Research Article

Environmental factors in the spatial variability of demersal fish in a subtropical estuary and adjacent continental shelf

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ABSTRACT. Quarterly collections of demersal fish were conducted between 2014 and 2018 on the adjacent continental shelf and in the Paranaguá Estuarine Complex (PEC). Univariate and multivariate statistical analyses were used to determine the abundance, richness, and composition of demersal fish assemblages and to list predictor variables responsible for the variability in these ecological descriptors by applying generalized linear models. The collected specimens of demersal fish (n = 25,179) were distributed across 19 orders, 31 families, and 72 species. Fish richness was explained by the following predictor variables: the percentage of fine sand in the sediment, the richness of the benthic megafauna, and sampling sites. The abundance was associated with the predictor variables of the percentage of very fine sand in the sediment, percentage of silt in the sediment, salinity, and sampling sites. Canonical correspondence analysis showed that the fish assemblage composition was strongly associated with the salinity gradient and positively correlated with benthic megafaunal species richness. As it is one of the last remnants of the Atlantic Forest, declared by UNESCO as a Natural Heritage of Humanity, the patterns observed in this study will support PEC's coastal management of current developmental demands, particularly related to port activities.

Keywords: demersal fish fauna; ecosystem; generalized linear models; Paranaguá Estuary; Brazil

INTRODUCTION

Fish assemblages are more often pressured in estuarine regions compared to other types of environments because of the significant variations in water mass circulation patterns, which vary daily and annually as estuaries are located at the interface between the ocean and continent (Paiva et al. 2008). However, these environments support considerable biodiversity, given

the high primary productivity resulting from the input of nutrients from rivers (Ricklefs 2003). Most estuary species use these environments for feeding, reproduction, growth, and development of larvae and juveniles (recruitment) and fundamental ecological processes in maintaining marine populations (Whitfield 1999, Isaac-Nahum 2006). Estuaries are subjected to a series of hydrological, oceanographic, and anthropogenic processes, thus creating a habitat with thermal

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and salinity gradients and variable concentrations of nutrients and pollutants (Wolanski 2007). All these processes influence fish distribution patterns in space-time and shape the diversity of assemblages owing to this environmental heterogeneity (Azevedo et al. 2007, Potter et al. 2015, Fujiwara et al. 2016).

Both on the continental shelf and in estuaries, changes in temperature, salinity, turbidity, dissolved oxygen, sediment composition, and depth can directly affect the diversity of fish assemblages (Jung & Houde 2003, Oliveira-Neto et al. 2004, Falcão et al. 2006, Possato et al. 2016, Gomes-Gonçalves et al. 2020, Molina et al. 2020, Santos et al. 2020). In estuaries, such factors vary over short distances and within small areas more than on the continental shelf, where changes are generally more dispersed. Thus, the tremendous environmental stress naturally occurring in estuaries can be easily exacerbated by small changes in the water column, directly reflecting highly adapted fauna with high physiological plasticity. In addition to the high variability in environmental conditions, ecological interactions with different taxonomic groups play an equally important role in structuring fish assemblages (Schluter & Ricklefs 1993).

In trophic terms, the distribution of demersal fish, for example, directly responds to the presence of benthic megafauna, one of their main food resources (Fujiwara et al. 2016). Therefore, these two assemblages are expected to exhibit a strong spatiotemporal relationship. However, ecological interactions between fish and benthic megafauna species can be complex and require better understanding (Quilez 2014).

Human activities have increased in recent decades and have impacted coastal and ocean ecosystems, especially concerning marine pollution, causing disturbances in these environments and altering habitats and the structure of biological assemblages (Kennish 2002). The increase in port activities and their maintenance through dredging alters the geomorphology, hydrography, and physiography of estuarine regions, consequently modifying the dynamics of fish fauna. It is noted, therefore, that the joint action of natural and anthropic factors can control the abundance, behavior, and selection of habitats of estuarine organisms, and from there, a thorough analysis of the impacts caused by human activities on these ecosystems is necessary.

Predicting the impacts of environmental, biological, and anthropogenic factors and their interactions on fish distribution patterns on continental shelves and estuaries is a complex task (Azevedo et al. 2007, Contente et al. 2011a). This study evaluated the impact of ecological differences on the structure of the demersal fish fauna. It aimed to provide an understanding of biotic and abiotic environmental changes, focusing on temporal and spatial variations in the Paranaguá Estuarine Complex (PEC) and the adjacent continental shelf. Using multivariate methods is essential to assess the diversity, understand the ecosystem, and attempt to predict future changes based on knowledge of the processes governing these changes over time and space. Given the high demand for port activities expansion in a region recognized by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) as a Natural Heritage of Humanity (UNESCO 1999), it is home to one of the last remnants of the Atlantic Forest biome on the planet, knowledge of the patterns of distribution and occurrence of demersal fish and the variables influencing these patterns is of paramount importance for coastal management processes in this region.

MATERIALS AND METHODS

Study area

The state of Paraná, southern Brazil's coast, is 98 km long (Bigarella et al. 1978) and has two important estuarine systems: PEC, located in the northern portion, and Guaratuba Bay on the southern portion of the coast. The PEC is located in the central northern region of the Paraná coast, a subtropical region of Brazil. It has an area of 612 km² (Angulo 1992), comprising five main water bodies: Antonina, Paranaguá, Laranjeiras, Guaraqueçaba, and Pinheiros bays (Lana et al. 2001). Ilha do Mel divides the mouth into two, which is of great ecological and tourism importance to the region.

The PEC is divided into two main orientation axes: the east-west axis, approximately 56 km in length, and the north-south axis, approximately 30 km in length (Andriguetto-Filho 1999). This region is inhabited by a large fishing community, who use fishing as the basis of their economy (Mendonça et al. 2017). Therefore, PEC has significant economic importance for the fishing, industrial, and tourism sectors, associated with the intense activities of two ports located in the complex (port of Paranaguá and port of Antonina) and a third port currently being constructed in the Pontal of Paraná (Cunha 2018).

