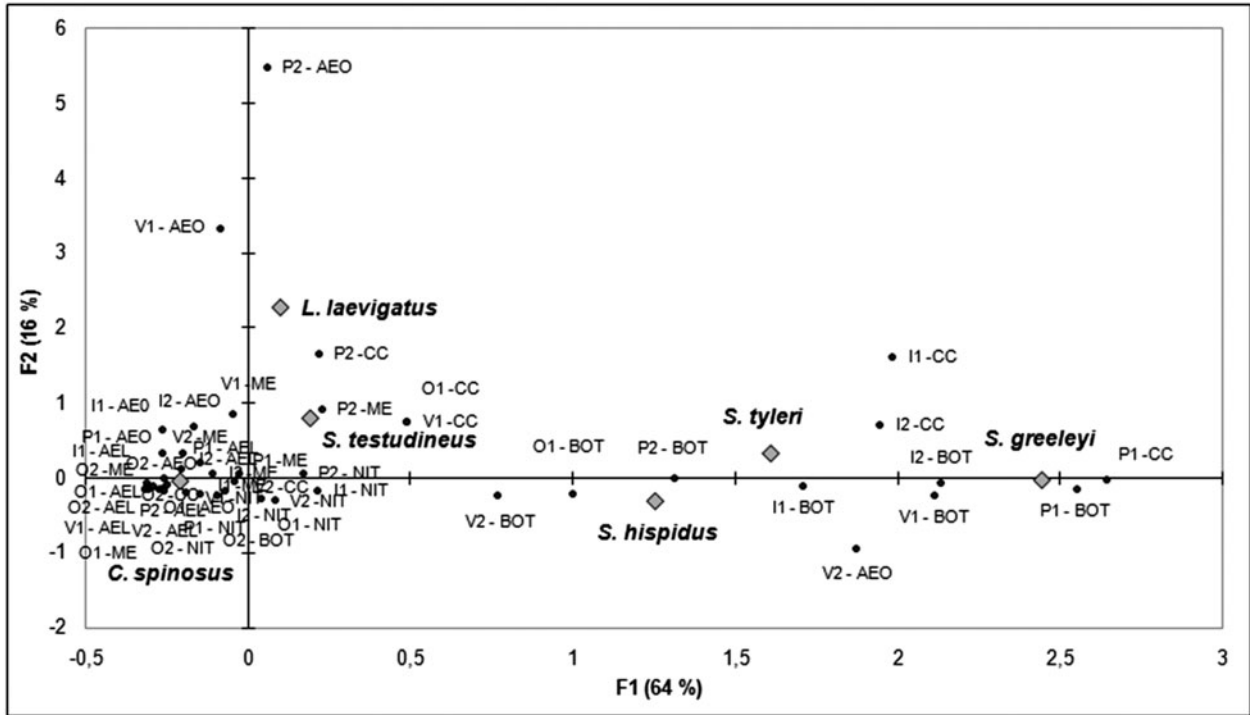


Fig. 3. Spatiotemporal analysis of Tetraodontiformes in Guanabara Bay between July 2005 and June 2007. BOT (station 4.2), NIT (station 4.1), CC (station 3.2), ME (stations 3.1, 5.1 and 5.2), AEL (stations 2.1 and 2.2) and AEO (stations 1.1 and 1.2); P = spring; V = Summer; O = autumn; I = winter; 1 = year 1; 2 = year 2.

However, this interaction between fish fauna and physico-chemical variables explains little of the variation in the distribution of the assemblage. Although the three canonical axes of the CCA were significant in the Monte Carlo test ($P > 0.01$

after 99 permutations), its total explicability was only 19.5% of the variation in the data. Temperature and salinity exhibited CV values of less than 10%, making the mean more representative as a centralizing measure. However, the mean

