# Local and regional ecological drivers of fish assemblages in Brazilian estuaries

**Ciro C. Vilar[1],\*, Jean-Christophe Joyeux[2], Tommaso Giarrizzo[3], Henry L. Spach[1], João P. Vieira[4], Teodoro Vaske-Junior[5,6]**

[1]Laboratório de Ecologia de Peixes, Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Sul, Pontal do Paraná, Paraná 83255-976, Brazil

[2]Laboratório de Ictiologia, Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Goiabeiras, Vitória, Espírito Santo 29075-910, Brazil

[3]Laboratório de Biologia Pesqueira e Manejo de Recursos Aquáticos, Universidade Federal do Pará, Terra Firme, Belém, Pará 66040-170, Brazil

[4]Laboratório de Ictiologia, Departamento de Oceanografia, Universidade Federal do Rio Grande, Rio Grande, Rio Grande do Sul 96201-900, Brazil

[5]Universidade Federal Rural de Pernambuco, Dois Irmão, Recife, Pernambuco 52171-900, Brazil

[6]*Present address:* Laboratório de Elasmobrânquios, Universidade Estadual Paulista Júlio de Mesquita Filho, Parque Bitaru, São Vicente, São Paulo 11330-900, Brazil

ABSTRACT: Spatial patterns in assemblage structures are generated by ecological processes that occur on multiple scales. Identifying these processes is important for the prediction of impact, for restoration and for conservation of biodiversity. This study used a hierarchical sampling design to quantify variations in assemblage structures of Brazilian estuarine fish across 2 spatial scales and to reveal the ecological processes underlying the patterns observed. Eight areas separated by 0.7 to 25 km (local scale) were sampled in 5 estuaries separated by 970 to 6000 km (regional scale) along the coast, encompassing both tropical and subtropical regions. The assemblage structure varied significantly in terms of relative biomass and presence/absence of species on both scales, but the regional variation was greater than the local variation for either dataset. However, the 5 estuaries sampled segregated into 2 major groups largely congruent with the Brazilian and Argentinian biogeographic provinces. Three environmental variables (mean temperature of the coldest month, mangrove area and mean annual precipitation) and distance between estuaries explained 44.8 and 16.3%, respectively, of the regional-scale variability in the species relative biomass. At the local scale, the importance of environmental predictors for the spatial structure of the assemblages differed between estuarine systems. Overall, these results support the idea that on a regional scale, the composition of fish assemblages is simultaneously determined by environmental filters and species dispersal capacity, while on a local scale, the effect of environmental factors should vary depending on estuary-specific physical and hydrological characteristics.

KEY WORDS: Fish communities · Estuarine fish · Spatial patterns · Multi-scale · Atlantic Ocean · Brazil

## INTRODUCTION

Identifying patterns of species distribution and revealing their causes are among the central goals of ecology. Typically, the ecological processes underlying the distribution of organisms operate at specific scales, and together can generate variability between sites separated by only a few millimetres to thousands of kilometres (Levin 1992). For these reasons, ecologists have recognised that multi-scale

approaches are necessary for a comprehensive understanding of the spatial patterns of community organisation and the factors controlling them (Wiens 1989, Levin 1992, Azovsky 2000). Once the scale(s) is identified at which variation is highest, hypotheses about the factors possibly causing the observed patterns can be generated and tested (Levin 1992).

In estuaries, spatial variability in the composition of fish assemblages has been attributed to a number of variables that act in a hierarchy of scales. In a regional context, there is evidence that assemblage composition can be influenced by factors such as the latitudinal temperature gradient, the width of the estuary mouth, tidal amplitude, mangrove area and rainfall (Vieira & Musick 1994, Blaber 2000, Ley 2005, Harrison & Whitfield 2006, Sheaves & Johnston 2009). Another factor possibly working on a large scale is the distance between estuaries, which may reflect differences in the recruitment and dispersal of certain species (Sheaves & Johnston 2009). On a local scale, in contrast, spatial patterns in the ichthyofauna structure have often been related to changes in salinity, depth, dissolved oxygen, transparency and the distance from the point of connection to the sea (Araújo et al. 2002, Barletta et al. 2005, Chagas et al. 2006, Vilar et al. 2011).

Although Brazil's coastline extends for approximately 8000 km, ranging from macrotidal equatorial estuaries in the north to subtropical microtidal estuaries in the south, studies investigating the composition of its estuarine fish assemblages have traditionally been conducted on a local scale (e.g. Garcia et al. 2001, Araújo et al. 2002, Barletta et al. 2005, Vilar et al. 2011). Consequently, there is still a severe lack of information regarding the geographical distribution and particularly the abundance of fish species along this latitudinal gradient, which has hindered the understanding of the biogeographic patterns and ecological processes driving the assemblages.

The few biogeographical studies undertaken previously, however, have identified some regional distinctions in the estuarine ichthyofauna along the coast of the country. Based on a dendrogram of species presence/absence data obtained from the literature, Vieira & Musick (1994) separated the fauna of the western Atlantic into 3 groups. From this analysis, 2 faunal components were defined on the coast of Brazil: (1) 'tropical', represented by fauna captured in estuaries located between Colombia and northeastern Brazil (10°N–11°S), and (2) 'warm-temperate', which includes estuaries distributed between the States of São Paulo and Rio Grande do Sul (24–32°S). The groups found in this analysis corre-

sponded in part to the Brazilian and Argentinian biogeographical provinces proposed by Briggs (1995), whose transition area is located in Cabo Frio (22°S). However, Araújo & Costa de Azevedo (2001) observed that the fish of Lagoa dos Patos and other estuaries in the south of the country (near 32°S) were substantially different from those found in systems in the adjacent southeastern region (22–28°S). All these results, therefore, indicate the existence of factors that limit the geographical distribution of species, although the identity of these factors remains to be empirically investigated.

To address this issue, the present study used data collected by the authors as part of the project 'Use and Appropriation of Coastal Resources' ('Uso e Apropriação de Recursos Costeiros'—RECOS, in Portuguese) from coordinated sampling in 5 estuaries distributed along the Brazilian coast between latitudes 0° and 32°S (for details, see Lana et al. 2006). The ichthyofauna of these estuaries was collected using standardized fishing gear and a similar sampling protocol, which yielded comparable databases. Using standardized procedures allowed us to appropriately analyse the presence of spatially-distinct faunal components along this extensive latitudinal gradient; something that had been suggested in previous studies using presence/absence data collected with disparate sampling methods (see Vieira & Musick 1994, Araújo & Costa de Azevedo 2001).

Based on a comprehensive dataset, this study aimed to (1) identify biogeographic patterns in the composition of estuarine ichthyofauna along the Brazilian coast, (2) quantify and compare the magnitude of variation in the compositions of assemblages between the local (i.e. within the estuaries) and regional (i.e. between estuaries) scales and (3) analyse the relative importance of a set of environmental and spatial variables in structuring local and regional fish assemblages. More precisely, the geographic patterns were investigated based on the contributions of the main families to the total species richness and the biomass captured in each estuary, as well as through the identification of the major species responsible for similarities and differences in ichthyofaunal composition among the systems.

## MATERIALS AND METHODS

### Study area

Five permanently open estuaries distributed between the Amazon delta and the extreme southern

Brazilian coast were studied (from north to south): Curuçá, Santa Cruz, Piraquê-Açú, Paranaguá and Lagoa dos Patos (Fig. 1). These systems represent the main coastal morphoclimatic domains of the country; encompassing an equatorial macrotidal zone with one of the largest mangrove areas in the world in the north (Curuçá; Kjerfve & Lacerda 1993), to a subtropical microtidal area dominated by salt marshes in the south (Lagoa dos Patos; Costa et al. 1997). Along this area, 3 oceanographic currents are present (Fig. 1). The North Brazil Current influences the north and northeast regions and flows towards the Caribbean. The Brazil Current flows southward, carrying relatively warm water to most of the coast. The Malvinas Current brings cold water from the temperate region to southern/southeastern Brazil (Peterson & Stramma 1991, Campos et al. 1996).

Geomorphologically, the estuaries sampled can be divided into 4 types: (1) drowned river valleys, formed by 2 channels that come together before flowing into the sea, with the mouth width relatively greater than the headwaters (e.g. Curuçá and Piraquê-Açú); (2) tectonic, originating from the flooding of a fault in the earth's surface, where the contribution of continental water is relatively small (e.g. Santa Cruz); (3) embayment, which is composed of several sub-estuaries, surrounded by a coastal plain that extends 50 km inland to the base of the Serra do Mar mountain range (e.g. Paranaguá); and (4) coastal lagoon, dominated by shallow areas, oriented parallel to the coast and connected to the ocean by a single channel (e.g. Lagoa dos Patos). The substrate in these estuaries is composed primarily of sand and mud, with the presence of some scattered rock formations. Additionally, extensive seagrass meadows occur within the Santa Cruz estuary (Medeiros et al. 2001). Impacts resulting from fishing and other anthropogenic activities such as recreational use, partial urbanisation of margins and release of untreated sewage, occur in all systems. For each estuary, other environmental information is shown in Table 1.

