

Spatiotemporal variation among demersal ichthyofauna in a subtropical estuary bordering World Heritage-listed and marine protected areas: implications for resource management

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Abstract. Benthic trawl surveys were performed to quantify the spatiotemporal distributions of teleosts and key abiotic associations throughout an ecologically important estuary within Brazil's Atlantic Forest biosphere. Approximately 52 000 fish (51% juveniles) representing 75 species were sampled, with residents accounting for 36 and 61% of total species and individuals respectively. Five artisanally important species comprised 77 and 81% of individuals and biomass respectively. *Cathorops spixii* was most abundant (>40% of total), whereas *Stellifer rastrifer*, *Aspistor luniscutis*, *Sphoeroides greeleyi* and *S. testudineus* collectively contributed towards 37 and 34% of individuals and biomass respectively. The abundance of *A. luniscutis*, *C. spixii* and *S. rastrifer* was negatively associated with salinity, whereas the presence of the latter two species was also positively associated with temperature, and *S. greeleyi* and *S. testudineus* (mostly adults) were more abundant in deeper areas. These relationships seemed to be affected by species-specific reproductive (*S. rastrifer*, *C. spixii* and *A. luniscutis*), habitat (*S. greeleyi* and *S. testudineus*) and prey preferences (juvenile *C. spixii* and *A. luniscutis*). Protection for these various species may be achieved via immediate fishing effort regulations, but more research is required to manage other anthropogenic effects. Such work should be a priority to ultimately preserve what is one of the most important South American biodiversity areas.

Additional keywords: biodiversity hotspot, estuary function, fish community, fish distribution, nursery, Paranaguá estuarine complex.

Received 8 September 2015, accepted 16 March 2016, published online 17 June 2016

Introduction

Estuaries represent the interface between fresh and salt water ecosystems, are highly productive and often support large species diversity, especially in tropical and subtropical regions (Martino and Able 2003). The diversity of teleosts in estuaries has been hypothesised to be a function of large spatial and temporal variations in environmental conditions (Pasquaud *et al.* 2015). Some fish are physiologically and ecologically adapted to spend their entire life cycle in estuaries (termed 'estuarine residents'; Potter *et al.* 1986; Potter and Hyndes 1999; Elliott *et al.* 2007), but a greater number of species are transients that use estuaries during particular life stages (Blaber and Blaber

1980; Claridge *et al.* 1986; Paterson and Whitfield 2000; Elliott *et al.* 2007).

Regardless of their residence status, among the most important factors affecting teleost distributions in estuaries are environmental parameters, including water temperature, salinity and depth, all of which vary temporally (e.g. due to rainfall) and spatially (e.g. with distance from the ocean; Jaureguizar *et al.* 2004). Species-specific tolerances to environmental variations often dictate estuarine distributions and migration patterns. Beyond environmental drivers, biotic factors such as predation, competition and reproduction can strongly affect spatial and temporal species assemblages and distributions. These

relationships often are complex and interconnected. For example, Remmert (1983) proposed that large-scale composition patterns and community structures reflect the broad responses of organisms to the physical environment, with key abiotic variations acting as a physiological sieve, whereas biotic interactions refine species distributions within an ecosystem (Menge and Olson 1990).

Because of their large biodiversity, estuaries are among the most economically valuable ecosystems on Earth, particularly for artisanal fisheries in developing countries (Costanza *et al.* 1997). The Paranaguá estuarine complex (PEC; Fig. 1) in southern Brazil is one such estuary (Diegues 1995; Possatto *et al.* 2015). Despite being heavily populated, the PEC is considered one of the most preserved Brazilian ecological environments (Sá *et al.* 2006). Among the various anthropogenic activities, port-related industries dominate, followed by artisanal fisheries, tourism, agriculture and aquaculture. Notwithstanding these activities, attempts have been made to protect large areas of the coastal zone through environmental legislation. This protection encompasses vast mangrove belts bordering the estuary, which serve as important habitat for various marine fauna, and are ecologically linked to the extended rainforest zone in the hinterland (Pichler *et al.* 2015; Possatto *et al.* 2015).

Numerous surveys and ecological studies on the fish fauna in the PEC have emphasised its biodiversity importance (e.g. Spach *et al.* 2003; Queiroz *et al.* 2007; Barletta *et al.* 2008; Contente *et al.* 2011; Passos *et al.* 2012, 2013). However, most studies have been limited to small spatial and temporal

scales, with no seasonal comparisons (but see Possatto *et al.* 2016). Such broader studies are important for estuaries like the PEC, which encompass the tropical–temperate transition zones (e.g. 25°S). At these latitudes, there are large annual fluctuations in environmental parameters, especially rainfall (~2500 mm year⁻¹ regionally), which would be expected to strongly affect fish distributions and assemblage compositions (Barletta *et al.* 2003). Understanding such complex spatiotemporal patterns of influence is imperative for the effective management of anthropogenic activities within estuarine systems (Whitfield and Elliott 2002; Ley 2005).

Considering the above, the aim of the present study was to quantify the broad spatiotemporal distributions of demersal fish and key abiotic associations in the PEC as a step towards supporting coherent management in what can be described as one of the most important South American marine biodiversity areas. More specifically, we tested the hypothesis that rainfall, water temperature, salinity and depth explain variability among ichthyofaunal assemblages.

Materials and methods

Study area

The PEC (48°25'W, 25°30'S) has a total surface area of ~61 200 ha and can be considered part of a larger interconnected subtropical estuarine system that includes Iguape-Cananéia Bay to the north (and on the southern coast of