This study focused on the PEC east-west axis, which includes the channel of waterways for ships to the berths of the ports of Paranaguá and Antonina. This axis is more than 50 km long and 7 km wide and includes the Antonina and Paranaguá bays. Notably, the external area, that is, on the adjacent continental shelf,
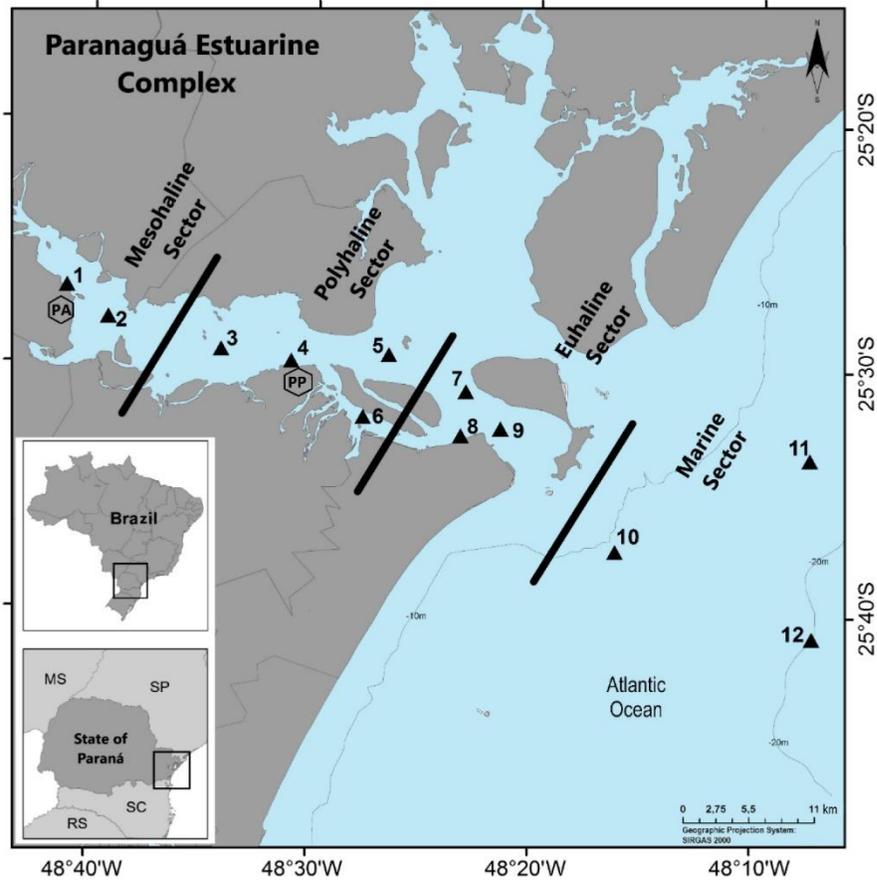
Figure 1. Location of the 12 sampling sites inside the Paranaguá Estuarine Complex and on the adjacent continental shelf on the coast of the state of Paraná. Highlights include the Ports of Antonina (PA) and Paranaguá (PP) and the salinity sectors (mesohaline: 1-2, polyhaline: 3-6, euhaline: 7-9, and marine: 10-12).

site 12 (outermost, located at the 20 m isobaths, Fig. 1), is the disposal site for the sediment dredged from the channel that provides access to the ports of this estuary and is called the external circular area 20 (ACE-20).

Data collection

Sampling was conducted quarterly between 2014 and 2018 at 12 sampling sites, and 144 samples were collected. The nine sites are located along the east-west axis of the PEC, and three are in the open sea (Fig. 1).

For sample collection, double trawls were conducted at each sampling site using a motorized wooden boat with an engine power of 60 Hp. The trawls had the same mesh sizes (42 and 26 mm stretched mesh openings in the bodies and cod ends, respectively), materials, and designs. Before each deployment, physical and chemical water data, such as salinity, temperature, pH, dissolved oxygen, and turbidity, were measured using a YSI ProDSS multiparameter probe, refractometer, and thermometer. Samples were also collected from the bottom sediment for sand particle

size analysis and to determine the percentage of silt and clay in the collected sediments.

Data processing

The collected samples were stored in plastic bags, kept on ice, and accurately identified according to the sampling site until arrival at the Fish Ecology Laboratory at the Center for Sea Studies (Universidade Federal do Paraná, UFPR). These samples were frozen until further screening and identification according to the Program for Monitoring Aquatic Biota and Determination of Bioindicators (LO 1173/2013-IBAMA) and authorization for the capture, collection, and transport of biological material (407/2014-IBAMA) for sample collection and processing. According to literature (e.g. Figueiredo 1978, Figueiredo & Menezes 1978, 1980a,b, 2000, Barletta & Corrêa 1992), all fish were identified to the lowest possible taxonomic level. Carcinofauna were identified using the bibliography described by Melo (1996, 1999).

All statistical analyses were performed using the computational environment R (R Development Core Team 2017). Generalized linear models (GLMs) were used to investigate the relationships between the abundance and richness of demersal fish with spatial, temporal, and environmental variables. In addition, six continuous variables were used: 1) water salinity, 2) water temperature, 3) dissolved oxygen, 4) hydrogenic potential, 5) the percentage of fine and very fine sand and silt in the sediment, and 6) species richness of the bycatch fauna, such as shrimp, crabs, squids, and starfish. In addition, three categorical variables (year, month, and sampling site) were used separately to predict demersal fish richness.

