# Factors influencing spatial patterns of the ichthyofauna of low energy estuarine beaches in southern Brazil

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Estuarine beaches are low energy environments found along the coast in several protected places around the world, such as estuaries, bays or areas protected by submerged bars or coral reefs. Although common, these places have been poorly studied. Using a seine net, six beaches were sampled along an environmental gradient for 12 months. During this period, an increase of the dominant species following the increase in salinity and energy values was observed, whilst the opposite pattern occurred for species richness and abundance. Univariate and multivariate analyses showed spatial and temporal variations between beaches and months. Depth and marginal habitats appear to be more important factors than wave height and period, temperature, salinity and pH, which are normally used to describe fish habitat utilization patterns in beaches and estuaries. Nevertheless, specific sampling designs should be proposed to evaluate properly these questions.

#### Keywords: fish, estuarine beaches, dominance, spatial variation

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## INTRODUCTION

Sandy ocean beaches cover only a small portion of Earth's total surface; and in Brazil, these areas extend along almost all the 9200 km of coastline (Hoefel, 1998). However, low energy sandy beaches are limited to gulfs, bays, barrier protected lagoons, islands protected by reefs or submerged bars and principally estuaries (Nordstrom, 1992; Jackson *et al.*, 2002; Goodfellow & Stephenson, 2005), which are common in southern and south-eastern Brazil (Borzone *et al.*, 2003).

Nordstrom (1992) defines estuarine beaches as sand, gravel or shell beaches located at partially closed places connected to an ocean or sea. In these areas, dominant sediment reworking processes are driven by local waves smaller than 0.25 m (Jackson *et al.*, 2002) with the wave formation centre not further than 50 km (Nordstrom, 1992; Jackson *et al.*, 2002). In addition, beach face widths have to be narrow, measuring less than 20 m in micro-wave regimes, and morphological features must include those inherited by highly energetic events (Jackson *et al.*, 2002). Borzone *et al.* (2003) suggested that these places give rise to a new morphodynamic environment type which is characterized as a transition between wavedominated sandy beaches and tide-dominated flats.

All morphological features generated by beach peculiarities have influenced the biotic communities of beach environments (Brow & McLachlan, 1990; Romer, 1990), and many

**Corresponding author:** C.W. Hackradt Email: hackradtcw@gmail.com studies have been dedicated to investigate their role in the fish life cycle. These investigations found a numerical prevalence of both few species and juvenile individuals (Lasiak, 1984, 1986; Santos & Nash, 1995; Gibson *et al.*, 1993; Clark *et al.*, 1996; Clark, 1997; Strydom, 2003). Most fish remained during short periods in this environment (Gibson *et al.*, 1993) and only a reduced number of species showed annual residence (Brown & McLachlan, 1990). Another important factor in beach environment is the high food availability due to continuous wave action, which makes nutrients available in the water column. This process favours phytoplankton enrichment, and consequently, the planktophagic organisms (McLachlan, 1980).

Previous studies have found greatest fish abundance during warmer months, decreasing with temperature reduction (Modde & Ross, 1981; Ross *et al.*, 1987; Gibson *et al.*, 1993; Santos & Nash, 1995; Clark *et al.*, 1996). These differences are attributed to the effect of the environmental set, such as wind, wave and water temperature (Lamberth *et al.*, 1995). However, some authors have found greatest abundances during spring rather than in the summer, as it was expected (Godefroid *et al.*, 1997; Félix *et al.*, 2007a).

Many authors have studied fish communities at Brazilian beaches. The first studies were focused on understanding spatial and temporal community patterns, characterizing species composition and comparing sites (Cunha, 1981; Paiva-Filho *et al.*, 1987; Monteiro-Neto *et al.*, 1990; Graça Lopes *et al.*, 1993; Monteiro-Neto & Musick, 1994; Giannini & Paiva-Filho, 1995; Saul & Cunningham, 1995; Teixeira & Almeida, 1998; Lopes *et al.*, 1999; Gomes *et al.*, 2003). Most recently, authors have investigated the daily ichthyofaunal variation and the influence of morphodynamic gradients (Gaelzer & Zalmon, 2003; Pessanha & Araújo, 2003).

With respect to the coast of Paraná, beach ichthyofauna is poorly studied, with few dispersed investigations, mainly on local comparisons between sandy beaches (Pinheiro, 1999), temporal variations (Godefroid *et al.*, 1997, 2004), ichthyoplankton (Godefroid *et al.*, 1999) and the influence of morphodynamism on fish community (Félix *et al.*, 2007b). Estuarine beaches were only evaluated based on species composition (Hackradt *et al.*, 2009) and temporal variation (Godefroid *et al.*, 1997; Félix *et al.*, 2006).