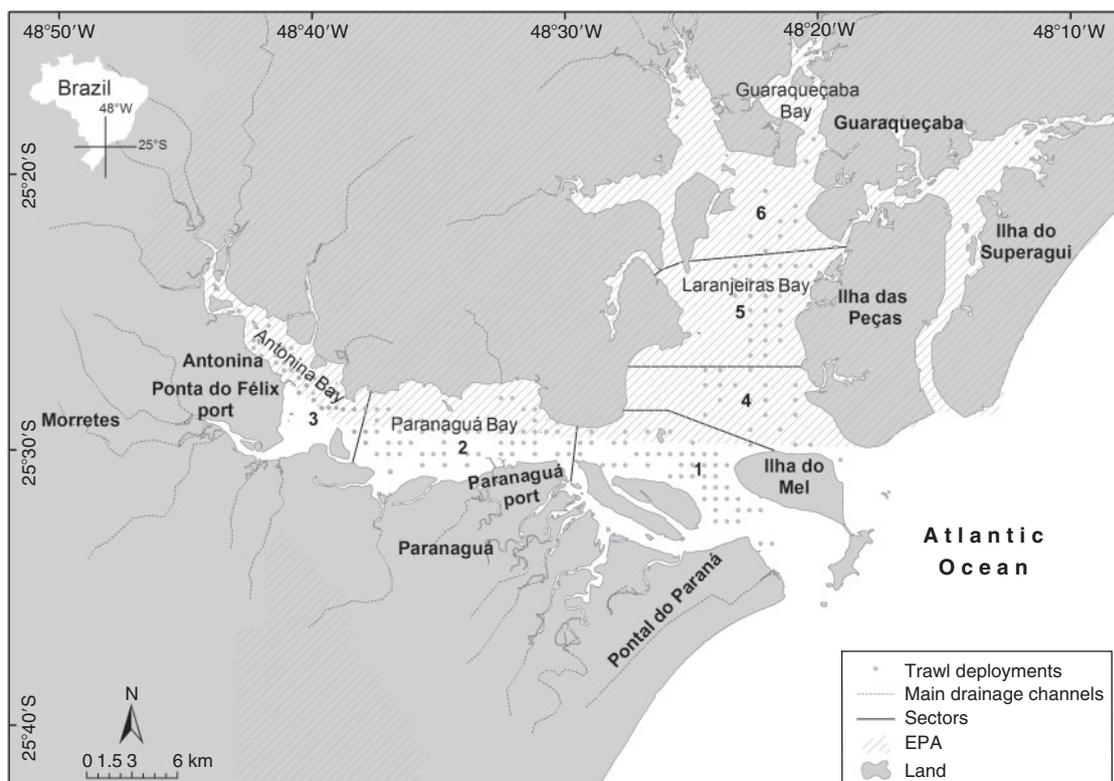


Fig. 1. Location of the Paranaguá estuarine complex in southern Brazil. Trawl deployments were made along six sectors in the east–west and north–south axes, namely outer (1 and 4), middle (2 and 5) and inner (3 and 6) sectors. EPA, Environmental Protected Area of Guaraqueçaba.

São Paulo; Lana *et al.* 2001; Noernberg *et al.* 2006; Fig. 1). Surrounded by one of the last remnants of Atlantic rainforest (2 071 685 ha), the PEC encompasses two conservational areas, namely the Superagui National Park (including Ilha do Superagui and Ilha das Peças) and the Environmental Protected Area of Guaraqueçaba, and borders a Natural World Heritage site (UNESCO 1999; Fig. 1). The system broadly separates into a 56-km long east–west axis forming Paranaguá and Antonina bays and a 40-km north–south axis constituting Laranjeiras and Guaraqueçaba bays (Fig. 1). Smaller segments connect various other water bodies, including Guaraqueçaba, Antonina, Pinheiros, Itaquí, and Benito bays and the Medeiros River (Lamour *et al.* 2004).

The PEC is characterised by a moderate vertical salinity gradient, with semidiurnal tides exhibiting diurnal inequality (maximum variation ~ 2.7 m) and consistent seasonal circulation and stratification (Marone *et al.* 2005). The climate is transitional tropical (mean annual rainfall ~ 2500 mm; Lana *et al.* 2001), with highly distinctive seasonality (wet summers and dry winters; Marone *et al.* 2005).

Sampling design

The east–west and north–south axes of the PEC were each divided into three sectors, comprising inner (Sectors 3 and 6 respectively), middle (Sectors 2 and 5 respectively) and outer (Sectors 1 and 4 respectively) areas (Fig. 1). The sectors were delineated according to substrate particle size, water temperature, density, chlorophyll, turbidity, salinity and suspended particulate matter (Lamour *et al.* 2004;). These variables were incorporated into a database and integrated by ArcGIS software (Esri Pty Ltd, Brisbane, Qld, Australia, see <https://esriaustralia.com.au/>). Using Hawth's Tools (developed for the ArcGIS software; Beyer 2004), random monthly sampling points were selected within each sector ($n = 6$ per sector). All sampling points comprised standardised grid sediments (>3 m depth and coarse grain size).

Between November 2012 and September 2013, each of the six sectors was sampled monthly using one of three penaeid trawls deployed across six replicate 5-min tows in a straight line (with the start and end positions marked using a global positioning system, GPS Map 76S, Garmin, Olathe, KS, USA, see <http://www.garmin.com/en-US>). The trawls were identical in terms of their mesh sizes (42- and 26-mm stretched mesh openings in the bodies and codends respectively), materials (0.6- and 1.0-mm diameter polyamide twine respectively) and designs (two seams, with lead-a-head and no sweeps), varying only slightly in their total opening lengths (9.44, 9.46 and 9.92 m). Each trawl was fished in a single-rig configuration (Broadhurst *et al.* 2013) from a 9-m canoe (18-kW engine size) and spread by two flat, rectangular otter boards (0.47×0.90 m and 17 kg each) attached to 10-mm diameter polyamide warps (total length 50 m). The trawl opening heights were all dictated by the otter board height and remained at ~ 0.46 m off the substratum.

Prior to each 5-min deployment, salinity and temperature were measured with a multiple sensor (ASTD 687; Alec Electronics Co., Ltd, Kobe, Japan, see <http://www.hydro-international.com/content/article/alec-electronics-co-ltd>). Depth was subsequently recorded at 1-min intervals using an echosounder (168 EX; Eagle Cuda, Eagle Electronics, Catoosa, OK USA, see <http://www.eaglenav.com/>). Rainfall data encompassing the estuary

catchment were obtained for each sampled month from Sistema meteorológico do Paraná (SIMEPAR; <http://www.simepar.br>, accessed 25 March 2014). At the end of each deployment, the codend was emptied onto a sorting tray and the fish separated, placed in plastic bags and kept on ice for transport to the laboratory. When more than 50 individuals of a species were caught, the excess was counted, weighed (to the nearest 1 g), discarded in the field and the data subsequently scaled. Elasmobranchs were released and not considered further here (because they comprised a separate study; Possatto *et al.* 2016).

The collected teleosts were identified to the highest possible taxonomic separation before being measured for total length (TL; to the nearest 1 cm) and weighed (as above). Up to 50 randomly selected individuals of each species from each deployment were also sexed and had their maturation stage (immature, maturing, mature or spent) determined following Vazzoler (1981). For analytical purposes, immature individuals were classified juveniles, whereas all other stages were deemed adults.

Data analyses

Fish abundances were standardised to per 0.1 ha trawled by multiplying the known trawled distance by the hypothesised wing-end spread of the trawl. The latter was estimated for each deployment by considering all relevant technical parameters (i.e. towing speed, water depth at 1-min intervals, length of warp deployed and trawl system area) within the Prawn Trawling Performance Model (Sterling 2005) and varied between 0.45 and 0.53 of the individual trawl headline lengths. To incorporate broader temporal scales and the potential effect of rainfall, we considered monthly rainfall patterns between 2003 and 2013 (from SIMEPAR) and aggregated each month into four seasons: early wet (October, November and December; mean \pm s.d. combined monthly rainfall of 235.1 ± 37.5 mm), late wet (January, February and March; 345.2 ± 73.2 mm), early dry (April, May and June; 136.2 ± 52.6 mm) and late dry (July, August and September; 146.0 ± 61.2 mm; Fig. 2).

Statistical analyses

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson *et al.* 2008) was used to test for spatiotemporal differences in measured environmental variables (temperature, salinity and depth) and fish assemblage characteristics. A three-factor PERMANOVA was used to test for differences in the abundances and assemblage structures of fish among seasons, axes and sectors. All factors were fixed and fully orthogonal. The multivariate analysis was based on the Bray–Curtis dissimilarity measure, whereas each univariate analysis was based on the Euclidean distance measure. Type III (partial) sums of squares were calculated using 9999 permutations of the residuals under a reduced model (multivariate analysis) and unrestricted permutations of the raw data (univariate analysis).