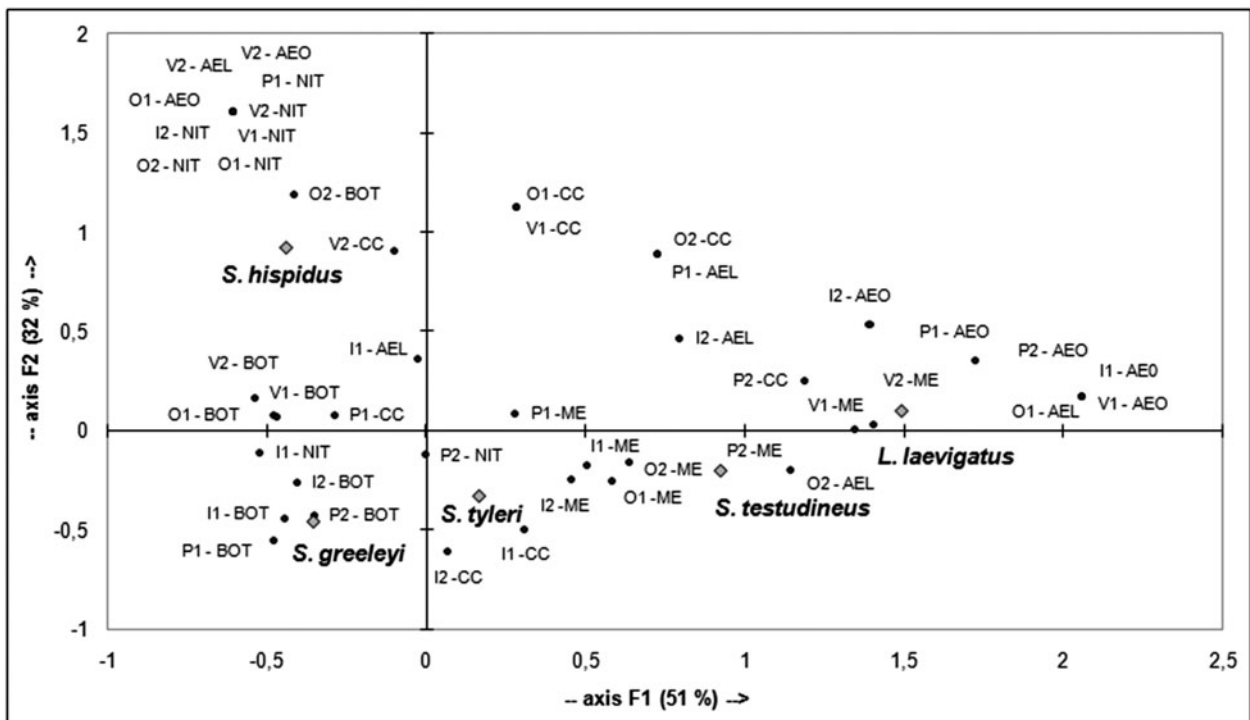


Fig. 4. Spatiotemporal analysis of Tetraodontiformes in Guanabara Bay between July 2005 and June 2007, excluding the dominant species *Chilomycterus spinosus*. BOT (station 4.2), NIT (station 4.1), CC (station 3.2), ME (station 3.1, 5.1 and 5.2), AEL (stations 2.1 and 2.2) and AEO (stations 1.1 and 1.2); P = spring; V = summer; O = autumn; I = winter; 1 = year 1; 2 = year 2.

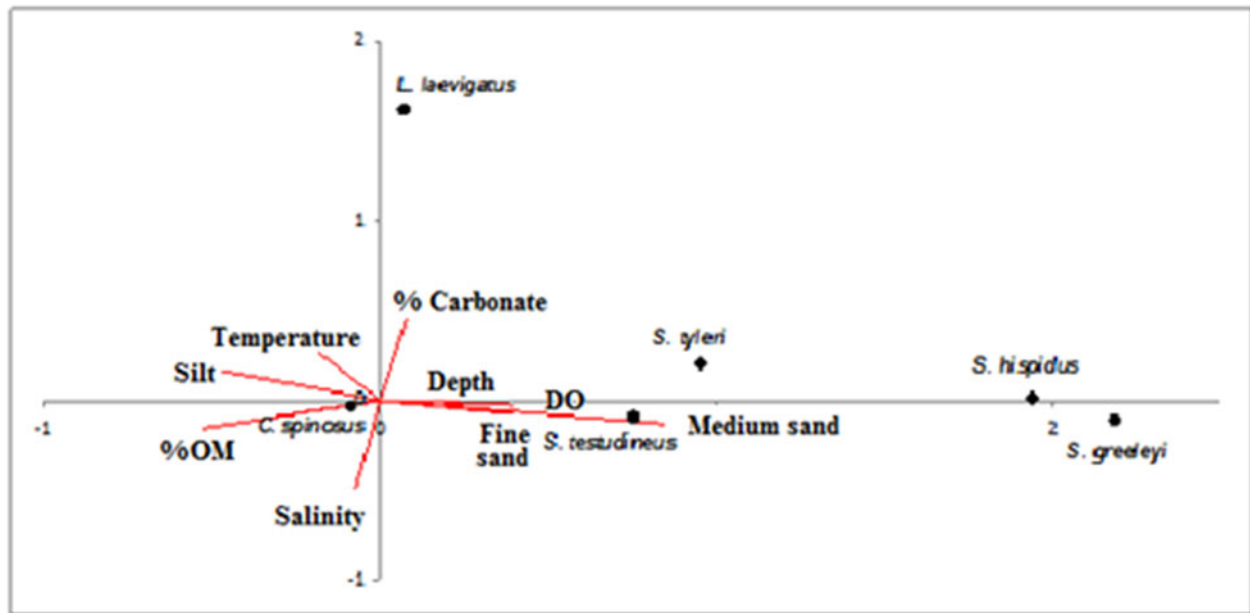


Fig. 5. Canonical analysis of the absolute frequencies, of Tetraodontiformes and environmental variables, in the tropical estuary of Guanabara Bay, between July 2005 and June 2007. Axis 1 (abscissa) = 13.9%; Axis 2 (ordered) = 4.4% of the variation in the data.

values of temperature and salinity varied little between species regardless of the spatiotemporal distribution of the sample, indicating homogeneity of the water conditions at the bottom (Table 4).

The frequency distribution with respect to particle size (Table 5) was more heterogeneous. The lower estuary species, such as *S. greeleyi* and *S. hispidus*, exhibited a clear preference for a thicker sediment composed primarily of sand (67% of specimens captured). By contrast, *S. testudineus*, *L. laevigatus* and *C. spinosus*, which were most common in the middle estuary, exhibited little preference for poor-quality sediment (>70% 'mixed') consisting of a mixture of silt, mud and sand.

Spherooides tyleri exhibited intermediate values, consistent with its distribution within the bay. *Lagocephalus laevigatus* was seldom captured on sandy bottoms but had a strong presence on finer sediments such as silt.