The variation inflation factor (VIF) function in the car package (Fox & Weisberg 2011) was used to test the multicollinearity of the predictor variables (Zuur et al. 2010). The Poisson distribution was used for richness data using the glm function. For abundance data, the adopted distribution was a negative binomial using the glm.nb function of the MASS package (Venables & Ripley 2002). The dredge function of the MuMIn package (Bartón 2022) was used, which selects the most significant models using the corrected Akaike information criterion (AICc), delta AIC, and Akaike weights among the models. The Akaike weight measures the relative probability of a model being the best among all applied models. These are normalized to sum 1 and interpreted as probabilities (Burnham & Anderson 2002). Next, those with a delta AIC value of <3 were selected. The average model interpreted the predictor variables based on their relative importance (RI > 90). The effects package effect function (Fox 2003) and the vegan package stripchart function (Oksanen et al. 2019) were used for graphic outputs.

Two asymmetric methods of canonical ordination were applied to evaluate the distribution of demersal fish species: canonical correspondence analysis (CCA) (Ter Braack 1986) and redundancy analysis (RDA) (Gittins 1985) with variance partition (RDAp) (Peres-Neto et al. 2006).

The CCA was applied to identify the influence of physical and chemical water variables (salinity, temperature, dissolved oxygen, and percentage of hydrogenic potential) and sediment texture variables (percentage of fine, very fine sand, and silt) on the distribution of demersal fish species with higher occurrence (>20% samples). The response matrix (demersal fish) was log-transformed $(y + 1)$ to minimize the effect of outliers, and the environmental variables were standardized $((x - \mu) / \sigma)$ before CCA was performed. Then, the *cca* function with direct selection procedure (*ordistep* function) was used in both vegan packages (Oksanen et al. 2019) to identify environmental variables that significantly explained the variation in the abundance matrix of demersal fish. Finally, for graphic output, the plot function of the RColorBrewer package was used (Neuwirth 2014).

RDA was conducted to identify the influence of physical and chemical water variables, sediment texture variables, and biotic variables (bycatch fauna abundance matrix) on the distribution of demersal fish species. Species of demersal fish and bycatch fauna with less than 10% occurrence in the samplings were considered rare and removed from the analysis to prevent an overweighting of their influence on the ordination results. Prior to performing the RDA, the response matrix (demersal fish) and the biotic predictor matrix were modified to homogenize the variation between species abundance using the Hellinger transformation (Legendre & Gallagher 2001) and make the data more appropriate for analysis using linear ordination methods (Peres-Neto et al. 2006). As with the CCA, the environmental variables were standar-dized $((x - \mu) / \sigma)$, and the *rda* function with a direct selection procedure (*ordistep* function) was used in both *vegan* packages (Oksanen et al. 2019). The next step involved a variance partition procedure (Peres-Neto et al. 2006) that was applied to the RDAp to identify the explanatory power of the environmental matrix and the biotic matrix in the distribution of demersal fish species (Legendre & Legendre 2012). The results of the variance partition were based on adjusted fractions of variation (Peres-Neto et al. 2006), and the randomization test was used to compute the significance levels. In the RDAp, the total percentage variation in the demersal fish matrix was broken down into pure and shared contributions of two sets of predictors (environmental and biotic matrices) assigned to different fractions based on variation-adjusted fractions (Radj2) (Peres-Neto et al. 2006).

RESULTS

Fish assemblage

We collected 25,179 demersal fish specimens distri-buted across 2 superclasses, 19 orders, 31 families, and 72 species. The families with the highest number of taxa were Sciaenidae (18 species) and Paralichthyidae (6 species). The remaining families were represented as single species. Although 72 species have been recorded along the estuary and continental shelf, more than 77% of all individuals belonged to only eight species, namely: *Cathorops spixii* (34.12%), *Stellifer rastrifer*

(22.15%), *Menticirrhus martinicensis* (6.37%), *Ctenosciaena gracilicirrhus* (4.19%), *Micro-pogonias furnieri* (3.26%), *Cynoscion microlepidotus* (2.44%), *Achirus lineatus* (2.44%), and *Stellifer brasiliensis* (2.31%). The other species were repre-sented by less than 1.7% of all individuals (Table 1).

Influence of environmental factors on demersal fish assemblages

The predictor variables that explained demersal fish richness was the percentage of fine sand in the sediment, benthic megafauna species richness (Table 2), and sampling sites (Table 3). Mean richness values were higher at sampling sites 5-8 (Fig. 2a). Richness was positively correlated with the percentage of fine sand in the sediment (Fig. 2b) and the benthic megafaunal species richness (Fig. 2c).

The following predictor variables explained the abundance of demersal fish: percentage of very fine sand in the sediment, percentage of silt in the sediment, salinity (Table 2), and sampling sites (Table 3). Abundance was positively correlated with the percentage of very fine sand in the sediment (Fig. 3b) and the percentage of silt in the sediment (Fig. 3c) and negatively correlated with salinity (Fig. 3d). The mean values of abundance were higher at sampling sites:1-5 (Fig. 3a).

In the CCA, the environmental variables that significantly explained the variation in fish abundance were the percentage of fine sand, very fine sand, and silt in the sediment and salinity. The first two CCA axes explained 5.7 and 1.3% of the data variation. The first axis explained 69% of the cumulative variation in the fish species-environmental variables relationship, whereas the second axis explained 16.1% of the cumulative variation (Fig. 4).

Cathorops spixii (cas), *Stellifer rastrifer* (str), *Symphurus tesselatus* (syt), and *Isopisthus parvipinnis* (isp) were more abundant in the polyhaline gradient and were correlated with higher percentages of silt in the sediment. In contrast, *Sphoeroides greeleyi* (spg), *Sphoeroides testudineus* (spt), *Chaetodipterus faber* (chf), and *Genidens genidens* (geg) were more abundant in the polyhaline and euhaline gradients and were correlated with lower percentages of very fine sand in the sediment. Conversely, *Diplectrum radiale* (dir), *Prionotus punctatus* (prp), *Eucinostomus argenteus* (eua), *Chilomycterus spinosus* (chs), *Citharichthys arenaceus* (cia), and *Ctenosciaena gracilicirrhus* (ctg) were more abundant in the polyhaline and euhaline gradients and were correlated with higher percentages of fine sand in the sediment.