Separate pairwise tests were subsequently used to assess which levels of each significant interactive factor differed for each level of the other factor using the PERMANOVA routine. The proportion of variation attributable to each factor and interaction in each model was calculated to facilitate interpretation of the results. Multivariate patterns of assemblages were determined and visualised using hierarchical agglomerative

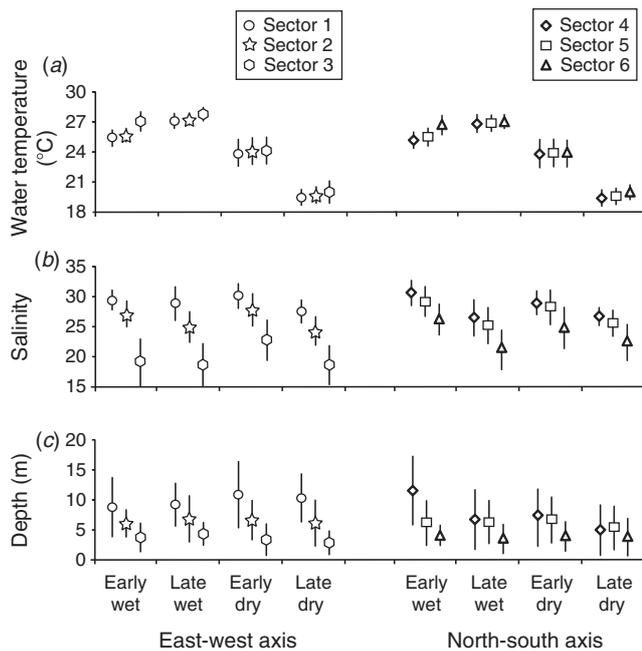


Fig. 3. Mean (\pm s.d.) water temperature (a), salinity (b) and depth (c) in the east–west and north–south axes of the Paranaguá estuarine complex sampled by sector and season between November 2012 and September 2013.

(16 species), Carangidae, Ariidae and Engraulidae (six species each), Achiridae (five species), Paralichthyidae and Tetradontidae (four species), Haemulidae (three species), and Cynoglossidae and Pristigasteridae (two species; Table 2). All other families were each represented by a single species (Table 2).

Only 11 species contributed more than 1% to the total number of fish sampled; representing 87% of all species sampled by number (Table 2). Five species dominated the assemblage, with *Cathorops spixii* the most abundant, accounting for 40 and 44% by number and weight of the total respectively (Table 2). *Stellifer rastrifer*, *Aspistor luniscutis*, *Sphoeroides greeleyi* and *S. testudineus* collectively contributed towards a further 37 and 34% of the total number and biomass respectively. All five species were residents, except *S. rastrifer* (Table 2). Because of *C. spixii* and *A. luniscutis*, the Ariidae family represented 46 and 62% by number and weight of the total respectively (Table 2).

Spatiotemporal variations in fish assemblages

Fish assemblage structure differed significantly due to the interactive effects of season, axis and sector, indicating complex spatiotemporal relationships (PERMANOVA, $P < 0.01$; Table 1). Cluster analysis identified four distinct assemblage groups at the 40% similarity level (Fig. 4). Group A comprised primarily teleosts collected in the middle (2) and inner (3) sectors along the east–west axis (Fig. 4). Three species, including *C. spixii*, *S. rastrifer* and *A. luniscutis*, contributed more than 90% towards the similarity matrix of this group (Fig. 4). Group B was the largest, containing 10 clusters mostly taken in the north–south sector in the late wet and early dry, with *C. spixii*, *S. rastrifer* and *S. greeleyi* contributing most to the similarity

matrix (Fig. 4). Group C contained four clusters taken in the late dry, whereas Group D contained only two samples taken in the early wet season (Fig. 4).

Spatiotemporal variations in the abundances of fish

Spatiotemporal patterns in the total species and individuals sampled, proportions of juveniles and transient species and abundances of the five key species (above) were complex (i.e. there were significant higher-order interactions in most PERMANOVAs; $P < 0.05$; Table 1). Nevertheless, some general patterns were evident. Pairwise analyses identified that a significantly greater number of total species were sampled in the late wet than the other seasons (pooled across axes and sectors; $P < 0.05$; Table 1; Fig. 5a).

The number of total individuals sampled per 0.1 ha differed significantly according to interactive effects of season and sector, as well as axis and sector ($P < 0.05$; Table 1). Specifically, more total individuals were sampled in the late wet season across all sectors in the north–south axis, but only in the middle and inner sectors (2 and 3) in the east–west axis (Fig. 5b). Similarly, more total individuals (pooled across seasons) were sampled in the middle and inner sectors in the east–west axis, but this was not the case in the north–south axis (Fig. 5b).

The proportion of transient species sampled differed significantly according to seasons, with the least sampled in the late dry across all sectors and both axes ($P < 0.001$; Table 1; Fig. 5c). Pairwise comparisons failed to detect any significant differences in the proportion of transient species sampled across the other seasons ($P > 0.05$; Fig. 5c). Further, the proportion of transient species returned a significant axis \times sector interaction ($P < 0.01$; Table 1; Fig. 5c). The pairwise tests identified that a greater proportion was sampled in the outer sector (1) but not middle or inner (2 and 3) sectors in the east–west axis than in the north–south axis ($P < 0.05$; Fig. 5c).

The proportion of juveniles sampled also differed significantly according to the interactive effects of several factors ($P < 0.05$; Table 1; Fig. 5d). Notably, the proportion of juveniles clearly differed according to season in the east–west axis, with the least sampled in the early wet and the most in the late wet and early dry seasons, but no such pattern was evident in the north–south axis (pairwise tests; Fig. 5d). Further, in the east–west axis, a lower proportion of juveniles was sampled in the middle sector (2) but again this was not evident in the north–south axis (Sector 5; Fig. 5d).

With regard to the five key species, all were recorded across all seasons, axes and sectors, but with significant spatiotemporal variations ($P < 0.05$; Table 1; Fig. 6). *Cathorops spixii* and *A. luniscutis* differed significantly according to the interactive effects of axis and sector ($P < 0.05$; Table 1; Fig. 6a, b). Across all seasons, *C. spixii* was significantly more abundant in the middle and inner sectors (2 and 3) than the outer (1) sector in the east–west axis, but this was not always the case in the north–south axis ($P < 0.05$; Fig. 6a). By comparison, *A. luniscutis* was most abundant in the inner sector (3) of the east–west axis (especially during the late wet season) than all other sectors within either axis, whereas across all seasons *S. rastrifer* differed significantly according to the interactive effects of season and both axis and sector ($P < 0.05$; Table 1; Fig. 6b, c), and was

Table 2. Families and species, and their absolute and relative frequencies (%) in numbers and weights, total length (TL; mean \pm s.d.) and ecological guilds sampled in the Paranaguá estuarine complex between November 2012 and September 2013
R, resident; T, transient