Despite the range of advances in studies of different beach environments and the great number of biological assessments at several estuarine habitats, such as mangroves, seagrass beds, tidal flats and water columns, estuarine beaches remain largely unstudied (Nordstrom, 1992; Hoefel, 1998). They are unique environments that differ from sandy beaches by presenting a stable substrate that allows fauna and flora attachment (Nordstrom, 1992). In this context, the aim of the present study is to understand the ichthyofaunal structuring at six estuarine beaches along a salinity–energy gradient inside the largest estuary in southern Brazil.

#### MATERIALS AND METHODS

#### Study area

The Bay of Paranaguá is described as a type B, partially-mixed estuary, with lateral heterogeneity (Knoppers et al., 1987). The estuary penetrates 50 km into the continent, with a mean width of 10 km and an average depth of 5.4 m (Noernberg et al., 2004). The occurrence of a salinity and energy gradient along the east-west axis divides the bay into three zones: (1) an external high energy region with average salinity of about 30, called the euhaline region, which includes the following beaches: Encantadas (EN: 25°33'49.1"S 48°19'05.1"W), Brasília (BR: 25°31′36.4″S 48°20′35.7″W), Coroinha (CO: 25°30'40.9"S 48°22'38.8"W) and Cobras' Island (IC: 25°29'03.1"S 48°25'50.6"W); (2) an intermediary, polyhaline region where Piaçaguera beach is located (PI: 25°29'03.1"S  $48^{\circ}29'40.0''W$ ; and (3) an innermost low energy and salinity region, called the oligo-mesohaline region, with salinity values between zero and 15, where Europinha beach is located (EU: 25°27'39.2"S 48°36'41.1"W) (Figure 1). Usually, waves are originated by south-eastern winds at the estuary mouth region, displaying on average half a metre height and three to seven seconds period duration. In stormy conditions, waves can reach a maximum of 3 m height (Lana et al., 2001).

# Data collection

Fish assemblages at the 6 locations were sampled during daylight hours, between 6.00 and 13.00 h from June 2005 to May 2006, using a beach seine net, 15 m long and 2.6 m height with a stretched mesh size of 5 mm. Three 20-m hauls were made at each site, separated 5 m apart to minimize the influence on the following haul. All sampling campaigns began at neap low tide, following the same beach visiting sequence. Hauls were pulled simultaneously and parallel to the beach face by two persons, one at each end of the net. All fish collected were identified to species level following Figueiredo & Menezes (1978, 1980, 2000) Fischer (1978), Menezes & Figueiredo (1980, 1985) and Barletta & Corrêa (1992). These were then weighed (g) and measured to the nearest 1 mm (total length and standard length), except when samples were very large. On such occasions, measurements were restricted to a subsample of 30 individuals per species. The excess was weighed, counted and incorporated as weight and number counts.

Environmental data were measured concomitantly with beach hauls: surface water salinity (using a refractometer), surface water temperature (through a mercury thermometer), pH (through a portable pH meter), wave height and wave duration. Wave height was taken with a 2-m ruler and obtained from the metric difference between crest and sea level of the largest waves breaking on the surf zone. Wave period was measured from the duration (in seconds) of 11 successive breaking waves divided by 10 to obtain the period of a single wave. This procedure was applied twice to produce an average.

Seasons of the year were defined as follows: summer (December, January and February), autumn (March, April and May), winter (June, July and August) and spring (September, October and November).

## Data analysis

To determine whether species can be classified as dominant, the following criteria have been used: frequency of occurrence in the samples exceeding 10%; abundance exceeding 1%; and, constant occurrence, i.e. present in at least eight collection months.

To test whether the abundance (N), number of species (S), catch weight (P), Margalef's richness (d), Pielou's evenness (J') and Shannon–Wiener diversity (H') were spatio-temporally different, two-way analysis of variance (ANOVA) (Pielou, 1969; Ludwig & Reynolds, 1988) was applied. Before conducting the test, biotic data were tested for homoscedasticity and normality by the Bartlett and Kolmogorov–Smirnov tests, respectively (Sokal & Rohlf, 1995). To fulfil ANOVA assumptions, abundance (N), catch weight (P), Pielou's evenness (J') and Shannon–Wiener diversity index (H') data were transformed by Log(x + 1). When differences were significant (P < 0.05), the *a posteriori* Student–Newman–Keuls test was used to identify which averages were different.