Additionally, *Stellifer brasiliensis* (stb), *Paralonchurus brasiliensis* (pab), and *Citharichthys spilopterus* (cis) were more abundant in the polyhaline and euhaline gradients and were correlated with higher salinity. *Achirus lineatus* (acl), *Cynoscion microlepidotus* (cym), *Menticirrhus americanus* (mea), and *Etropus crossotus* (etc) showed no correlation with the measured environmental variables.

The RDA analysis showed that environmental and biotic variables significantly explained the distribution of demersal fish species (Table 4). The percentage of variation in the demersal fish matrix explained by environmental variables was 11.6% and by biotic variables was 21.9% (Table 4).

The physical sediment texture variables (e.g. percentage of fine sand and silt) and chemical variables (salinity, temperature, and dissolved oxygen) explained the distribution of the demersal fish species assessed in this study. The spatial and temporal distributions of the key megafauna, such as *Xiphopenaeus kroyeri*, *Farfantepenaeus brasiliensis*, *F. paulensis*, *Rimape-naeus constrictus* (shrimp), *Callinectes ornatus*, *C. danae*, *Callinectes* sp. (crab), *Hepatus pudibundus* (crab), *Clibanarius vittatus* (hermit crab), *Lolliguncula* sp. (squid), and *Luidia* sp. (starfish) are also shown in Table 4.

The RDAp showed the explanatory power of the environmental and biotic matrices and the correlation between these predictor matrices in the response of the demersal fish abundance matrix. These predictor matrices pure and shared effects are important in the distribution of demersal fish species.

The total amount of variation in the fish abundance matrix explained by the predictor matrices was 22.3% (Fig. 4). The pure biotic fraction (12.7%) mainly explained the distribution of fish species, followed by the fraction shared between environmental and biotic variables (5%), and the pure environmental fraction (4.6%).

DISCUSSION

In this study, we found that the composition and structure of fish communities in general in the PEC and adjacent continental shelf follow a pattern observed in tropical western Atlantic estuaries (Blaber 1997, 2002), with a predominance of species of the family Sciaenidae, which in this study represented more than 51% of all recorded families. For example, in a survey of the fish fauna on Santa Catarina Island in southern Brazil, of the 58 species recorded, 20 were classified as Sciaenidae (Ribeiro et al. 2019). A pioneering survey

Table 1. Taxonomic classification of ichthyofauna captured quarterly between 2014 and 2018 and the number of individuals per sector. Sectors: Mesohaline (Meso), Polyhaline (Poly), Euhaline (Euha), and Marine (Mar).

Species	Meso	Poly	Euha	Mar
Actinopterygii				
Acanthuriformes				
Sciaenidae				
Bairdiella ronchus (Cuvier, 1830)	0	0	1	1
Ctenosciaena gracilicirrhus (Metzelaar, 1919)	0	311	404	343
Cynoscion acoupa (Lacépède, 1801)	1	0	0	0
Cynoscion jamaicensis (Vaillant & Bocourt, 1883)	1	0	2	3
Cynoscion leiarchus (Cuvier, 1830)	2	119	61	4
Cynoscion microlepidotus (Cuvier, 1830)	26	463	93	35
Isopisthus parvipinnis (Cuvier, 1830)	39	284	7	74
Larimus breviceps Cuvier, 1830	0	0	1	111
Macrodon atricauda (Günther, 1880)	8	99	3	25
Menticirrhus cuiaranensis (Holbrook, 1847)	3	55	73	25
Menticirrhus martinicensis (Cuvier, 1830)	24	687	681	213
Micropogonias furnieri (Desmarest, 1823)	44	633	100	45
Nebris microps Cuvier, 1830	0	0	0	5
Paralonchurus brasiliensis (Steindachner, 1875)	6	50	11	206
Stellifer brasiliensis (Schultz, 1945)	0	295	63	224
Stellifer rastrifer (Jordan, 1889)	666	4183	64	668
Stellifer stellifer (Bloch, 1790)	0	80	0	0
Umbrina coroides Cuvier, 1830	0	0	0	1
Aulopiformes				
Synodontidae				
Synodus intermedius (Agassiz, 1829)	0	4	2	7
Batrachoidiformes				
Batrachoididae				
Porichthys porosissimus (Cuvier, 1829)	0	2	0	20
Carangiformes				
Carangidae				
Selene vomer (Linnaeus, 1758)	0	11	2	0
Clupeiformes				
Engraulidae				
Lycengraulis grossidens (Spix & Agassiz, 1829)	2	21	0	0
Pristigasteridae				
Pellona harroweri (Fowler, 1917)	0	40	7	84
Gadiformes				
Phycidae				
Urophycis brasiliensis (Kaup, 1858)	0	0	2	16
Gobiiformes				
Gobiidae				
Bathygobius soporator (Valenciennes, 1837)	1	0	0	0
Ctenogobius shufeldti (Jordan & Eigenmann, 1887)	0	1	2	0
Lophiiformes				
Ogcocephalidae				
Ogcocephalus vespertilio (Linnaeus, 1758)	0	1	2	0
Moroniformes				
Ephippidae				
Chaetodipterus faber (Broussonet, 1782)				
Mulliformes	26	81	156	6
Mullidae				
Mullus argentinae Hubbs & Marini, 1933	0	0	0	126
Ophidiiformes				