Family	Species	<i>n</i> (%)	Weight (g) (%)	TL (cm)	Guild
Achiridae	<i>Achirus declivis</i>	133 (0.2)	7126 (0.7)	12.6 \pm 3.2	R
	<i>A. lineatus</i>	506 (1.0)	11 586 (1.1)	9.9 \pm 1.7	R
	<i>Catathyridium garmani</i>	22 (<0.1)	807 (0.1)	11.3 \pm 2.1	R
	<i>Trinectes paulistanus</i>	76 (0.1)	1068 (0.1)	8.5 \pm 1.3	R
	<i>T. microphthalmus</i>	1 (<0.1)	2 (<0.1)	4.3	T
Ariidae	<i>Aspistor lumiscutis</i>	3084 (5.9)	160 116 (14.9)	14.8 \pm 7.2	R
	<i>Bagre bagre</i>	9 (<0.1)	38 (<0.1)	8.3 \pm 1.8	T
	<i>Cathorops spixii</i>	20 662 (39.6)	472 303 (43.9)	12.5 \pm 4.3	R
	<i>Genidens barbatus</i>	16 (<0.1)	771 (0.1)	17.2 \pm 3.1	T
	<i>G. genidens</i>	373 (0.7)	34 794 (3.2)	17.9 \pm 8.5	T
	<i>Notarius grandicassis</i>	119 (0.2)	3944 (0.4)	12.0 \pm 5.4	R
Batrachoididae	<i>Opsanus beta</i>	5 (<0.1)	330 (<0.1)	13.9 \pm 5.2	R
Carangidae	<i>Chloroscombrus chrysurus</i>	108 (0.2)	299 (<0.1)	6.1 \pm 1.3	T
	<i>Hemicarax amblyrhynchus</i>	8 (<0.1)	110 (<0.1)	9.5 \pm 3.7	T
	<i>Oligoplites saurus</i>	12 (<0.1)	62 (<0.1)	8.5 \pm 1.3	T
	<i>Selene setapinnis</i>	41 (<0.1)	171 (<0.1)	6.2 \pm 1.3	T
	<i>S. vomer</i>	86 (0.2)	253 (<0.1)	5.3 \pm 1.3	T
	<i>Trachinotus carolinus</i>	1 (<0.1)	288 (<0.1)	27.2	T
	<i>Centropomus parallelus</i>	1 (<0.1)	216 (<0.1)	29.5	R
Clupeidae	<i>Harengula clupeola</i>	9 (<0.1)	258 (<0.1)	13.1 \pm 3.0	T
Cynoglossidae	<i>Symphurus diomedianus</i>	1 (<0.1)	27 (<0.1)	13.2	T
	<i>S. tessellatus</i>	717 (1.4)	18 270 (1.7)	14.5 \pm 2.3	T
Diodontidae	<i>Chilomycterus spinosus spinosus</i>	124 (0.2)	9040 (0.8)	9.4 \pm 4.1	R
Eleotridae	<i>Eleotris pisonis</i>	8 (<0.1)	32 (<0.1)	6.6 \pm 1.8	R
Engraulidae	<i>Anchoa spinifer</i>	3 (<0.1)	55 (<0.1)	13.6 \pm 3.4	R
	<i>A. tricolor</i>	2 (<0.1)	13 (<0.1)	8.7 \pm 0.3	R
	<i>Anchovia clupeoides</i>	7 (<0.1)	165 (<0.1)	13.7 \pm 4.2	T
	<i>Anchoviella lepidostole</i>	8 (<0.1)	75 (<0.1)	9.7 \pm 1.9	R
	<i>Cetengraulis edentulus</i>	4 (<0.1)	102 (<0.1)	14 \pm 0.7	T
	<i>Lycengraulis grossidens</i>	92 (0.2)	1358 (0.1)	12.1 \pm 2.1	T
	<i>Chaetodipterus faber</i>	475 (0.9)	6795 (0.6)	6.8 \pm 1.8	T
	<i>Urophycis brasiliensis</i>	3 (<0.1)	12 (<0.1)	7.8 \pm 2.7	T
Gerreidae	<i>Eucinostomus argenteus</i>	31 (<0.1)	485 (<0.1)	9.8 \pm 2.0	T
Gobiidae	<i>Gobionellus oceanicus</i>	5 (<0.1)	38 (<0.1)	10.0 \pm 5.4	R
Haemulidae	<i>Conodon nobilis</i>	2 (<0.1)	57 (<0.1)	9.0 \pm 8.8	T
	<i>Genyatremus luteus</i>	154 (0.3)	2448 (0.2)	8.4 \pm 3.0	R
	<i>Pomadasys corvinaeformis</i>	1037 (2.0)	8880 (0.8)	8.0 \pm 0.9	T
Lutjanidae	<i>Lutjanus synagris</i>	2 (<0.1)	18 (<0.1)	8.2 \pm 0.1	T
Monacanthidae	<i>Stephanolepis hispidus</i>	10 (<0.1)	197 (<0.1)	8.7 \pm 3.1	R
Paralichthyidae	<i>Citharichthys arenaceus</i>	4 (<0.1)	86 (<0.1)	11.0 \pm 2.1	R
	<i>C. spilopterus</i>	424 (0.8)	6631 (0.6)	10.9 \pm 2.6	R
	<i>Etropus crossotus</i>	705 (1.3)	8809 (0.8)	9.8 \pm 2.0	R
	<i>Paralichthys orbignyanus</i>	9 (<0.1)	6717 (0.6)	32.9 \pm 16.5	T
Polynemidae	<i>Polydactylus virginicus</i>	1 (<0.1)	11 (<0.1)	10.7	T
Pomatomidae	<i>Pomatomus saltatrix</i>	8 (<0.1)	588 (0.1)	18.3 \pm 5.2	T
Pristigasteridae	<i>Chirocentron bleekermanus</i>	268 (0.5)	379 (<0.1)	6.1 \pm 0.9	T
	<i>Pellona harroweri</i>	472 (0.9)	2033 (0.2)	7.0 \pm 1.9	T
Sciaenidae	<i>Bairdiella ronchus</i>	2 (<0.1)	37 (<0.1)	11.6 \pm 1.3	R
	<i>Ctenosciaena gracilicirrhus</i>	37 (<0.1)	150 (<0.1)	6.6 \pm 1.2	T
	<i>Cynoscion acoupa</i>	3 (<0.1)	22 (<0.1)	9.8 \pm 0.9	T
	<i>C. jamaicensis</i>	138 (0.3)	1221 (0.1)	9.2 \pm 2.0	T
	<i>C. leiarchus</i>	516 (0.1)	6300 (0.6)	8.5 \pm 4.2	T
	<i>C. microlepidotus</i>	474 (0.9)	5425 (0.5)	9.3 \pm 4.0	R
	<i>Cynoscion</i> sp.	83 (0.1)	80 (<0.1)	4.3 \pm 1.2	
	<i>Isopisthus parvipinnis</i>	945 (1.8)	5058 (0.5)	7.8 \pm 2.0	T
	<i>Larimus breviceps</i>	1 (<0.1)	3 (<0.1)	7.1	T
	<i>Macrodon ancylodon</i>	450 (0.9)	5972 (0.6)	12.1 \pm 3.7	T

(Continued)

Table 2. (Continued)