## Data acquisition

### Ichthyofauna

Between April 2003 and July 2004, 40 areas, separated by 0.7 to 25 km (local scale) were sampled in the subtidal of 5 estuaries (8 areas in each estuary). These estuaries were separated by 970 to 6000 km (regional scale) along the Brazilian coast, covering tropical (Curuçá, Santa Cruz and Piraquê-Açú) and subtropical (Paranaguá and Lagoa dos Patos) regions. The sampling areas were chosen to represent a large gradient of environmental conditions within these systems. The straight-line distance among them ranged between 1.5 and 8 km at Curuçá, 0.7 and 10 km at Santa Cruz, 1 and 6 km at Piraquê-Açú, 2 and 25 km at Paranaguá and 1.3 and 14 km at Lagoa dos Patos. In each area, 1 (at Santa Cruz) or 2 (in the other estuaries) samples were collected during each sampling occasion. An otter trawl (10.43 m footrope and 8.62 m headrope, with 13 and 5 mm mesh-size in the body and in the cod-end, respectively) was towed by a boat for 4 to 15 min to collect fish. Captured individuals were kept on ice and subsequently identified and weighed (wet weight in g) in the laboratory. All estuaries were sampled during the day (06:30 h to 18:00 h) in neap tides using the same fishing equipment. Sampling occurred monthly in Piraquê-Açú (for 13 mo, n = 204), bimonthly in Curuçá (7 sampling periods, n = 111), in Lagoa dos Patos (7 sampling periods, n = 112) and in Paranaguá (6 sampling periods, n = 91), and seasonally in Santa Cruz (4 sampling periods, n = 31), resulting in a database with 549 samples.
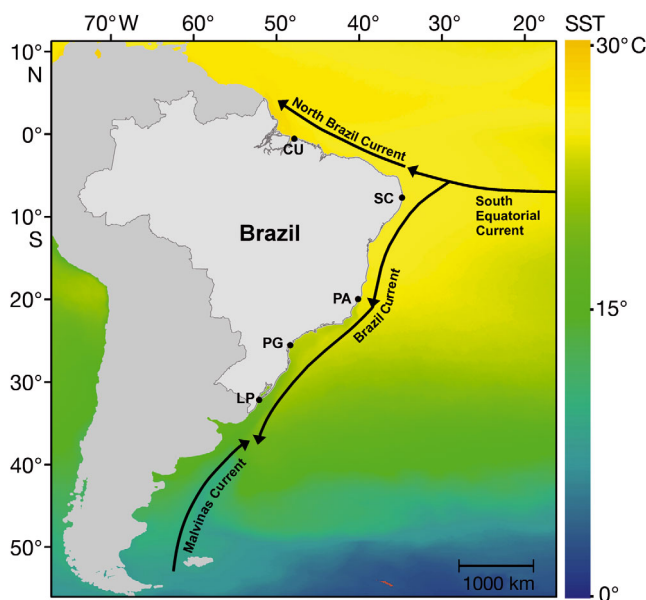


Fig. 1. Location of the 5 sampled estuaries, sea surface temperature (average from 2003 to 2007 with 0.05 degree resolution; MODIS Aqua Level-3) and the major superficial currents (modified from Peterson & Stramma 1991) influencing the Brazilian coast. CU: Curuçá; SC: Santa Cruz; PA: Piraquê-Açú; PG: Paranaguá; LP: Lagoa dos Patos

Table 1. Local- and regional-scale environmental variables measured or obtained from the literature for each estuary. Values of local variables correspond to the means (min.–max.); '–' indicates variables were not measured

| | Curuçá 0° 33′ S, 47° 50′ W | Santa Cruz 7° 41′ S, 34° 50′ W | Piraquê-Açú 19° 57′ S, 40° 09′ W | Paranaguá 25° 32′ S, 48° 20′ W | Lagoa dos Patos 32° 09′ S, 52° 05′ W |
|---|---|---|---|---|---|
| **Local-scale variables** | | | | | |
| Salinity | 17.4 (6.1–40.8) | 29.4 (24.7–35) | 28.4 (0.4–37.9) | 25.5 (20.5–29.5) | 5.7 (0–19.4) |
| Water temperature (°C) | 26.3 (20.6–31) | 28.7 (27.2–30) | 25.7 (22.5–29.7) | 23.6 (17.8–29.2) | 19.5 (11–25) |
| Dissolved oxygen (mg l$^{-1}$) | 5.4 (3.3–8.4) | – | – | – | – |
| Secchi transparency (m) | – | 1.7 (1.2–2.8) | – | 1.9 (1.1–3.6) | 0.6 (0.15–1.5) |
| Depth (m) | 3.7 (2–7.5) | 4.4 (1.5–6.6) | 5.1 (1.3–11) | 4.8 (2.5–7.7) | – |
| Distance from estuary mouth (km) | 14.7 (11.5–18.8) | 5.6 (1.5–8.7) | 5.4 (2.6–8.8) | 17.4 (9.8–23) | 22.3 (12.9–30.9) |
| **Regional-scale variables** | | | | | |
| Mean annual water temperature (°C) | 26.3 | 28.2[a] | 25.7 | 23.6 | 19.5 |
| Mean water temperature in the coldest month (°C) | 21 | 26.8[a] | 23.2 | 18.3 | 11.2 |
| Tidal range (m)[b] | 4.7 | 2.2 | 1.5 | 1.8 | 0.4 |
| Mouth width (m) | 4465 | 2759 | 291 | 5616 | 588 |
| Estuary area (km$^2$) | 200[c] | 824[a] | 5.1[d] | 551.8[e] | 10360[f] |
| Mangrove area (km$^2$) | 116[c] | 28.1[a] | 12.3[d] | 295[e] | 0[g] |
| Mean annual precipitation (mm)[h] | 2526 | 2394 | 1250 | 2500 | 1300 |
| Distance between estuaries (km) | 0 | 1845 | 3445 | 4742 | 6000 |

Sources: [a]Medeiros et al. (2001), [b]Brazilian Navy Hydrographic and Navigation Directorate (www.mar.mil.br/dhn/chm/tabuas/index.htm), [c]Giarrizzo & Krumme (2007), [d]Barroso (2004), [e]Noernberg et al. (2004), [f]Garcia et al. (2001), [g]Kjerfve & Lacerda (1993), [h]National Agency of Waters (hidroweb.ana.gov.br/). For the other variables/regions, see 'Materials and methods'

Only the taxa identified to the species level and whose natural ranges included the Brazilian coast were considered in subsequent analyses. The taxa included in this study as *Stellifer* sp. and *Mugil* sp. refers to species that are distinct from their congeners but yet undescribed (Menezes et al. 2003). The taxonomic classification and species nomenclature follows Eschmeyer (2011).

### Local-scale predictors of assemblages

Five environmental parameters were tested as local-scale predictors of fish assemblages (Table 1). The over-water distance from each sampling area to the mouth of the estuary was determined using a Geographic Information System (GIS; Google Earth). The other variables were measured before each trawl (at Piraquê-Açú and Paranaguá) or immediately after the first trawl within each area (at Curuçá, Santa Cruz and Lagoa dos Patos) on each sampling trip; exceptions were depth at Curuçá (measured at the beginning and end of each trawl) and Paranaguá (measured at each minute of trawling). Where multiple readings were taken, the mean of each variable per area was used in the analysis.

### Regional-scale predictors of assemblages

Eight variables describing the spatial relationships between estuaries (i.e. distance) as well as the physiographic and hydrological characteristics were obtained for each estuary (Table 1). Four of these variables (mangrove area, mean annual precipitation, tidal amplitude and estuary area) were taken from the literature (presented in Table 1), while 2 variables (width of estuary mouth and distance between estuaries) were measured using satellite images and GIS. An additional 2 variables (mean and minimum water temperature) were obtained from the literature (for Santa Cruz) or obtained during field collections (other estuaries). The distance between estuaries was measured from Curuçá by following the coastline without considering the indentations, to represent the shortest possible distance between any 2 locations. The width of the estuary mouth was obtained from the shortest distance between the margin edges at the point where one or both of them turn and follow the direction of the coast. In estuaries with more than one connection to the sea (i.e. Curuçá, Santa Cruz and Paranaguá), the sum of the widths of all connections was used. The mean annual precipitation data obtained from the

literature for the drainage basin of each estuary covered a time series ≥10 yr.