The spatiotemporal distributions of the six main Tetraodontiformes species, based on total number and total weight help visualize the patterns described by the hierarchical and correspondence analysis, specially the population peak for *C. spinosus* observed during the austral summer and autumn of 2007, and its preference for the middle estuary (Figures 6 and 7). A similar preference can be seen in *L. laevigatus* and *S. testudineus*. In contrast, *S. hispidus* and *S. greeleyi* were more

Table 4. Weighted averages and coefficients of variation of abiotic parameters at the time of capture of the main Tetraodontiformes species in Guanabara Bay between July 2005 and June 2007.

	<i>S. greeleyi</i>			<i>S. testudineus</i>			<i>S. tyleri</i>		
	Mean	CV%	N	Mean	CV%	N	Mean	CV%	N
Bottom water									
Average depth (m)	7.5	47.6	525	6.2	65.6	51	7.9	71.5	61
Temperature (°C)	23.1	7.1	199	23.6	8.8	20	23.3	6.9	31
Salinity	32.5	4.4	199	30.9	5.1	20	32.4	4.8	31
DO (mg L ⁻¹)	5.05	40.87	199	5.06	42.77	20	4.04	48.66	31
Saturation (%)	65.3	42.8	175	71.5	47	19	53.6	43.8	27
Carbonate (%)	5.6	126.5	501	4.33	169.6	46	4.59	116.2	57
OM (%)	3.03	136	501	7.64	58.9	46	7.38	72.3	57
N total			525			51			61
	<i>L. laevigatus</i>			<i>S. hispidus</i>			<i>C. spinosus</i>		
Average depth (m)	5.7	63.2	353	7.9	53	247	6.01	61.7	14,837
Temperature (°C)	24.2	7	178	23.2	8.9	136	23.7	5.7	9706
Salinity	31.7	6.4	178	32.5	4.3	136	32.5	4.2	9706
DO (mg L ⁻¹)	3.33	43.33	175	5.34	39.02	136	3.53	62.19	9706
Saturation (%)	41.5	53.7	169	71.4	41.3	127	48.2	61.4	9308
Carbonate (%)	4.43	156.3	338	4.17	154.5	221	2.72	152.2	13,610
OM (%)	9.17	49.6	337	3.65	143	221	9	54.8	13,610
N total			353			247			14,837

Table 5. Distribution of the absolute and percentage frequencies, of the major Tetraodontiformes species, by sediment according to Folk's textural classification, in Guanabara Bay, between July 2005 and June 2007.

Folk's Texture class	<i>S. greeleyi</i>		<i>S. testudineus</i>		<i>S. tyleri</i>		<i>L. laevigatus</i>		<i>S. hispidus</i>		<i>C. spinosus</i>	
	N	%	N	%	N	%	N	%	N	%	N	%
Sand	334	66.7	8	22.9	14	24.6	17	5.0	147	66.5	1335	9.8
Clay	8	1.6	-	-	-	-	-	-	-	-	39	0.3
Mud	13	2.6	-	-	5	8.8	26	7.7	20	9.0	1097	8.1
Silt	1	0.2	2	5.7	3	5.3	48	14.2	10	4.5	1477	10.9
Mixed	145	28.9	25	71.4	35	61.4	247	73.1	44	19.9	9662	71.0
Total	501		35		57		338		221		13,610	

commonly found in the lower estuary. Only *S. tyleri* showed no distinction in total capture between middle and lower estuary.

Functional guilds of the estuary

The analysis of each species population pattern was compared with the existing data in the specialized literature.

Seven species can be classified as *Marine estuarine opportunist*, a subdivision of *Marine migrants*, due to the constant presence as indicated by their high frequency of occurrence and wide use of the estuary. Only two species, *Aluterus heudelotti* and *A. schoepfi*, are considered *Marine stragglers*, due to the low occurrence and restriction to the lower estuary (Table 6).