Data on species abundance (log transformed) were converted into similarity matrices using the Bray-Curtis similarity index, with all field points separated by seasons. Following, ANOVA results were displayed on a dendrogram using group average linking (cluster), and an ordination plot, generated by a non-metric multidimensional scaling (MDS) procedure (Clarke & Warwick, 1994). To evaluate the statistical importance of group formation, a similarity analysis (ANOSIM) was performed and, to reveal species contribution to group formation, a similarity of percentages (SIMPER) procedure was conducted subsequently. To evaluate the correlation level between environmental data that best explained fish community patterns, the BIOENV routine was applied.

#### RESULTS

Environmental results showed beach singularities and marked temporal differences. Temperature reached highest values

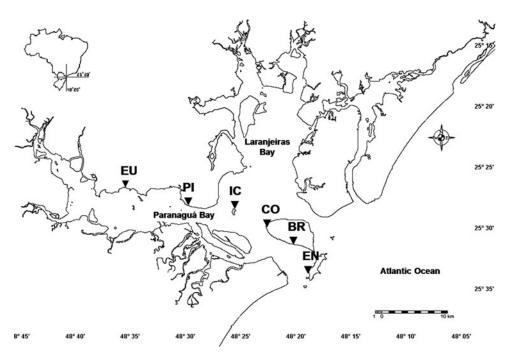


Fig. 1. Paranaguá Bay estuarine complex. Map showing the six studied beaches (EU, Europinha; PI, Piaçaguera; IC, Cobras' Island; CO, Coroinha; BR, Brasília; EN, Encantadas).

during summer months and lowest in early spring, varying equally in space (Figure 2A). Salinity was high during winter and the opposite trend was observed in summer and spring months, with lower values at inner beaches and higher values at outermost areas (Figure 2B). Lowest pH values were found at the most internal beach (Europinha) whilst higher values occurred on beaches at Mel Island (Coroinha, Brasilia and Encantadas). Temporally, larger pH values were registered in November, December and February (Figure 2C). Morphodynamic data, i.e. wave height and period, displayed higher values towards the external beaches and the opposite on the inner beaches. Encantadas showed the highest wave height values (Figure 2D, E) and depth was greatest at Cobras' Island beach (140 cm), followed by Encantadas (90 cm), Brasilia (70 cm), Piaçaguera (65 cm), Coroinha (50 cm) and Europinha (20 cm).

Ichthyofaunal composition was different amongst the studied beaches. Family and species numbers and number of exclusive species were greater at the intermediate sector, Cobras' Island, decreasing in the direction of the outermost beaches, Europinha and Encantadas. Nonetheless, catch weight displayed a reverse trend, with larger values at the outermost beaches. Abundance was greater at Piaçaguera (5281), Europinha (4607) and Cobras' Island (3303) and smallest at Brasilia (1129) (Table 1). Dominance increased gradually in relation to exposure level, except for a high level of dominance found at Piaçaguera beach (Figure 3).

Some beaches have been characterized by dissimilar species occurrences and abundance levels. Although *Mugil* spp. and *Atherinella brasiliensis* have been abundant and common in all beaches, they were more representative at Europinha and Piaçaguera, the latter amounting for 80% of the total catch in number. Nevertheless, the occurrence of *Centropomus pararellus*, *Cathorops spixii*, *Caranx hippos*, *Stellifer stellifer* and *Sardinella brasiliensis* at Europinha and *Scomberomorus* sp., *Microgobius* sp., *Ctenogobius shufeldti* and *Centropomus*  undecimalis at Piaçaguera, illustrate the differential spatial utilization of the studied beaches by the species. A great number of uncommon species was caught at Cobras' Island beach. The species Paralichthys orbignyanus, Achirus lineatus, Ophichthus gomesii, Rhinobatos percellens, Mycteroperca sp., Stephanolepis hispidus, Pomadasys ramosus, Bathygobius soporator, Fistularia tabacaria, Syngnathus elucens and Lagocephalus laevigatus were caught exclusively at this beach. However, at the exposed beaches (Coroinha, Brasilia and Encantadas), only Sphyraena tome; Platanichthys platana and Caranx latus; Umbrina coroides and Sparidae juveniles occurred exclusively there (Table 1).

Month and site (beach) factors were considered fixed in the two-way ANOVA. Abundance, species richness, weight, Margalef richness and Pielou evenness data were significant on factors interaction, whilst Shannon–Wiener diversity differed only amongst months (Table 2). According to *post-hoc* tests, high abundance values were found in February and March, and were different in June and July when lower catches occurred. Spatially higher catches in number, owing to *Atherinella brasiliensis* and *Mugil* spp. captures at Piaçaguera, Cobras' Island and Encantadas, caused them to differ from the others beaches (Figure 4A).