## Data analysis

Initially, data were standardized to avoid potential problems associated with differences in trawl duration (4 to 15 min). Standardized values were calculated by dividing the biomass of each fish species in a given sample by the total biomass captured in that sample (×100; hereafter relative biomass). Relative biomass data were square-root transformed, recoded as presence/absence and analysed using PRIMER v6 (Clarke & Warwick 2001) and the PERMANOVA+ add-on package (Anderson et al. 2008). Square-root transformed biomass data reveal patterns of both the most and intermediately abundant species, as they tend to have larger quantitative differences between samples. On the other hand, presence/absence data tend to emphasize the rare species, as the abundant species tend to occur in a large number of samples and contribute little to the differentiation of the assemblages (Clarke & Warwick 2001).

Geographic patterns of similarity were analysed from the means of transformed relative biomass and the presence/absence data of each species per site using the Bray-Curtis and Sørensen indices, respectively. The resulting similarity matrices were subjected to hierarchical cluster analysis using the unweighted pair-group average (UPGMA). Similarity profile tests (SIMPROF) were performed to investigate the significance of groupings in each cluster analysis (Clarke et al. 2008). This test compares a true similarity profile calculated by ranking the similarity matrix with a mean profile created by permuting the values of each species among the samples (here estuaries) and recalculating the profile repeatedly. A statistic (π) is then calculated as the deviation of the real profile from the mean permuted profile. The observed value of π is compared with its null distribution generated by permutations to determine significance (Clarke et al. 2008).

Spatial differences in the relative biomass and the presence/absence of species were tested using a permutational multivariate ANOVA (PERMANOVA; Anderson et al. 2008), considering the estuaries (5 levels, fixed) and areas (8 levels, random, nested within estuaries) as factors. The components of variation for each term included in the analyses were also calculated to quantify the variation in assemblage composition within- and between-estuaries. *A poste-*

*riori* paired comparisons were performed with distance-based permutational *t*-tests (Anderson et al. 2008) using similarity matrices built from all samples (n = 542 after exclusion of 7 samples with zero individuals from Lagoa dos Patos). Significance levels were determined from 4999 permutations of residuals under a reduced model for each term analysed (Anderson 2001). PERMANOVA and permutational *t*-test were applied in the present study because they can handle unbalanced sampling designs (Anderson et al. 2008).

When paired *t*-test detected significant differences in assemblage composition between estuaries, a similarity percentages analysis (SIMPER) was performed on the relative biomass data to identify the species contributing most to within-estuaries similarity (i.e. characteristic species) and between-estuaries dissimilarity (i.e. discriminating species; Clarke and Warwick 2001). Non-metric multidimensional scaling (nMDS) was used to visualise the variability of assemblages, considering both the transformed relative biomass (using Bray-Curtis) and the presence/absence data (using Sørensen).

To test whether changes in assemblage structure between the estuaries were correlated with the regional-scale predictors, distance-based linear models (DistLM; Anderson et al. 2008) were applied using 2 sets of analyses: conditional test with forward selection, in which the predictor variable with the greatest coefficient of determination is selected first, followed by the variable with the greatest coefficient after inclusion of the first (i.e. partial $r^2$), and so on, until it is no longer possible to increase the total variance explained by the model (i.e. $R^2$); and the marginal test, in which the variance explained by each variable is calculated independently of the others, as in a simple regression (i.e. $r^2$). When 2 predictors were redundant (i.e. Spearman correlation > 0.8), only the most explicative was considered in the conditional tests.

The relationship between the site-averaged relative biomass data and the local-scale predictors was analysed independently for each estuary on each sampling occasion using DistLM. As the tests were repeated separately for each sampling occasion, the spatial 'effect' (if any) of environmental variables on the local distribution of the species was isolated, and any effect related to the assemblage differences between sampling occasions for a given sampling area (i.e. temporal effect) was discarded. To determine the relative importance of each predictor, an approach based on 2 complementary metrics was adopted: (1) the coefficients of determination ($r^2$) of

the predictors when modelled separately in DistLM marginal tests (described above) and (2) the prevalence, defined as the proportion of times a given predictor was significantly correlated (i.e. $p \le 0.05$) with the spatial structure of the assemblages relative to the total number of times it had been tested. The first measure provides information regarding the magnitude of the relationship between environmental variables and the spatial structure of the fish assemblages, while the second indicates whether the frequency of that relationship was stronger than expected by chance. These analyses were conducted for 4 of the 5 estuaries sampled; Santa Cruz was not included due to the lack of local abiotic data for some of the sampling events. The conditional test was also used to model the total variance explained by the local-scale environmental variables, when they were analysed together. DistLM tests were based on log-transformed predictor variables, Bray-Curtis similarity and 999 permutations (Anderson et al. 2008).

Finally, a one-way nonparametric ANOVA (np-ANOVA) was applied to compare the $r^2$ values between the local-scale predictors, considering each estuary separately. These analyses were performed with matrices of the Euclidean distances between the coefficients of determination of each variable, using the same procedures as described above for PERM-ANOVA. As all DistLM analyses to test the effect of the local-scale predictors were performed on an equal number of observations (n = 8 areas per estuary), no correction of the coefficient of determination was necessary.

## RESULTS

### Assemblage composition along the coast

Samples collected in the 5 estuaries along the Brazilian coast yielded 646 kg of fish, which represented 184 species belonging to 118 genera and 56 families (listed in Table S1 in the Supplement at www.int-res.com/articles/suppl/m485p181_supp.pdf). At all sites except Santa Cruz, the species accumulation curve tends to stabilize, suggesting that the sampling effort was adequate for the characterisation of most assemblages (Fig. S1 in the Supplement). Overall, Sciaenidae had the greatest richness (22 species), followed by Engraulidae (13), Ariidae (10), Carangidae (10), Achiridae, Gobiidae and Paralichthyidae (8 each). Ariidae provided most of the total biomass (32.5%), followed by Sciaenidae (12.8%), Tetraodontidae (11.7%), Achiridae (7.4%), Diodontidae (6.9%),

Gerreidae (3.6%) and Lutjanidae (3.6%). The total number of species recorded ranged from 82 in Piraquê-Açú to 37 in Lagoa dos Patos. More than half of the species (53.8%; 99) occurred only in a single estuary, and a small proportion (8.7%; 16) occurred in 4 estuaries (none occurred in all 5 estuaries). The only locally endemic species was *Parapimelodus nigribarbis*, which occurs only in the basin of Lagoa dos Patos.

The most representative species in terms of biomass differed between estuaries, and several of these were exclusive to one estuary (Fig. 2). In Curuçá, for example, *Cathorops agassizii* (17.6%), *Stellifer naso* (15.2%) and *Sciades herzbergii* (7.3%) were among the 5 dominant species in terms of biomass, but were not captured anywhere else. Similarly, *Bagre marinus* (18%) had the highest contribution in Santa Cruz and was absent in the other estuaries, as well as 3 of the 4 species with the greatest biomass percentages in Lagoa dos Patos (i.e. *Geophagus brasiliensis*, *Hoplias malabaricus* and *Paralichthys orbignyanus*). In contrast, *Cathorops spixii* had the third highest contribution in Curuçá (9.1% of total biomass) and ranked first in Paranaguá (42.6%). *Chilomycterus spinosus* (26.1%), *Sphoeroides testudineus* (18.2%), *Lutjanus synagris* (6.8%) and *Achirus declivis* (5.5%) were dominant in Piraquê-Açú, while *Genidens genidens* (20.0%), *Pomadasys corvinaeformis* (5.8%) and *Chaetodipterus faber* (5.1%) dominated in Paranaguá. Species that exhibited a geographic consistence in abundance include *Colomesus psittacus* in northern estuaries (7.7% in Curuçá and 11.4% in Santa Cruz) and *G. genidens* in southern estuaries (20.0% in Paranaguá and 5.3% in Lagoa dos Patos) (Fig. 2). The proportion of total biomass represented by the dominant species increased southward from about 18% in Curuçá and Santa Cruz to 44.2% in Lagoa do Patos (Fig. 2).