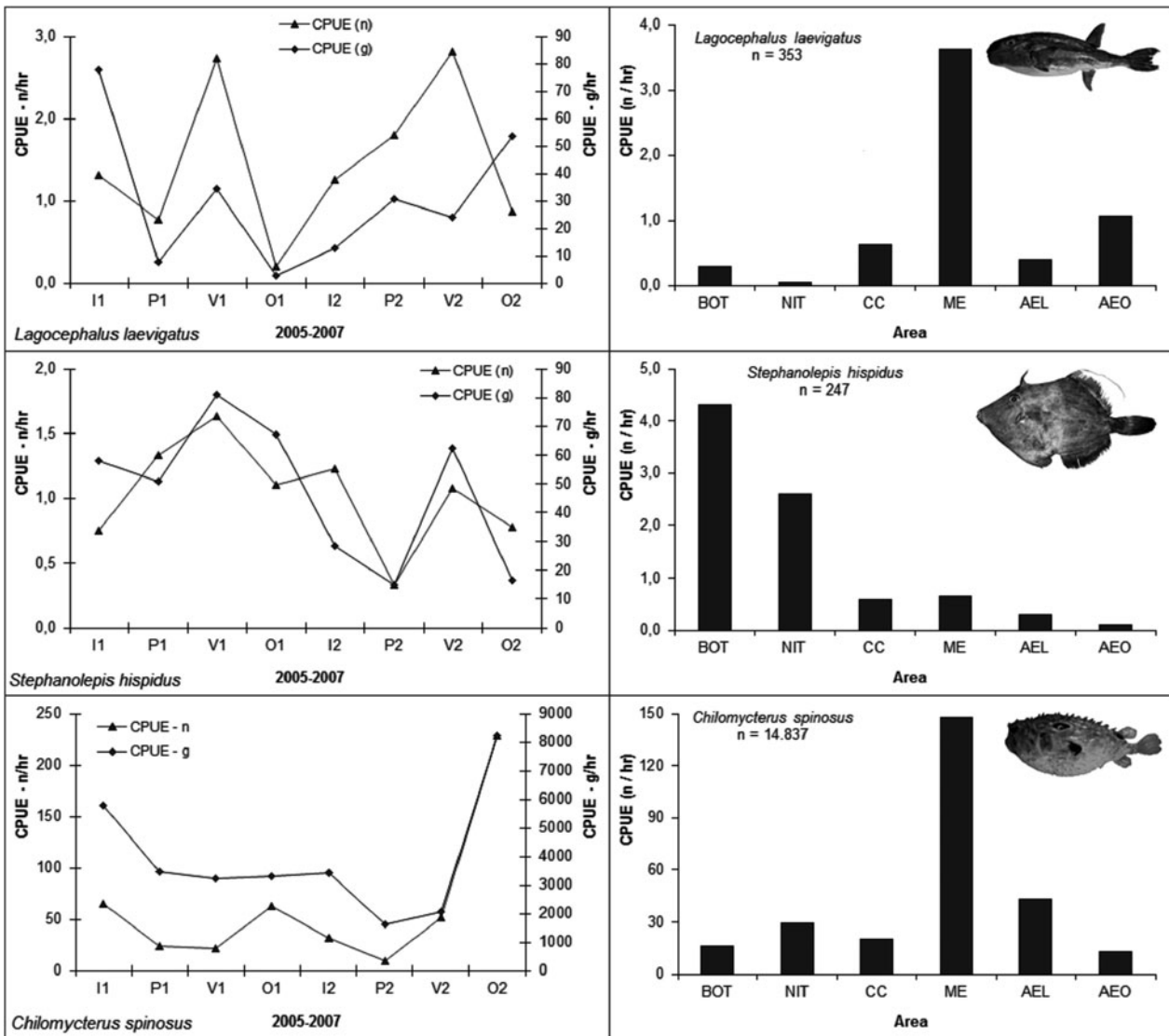


Fig. 6. Spatiotemporal distributions of *Lagocephalus laevigatus*, *Stephanolepis hispidus* and *Chilomycterus spinosus*, based on total n/CPUE and total w/CPUE, in Guanabara Bay between July 2005 and June 2007.