Continuation

Species	Meso	Poly	Euha	Mar
Ophidiidae				
Ophidion holbrooki Putnam, 1874	0	0	0	9
Perciformes				
Gerreidae				
Diapterus rhombeus (Cuvier, 1829)	0	2	1	4
Eucinostomus argenteus Baird & Girard, 1855	0	122	33	69
Eucinostomus gula (Quoy & Gaimard, 1824)	1	13	29	7
Haemulidae				
Conodon nobilis (Linnaeus, 1758)	0	1	5	17
Genyatremus luteus (Bloch, 1790)	20	28	0	4
Haemulon aurolineatum Cuvier, 1830	0	0	0	2
Haemulopsis corvinaeformis (Steindachner, 1868)	16	32	77	87
Orthopristis rubra (Cuvier, 1830)	0	0	2	11
Lutjanidae				
Lutjanus synagris (Linnaeus, 1758)	0	0	1	0
Priacanthidae				
Heteropriacanthus cruentatus (Lacépède, 1801)	0	0	2	2
Scorpaenidae				
Scorpaena brasiliensis Cuvier, 1829	0	0	2	0
Serranidae				
Diplectrum formosum (Linnaeus, 1766)	0	0	0	21
Diplectrum radiale (Quoy & Gaimard, 1824)	0	24	58	44
Triglidae				
Prionotus punctatus (Bloch, 1793)	1	146	184	111
Pleuronectiformes				
Achiridae				
Achirus declivis Chabanaud, 1940	1	27	1	0
Achirus lineatus (Linnaeus, 1758)	4	289	336	6
Catathyridium garmani (Jordan, 1889)	4	5	0	0
Trinectes microphthalmus (Chabanaud, 1928)	0	0	1	14
Trinectes paulistanus (Miranda Ribeiro, 1915)	0	2	2	10
Cynoglossidae				
Symphurus tessellatus (Quoy & Gaimard, 1824)	15	178	33	23
Paralichthyidae				
Citharichthys arenaceus Evermann & Marsh, 1900	0	32	70	80
Citharichthys macrops Dresel, 1885	0	0	3	65
Citharichthys spilopterus Günther, 1862	1	54	37	38
Etropus crossotus Jordan & Gilbert, 1882	0	96	111	38
Paralichthys patagonicus Jordan, 1889	0	0	2	0
Siluriformes				
Ariidae				
Cathorops spixii (Agassiz, 1829)	2347	5789	405	55
Genidens barbus (Lacepède, 1803)	190	52	24	0
Genidens genidens (Cuvier, 1829)	25	182	188	0
Syngnathiformes				
Dactylopteridae				
Dactylopterus volitans (Linnaeus, 1758)	0	2	2	68
Syngnathidae				
Hippocampus reidi Ginsburg, 1933	0	0	1	0
Tetraodontiformes				
Balistidae				
Balistes capriscus Gmelin, 1789	0	0	1	7
Chilomycterus spinosus (Linnaeus, 1758)	1	30	41	61

Continuation

Species	Meso	Poly	Euha	Mar
Monacanthidae				
Stephanolepis hispida (Linnaeus, 1766)	0	1	7	0
Tetraodontidae				
Lagocephalus laevigatus (Linnaeus, 1766)	0	1	0	0
Sphoeroides greeleyi Gilbert, 1900	0	96	268	1
Sphoeroides spengleri (Bloch, 1785)	0	24	10	3
Sphoeroides testudineus (Linnaeus, 1758)	2	61	123	3
Sphoeroides tyleri Shipp, 1972	0	7	8	3
Chondrichthyes				
Myliobatiformes				
Dasyatidae				
Hypanus guttatus (Bloch & Schneider, 1801)	2	13	1	1
Rhinopristiformes				
Rhinobatidae				
Pseudobatos percellens (Walbaum, 1792)	0	18	40	5
Zapteryx brevirostris (Müller & Henle, 1841)	0	0	0	10
Torpediniformes				
Narcinidae				
Narcine brasiliensis (Olfers, 1831)	0	1	4	1

in northern Brazil (Vinson et al. 2004) showed that because of the importance of the family Sciaenidae in that ecosystem (Barletta-Bergan et al. 2002), it was necessary to deepen it using more refined techniques with phylogenetic studies. According to Vieira & Musick (1994), in western Atlantic estuaries, the family Sciaenidae is among the most abundant when bottom trawling is used as a collection method.

The composition of estuarine fish populations changes constantly and drastically because of the variability in environmental conditions and the specified tolerance limits of certain species to environmental changes (Kennish 1990). The complexity of determining and quantifying the effects of abiotic and biotic parameters on the spatial and temporal variation in the abundance and richness of estuarine fish is directly linked to the synergistic interactions specific to each environment (Blaber 2002). In this sense, using mathematical methods to evaluate fish species in the PEC and adjacent continental shelf of Paraná, variables such as the percentage of very fine sand and silt in the sediment composition, water salinity, bycatch fauna richness, and sampling sites were defined as the main drivers of spatial and temporal variation in abundance and richness according to the proposed models and the predictor variables tested.

The higher abundance of fish in sites 1-5 (mesohaline and polyhaline sectors) is directly linked to the locations with the greatest increase in nutrients and organic matter, both natural and anthropogenic. Patterns that are also recorded in other estuaries in Brazil, such as the highest mean density and biomass of fish recorded in the upper estuary of the Mabucaba River in Rio de Janeiro (Neves et al. 2010) and in estuaries in southern Africa showed a preference for shallow upstream waters for shelter and refuge from predators (Harrison & Whitfield 2006). Shallower zones upstream of the Paranaguá Estuary have salinities ranging from 5 to 25 and are classified as polyhaline or mesohaline (Neto & Lana 1997, Lana et al. 2001, Passos et al. 2013). These environments show higher deposition of fine sediments (silt, clay, and very fine sand) with high levels of organic matter and nutrients, as they are transition environments with significant productivity (Miranda et al. 2002, Paiva et al. 2005, Cattani & Lamour 2016).

The shallower upstream areas (sites 1 to 5, where greater abundances of fish were recorded) are favorable habitats that several fish species rely on for food, reproduction, growth, or shelter from predators, called "nurseries" or breeding areas. These brackish water environments have a high representation and abundance of juveniles (Araújo et al. 1998, Spach et al. 2004, Falcão 2006, Félix et al. 2006). Our results are congruent with those reported for other Brazilian estuaries, showing a high abundance of euryhaline fishes with particular physiological conditions adapted for brackish and saltwater (Contente et al. 2011b).