In all locations, Sciaenidae (together with Gerreidae in Lagoa dos Patos) was the most species-rich family (Fig. 3). For Achiridae and Engraulidae, the number of species decreased progressively from

Fig. 2. Regional variation in the relative biomass of the most abundant fish species caught in 5 estuaries on the Brazilian coast: Curuçá (CU), Santa Cruz (SC), Piraquê-Açú (PA), Paranaguá (PG) and Lagoa dos Patos (LP). The diameter of the circle is proportional to the species' percentage contribution to total biomass captured in each estuary. The percentage value of the most abundant species in each estuary is presented for comparative purpose. ●: contributes ≤1% of the total biomass captured in each estuary; (+) present but not captured; (–) absent
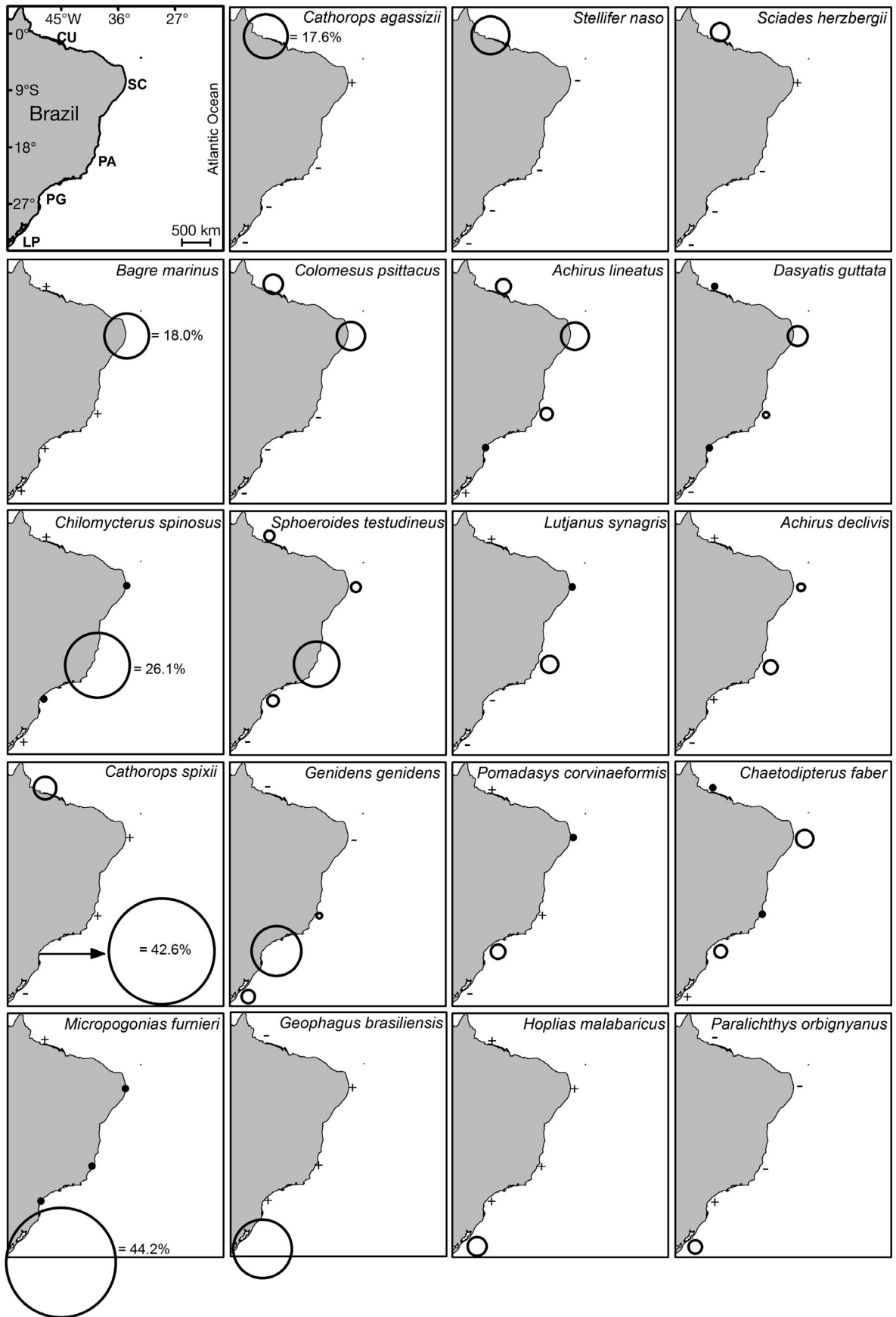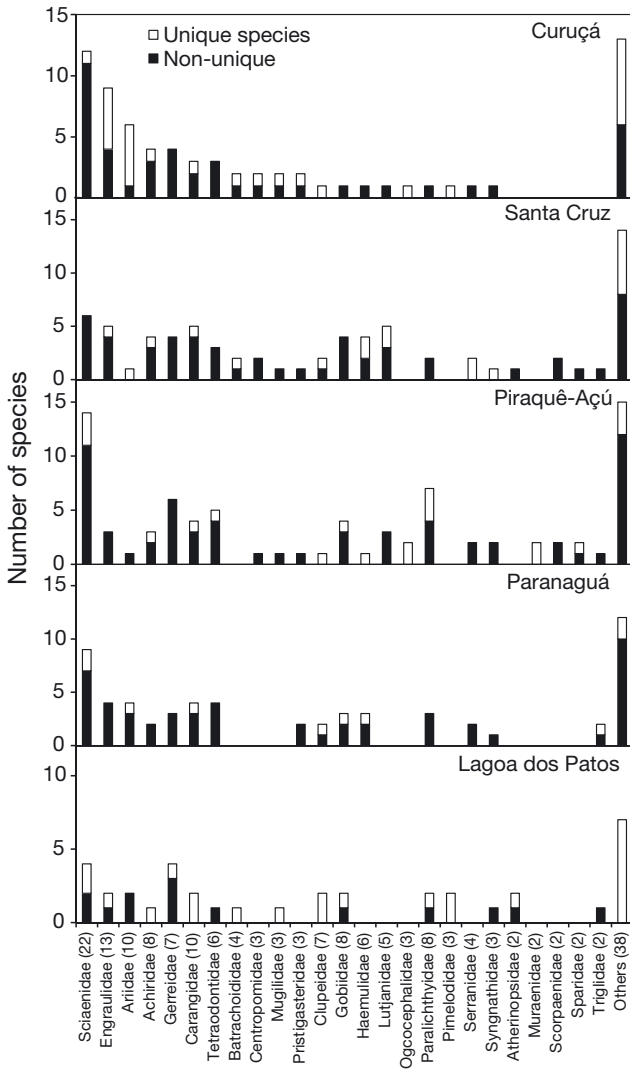
Fig. 3. Regional distribution of the number of fish species for the richest (≥2 species) families in each estuary, with the total number of species belonging to each family shown in parentheses. The species are divided into unique species (occurring in only one estuary) and non-unique species (occurring in more than one estuary)
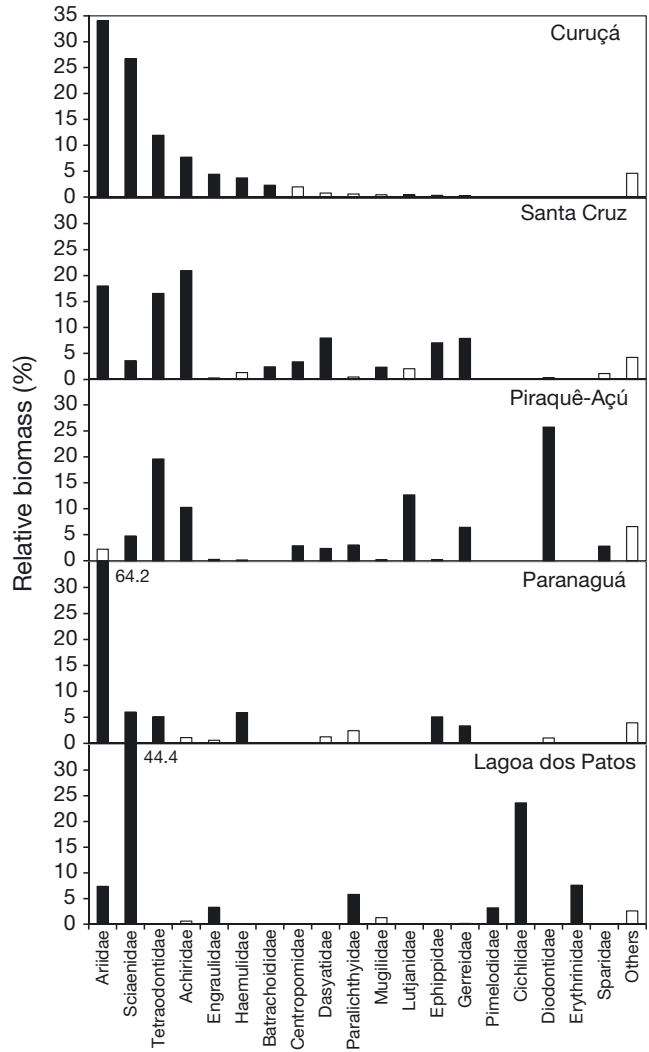


Fig. 4. Regional variations in the relative biomass of fish families in each estuary. Black bars: those families collectively responsible for ca. 90% of the total biomass caught in each system; white bars: less important families

north to south, while Lutjanidae occurred only in the estuaries north of Paranaguá and was particularly rich in Santa Cruz (5 species). Paralichthyidae had the highest number of species in Piraquê-Açú (7), located in the centre of the Brazilian coast, with species richness gradually decreasing towards the estuaries present at either end of the coast (Fig. 3).