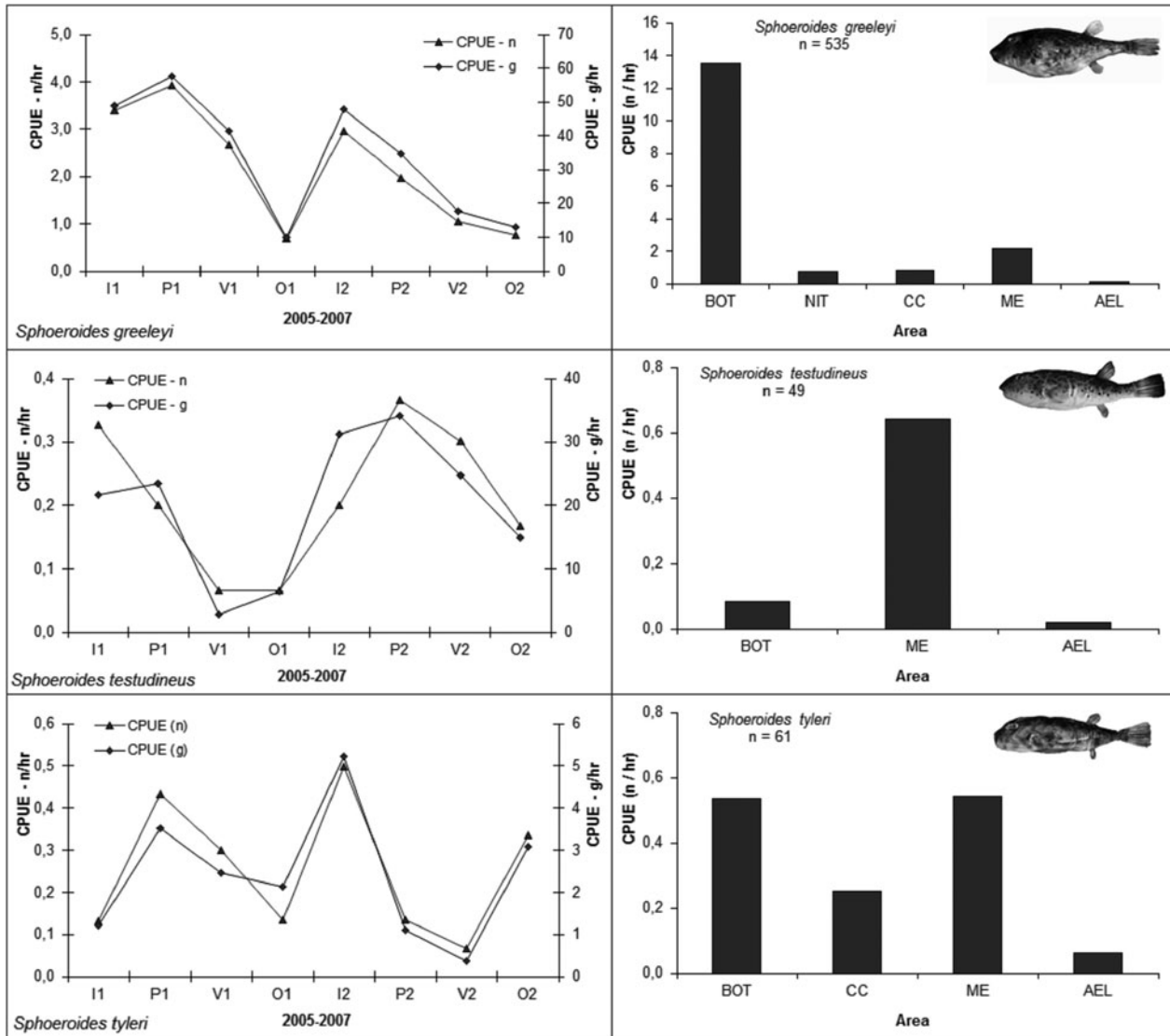


Fig. 7. Spatiotemporal distributions of *Sphaeroides greeleyi*, *S. testudineus* and *S. tyleri*, based on total n/CPUE and total w/CPUE, in Guanabara Bay between July 2005 and June 2007.

DISCUSSION

The distribution and abundance of fishes in tropical estuaries are controlled by a complex combination of factors acting simultaneously and directly or indirectly on ichthyofauna (Sosa-López *et al.*, 2007; Blaber, 2013). The type and duration of the response to these parameters are unique for each species and generate spatiotemporal variations in patterns of diversity and the usage of the estuary by each taxon (Barletta-Bergan *et al.*, 2002; Silva-Júnior *et al.*, 2013). The species of Tetraodontiformes captured in the tropical estuary of Guanabara Bay exhibited diverse modes of occupation of the estuarine complex. The distinctions identified in the present study may reflect the variety of morphological, physiological and behavioural adaptations exhibited by fishes of this order.

Of the taxa recorded in this study, the genus *Aluterus* was solely associated with the pelagic environment of the coastal areas. This genus is of commercial importance, is part of the diet of large pelagic predators (Rosas-Alayola *et al.*, 2002)

and inhabits floating *Sargassum* beds (Rooker *et al.*, 2006). However, specimens of *Aluterus* are also captured by shrimp trawlers along the coastal reefs (López-Peralta & Arcila, 2002), which indicates that these species have a demersal habit at some point in their life cycle, possibly an ontogenetic segregation. Their presence in shrimp bycatch confirms their vulnerability to bottom trawl nets. Moreover, in shallow estuaries such as Guanabara Bay, trawl fishing on the bottom captures a significant portion of the community due to the small pelagic water column (Selleslagh & Amara, 2008). In addition, catch also occurs during the ascent and descent of the net (Vianna & Almeida, 2005). Therefore, it is safe to assume that both species of *Aluterus* are not part of the estuarine ichthyofauna of Guanabara Bay, being limited to be only occasional visitors.

The length of the study period enabled the observation of a population explosion of *Chilomycterus spinosus*. The few available previous studies indicate that this is a recent event because such high numbers of this species have not been

Table 6. Classification of the identified species of Tetraodontiformes within functional groups, according to the analyses of a 2-year twice-monthly sampling effort, in five distinct areas of Guanabara Bay (July 2005 to June 2007).

Species	Reproduction	Salinity	Distribution	FO (%)	Estuary	Classification (Elliot <i>et al.</i> , 2007)
<i>Acanthostracion</i> sp.	Spawning occurs in open waters ¹	Euryhaline Marine ²	Two possible species with a mostly overlapping distribution. Western Atlantic, from the north-eastern USA to Argentina ^{3,4,5}	2.1	LE	Inconclusive
<i>Aluterus heudelotii</i>	Spawning occurs in open waters, moving later to coastal areas ⁶	Stenohaline Marine ^{4,7}	Amphi-Atlantic. Western Atlantic, from Massachusetts (United States) and Bermuda to Santa Catarina (Brazil) ^{3,5}	4.2	LE	Marine straggler
<i>Aluterus schoepfi</i>		Stenohaline Marine ^{4,7}	Western Atlantic, from Nova Scotia (Canada) to Santa Catarina (Brazil) ^{3,5}	6.3	LE	Marine straggler
<i>Chilomycterus reticulatus</i>	Preferential spawning ground unknown. Juvenile pelagic and adults associated with reefs and seagrass beds ^{8,9}	Euryhaline Marine ¹⁰	Circumglobal. Western Atlantic, from New Jersey to Rio de Janeiro (Brazil) ^{a,3,8}	2.1	ME	Marine Estuarine Opportunist
<i>Chilomycterus spinosus</i>		Euryhaline Marine ¹⁰	Amphi-Atlantic, divided in two subspecies: <i>C. s. mauretanicus</i> (Le Danois, 1954), restricted to the Eastern Atlantic; and <i>C. s. spinosus</i> , restricted to the Western Atlantic, from Suriname to Argentina ^{3,8}	100	Widespread	Marine Estuarine Opportunist
<i>Lagocephalus laevigatus</i>	Adults inhabit offshore areas, while juveniles are found in shallower waters. Probable use of estuaries as nursery ground. ¹¹	Euryhaline Marine ¹⁰	Amphi-Atlantic. Western Atlantic, from Newfoundland (Canada) to Argentina ³	85.4	UE/ME	Marine Estuarine Opportunist
<i>Sphoeroides greeleyi</i>	Spawning in estuary ¹² Assumed to be similar <i>S. maculatus</i> (Spawn occurs in all inhabited areas) ^{13,14}	Euryhaline Marine ¹⁰	Western Atlantic, from Belize to Paraná Brazil) ^{3,15}	95.8	Widespread	Marine Estuarine Opportunist
<i>Sphoeroides testudineus</i>	Spawning in estuary. ¹⁶ Assumed to be similar <i>S. maculatus</i> (Spawn occurs in all inhabited areas) ^{13,14}	Euryhaline Marine ^{10,17}	Western Atlantic, from New Jersey to Santa Catarina ³	50.0	Widespread	Marine Estuarine Opportunist
<i>Sphoeroides tyleri</i>	Assumed to be similar <i>S. maculatus</i> (Spawn occurs in all inhabited areas) ^{13,14}	Euryhaline Marine ¹⁷	Western Atlantic, from Nova Scotia to Santa Catarina ³	60.4	Widespread	Marine Estuarine Opportunist
<i>Stephanolepis hispidus</i>	Spawning associated with seaweed and beaches for both larvae and juvenile. ⁶ Spawns in offshore waters. ¹⁸ Seems to follow the same pattern described for <i>Aluterus</i> spp. ¹⁹	Euryhaline Marine	Amphi-Atlantic. Western Atlantic, from Nova Scotia to Uruguay. ^{3,5}	91.7	Widespread	Marine Estuarine Opportunist