Table 2. Selection of generalized linear models for richness (riq) and abundance (abund) of demersal fish with continuous variables as predictors. abuac: benthic megafauna species abundance, aref: fine sand in the sediment (%), aremf: very fine sand in the sediment (%), od: dissolved oxygen, riqac: benthic megafauna species richness, sal: salinity, silt: silt in the sediment (%), temp: water temperature, pH: hydrogenic potential, RI: relative importance of predictor variables. Predictor variables with RI > 0.9 are in bold. Models with delta AIC > 3 were not shown.

Models for richness	df	logLik	AICc	delta	weight
riq ~ **aref** + **riqac**	4	-569.6	1147.3	0.00	0.09
riq ~ **aref** + **riqac** + silte	5	-568.9	1148.1	0.77	0.06
riq ~ **aref** + od + **riqac**	5	-569.1	1148.5	1.20	0.05
riq ~ **aref** + aremf + **riqac**	5	-569.2	1148.6	1.27	0.05
riq ~ **aref** + pH + **riqac**	5	-569.2	1148.7	1.37	0.04
riq ~ **aref** + **riqac** + temp	5	-569.4	1149.2	1.86	0.03
riq ~ **aref** + aremf + **riqac** + silte	6	-568.5	1149.3	2.00	0.03
riq ~ **aref** + **riqac** + sal	5	-569.6	1149.4	2.09	0.03
riq ~ **aref** + pH + **riqac** + silte	6	-568.5	1149.4	2.12	0.03
riq ~ **aref** + od + **riqac** + silte	6	-568.6	1149.6	2.26	0.03
riq ~ **aref** + aremf + od + **riqac**	6	-568.7	1149.8	2.45	0.03
riq ~ **aref** + **riqac** + silte + temp	6	-568.8	1149.9	2.63	0.02
riq ~ **aref** + od + pH + **riqac**	6	-568.8	1150.0	2.64	0.02
riq ~ **aref** + aremf + pH + **riqac**	6	-568.8	1150.0	2.67	0.02
riq ~ **aref** + **riqac** + sal + silte	6	-568.9	1150.2	2.87	0.02
RI: aref = 1; riqac = 1					
Models for abundance	df	logLik	AICc	delta	weight
abund ~ abuac + **aremf** + **sal** + **silte**	6	-1212.6	2437.5	0.00	0.13
abund ~ **aremf** + **sal** + **silte**	5	-1213.6	2437.5	0.03	0.12
abund ~ **aremf** + od + **sal** + **silte**	6	-1213.4	2439.1	1.60	0.06
abund ~ abuac + **aremf** + od + **sal** + **silte**	7	-1212.4	2439.4	1.87	0.05
abund ~ **aremf** + **sal** + **silte** + temp	6	-1213.6	2439.5	2.03	0.05
abund ~ abuac + **aremf** + pH + **sal** + **silte**	7	-1212.5	2439.6	2.08	0.04
abund ~ abuac + **aremf** + **sal** + **silte** + temp	7	-1212.5	2439.6	2.10	0.04
abund ~ abuac + **aremf** + aref + **sal** + **silte**	7	-1212.5	2439.6	2.10	0.04
abund ~ **aremf** + pH + **sal** + **silte**	6	-1213.6	2439.6	2.11	0.04
abund ~ aref + **aremf** + **sal** + **silte**	6	-1213.6	2439.6	2.14	0.04
RI: aremf = 1; sal = 1; silte = 1					

These fish species have generally been characterized as omnivorous and opportunistic, with rapid growth and short life cycles (Blaber 1997, Contente et al. 2011a,b).

Unlike fish abundance, which was higher upstream of the estuary, the highest richness indices were recorded at sites 5-8. These sites are deeper than the innermost points, with salinity ranging from 15 to 25, and are classified as euhaline and polyhaline (Neto & Lana 1997, Lana et al. 2001, Passos et al. 2013). Higher richness values in estuarine areas under the marine influence have been observed in other estuaries, such as the Mabucaba River, an open tropical estuary in Brazil in Rio de Janeiro (Neves et al. 2010), as well as in open temperate estuaries in the USA, southern New Jersey (Martino & Able 2003), and coastal marine environ-

ments, such as the Lagarto River in Yucatan, Mexico (Vega-Cendejas & Santillana 2004).

Species richness is usually high in regions close to estuary mouths because of the influence of salinity (Elliott et al. 1990, Neves et al. 2010), which favors the occurrence of marine species in these regions under high tide conditions. Therefore, salinity is a key variable influencing fish species richness in estuarine habitats (Elliott et al. 1990). Neves et al. (2010) suggested that salinity could be a driving force that establishes these patterns of higher richness in euryhaline stretches of estuaries, that is, closer to the marine environment. In addition to salinity, bycatch fauna richness was a key predictor variable that influenced the abundance and richness of fish assembla-

Table 3. Selection of generalized linear models for richness (riq) and abundance (abund) of demersal fish with categorical variables as predictors. RI: relative importance of predictor variables. Models with delta AIC > 3 were not shown. Predictor variables with RI > 0.9 are in bold. Akaike's information criteria (AIC).