Family	Species	n (%)	Weight (g) (%)	TL (cm)	Guild
	<i>Menticirrhus americanus</i>	454 (0.9)	21 489 (2.0)	15.2 ± 4.8	T
	<i>Micropogonias furnieri</i>	981 (1.9)	5221 (0.5)	7.7 ± 2.1	T
	<i>Nebris microps</i>	3 (<0.1)	211 (<0.1)	18.7 ± 5.7	T
	<i>Paralonchurus brasiliensis</i>	140 (0.3)	3431 (0.3)	13.6 ± 2.6	T
	<i>Stellifer brasiliensis</i>	188 (0.4)	1211 (0.1)	8.2 ± 1.2	T
	<i>S. rastrifer</i>	11 898 (22.8)	77 394 (7.2)	8.3 ± 1.8	T
	<i>S. stellifer</i>	283 (0.5)	3833 (0.4)	10.1 ± 2.0	R
Serranidae	<i>Diplectrum radiale</i>	108 (0.2)	3491 (0.3)	13.1 ± 2.2	T
Sphraenidae	<i>Sphyaena guachancho</i>	2 (<0.1)	424 (<0.1)	34.5 ± 4.9	T
Stromateidae	<i>Pepilus paru</i>	59 (0.1)	1271 (0.1)	9.7 ± 2.3	T
Syngnathidae	<i>Hippocampus reidi</i>	4 (<0.1)	19 (<0.1)	9.3 ± 2.2	R
Synodontidae	<i>Synodus foetens</i>	12 (<0.1)	848 (0.1)	21.1 ± 5.8	T
Tetraodontidae	<i>Lagocephalus laevigatus</i>	6 (<0.1)	393 (<0.1)	10.4 ± 8.5	T
	<i>Spherooides greeleyi</i>	2781 (5.3)	50 198 (4.7)	9.0 ± 1.0	R
	<i>S. spengleri</i>	321 (0.6)	1839 (0.2)	5.6 ± 1.7	T
	<i>S. testudineus</i>	1713 (3.2)	108 458 (10.1)	13.3 ± 2.7	R
Trichiuridae	<i>Trichiurus lepturus</i>	10 (<0.1)	359 (<0.1)	31.8 ± 14.3	T
Triglidae	<i>Prionotus punctatus</i>	659 (1.3)	3736 (0.3)	7.1 ± 1.9	T
Total		52 119	1 075 956		

most abundant in the late wet season across all sectors in the north–south axis, but only in the middle and inner sectors (2 and 3) in the east–west axis (Fig. 6c).

Neither *S. greeleyi* nor *S. testudineus* exhibited broad, overall seasonal differences in abundances ($P > 0.05$; Table 1; Fig. 6d, e). *Spherooides greeleyi* predominantly occurred in the north–south axis ($P < 0.05$; Fig. 6d). By comparison, the abundance of *S. testudineus* exhibited a significant axis \times sector effect, with the most individuals in the outer sector (4) of the north–south axis, but this was not evident in the east–west axis (Fig. 6e).

Environmental correlates with fish assemblage parameters

Water temperature was significantly related to the Euclidean distance matrices of the total assemblage structure, and the numbers of total species, total individuals, *C. spixii* and *S. rastrifer* ($P < 0.01$; Table 3). However, the observed relationships were generally weak, with water temperature explaining between 3.4 and 10.0% of the variation (R^2 value) in each analysis (Table 3). Salinity was significantly related to the Euclidean distance matrix of the assemblage structure, and the numbers of total individuals, *C. spixii*, *S. rastrifer* and *A. luniscutis* ($P < 0.01$; Table 3). The amount of variation explained by salinity was greatest (9.3%) for the latter species (Table 3). Water depth was significantly related to assemblage structure and the abundances of *S. greeleyi* and *S. testudineus*, but these relationships were similarly weak, accounting for less than 3.1% of the variation among samples ($P < 0.05$; Table 3). When all three parameters were included in a sequential regression, their combined total relationship was significant in each analysis, except for total species, *S. greeleyi* and *S. testudineus* ($P < 0.05$; Table 3). Nevertheless, the combined relationships only marginally improved the amount of variation explained over the single relationship (Table 3).

Discussion

The findings of the present study reiterate the importance of environmental parameters, especially salinity and temperature, for explaining spatiotemporal variation among the abundances of dominant estuarine species (Greenwood and Hill 2003; Jaureguizar *et al.* 2004; Akin *et al.* 2005; Garcia *et al.* 2012). These results can be discussed by first considering the environmental fluctuations, followed by underlying resource requirements according to species-specific life-history needs, and ultimately used to support existing and future resource management plans for the area.

Environmental variation

The entire PEC receives considerable rainfall during the warm wet season (e.g. up to 450 mm per month between October and March) and with cascading effects on salinity. This was especially evident in the east–west axis, which is characterised by several large rivers at the inner sector (Noernberg *et al.* 2006). This sector consistently had the lowest salinities, contributing towards greater environmental variability across the entire axis. In contrast, in addition to having less freshwater input from rivers, the north–south axis is shallower, shorter and wider ($\sim 40 \times 13$ km) than the east–west axis ($\sim 56 \times 7$ km), and therefore more amenable to seawater penetration (thus greater salinities throughout its entirety).

Regardless of rainfall and geographical differences, salinity increased in both axes towards the ocean, which is typical of estuarine systems owing to abiotic gradients resulting from the convergence of adjacent marine and freshwater environments (e.g. Day 1981). The warmest temperatures (as may be expected) were observed across all sectors and both axes during the late wet season (summer–autumn) and coolest in the late dry season (winter–spring). Depth did not present a specific pattern in the PEC. These spatial and temporal variations in water

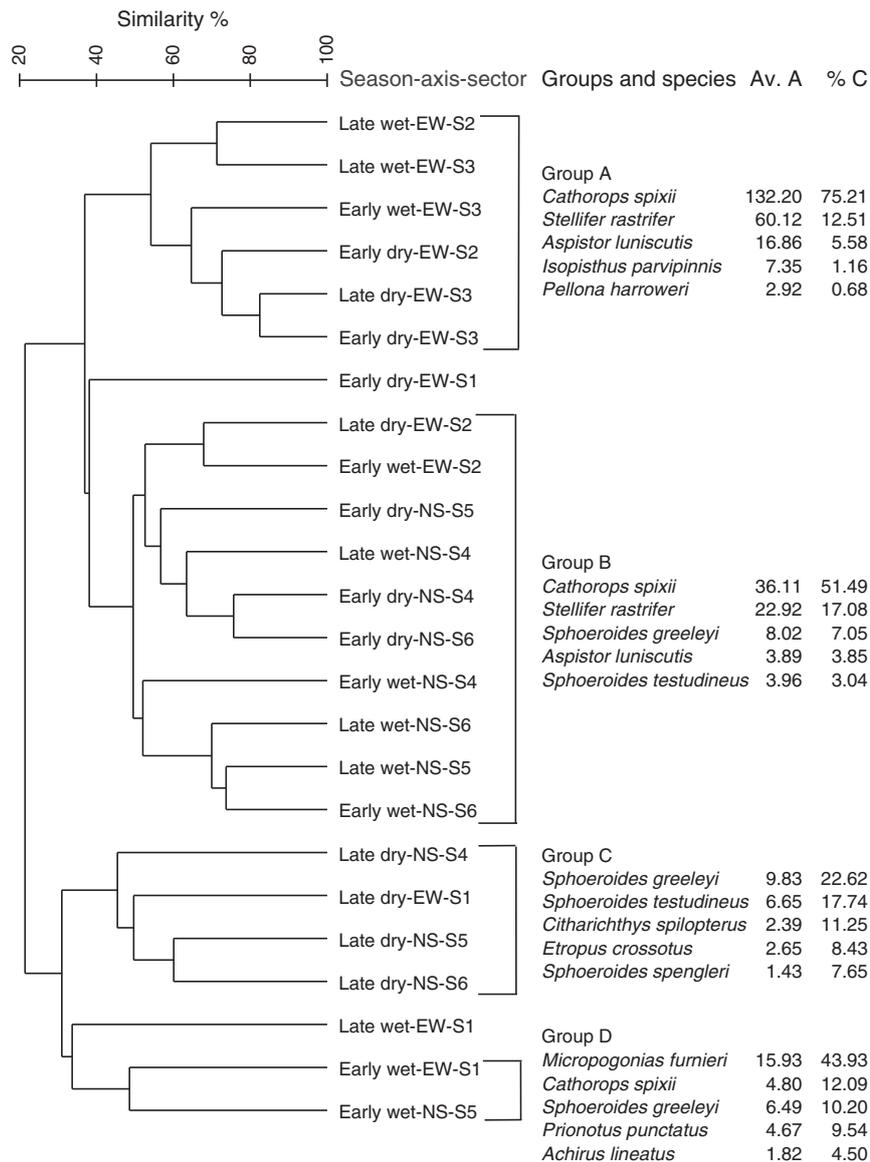


Fig. 4. Cluster dendrogram based on Bray–Curtis similarity measures, and similarity percentage analyses on fish species density data from the Paranaguá estuarine complex. The cluster analysis identified four distinct assemblage groups at the 40% similarity level (Groups A–D). EW, east–west; NS, north–south; S, sector; Av. A, average similarity; % C, percentage contribution.