^aIn Brazil, known only from few specimens from Rio de Janeiro (Menezes *et al.*, 2003).

The classification was further complemented with published data for the species or, if unavailable, a congeneric species. References: ¹Schärer *et al.*, 2009; ²García-Hernández *et al.*, 2009; ³Menezes *et al.*, 2003; ⁴McEachran & Fechtel, 2005; ⁵Matsuura, 2015; ⁶Zapfe & Lyczkowski-Shultz, 2006; ⁷Figueiredo & Menezes, 2000; ⁸Leis, 2006; ⁹Sommer *et al.*, 1996; ¹⁰Vilar *et al.*, 2011; ¹¹Denadai *et al.*, 2012; ¹²Schultz *et al.*, 2002; ¹³Sibunka & Pacheco, 1981; ¹⁴Lyczkowski-Shultz, 2006; ¹⁵Shipp, 2003; ¹⁶Rocha *et al.*, 2002; ¹⁷Azevedo *et al.*, 2007; ¹⁸Mancera-Rodríguez & Castro-Hernández, 2015; ¹⁹Mancera-Rodríguez & Castro-Hernández, 2004; LE: Lower estuary; ME: Middle Estuary; UE: Upper estuary.

previously recorded. Furthermore, the absence of records of similar behaviour by Diodontidae species in other estuaries in Brazil and other parts of the world indicates that this may be a unique feature of the Guanabara Bay. In a recent study conducted in a nearby tropical estuary (23°S), *C. spinosus* was only identified in the middle part of the estuary and

did not exhibit the dominance observed in the present study (Neves *et al.*, 2011). These results suggest an environmental imbalance in the bay that favoured this species, which is usually less prevalent. However, the identification of the factors that favour this species is hampered by a lack of knowledge about the fish fauna in the bay and their interactions with

this tropical estuarine complex. Thus, while this initial investigation of the distribution of Tetraodontiformes and the factors regulating this distribution clarifies some aspects of the ecology of Tetraodontiformes in estuarine environments, it primarily raises new questions and hypotheses.

The structure of an estuarine fish assemblage depends on various interrelated factors. In tropical estuaries, salinity is often viewed as the most relevant parameter for fish diversity due to different levels of tolerance to the salt gradient exhibited by species (Spach *et al.*, 2003; Whitfield & Harrison, 2003; Vega-Cendejas & Santillana, 2004; Sosa-López *et al.*, 2007). Such studies, however, often observe a wide range of variation in this parameter, including extremes of hypo- and hypersalinity. Such extremes were not observed in the estuary of Guanabara Bay. The lowest and highest salinity values were 15 and 34, respectively, and the seasonal variation in salinity followed local rainfall patterns (inversely related) (Silva-Júnior *et al.*, 2013). However, water dilution in the bay during the rainy season is confined to the superficial layers, creating a vertical gradient in the water column that results in a halocline. Therefore, the minimum salinity near the seabed does not reach 26 and does not exhibit marked seasonality (Paranhos & Mayr, 1993). Thus, the influence of salinity on temporal variations in the fish fauna of the tropical estuary is reduced, while its contribution to the spatial distribution of species is enhanced.

However, the present study reveals that the main species of Tetraodontiformes were exposed to an even smaller range of variation in salinity. This suggests that, in addition to being good osmoregulators, Tetraodontiformes possess mechanisms to avoid diluted waters, such as moving to more stable regions in response to strong discharges of fresh water during the rainy season, as suggested by Barletta *et al.* (2008), or following tidal movements and only exploring the inner regions during high tide. In a nearby estuary, the Sepetiba Bay (23°S), *Spherooides testudineus* and *S. greeleyi* were associated with low tide and high transparency (Pessanha & Araújo, 2003), suggesting that these species primarily use the lower estuary regardless of the tide. Emigration to more hydrologically stable regions, such as the coastal area, may explain the reduction in abundance of *Spherooides* spp. at the end of the rainy season. The lack of a correlation between rainfall and species abundance indicates that other factors likely regulate immigration during the summer.