Models for richness	df	logLik	AICc	delta	weight
riq ~ **site** + year	17	-537.6	1112.3	0.00	0.64
riq ~ **site**	13	-542.9	1113.6	1.36	0.32
RI: site = 1					
Models for abundance	df	logLik	AICc	delta	weight
abund ~ **site** + year	17	-1178.8	2396.7	0.00	0.70
abund ~ **site**	13	-1184.9	2397.7	3.00	0.15
RI: site = 1					
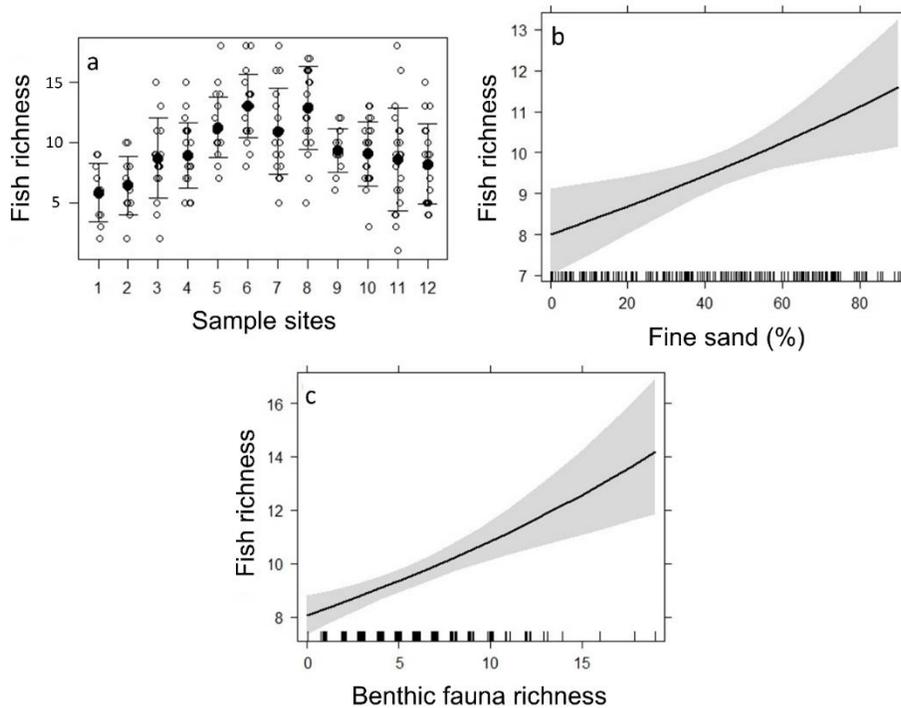
Figure 2. Variables selected (relative importance of predictor variables; RI > 90) to compose the demersal fish richness models. a) Relationship between mean values of demersal fish richness with sampling sites. Circles correspond to samplings (216 in total), filled circles correspond to mean, and up and down intervals correspond to standard deviation, b) relationship between the demersal fish richness with the percentage of fine sand in the sediment, c) relationship between the demersal fish richness with benthic megafauna species richness. In b-c, the solid line represents the relationship between the response variable and the predictor variable, and the shaded part corresponds to the standard deviation.

ges in this study, which was directly related to the abundance and richness of demersal fish. The prey-predator relationships between demersal fish species of the family Sciaenidae that feed on benthic megafauna (shrimp and mollusks) justify the relevance of bycatch fauna richness in the patterns of occurrence of demersal fish species (Camargo & Isaac 2004, Quilez 2014).

From the association of datasets regarding the abundance of demersal fish species and environmental data, the results of the CCA revealed a strong relationship between the families Sciaenidae (represented by five species) and Ariidae (represented by three species) with the mesohaline and euhaline environments of the estuary, owing to salinity levels above 15. In addition, our findings highlight the influence of sedimentary factors, such as the fine sand and silt in these environments, which are intrinsic due to local geomorphology (Cattani & Lamour 2016) and directly re-
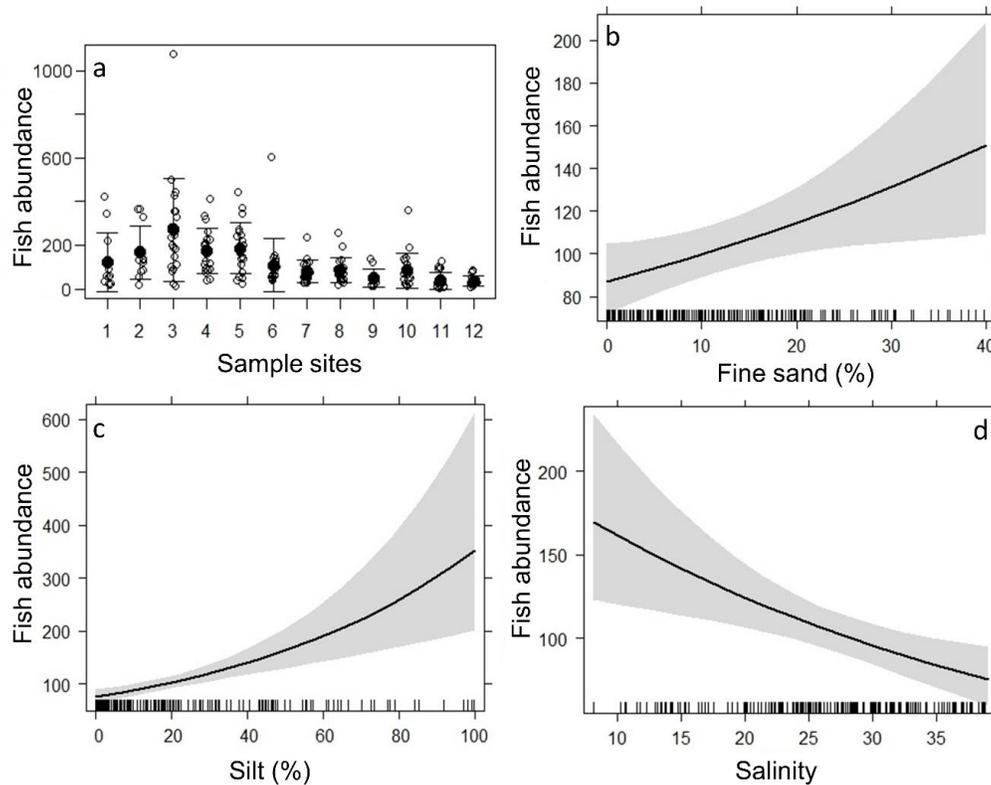
Figure 3. Variables selected (relative importance of predictor variables; RI > 90) to compose demersal fish abundance models. a) Relationship between mean values of the abundance of demersal fish with sampling sites. Circles correspond to samplings (216 in total), filled circles correspond to mean, and up and down intervals correspond to standard deviation, b) relationship between the abundance of demersal fish with the percentage of very fine sand in the sediment, c) the percentage of silt in the sediment, and d) salinity. In b-d, the solid line represents the relationship between the response variable and the predictor variable, and the shaded part corresponds to the standard deviation.