attributes affected the distributions of assemblage structure and key species, with clear inter- and intra-axes spatial differences.

Assemblage composition

Prior to focussing on the extent to which the above variations in environmental parameters were reflected in the patterns and distributions of assemblages and key species, the fishing gear selectivity warrants some mention for possible confounding effects, especially among estimating juvenile abundances. In particular, because the trawls all fished the lower 0.46 m of the water column and their mesh sizes were quite small, it is possible that they selected proportionally smaller individuals. Conversely, the logistics of trawling meant that we were forced away from

some very shallow areas, which may have precluded sampling some juveniles and small species (i.e. depth-dependant effects on sizes; Pichler *et al.* 2015). Such variables could either over- or underestimate absolute fish abundances per 0.1 ha. Nevertheless, because we maintained the same sampling gear and sites across time, the observed abundances are representative of relative differences.

Similar to studies in other channel estuaries, the sampled ichthyofauna in the PEC was diverse, comprising adults and juveniles of both resident and transient species (Allen *et al.* 2006). Nevertheless, only a small component of the total ichthyofauna dominated samples, which is also true in other estuarine systems (Whitfield 1999; Akin *et al.* 2005). Such a

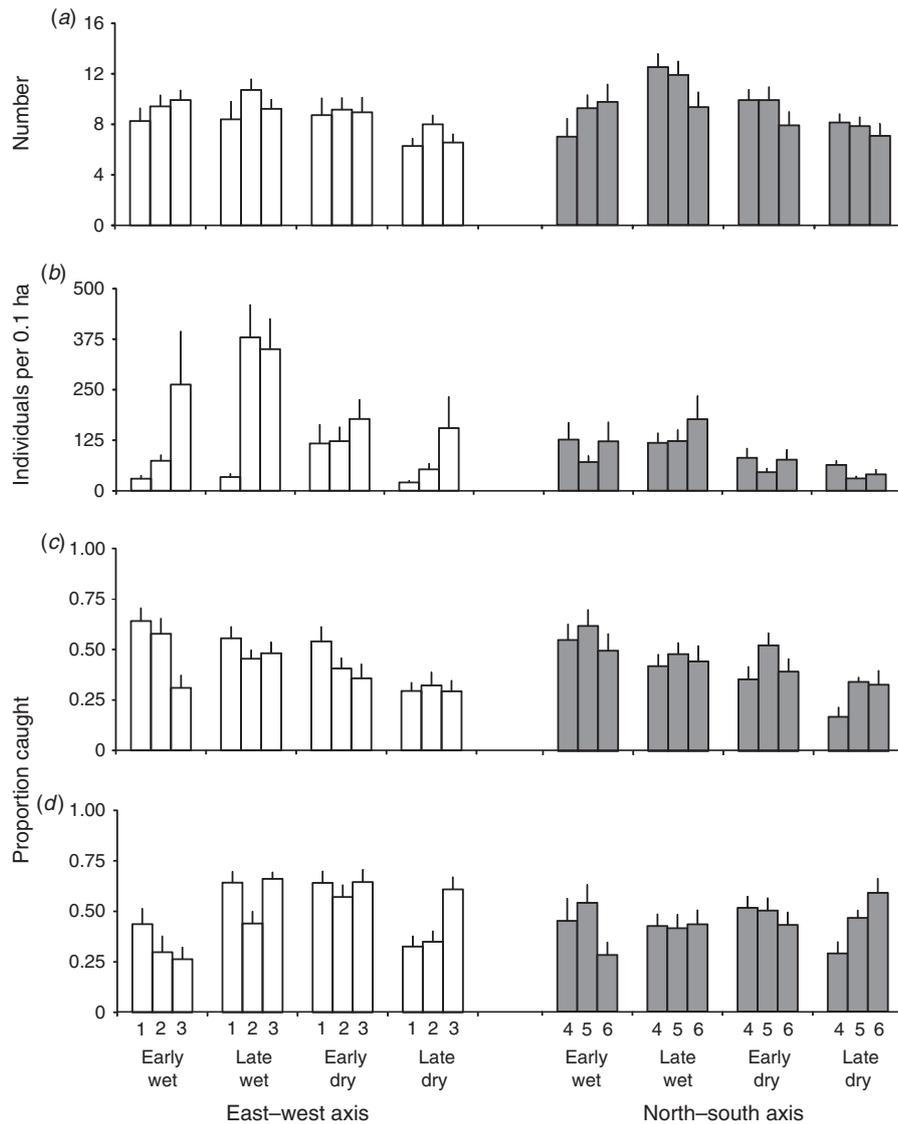


Fig. 5. Mean (\pm s.e.m.) numbers of total (a) species and (b) individuals per 0.1 ha, as well as the proportions of (c) transient species and (d) juveniles sampled between November 2012 and September 2013 across four seasons and three sectors in each of the two axes in the Paranaguá estuarine complex.

result is often attributed to the dynamic and variable estuarine environment, in which few species are adapted to live owing to the necessity for broad tolerances to fluctuating abiotic conditions (Whitfield 1999; Barletta *et al.* 2005, 2008). The dominant species here included four residents (*C. spixii*, *A. luniscutis*, *S. testudineus* and *S. greeleyi*) and one transient (*S. rastrifer*), and their distributions contributed greatly to the observed spatiotemporal variations in assemblage structure. However, each of the individual species requirements were somewhat divergent, reflecting their species-specific life histories.

Specifically, *C. spixii* and *A. luniscutis* belong to Ariidae, which is among the most important teleost families in tropical and subtropical estuaries (Lowe-McConnell 1987; Barletta and Blaber 2007; Barletta *et al.* 2008; Dantas *et al.* 2010). The

success of this family in transitional waters is a consequence of their eury-thermohaline capacity, Weberian apparatus (i.e. connecting the swim bladder to inner ear, increasing their environmental perception) and parental care (Burgess 1989; Dantas *et al.* 2010). Similarly, *S. greeleyi* and *S. testudineus* are tetraodontids, a family also adapted to a wide range of habitats and environmental conditions (Nelson 1994). More locally, the abundant transient *S. rastrifer* is among the most common, inhabiting the shallow continental shelf of the Paraná coast and the broader south-west Atlantic Ocean (Godefroid *et al.* 2004). All five species are retained by artisanal fishers (Coelho *et al.* 1986; Reis 1986), including the two tetraodontids, despite the dangers of tetrodotoxin in their meat (Haddad Junior 2003).