However, fish can be indirectly influenced by salinity, i.e. by affecting the distribution of species that feed the fish fauna. In Guanabara Bay, the abundance and distribution of the shrimp *Farfantepenaeus brasiliensis* (Latreille, 1817) (Gomes *et al.*, 2013) and the crab *Callinectes ornatus* (Ordway, 1863) (Keunecke *et al.*, 2012) fluctuate in response to environmental changes, such as changes in the salt gradient caused by rainfall. Hence, the distributions of carcinophagous species should change in response to the displacement of its preferred prey. Despite the lack of information on the feeding habits of the local Tetraodontiformes, this pattern may apply to the Tetraodontidae species, as *S. testudineus* and *L. laevigatus*, already known as shellfish feeders (Santos & Rodriguez, 2011; Denadai *et al.*, 2012).

Despite the greater academic interest in the environmental health of the different ecosystems along the estuarine complex, as well as the public outcry for the improvement of the environmental conditions of the bay, Guanabara Bay remains a highly impacted environment. While the lower

estuary enjoys greater exposure to cleaner coastal waters, the upper portions of the bay, especially the western and north-western sectors, receive the majority of the drainage from metropolitan Rio de Janeiro (Ribeiro & Kjerfve, 2002). Furthermore, the concentrations of heavy metals (Fe, Mn, Zn, Cu, Pb, Cr and Ni) were found to be very high in urban street sediments, which are a potential source of these pollutants in the bay, being higher in densely populated areas (Pereira *et al.*, 2007). The sediment is also severely impacted by the continuous input of domestic sewage and industrial effluent; the surface sediment layer is suboxic or anoxic (Silva *et al.*, 2008). The existing facilities for sewage treatment and waste disposal are insufficient to halt the environmental degradation. Ribeiro & Kjerfve (2002) estimated that in order to achieve pre-1950 conditions, it would be necessary to properly treat 80–90% of all domestic and industrial sewage, far from the 15% that is presently treated.

Despite the spatiotemporal segregation between species, it was not possible to characterize their preferred habitats in terms of abiotic factors. The low explicability of the CCA (Figure 5) can be attributed to the wide variation in parameters such as depth, OD, saturation, carbonates and organic matter (Table 4). Therefore, the core values presented were not informative and could not be used to characterize the habitat occupied by each species. However, the large deviation provided important information on the tolerance of these fish to factors indicative of eutrophication. Tetraodontiformes species exhibited a wide tolerance to conditions of eutrophication resulting from pollution, such as changes in OD, saturation and OM% in the sediment. However, the majority of these species avoid extreme conditions, as evidenced by the higher fish abundance in the low and medium estuaries. The higher level of occupation of the lower estuary by *Stephanolepis hispidus* and *S. greeleyi* and of the middle estuary by *S. testudineus*, *L. laevigatus* and *C. spinosus* might reflect variations in levels of tolerance to these inhospitable conditions, leading to the hypothesis that water renewal and not isolated variables determines the distribution of estuarine species (Bouchereau & Chaves, 2003). According to this reasoning, *L. laevigatus* and *C. spinosus* are the species most tolerant to eutrophic conditions because they consistently occur in the most affected regions of the bay. Oziolor & Matson (2015) published a thorough review on fish population adaptation to anthropogenic pollution, where they support the idea that euryhaline species, as *C. spinosus* and *L. laevigatus*, are naturally adapted to a stressed environment. These conditions produce robust species that may be able to adapt to levels of pollution that are lethal to other species, as observed for *Fundulus heteroclitus* in urban estuaries of the Atlantic coast of the USA (Whitehead *et al.*, 2012). As environmental conditions in the bay deteriorate, this physiological trait could be highly beneficial to these species. However, the abundances of species in the central channel, which undergoes constant water renewal that reduces its susceptibility to the cumulative effects of pollution, are comparable with those in internal, eutrophic areas.

The low capacity of abiotic parameters to explain the distribution of estuarine fish species has also been observed in environments in which variations in these factors are sharper and more seasonal (Maes *et al.*, 2004; Selleslagh & Amara, 2008). In the present study, the small spatial and temporal variations in parameters such as salinity and

temperature, combined with the possible tolerance of species to variations in other factors, minimized the influence of these variables on this group of fish. Moreover, these results indicate a major role of other elements in structuring the community as well as a crucial role of biotic phenomena in this process, as previously recorded by Kupschus & Tremain (2001) in a subtropical estuary.

Spatiotemporal variations in fish assemblages tend to reflect peaks in the abundances of the main species (Selleslagh & Amara, 2008). The interference of *C. spinosus* with the frequencies of other species of Tetraodontiformes is quite clear. During the autumn of both years of the study, the high capture rate of *C. spinosus* was accompanied by a decline in the CPUE for other species. Even *S. greeleyi* and *S. hispidus*, which exhibited a preference for the lower estuary, in which *C. spinosus* was less dominant, became scarce during these periods. The other Diodontidae, *Chilomycterus reticulatus* was completely excluded from the system, despite being a euryhaline species.