In terms of relative biomass, Sciaenidae was again important in all estuaries, being among the 7 families with the largest contributions. The capture of Sciaenidae varied from 44.4% of the total biomass in Lagoa dos Patos to 3.6% in Santa Cruz (Fig. 4). Addi-

tionally, Ariidae contributed greatly to the fauna captured to the north (Curuçá and Santa Cruz) and south (Paranaguá and Lagoa dos Patos) of Piraquê-Açú, where they contributed only 2.2% of the total biomass. The highest percent biomass for Achiridae occurred in tropical estuaries, where their contributions reached 7.7% in Curuçá, 21.0% in Santa Cruz and 10.2% in Piraquê-Açú. In contrast, other relatively important families at Lagoa dos Patos, such as Cichlidae (23.6%), Erythrinidae (7.6%) and Pimelodidae (3.2%), were missing or not representative in other locations (Fig. 4).

The cluster analyses based on relative biomass and presence/absence of species aggregated 4 estuaries (Curuçá, Santa Cruz, Piraquê-Açú and Paranaguá)

into a group well differentiated from the estuary located further south (Lagoa dos Patos), with the division occurring at a level of similarity of 5.1% and 14.9%, respectively (Fig. 5). The Santa Cruz, Piraquê-Açú and Paranaguá estuaries formed a subgroup separated at the 36.6% similarity level from Curuçá, but only in the analysis considering presence/absence. All these clusters were significant (SIMPROF; Fig. 5). The true similarity profile calculated from the 5 estuaries differed markedly from the mean permuted profile for both relative biomass ($\pi$ = 8.4, p = 0.001) and presence/absence ($\pi$ = 5.9, p = 0.001). In the presence/absence analysis, however, the subgroup was separated from Curuçá by only $\pi$ = 2.5 (p = 0.042).

In the SIMPER analysis, *Achirus lineatus* ranked in the top 8 most important species for fauna characterisation at all sites with the exception of Lagoa dos Patos (where it was absent), with a particularly high contribution in the 3 northern estuaries (Curuçá, Santa Cruz and Piraquê-Açú; Table 2). Of the remaining species, *Stellifer naso*, *Cathorops agassizii* and *Cathorops spixii* contributed the most to the characterisation of the fauna of Curuçá, while *Diap-*
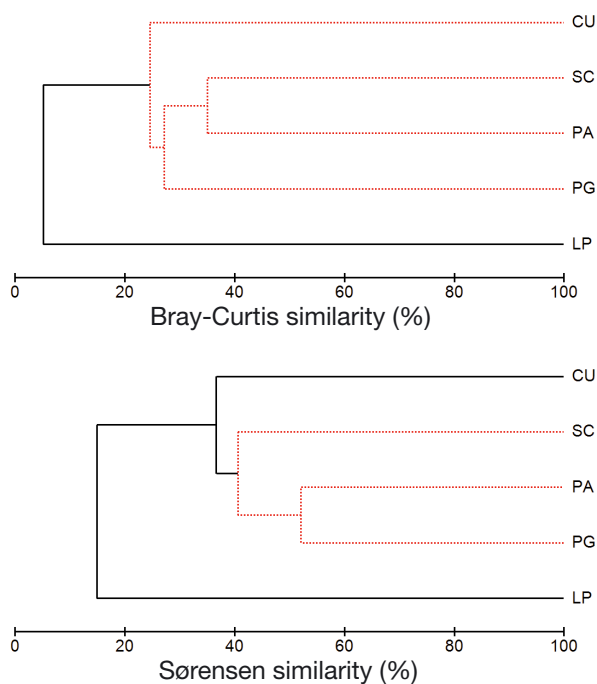


Fig. 5. Hierarchical cluster analysis derived from the Bray-Curtis similarity of square-root transformed relative biomass data (above) and the Sørensen similarity of presence/absence data (below) of fish species collected at 5 estuaries along the Brazilian coast. Significant groups (p < 0.05) determined by similarity profile test (SIMPROF) are indicated by black lines. Estuaries labelled according to Fig. 1

*terus auratus*, *Bagre marinus*, *Chaetodipterus faber* and *Symphurus plagusia* were typical of Santa Cruz. Other species, such as *Chilomycterus spinosus*, *Lutjanus synagris* and *Sphoeroides testudineus*, had relatively high biomass at Piraquê-Açú and were the most important in the characterisation of the fauna at this estuary. The species characterizing Paranaguá were *Genidens genidens*, *Eucinostomus argenteus*, *C. spixii* and *Etropus crossotus*, and those typical of Lagoa dos Patos were *Micropogonias furnieri*, *Lycengraulis grossidens* and *Geophagus brasiliensis* (Table 2).

## Comparison of local and regional variability

Relative biomass and presence/absence data were significantly different among estuaries (PERM-ANOVA for relative biomass: pseudo-$F_{4,503}$ = 22.8, p < 0.001; presence/absence: pseudo-$F_{4,503}$ = 28.8, p < 0.001) and between areas within them (relative biomass: pseudo-$F_{35,503}$ = 2.5, p < 0.001; presence/absence: pseudo-$F_{35,503}$ = 2.6, p < 0.001). However, the components of variation showed that for both data sets, these differences were much greater at the regional scale (mean relative biomass dissimilarity: 38.5%; mean presence/absence dissimilarity: 41.0%) than at the local scale (17.8%; 17.0%). Paired *t*-tests indicated that all estuaries differed significantly for both the quantitative and qualitative data (p < 0.001 in all tests).

These results were supported by the nMDS ordinations made with the relative biomass and presence/absence. In both analyses, the points representing the assemblages of the 8 sampled areas for each location were primarily distributed in accordance with the estuaries and, secondarily, according to the location inside each of them (Fig. 6). The only exceptions were 2 Santa Cruz points which formed a separate group in the presence/absence analysis. However, this group was strongly influenced by relatively low species richness in these areas (12 species), which resulted in a high Sørensen similarity (40%) even with only 3 shared species. There was no overlap among the assemblages of the 5 estuaries in ordination plots (Fig. 6). The Lagoa dos Patos assemblage was the most distinct compared to all of the other estuaries, remaining relatively isolated.

The most important species to discriminate the assemblage of Curuçá from those of other estuaries were *Stellifer naso* and *Cathorops agassizii* (Table 3). *Achirus lineatus* and *Bagre marinus* ranked among the top 3 discriminator species of Santa Cruz in all

Table 2. Species contributing most to within-estuaries similarity according to the similarity percentages analysis (SIMPER) based on relative biomass data. The percentage of the contribution for the within-estuaries similarity and the rank (superscript number) of each species are also shown

| Species | Curuçá | Santa Cruz | Piraquê-Açú | Para-naguá | Lagoa dos Patos |
|---|---|---|---|---|---|
| *Stellifer naso* | $22.42^1$ | | | | |
| *Cathorops agassizii* | $16.92^2$ | | | | |
| *Achirus lineatus* | $7.65^3$ | $18.89^1$ | $7.73^4$ | $5.41^8$ | |
| *Cathorops spixii* | $7.53^4$ | | | $10.72^3$ | |
| *Stellifer rastrifer* | $6.54^5$ | | | | |
| *Genyatremus luteus* | $6.14^6$ | | | | |
| *Colomesus psittacus* | $5.46^7$ | $4.13^8$ | | | |
| *Sphoeroides testudineus* | $4.98^8$ | $2.07^{12}$ | $16.16^3$ | $7.72^6$ | |
| *Sciades herzbergii* | $4.67^9$ | | | | |
| *Symphurus plagusia* | $3.43^{10}$ | $8.28^5$ | | | |
| *Lycengraulis grossidens* | $1.9^{11}$ | | | | $12.72^2$ |
| *Batrachoides surinamensis* | $1.47^{12}$ | | | | |
| *Citharichthys spilopterus* | $1.41^{13}$ | | | | |
| *Diapterus auratus* | | $15.47^2$ | $1.71^7$ | | |
| *Bagre marinus* | | $9.58^3$ | | | |
| *Chaetodipterus faber* | | $9.13^4$ | | $8.39^5$ | |
| *Bairdiella ronchus* | | $7.67^6$ | | | |
| *Achirus achirus* | | $6.72^7$ | | | |
| *Diapterus rhombeus* | | $2.97^9$ | $1.3^{10}$ | | |
| *Sphoeroides greeleyi* | | $2.68^{10}$ | $2.92^6$ | | |
| *Achirus declivis* | | $2.44^{11}$ | $5.31^5$ | | |
| *Chilomycterus spinosus* | | | $36.56^1$ | | |
| *Lutjanus synagris* | | | $16.39^2$ | | |
| *Symphurus tesselatus* | | | $1.61^8$ | | |
| *Eucinostomus gula* | | | $1.44^9$ | | |
| *Genidens genidens* | | | | $25.37^1$ | |
| *Eucinostomus argenteus* | | | | $11.2^2$ | |
| *Etropus crossotus* | | | | $9.93^4$ | |
| *Menticirrhus americanus* | | | | $5.47^7$ | |
| *Diplectrum radiale* | | | | $4.53^9$ | |
| *Pomadasys corvinaeformis* | | | | $1.93^{10}$ | |
| *Micropogonias furnieri* | | | | | $73.43^1$ |
| *Geophagus brasiliensis* | | | | | $5.03^3$ |

relative species biomass (e.g. p = 0.001 in the marginal tests). Among them, the mean temperature of water in the coldest month explained most of the variability in assemblage structure (22.8%), and the width of the estuary mouth had the lowest explanation (17%; Fig. 7). The model constructed using the forward procedure identified 4 factors that were significantly related to variability in the biotic data (i.e. mean temperature of the coldest month, distance between estuaries, mangrove area and mean annual precipitation), explaining together 61.2% of the total variance. The variables with the largest contributions in the model were the mean temperature of water in the coldest month and distance between estuaries, which explained 22.8% and 16.3% of the variance in relative species biomass, respectively (Fig. 7).