flect on the structuring of these demersal assemblages. The predominance of the families Sciaenidae and Ariidae has previously been related to environments further away from the sea in the Caeté Estuary (Barletta et al. 2005), Sepetiba Bay (Azevedo et al. 2007), and Lagoa dos Patos Estuary (Chao et al. 1982), corroborating our results,

In addition to salinity and the texture variables of the sediment, such as the percentage of fine sand and silt in explaining the distribution of demersal fish species, the variables temperature and dissolved oxygen showed significant values that explained the spatial and temporal distribution of fish species. Based on the redundancy analysis, the variation in the demersal fish matrix explained by the environmental variables was 11.6%. However, in this study, a higher percentage of this variation could be explained as it was directly influenced by biotic variables (21.9%). Therefore, the fish assemblage structure was mainly explained by structuring the bycatch megafauna. The

Atlantic seabob shrimp *Xiphopenaeus kroyeri* presented the highest abundance among all other megafauna species. Atlantic seabob shrimp and other decapod species, such as *Callinectes danae* and *C. ornatus*, are important food resources for fish belonging to the family Sciaenidae (Quilez et al. 2014). Shallower sites may harbor a greater abundance and richness of demersal fish because of the higher abundance of prey, especially juvenile shrimps that seek shallower areas to develop (Andriguetto-Filho et al. 2016), favoring predation by demersal fish.

Temperature and dissolved oxygen are important parameters influencing fish fauna's distribution and occurrence patterns, acting on medium- and short-term temporal scales, respectively (Araújo & Azevedo 2001, Blaber 2002). Despite the relatively low explanation of these variables in the analysis (RDAp), which comprises the pure and shared explanatory power of the environmental and biotic predictor matrices on the distribution of demersal fish species, other variables

Figure 4. Canonical correspondence analysis (CCA) diagram. aref: fine sand in the sediment (%), silt: silt in the sediment (%), aremf: very fine sand in the sediment (%), sal: salinity. Demersal fish species: *Cathorops spixii* (cas), *Stellifer rastrifer* (str), *Symphurus tesselatus* (syt), *Isopisthus parvipinnis* (isp), *Sphoeroides greeleyi* (spg), *Sphoeroides testudineus* (spt), *Chaetodipterus faber* (chf), *Genidens genidens* (geg), *Diplectrum radiale* (dir), *Prionotus punctatus* (prp), *Eucinostomus argenteus* (eua), *Chilomycterus spinosus spinosus* (chs), *Citharichthys arenaceus* (cia), *Ctenosciaena gracilicirrhus* (ctg), *Stellifer brasiliensis* (stb), *Paralonchurus brasiliensis* (pab), *Citharyctis spilopterus* (cis), *Achirus lineatus* (acl), *Cynoscion microlepidotus* (cym), *Menticirrhus americanus* (mea) and *Etropus crossotus* (etc).

Table 4. Results of the redundancy analysis for the demersal fish matrix as a response, also using Akaike's information criteria (AIC). Values in parentheses show i) the percentage of variation in the demersal fish matrix, explained by physical and chemical water, sediment texture, and biotic variables, ii) significance values.

Environmental	Selected variable	AIC	F	*P*
Demersal fish (11.6; 0.001)	% of fine sand in the sediment	-88.22	14.25	0.005
	Salinity	-92.50	6.28	0.005
	Temperature	-93.14	2.61	0.015
	% of silt in the sediment	-93.11	1.93	0.020
	Dissolved oxygen	-93.05	1.85	0.050
Biotic	Selected variable	AIC	F	*P*
Demersal fish (21.9; 0.001)	*Xiphopenaeus kroyeri*	-98.21	25.05	0.005
	Farfantepenaeus brasiliensis	-101.79	5.58	0.005
	Clibanarius vittatus	-103.25	3.42	0.005
	Callinectes sp.	-104.80	3.50	0.005
	Callinectes danae	-106.13	3.26	0.005
	Lolliguncula sp.	-106.60	2.39	0.015
	Hepatus pudibundus	-107.20	2.53	0.010
	Rimapenaeus constrictus	-107.20	1.87	0.015
	Farfantepenaeus paulensis	-107.35	2.10	0.015
	Luidia sp.	-107.38	1.93	0.010
	Callinectes ornatus	-107.76	2.26	0.015

(geochemical, hydrological, and anthropogenic) act synergistically in fish fauna patterns (Mariani 2001).

Considering the complexity of the role of environmental processes in ecological processes, other factors not evaluated in this study may have contributed to the low explanatory values of our purely environmental, purely biotic, and shared variables. The lack of measurements of certain factors, such as environmental disturbances, anthropogenic factors, and ecological interactions, can act as underlying causes in the final explanation, making it difficult to distinguish what is explained by the measured variables of the purely stochastic portion (Borcard et al. 1992).

Our results showed that environmental and biological variables significantly explained the spatial and temporal distribution of abundance and richness of demersal fish assemblages from the Paranaguá Estuary and the adjacent continental shelf.

Considering the results evidenced in the euhaline and polyhaline sectors, which showed greater fish richness and a certain "stability" of the environment, we can infer that these sites have strong resilience, given that these sectors are under a strong anthropogenic influence. Focused attention on the strategic planning of competent bodies in these sectors is required.

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