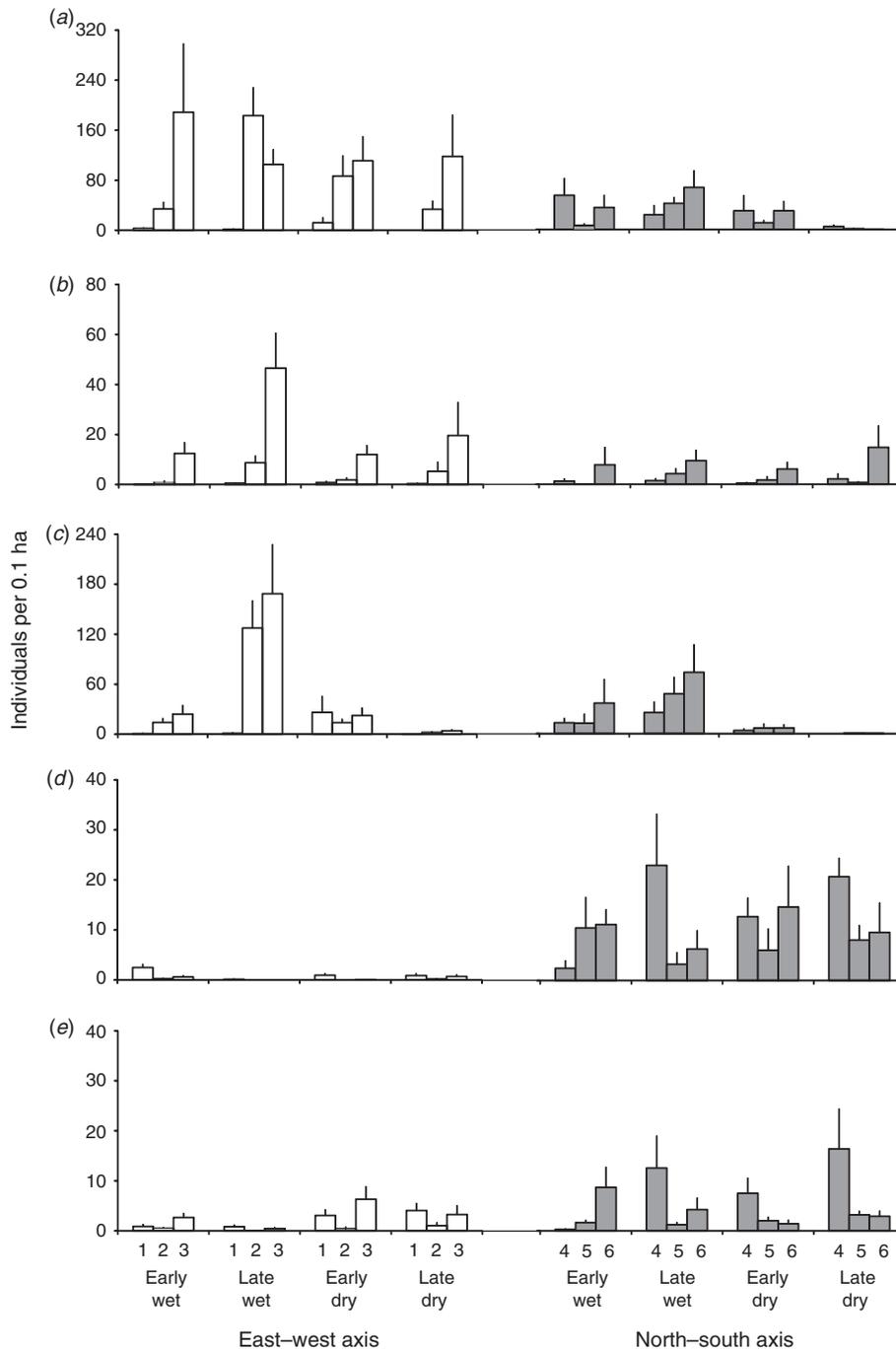


Fig. 6. Mean (\pm s.e.m.) numbers of (a) *Cathorops spixii*, (b) *Aspistor luniscutis*, (c) *Stellifer rastrifer*, (d) *Spherooides greeleyi* and (e) *Spherooides testudineus* individuals per 0.1 ha sampled between November 2012 and September 2013 across four seasons and three sectors in each of two axes in the Paranaguá estuarine complex.

Spatiotemporal variations in abundances

Notwithstanding the presence of the five key species throughout the sampled year, there were intraspecific spatiotemporal variations in their patterns of abundances. *Stellifer rastrifer* followed a clear seasonal trend, demonstrating a preference for

the less saline waters of the inner and middle sectors in the east-west axis during the late wet season. The same pattern was previously reported for this species in the PEC (Barletta *et al.* 2008) and other estuaries (Giannini and Paiva Filho 1990; Chaves and Vendel 1997). Such preferences may reflect

Table 3. Summary of distance-based linear model (DISTLM) analyses relating environmental variables to the Euclidean distance matrix for the total assemblage structure, the numbers of total species and individuals and the five key species sampled in the Paranaguá estuarine complex between November 2012 and September 2013
 ns, not significant; *, $P < 0.05$; **, $P < 0.01$. T, temperature; S, salinity; D, depth

	Temperature			Salinity			Average depth			Combined factors			
	Pseudo-F	P-value	%	Pseudo-F	P-value	%	Pseudo-F	P-value	%	Factors	Pseudo-F	P-value	%
Assemblage structure	24.04	**	5.751	13.571	**	3.33	8.843	**	2.195	T+S+D	17.964	**	12.935
Number of total species	43.547	**	9.953	2.144	ns	5.412	0.463	ns	1.173	T only			
Number of total individuals	32.457	**	7.611	11.445	**	2.823	0.216	ns	0.054	T+S+D	6.348	*	11.527
<i>Cathorops spixii</i>	13.826	**	3.39	10.939	**	2.701	0.117	ns	0.029	T+S+D	5.7	*	7.218
<i>Stellifer rastrifer</i>	32.788	**	7.682	9.301	**	2.306	0.009	ns	0.002	T+S	8.697	**	9.681
<i>Aspistor luniscutis</i>	2.073	ns	0.523	40.614	**	9.345	2.218	ns	0.559	S+D	5.341	*	10.56
<i>Sphoeroides greeleyi</i>	1.731	ns	0.437	1.261	ns	0.319	12.586	**	3.095	D only			
<i>Sphoeroides testudineus</i>	3.108	ns	0.783	0.001	ns	0.023	7.608	*	1.895	D only			

reproductive behaviour (Queiroz *et al.* 2006), considering that, like some other transients, *S. rastrifer* mainly spawns in the upper estuary during spring and summer in response to warmer water temperatures, and clearly with a broad tolerance to fluctuating salinity (Chaves and Vendel 1997).

The other four dominant species were all residents and although they exhibited slightly divergent patterns in abundances, most were strongly affected by rainfall and water temperature, patterns that ultimately contributed towards the observed differences in broader categories (total species and numbers and assemblage structure). Specifically, like *S. rastrifer*, *A. luniscutis* and, to a lesser extent, *C. spixii* were more abundant in the wet, especially in the warmer, shallow and less saline waters of the inner sectors (3 and 6) and particularly the east–west axis. This pattern was also presumably in response to summer spawning, because the proportion of juveniles was greater across both axes during the early dry season, and in the east–west axis during the late wet season. These observations are supported by Fávaro *et al.* (2005), who suggested that *C. spixii* reproduce between September and November (i.e. the early wet season).