## Local determinants of assemblages

No significant differences were detected between the coefficients of determination of the explanatory variables in any estuary (Table 4). However, based on the percentage of DistLM tests with significant results (i.e. prevalence), the most important variables were salinity, distance from estuary mouth (DEM) and temperature (each with 28% of tests significant) in Curuçá; depth and temperature (both with 25%) in Piraquê-Açú; salinity (33%), DEM and depth (both with 16.6%) in Paranaguá; and DEM (42.8%) and transparency (25%) in Lagoa dos Patos (Table 4). The best models obtained by the forward conditional tests explained between 95.2% (in Curuçá) and 65.1% (in Piraquê-Açú) of the total variability in the relative biomass of the species (Table 4). These results support the hypothesis that all variables analysed are potential drivers of the spatial structures of fish assemblages and also highlight clear changes in their relative importance between estuaries.

paired SIMPER comparisons, whereas the major contributions to differentiate the fauna of Piraquê-Açú came from *Chilomycterus spinosus* and *Sphoeroides testudineus*. *Genidens genidens* and *Cathorops spixii* had the greatest contribution to distinguish the assemblage of Paranaguá from that of other estuaries, and *Micropogonias furnieri* and *Lycengraulis grossidens* to distinguish the fauna of Lagoa dos Patos.

### Regional determinants of assemblages

When tested separately, all 8 predictor variables were significantly related to the regional variation in

Table 3. Species contributing most to between-estuaries dissimilarity according to the similarity percentages analysis (SIMPER) based on relative biomass data. Species are listed in decreasing order of their contribution to distinguish the estuary at the top of column from the others

| | Curuçá (CU) | Santa Cruz (SC) | Piraquê-Açú (PA) | Paranaguá (PG) | Lagoa dos Patos (LP) |
|---|---|---|---|---|---|
| **CU** | | *Achirus lineatus*<br>*Bagre marinus*<br>*Diapterus auratus*<br>*Chaetodipterus faber*<br>*Achirus achirus* | *Chilomycterus spinosus*<br>*Sphoeroides testudineus*<br>*Lutjanus synagris*<br>*Achirus declivis*<br>*Lutjanus jocu* | *Genidens genidens*<br>*Cathorops spixii*<br>*Sphoeroides testudineus*<br>*Chaetodipterus faber*<br>*Eucinostomus argenteus* | *Micropogonias furnieri*<br>*Lycengraulis grossidens*<br>*Citharichthys spilopterus*<br>*Geophagus brasiliensis*<br>*Parapimelodus nigribarbis* |
| **SC** | *Stellifer naso*<br>*Cathorops agassizii*<br>*Colomesus psittacus*<br>*Cathorops spixii*<br>*Sphoeroides testudineus* | | *Chilomycterus spinosus*<br>*Sphoeroides testudineus*<br>*Lutjanus synagris*<br>*Achirus declivis*<br>*Sphoeroides greeleyi* | *Genidens genidens*<br>*Sphoeroides testudineus*<br>*Cathorops spixii*<br>*Eucinostomus argenteus*<br>*Etropus crossotus* | *Micropogonias furnieri*<br>*Lycengraulis grossidens*<br>*Geophagus brasiliensis*<br>*Citharichthys spilopterus*<br>*Parapimelodus nigribarbis* |
| **PA** | *Stellifer naso*<br>*Cathorops agassizii*<br>*Achirus lineatus*<br>*Cathorops spixii*<br>*Stellifer rastrifer* | *Achirus lineatus*<br>*Bagre marinus*<br>*Diapterus auratus*<br>*Chaetodipterus faber*<br>*Bairdiella ronchus* | | *Genidens genidens*<br>*Cathorops spixii*<br>*Eucinostomus argenteus*<br>*Chaetodipterus faber*<br>*Etropus crossotus* | *Micropogonias furnieri*<br>*Lycengraulis grossidens*<br>*Geophagus brasiliensis*<br>*Citharichthys spilopterus*<br>*Parapimelodus nigribarbis* |
| **PG** | *Stellifer naso*<br>*Cathorops agassizii*<br>*Achirus lineatus*<br>*Stellifer rastrifer*<br>*Colomesus psittacus* | *Achirus lineatus*<br>*Chaetodipterus faber*<br>*Bagre marinus*<br>*Diapterus auratus*<br>*Bairdiella ronchus* | *Chilomycterus spinosus*<br>*Sphoeroides testudineus*<br>*Lutjanus synagris*<br>*Achirus lineatus*<br>*Achirus declivis* | | *Micropogonias furnieri*<br>*Lycengraulis grossidens*<br>*Geophagus brasiliensis*<br>*Citharichthys spilopterus*<br>*Parapimelodus nigribarbis* |
| **LP** | *Stellifer naso*<br>*Cathorops agassizii*<br>*Cathorops spixii*<br>*Achirus lineatus*<br>*Colomesus psittacus* | *Achirus lineatus*<br>*Bagre marinus*<br>*Diapterus auratus*<br>*Chaetodipterus faber*<br>*Bairdiella ronchus* | *Chilomycterus spinosus*<br>*Sphoeroides testudineus*<br>*Lutjanus synagris*<br>*Achirus lineatus*<br>*Achirus declivis* | *Genidens genidens*<br>*Cathorops spixii*<br>*Eucinostomus argenteus*<br>*Chaetodipterus faber*<br>*Sphoeroides testudineus* | |

## DISCUSSION

### Biogeographic patterns

Some biogeographic patterns emerged from the comparisons of fauna captured in the estuaries spread over ~6000 km along the Brazilian coast. These patterns are clearly observed when the occurrences, relative biomasses and/or species richness of some families are compared. For example, Batrachoididae, Achiridae, Centropomidae and Lutjanidae were richer and more abundant in tropical estuaries (Curuçá, Santa Cruz and Piraquê-Açú) than in the subtropics (Paranaguá and Lagoa dos Patos; Figs. 3 & 4). In contrast, the relative biomass of Paralichthyidae contributed more to the assemblage at Lagoa dos Patos (32° S) (Fig. 4), mainly owing to the capture of a temperate-affinity species (*Paralichthys orbignyanus*). Diodontidae, represented solely by *Chilomycterus spinosus* in this study, was abundant only in Piraquê-Açú (Fig. 4), where 92% of its total biomass was captured. Although this species was not among the most abundant in the inner-portion of a nearby estuary (Chagas et al. 2006), it ranked among the dominant species in terms of biomass at this estuary's inlet (Araujo et al. 2008) and on soft bottom of the shallow shelf (Pinheiro et al. 2009), suggesting a general pattern for the region (~19 to 21° S).