Such conflicts exist due to the competitive interaction between species for food and space. In the studied tropical estuary, *C. spinosus* appears to exploit its broad tolerance of environmental changes as well as its larger size and morphological characteristics. Its permanently erect spines and large capacity to inflate make this puffer unlikely to be found within multispecific schools. To a lesser extent, some of the other species also appear to interact competitively. However, the high degree of spatial segregation between species is evident in the fact that none of the areas harboured all of the species.

The spatial and temporal segregation between species results in the sharing of resources and, consequently, a reduced probability of competition between them if resources become scarce (Wootton, 1998). Therefore, the taxa that share the most densely populated areas rarely overlap in time. *Stephanolepis hispidus*, for example, seems to avoid BOT when *S. greeleyi* is very abundant and occupies the other side of the lower estuary (NIT) at these times of the year. *Sphoeroides testudineus* also becomes rarer in the middle estuary during the summer, when *L. laevigatus* appears in large numbers in this area. Seasonal movement patterns, however, usually have a reproductive motivation or are ontogenetic (Wootton, 1998). Therefore, for fish species that use the estuary, the pattern of occurrence within that environment depends both on variations in the parameters of the ecosystem and on the phenomena that occur along the coast.

Guilds and the occupation of the estuary

Estuarine fish guilds are primarily determined by the spatial and seasonal occurrence of the species in these environments. These settlement patterns reflect short- and long-term migrations, physiological adaptations and multiple interactions between fish and the ecosystem (Elliott *et al.*, 2007; Blaber, 2013). Most fish associated with estuaries use these environments opportunistically, and Tetraodontiformes in the studied estuary are no exception. A dependent relationship with the estuary could not be detected in any of the species analysed because even those more closely associated with the environment were also captured in the coastal region (e.g. Vianna & Almeida, 2005). Therefore, seven of the 10 species were grouped together in the guild of Marine Estuarine Opportunist species. Only *Aluterus heudelotii* and

A. schoepfii were considered marine stragglers due to their strong association with the coastal pelagic environment, their restriction to the lower estuary stations and their absence in any other list of estuarine fish species found in Brazil. The boxfish *Acanthostracion* sp. could not be classified due to being represented by a single unspecified juvenile.

Although they belong to the same functional group, the estuarine-opportunist species exhibited distinct uses of the estuary. However, all had been previously recorded in other Brazilian estuaries (e.g. Chagas *et al.*, 2006; Queiroz *et al.*, 2006), suggesting that their relationship with the estuarine environment is not exclusive to the studied bay. The puffers *Sphoeroides* spp. have also been reported as estuarine residents in Paranaguá Bay, another coastal estuary of the south-western Atlantic (25°S) (Spach *et al.*, 2003).

These small puffers seem to be able to close their life cycle in the estuary, indicating a complex system of segregation by age and depth migrations between the main channel and the marginal regions. *Sphoeroides testudineus* has even been recorded in the larval stage in the tropical estuary of Guanabara Bay (Castro *et al.*, 2005), suggesting that reproduction occurs within the estuary. An *Acanthostracion* sp. larva was also collected by the authors in the central channel of the bay. However, this fixed sampling station at the entrance of the bay does not confirm the occurrence of reproduction inside the bay. On the contrary, in these early stages of life, individuals of Tetraodontiformes migrate from the sea into the estuary using the strong tidal flow in the central channel.

The puffer *L. laevigatus* is considered estuarine-dependent in the Patos Lagoon (30°–31°S), the southernmost estuary of the Brazilian coast. Its distribution in the studied estuary could confirm this classification if the occurrence of the young stratum sampled here was unique to estuarine environments. However, this is not the case, as shown by Vianna & Almeida (2005), because specimens of this stratum were caught in the coastal zone. This evidence does not exclude the possibility that species could be using the bay as a feeding ground more extensively, indicating the adaptability of the young to estuarine conditions. As for *S. hispidus* and *C. spinosus*, the strong association of these species with the estuary is not indicative of dependence *per se*. These two taxa use the bay as a nursery and remain inside the bay until they reach sexual maturity.

The filefishes *Aluterus* spp. and *S. hispidus* are sensitive to the progressive worsening of environmental conditions from the estuary's opening towards the innermost parts of the bay, but *C. spinosus* uses different ecological domains of this water body. The environmental, biotic and abiotic conditions within the bay during the 2 years examined in this study were extremely favourable to *C. spinosus* and permitted their interaction with a tropical estuarine complex in a form never before reported. Aside from the complex hydrobiological dynamics already expected for an estuary of its size, the current state of the bay reflects centuries of human interference. Therefore, the relative importance of the species most sensitive to pollution and fishing pressure will decrease within the estuarine ichthyofauna over time. By contrast, robust, resilient and commercially unimportant fishes, such as the species of Tetraodontiformes identified in this study, particularly *C. spinosus*, will begin to dominate these communities. This trend is indicative of an imbalance in ecosystem dynamics.

The diagnosis of the causes and consequences of a phenomenon such as the population explosion of a species of Diodontidae in an estuarine environment requires further study. Data concerning Tetraodontiformes in ichthyofaunal studies are usually limited to checklists. Their low abundance and lack of commercial interest rarely inspire studies of this morphologically unique order. However, the diversity of relationships between these fishes and the estuarine environment, as well as the range of uses demonstrated by a single guild, indicates that the group has great ecological potential. The lack of studies of the tropical estuaries of the Brazilian and South American coast in general, as demonstrated by Blaber (2013), hinders an understanding of the complex interactions between these systems.

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