Reproduction during the wet season would positively benefit most teleosts, because the rainfall increases nutrients in the water, causing cascading effects on primary and secondary productivity (Barletta *et al.* 2003). For example, juveniles would have more nutrients for food supplies and, because of the warmer water, their growth should be maximised (Deegan 1990). Further, increased water turbidity may reduce predation (Blaber 2000).

In contrast with the other dominant species, both tetraodontids (*S. greeleyi* and *S. testudineus*) were less affected by rainfall and more so by water depth, being most abundant in the more consistently shallower marine-dominated waters of the north–south axis year-round. Tetraodontids often inhabit shallow unvegetated margins of estuaries, where they can complete their entire life cycle. Potentially, these species may be more adapted to the consistent conditions observed in the north–south axis, or greater availability of suitable habitat (shallow water with adjacent mangroves). Other studies have demonstrated a preference by tetraodontids for such areas (Rocha *et al.* 2002; Schultz *et al.* 2002; Fávaro *et al.* 2009; Pichler *et al.* 2015).

Almost all *S. testudineus* and *S. greeleyi* caught in the present study were adults. However, juveniles should have been present because Rocha *et al.* (2002) and Schultz *et al.* (2002) identified reproductive periods of between September and January for *S. testudineus* and between November and January for *S. greeleyi*, which coincide with the timings of the other species above. A possible reason for the lack of sampled juveniles is that, owing to their poor swimming ability, they frequented shallower areas (mangroves, shallow seagrass beds and mud flats) with greater densities of food (Robertson and Duke 1990; Pichler *et al.* 2015) and slower-moving waters than our trawled sites. The potential for such size-specific spatial separation reiterates the importance of considering bias in sampling gears, and ultimately using various fishing gears (with overlapping selectivity) across different areas to quantify absolute distributions (Gray *et al.* 2006).

Variation in the spatiotemporal distributions of individual species and the possible explanatory factors extend to the

broader categories of total species and individuals, and the proportions of transients and juveniles. For example, regardless of axes, the number of total species sampled was greatest during the late wet season. As for *S. rastrifer* and *A. luniscutis*, this greater abundance of fish could potentially be due to more available food (Robertson and Duke 1990). In addition, Ariidae (which collectively accounted for approximately half the total catch) are known to use low saline waters for reproduction and recruitment (Barbieri *et al.* 1992).

The proportion of transients was greatest in the outer sector in many seasons across the east–west axis, and well represented in the outer sector at the north–south axis, presumably owing to ocean proximity. However, this result was clearly driven by a conglomeration of species other than the only dominant transient, *S. rastrifer* (which was recorded at low abundances in both outer sectors). This pattern mirrors many other tropical and temperate estuaries where transients mostly remain in the lower, marine-dominated reaches of estuaries (Woodland *et al.* 2012). These areas probably provide more shelter and food resources than adjacent coastal waters, hence estuaries are often nursery habitats for transient coastal species, which are then exploited (Potter and Hyndes 1999; Vasconcelos *et al.* 2010). Relevant species here included *Pomadasys corvinaeformis*, *Macrodon ancylodon*, *Cynoscion leiarchus*, *Isopisthus parvipinnis* and *Micropogonias furnieri*, all of which are caught across all life stages in artisanal fisheries in both in the PEC and adjacent coastal waters.

Conclusions and management implications

Despite the PEC being one of the most preserved estuaries in Brazil, anthropogenic developments and disturbances are apparent, especially in the east–west axis, which has a large port and greater urbanisation with more marine debris (Possatto *et al.* 2015), maritime traffic (Guebert *et al.* 2013), domestic discharge and sewage (Kolm *et al.* 2002; Martins *et al.* 2011) than the north–south axis. Nevertheless, it is clear that like the rest of the PEC, the east–west axis remains important to resident and transient teleosts, the movements of which are driven by a combination of abiotic and biotic factors, including rainfall (which affects salinity and turbidity), temperature, reproduction, recruitment and habitat preferences.

In terms of protecting the key species identified, attempts could be directed towards either: (1) improving existing fishing gear selectivity; or, perhaps (2) greater spatial and temporal regulation of effort. Specifically, several passive fishing gears are used in the PEC, including bottom and drift gill nets and hook-and-line, whereas the adjacent waters are subjected to intensive artisanal penaeid trawling effort (Silva *et al.* 2011, 2012). Of these gears, bottom-set gill nets and trawls are the least selective, typically capturing various benthic teleosts, including juveniles of the key species identified herein. Future research would benefit from assessing the relative selectivity of existing gears for mitigating unwanted catches at identified key places and times within the PEC (e.g. the inner and middle sectors of the east–west axis), and possibly simply choosing more selective existing gear configurations over others. Technology to reduce the bycatches of key species by adjacent penaeid trawlers is readily available and should be immediately

enforced by state and federal governments (Silva *et al.* 2011, 2012).

Regardless of fishing gear, some spatial and temporal regulation is also probably warranted. Because most species appear to reproduce during the wet season, restricting fishing in the middle and upper sectors of the east–west axis or even widespread closures during the late wet season may improve recruitment and reduce the mortalities of *C. spixii*, *S. rastrifer* and *A. luniscutis* during their reproduction. Legislation already exists for such strategies, which has been used previously to protect other economically important species in southern Brazil, including *Centropomus* spp., *Pomatomus saltatrix*, *Micropogonias furnieri* and *Sardinella brasiliensis* (ICMBio 2015). It remains to be seen whether existing policy makers have the capacity to expand on previous efforts.

Managing anthropogenic activities beyond fishing is somewhat more difficult, although it is clear that biodiversity conservation requires consideration of all impacts across all sectors and axes, as well as the broader coastal areas. Other studies have revealed considerable port contamination close to what were identified herein to be important areas for teleost reproduction (Santos *et al.* 2009; Liebezeit *et al.* 2011; Martins *et al.* 2011, 2015; de Abreu-Mota *et al.* 2014). Obviously, such effects would be best mitigated through far more stringent government control over domestic and industrial effluents.

Notwithstanding the need for coherent conservation strategies in the PEC (and adjacent coastal areas), there exist convoluted, social and bureaucratic conflicts concerning regional environmental resource exploitation (Andrighetto-Filho *et al.* 2009). An overt complexity of existing legislative processes needs to be considered along with the socioeconomic effects of anthropogenic impacts (especially fisheries), and perhaps ideally through greater consultation among key stakeholders (Andrighetto-Filho *et al.* 2009). Such work should be considered a priority if we hope to preserve what is one of the most important biodiversity areas in South America.

Acknowledgements

The authors acknowledge Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; www.capes.gov.br, accessed 1 September 2015) for funding F. E. Possatto's Ph.D. scholarship. H. L. Spach is a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellow and M. K. Broadhurst is a CAPES visiting researcher. Thanks are extended to Dr Kirk Winemiller for reviewing the work and for receiving F. E. Possatto at Texas A&M University, David Sterling for help calculating trawl parameters, Lilyane Santos, André Cattani, Kamila Maier, Nathalie Martins, Kelly Padovani, Bruna Oliveira and Juliane Santos for help with field sampling and Pâmela Cattani for the map.

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