In contrast, a recurrent feature in most estuaries was the high biomass contribution from the families Ariidae and Sciaenidae (Fig. 4), which is similar to that observed in the catches from other tropical and subtropical estuaries in the Western Atlantic (e.g. Vieira & Musick 1994, Araújo et al. 2002, Jaureguizar et al. 2004, Barletta et al. 2005), tropical
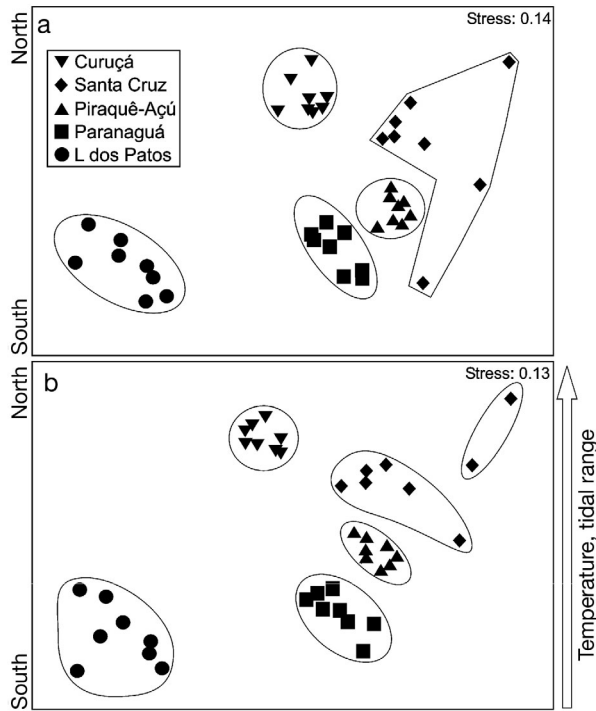
Fig. 6. Non-metric multidimensional scaling (nMDS) ordinations derived from (a) the mean relative biomass and (b) the presence/absence data of each species captured in 8 areas sampled in each estuary. The groups were defined using similarity cut-off levels of 21% (for relative biomass) and 38% (for presence/absence) in the cluster analysis (not shown)
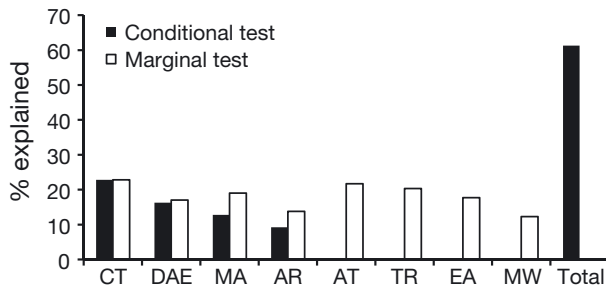


Fig. 7. Percent variation in the assemblage composition explained by the regional-scale variables according to the conditional test (partial) and marginal tests based on the mean relative biomass of each species in the 8 sampling areas within 5 estuaries (n = 40). The total variations explained by the conditional test including CT+DAE+MA+AR are also shown. The relationships were significant for all variables in the marginal tests and the 4 variables included in the conditional test by the forward selection method (p = 0.001 in all cases). CT: mean water temperature in the coldest month; DAE: distance among estuaries; MA: mangrove area; AR: mean annual rainfall; AT: mean annual water temperature; TR: tidal range; EA: estuary area; MW: mouth width

Table 4. Mean coefficients of determination (Mean $r^2 \pm$ SE) derived from marginal distance-based linear models (DistLM) and the prevalence of local predictors of fish assemblages in each estuary (n = 8 in each test). The results of npANOVAs comparing the coefficients of determination of the predictors and the forward conditional tests ($R^2$) with the greatest explanatory power (including all predictors) are also shown. N: number of marginal DistLM tests made for each predictor. Note that some variables were not measured in the 4 estuaries (see 'Materials and methods' for details) and that the marginal tests were made for 12 of the 13 months sampled in Piraquê-Açú due to the unavailability of predictor variables on one occasion (July 2004)

| Estuary | Predictors | N | Mean $r^2$ ($R^2$) | Prevalence |
|---|---|---|---|---|
| Curuçá (pseudo-$F_{4,30}$ = 1.39, p = 0.256, n = 34) | | | | |
| | Salinity | 7 | 18.6 ± 2.4 | 28.5 |
| | Dist. mouth | 7 | 18.5 ± 1.8 | 28.5 |
| | Temperature | 7 | 17.9 ± 2.3 | 28.5 |
| | Oxygen | 7 | 16.8 ± 1.9 | 14.2 |
| | Depth | 7 | 13.0 ± 1.3 | 0 |
| | Total explained | | (95.2) | |
| Piraquê-Açú (pseudo-$F_{3,44}$ = 1.21, p = 0.317, n = 47) | | | | |
| | Depth | 12 | 18.7 ± 1.9 | 25.0 |
| | Temperature | 12 | 17.4 ± 2.2 | 25.0 |
| | Salinity | 12 | 15.9 ± 1.7 | 16.6 |
| | Dist. mouth | 12 | 14.2 ± 1.1 | 0 |
| | Total explained | | (65.1) | |
| Paranaguá (pseudo-$F_{4,25}$ = 1.37, p = 0.261, n = 29) | | | | |
| | Salinity | 6 | 20.1 ± 4.0 | 33.3 |
| | Depth | 6 | 18.9 ± 4.4 | 16.6 |
| | Dist. mouth | 6 | 19.4 ± 3.0 | 16.6 |
| | Transparency | 6 | 17.5 ± 1.7 | 0 |
| | Temperature | 6 | 11.0 ± 1.5 | 0 |
| | Total explained | | (78.3) | |
| L. dos Patos (pseudo-$F_{3,21}$ = 0.52, p = 0.663, n = 24) | | | | |
| | Dist. mouth | 7 | 24.4 ± 4.7 | 42.8 |
| | Transparency | 4 | 14.0 ± 7.3 | 25.0 |
| | Salinity | 7 | 19.8 ± 5.6 | 14.2 |
| | Temperature | 7 | 17.1 ± 5.8 | 14.2 |
| | Total explained | | (80.0) | |

Eastern Atlantic, Indo-West Pacific and (for Ariidae) northeastern Australia (Blaber 2000, Ley 2005). These families are widely distributed worldwide and occur in freshwater, estuarine and marine environments (Nelson 2006), which indicates a great evolutionary plasticity. Interestingly, both are capable of emitting sounds through structures that have undergone convergent evolution and that can be used to intimidate predators, for sexual attraction and in agonistic interactions with competitors (Helfman et al. 2009). Members of Ariidae, in particular, have a set of adaptations that are important for explaining the success of this family, such as (1) the presence of stingers (usually poisonous) in the dorsal and pectoral fins, (2) chemical anti-predator alarms (Schreckstoff), (3) a

wide variability in thermal tolerance (eurythermia) and (4) the Weberian apparatus (Halstead et al. 1990, Nelson 2006, Marceniuk & Menezes 2007, Helfman et al. 2009). The relatively high number of Sciaenidae species (Fig. 3) with different trophic characteristics (e.g. from omnivorous to piscivorous; Chaves & Vendel 1998, Chaves & Umbria 2003) appears to further contribute to the abundance of this family in this and other studies. However, even though many families were shared among the estuaries, most species were not widely distributed.

The substantial distinction between the ichthyofauna of Lagoa dos Patos and those of other estuaries (see Fig. 5) is highlighted by the fact that about 62 % (23) of species captured at Lagoa dos Patos were not recorded elsewhere. This is principally due to the capture of species that occur only in the temperate region of the southwestern Atlantic — e.g. *Trachinotus marginatus*, *Platanichthys platana*, *Brevoortia pectinata*, *Symphurus jenynsi*, *Anchoa marinii*, *Paralichthys orbignyanus* and *Percophis brasiliensis* (Menezes et al. 2003) — and to the presence of continental species — e.g. *Odontesthes argentinensis*, *Hoplias malabaricus*, *Geophagus brasiliensis*, *Parapimelodus nigribarbis*, *Pimelodus maculatus*, *Charax stenopterus* and *Cyphocharax voga* (Buckup et al. 2007). Three of the latter species ranked among the 4 dominant in biomass and/or are among the most important in distinguishing the local fauna (Fig. 2, Table 3), reflecting the high continental influence in the Lagoa dos Patos. The presence of a relatively narrow inlet (588 m for a water body of 10 360 km$^2$) and the low tidal range (47 cm) contribute to the relatively low average salinity (5.7 vs. ≥17.4 in other estuaries), which favours the occurrence of freshwater taxa and the biomass dominance of so-called 'estuarine-dependent' species, such as *Micropogonias furnieri*.

The separation of the ichthyofauna at Curuçá from those at other tropical locations (Fig. 5, below) was due to the capture of species that occur only (or predominantly) in warm and turbid waters influenced by the discharge of Amazonian rivers in north Brazil (about 4° N to 3° S). This group of species is composed of *Aspredinichthys tibicen*, *Amphiarius rugispinis*, *Ogcocephalus nasutus*, *Stellifer naso, Anchoviella guianensis*, *A. cayennensis*, *Pterengraulis atherinoides* and *Apionichthys dumerili*. One, *S. naso*, had a relatively high biomass and is the most important species in distinguishing Curuçá ichthyofauna (Fig. 2, Table 3). With the exception of *O. nasutus*, these are typically estuarine or freshwater species that occur primarily within estuaries and that may have limited capacity to disperse over long distances.

Overall, the geographical structure of the fauna illustrated by cluster analyses is consistent with the new arrangement of the Brazilian and Argentinian biogeographic provinces proposed by Briggs & Bowen (2012). The realignments proposed by these authors are based on the validation, or refutation, of the provinces (as originally defined by Briggs 1995) using a comprehensive data set of Atlantic reef fishes that suggested an extension of the Brazilian province toward the south (28°S; see Floeter et al. 2001, 2008). In fact, the sharp drop observed in similarity between Lagoa dos Patos and the other estuaries suggests a transition from one to another biogeographical entity in southern Brazil (Fig. 5) that coincides with a reduction in water temperature (Fig. 1, Table 1).

## Local vs. regional variability

The composition of fish assemblages differed at the regional and local scales, but the variability was much higher at the regional scale (Fig. 6). As the distances between estuaries (970 to 6000 km) were relatively large compared with those of the points sampled within them (0.7 to 25 km), these results are consistent with the scale of variation of many physical properties of nature which tend to increase continuously with distance (Bell et al. 1993). A pattern of variability similar to that identified here was obtained for the fish fauna on unconsolidated and consolidated substrates of the northwest coast of Australia (Travers et al. 2010), for Caribbean coral reefs (Pandolfi 2002) and for trees in the Amazon (Tuomisto et al. 2003). Paradoxically, on the northeast coast of Australia, the variability in the compositions of ichthyofauna was higher among estuaries within the same bay (separated by <20 km) than between bays (separated by >100 km; Sheaves 2006).

The few studies that analysed the spatial variability of estuarine fish assemblages using a nested design provided seemingly conflicting results (e.g. this study vs. Sheaves 2006). However, this disparity likely reflects differences in the geographical range covered by these investigations, which can strongly influence the pattern of variability identified (Wiens 1989, Levin 1992). Samples in this study extended over ~6000 km of coastline covering 2 zoogeographical regions, whereas the study conducted by Sheaves covered a smaller extent (~180 km). Theoretically, as the sampled area increases, a greater proportion of spatial heterogeneity is represented as a greater variety of landscape elements is included in the study area (Wiens 1989). Thus, in nested analyses where

the larger scale investigated covers climatically and biologically distinct areas, as in this study, it is likely that the variability in the taxonomic composition of the assemblages will be greater on the broadest scale.

## Relative importance of regional ecological processes

Among the 8 regional predictors of the assemblages, the mean temperature of the coldest month and the distance between estuaries independently explained most of the variation in relative species biomass (Fig. 7). These results indicate that thermal preference or physiological constraints associated with temperature, and the dispersal capacity of each species are the major large-scale processes driving the structure of the assemblages. In fact, the idea that temperature is the primary driver of the geographical distribution of species has received strong empirical support in the literature, both for aquatic and terrestrial environments (Roy et al. 1998, Field et al. 2009). In relation to ichthyofauna, for example, temperature explained approximately 60% of the variability in the assemblages of South African estuaries (Harrison & Whitfield 2006), 41% of the variability in the assemblages on the shallow shelf and 53% in reef areas of Australia (Travers et al. 2010), and played an important role in distinguishing reef ichthyofauna along the Brazilian coast (Floeter et al. 2001). As expected, the mean water temperature in the coldest month of the 5 estuaries sampled decreased from north to south, ranging from 26.8°C in Santa Cruz (7° 41′ S) to 11.2°C in Lagoa dos Patos (32° 09′ S) (Table 1). This result broadly fits with the distribution of estuary samples along the nMDS ordinations based on relative biomass and the presence/absence of species (Fig. 6).

In a similar way, the significant effect of distance between the estuaries on the structuring of fish assemblages is compatible with the contemporary view that marine populations remain more isolated than previously considered (Cowen et al. 2006, Levin 2006). This has been corroborated by molecular analyses that revealed a reduced connectivity among marine fish populations. For example, on the Atlantic coast of South America, genetic studies identified not only geographically isolated populations for an estuarine species that inhabits semi-enclosed environments such as bays and lagoons (e.g. *Atherinella brasiliensis*; Stoiev 2009), but also for a marine species that lives on the shelf and occasionally enters

estuaries (e.g. *Macrodon ancylodon*; Santos et al. 2003). In both cases, the genetic heterogeneity of populations was positively correlated with geographic distance. These results parallel the prediction of neutral theory of biogeography, in which the dispersal limitation of species is one of the major factors responsible for the differences in species composition among sites (Hubbell 2001).

Mangrove area and mean annual rainfall were also important factors for the regional structuring of fish assemblages (Fig. 7). Mangroves are known to attract several species of fish owing to the provision of protection from predators, increased food availability and foraging efficiency within this habitat (Blaber 2000, Laegdsgaard & Johnson 2001). Correspondingly, some species identified by SIMPER analysis as being characteristic of 2 or more mangrove-fringed estuaries, such as *Cathorops spixii*, *Colomesus psittacus* and *Sphoeroides testudineus*, were also predominant in catches in mangrove channels reported by other authors (Giarrizzo & Krumme 2007, Oliveira-Neto et al. 2008). However, dependency on this ecosystem is possibly restricted to *C. psittacus*, which is known to feed primarily within mangroves (Krumme et al. 2007).

It is important to note, finally, that changes in rainfall can be ecologically important because they usually alter other factors that are directly related to the distribution and abundance of fish species in estuaries, including salinity, transparency, productivity and the depths of these environments (Garcia et al. 2001, Whitfield 1999, this study). Therefore, the significant and singular (although relatively weak) correlation of mean annual rainfall with the biotic data (Fig. 7) should actually represent the effect of these and correlated variables, but not rainfall itself. These results are supported by previous studies that also reported indirect effects of rainfall on the dynamics of the ichthyofauna in Lagoa dos Patos (Garcia et al. 2001) and in several other estuaries in South Africa (see Whitfield 1999 for a review).

## Relative importance of local ecological processes

At the local scale, the relative importance of environmental variables as predictors of fish assemblages varied in relation to estuaries, although the average $r^2$ for salinity was slightly higher in 2 of the 4 locations (Curuçá and Paranaguá, see Table 4). As salinity has been considered by several studies to be important for the spatial structure of estuarine fish assemblages (e.g. Barletta et al. 2005, Vilar et al.

2011), this result was partially expected. In contrast, the prevalence values for temperature (especially in Curuçá and Piraquê-Açú) were unexpected, since this variable has been previously associated with temporal variation, but not with the local-scale spatial variation in ichthyofauna (e.g. Bacheler et al. 2009, Vilar et al. 2011). However, this inconsistency seems to be related to the fact that, commonly, the spatial and temporal effects of explanatory variables in species distribution have been analysed together, making it impossible to determine the operational scale (i.e. spatial or temporal). Thus, these results highlight the need for spatially explicit analyses for a detailed interpretation of the relationship between the spatial structure of the fauna and possible ecological drivers.

The distance from the mouth of the estuary also had an important role as a predictor of fish assemblage composition, especially in the Lagoa dos Patos and Curuçá (Table 4). As the measurement of this variable can be performed using GIS, it is relatively easy, inexpensive and fast to obtain compared with other predictors. Thus, these attributes make it particularly attractive as a predictor of the relative biomass of species, especially where data are scarce or nonexistent. Depth had a considerable role as predictor of the fish assemblages at Piraquê-Açú and Paranaguá (Table 4), similar to that observed in Vitória Bay (southeastern Brazil), where depth had the most influence on species abundance (Chagas et al. 2006). However, none of the 7 DistLM analyses performed for Curuçá revealed a significant correlation between depth and the biotic data, showing an inconsistency between estuaries. For transparency, of the 10 DistLM tests performed (6 in Paranaguá and 4 in Lagoa dos Patos), only one was significant for Lagoa dos Patos, which resulted in a relatively high prevalence in this estuary, although it had a relatively low $r^2$ (Table 4). Overall, the heterogeneity in the relative importance of environmental variables between estuaries emphasises the role of idiosyncratic physical and hydrological features in determining the spatial structure of the fauna, and that the effects of these variables must be examined individually.

## CONCLUSIONS

Our results showed that, although the composition of fish assemblages is significantly different at both local and regional scales, the variability in composition of the fauna is much higher between estuaries than between sampling sites within them. The analy-sis correlating the relative biomass of species with a set of environmental and spatial variables provided some evidence of the main processes generating and maintaining this pattern of variability. At the regional scale (between estuaries), the variability in relative biomass of the species was explained by 3 independent environmental variables (in decreasing order: mean water temperature of the coldest month, mangrove area and mean annual precipitation) and by the distance between estuaries. At the local scale (between sampling sites within a given estuary), all predictors examined can act as modulators of the spatial structure of the assemblages, but their relative importance differs among estuaries. Overall, these results provide support for the idea that the geographic patterns in the compositions of the assemblages are simultaneously determined by environmental filters (especially water temperature) and the dispersal capacity of species, while local-scale spatial patterns are additionally influenced by other variables that vary in importance depending on estuary-specific physical and hydrological characteristics.

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