Higher mean weight values were registered during warmer months, which differed statistically from cold ones. Europinha, Piaçaguera and Cobras' Island showed significantly higher average values in December, February, March and May, in contrast to the remaining beaches (Figure 4B). Species richness was always higher in Europinha, Cobras' Island and Encantadas than Piaçaguera and Brasilia, despite the temporal variation, which presented two marked high points, one in September and the second in February and March (Figure 4C).

Ecological indices, Margalef's richness and Pielou's evenness, changed mainly between late winter-early spring and summer due to high contributions from Cobras' Island and

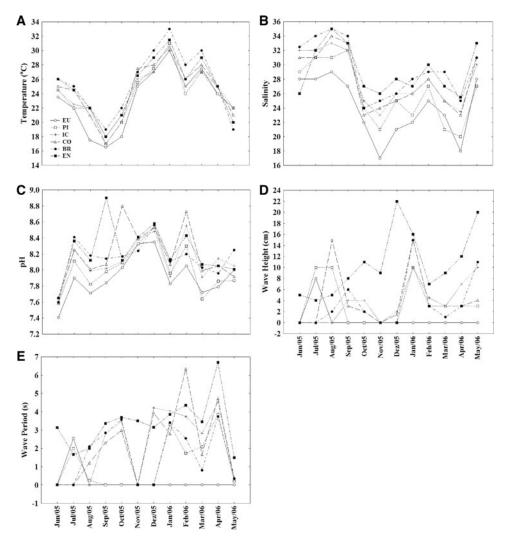


Fig. 2. Environmental data collected at six beaches sampled: (A) temperature in <sup>o</sup>C; (B) salinity; (C) pH; (D) wave height in centimetres; (E) wave period in seconds.

Europinha (Figure 4D, E). Shannon – Wiener diversity indices were only different between months, with spring and summer months distinguished from winter ones (Table 2; Figure 4F).

According to ANOVA results, multivariate analysis was conducted considering months grouped within seasons. Despite high values of stress, four groups were formed in each MDS and cluster combination plots. In winter, under 50% of similarity, groups A and B pooled an inner beach (Europinha) and two outermost locations (Coroinha and Encantadas), respectively, whilst groups C and D included intermediate beaches (Figure 5A). ANOSIM showed low significance levels and correlation, 0.207 (Table 3); but according to species occurrence and abundance indicated by SIMPER, internal similarities were greater than 50%, except for group B (22%). In addition, high dissimilarity percentages were found between groups, principally due to contributions from Cathorops spixii, Anchoa parva, Sphoeroide greeleyi, Atherinella brasiliensis, Anchoa tricolor and Harengula *clupeola* (Table 4).

During spring, minor differentiations were observed; group A included Piaçaguera (September and November) and Cobras' Island (September and October), group B pooled November Europinha and Coroinha with September and October Brasilia. Group C also joined Brasilia (November) and Europiunha (October), and the last group, D, included Encantadas (October and November) and Cobras' Island (November) (Figure 5B). A low correlation level between groups was demonstrated by ANOSIM results (0.253) (Table 3). SIMPER analysis exhibited 45% of internal similarity, with the greatest value (58%) at group B. High dissimilarities between groups (always greater than 65%) were attributed to the occurrence and abundance of engraulid juveniles, A. brasiliensis, Mugil spp., Sphoeroides greeleyi, Sphoeroides testudineus, Menticirrhus americanus, Harengula clupeola and Trachinotus carolinus (Table 4).

Greater segregation between beaches was observed in summer, when a lower stress value was observed (0.16) and confounded Cobras' Island with the remaining beaches. Group A consisted of Piaçaguera, Europinha (December) and Cobras' Island (January). Group B was formed by the February Cobras' Island and Brasília and group C only by Encantadas. Group D pooled intermediate beaches: Cobras' Island (December), Coroinha (January and February) and Brasilia (December and January) (Figure 5C). ANOSIM correlation was also higher, 0.449, with high significance level, 60% (Table 3). More than 50% of internal similarity and dissimilarity between groups were observed on SIMPER results, and *Mugil* spp., *Atherinella brasiliensis, Trachinotus carolinus*,

Table 1. Species abundance, total relative frequency, preferential habitat and species association to coastal habitat caught at the six beaches studied at Paranaguá Bay, Paraná, Brazil (EU, Europinha; PI, Piaçaguera; IC,
Cobras' Island; CO, Coroinha; BR, Brasília; EN, Encantadas; *, dominant species; M, marine; E, estuary; ME, marine and estuary; S, soft bottom; RR, rock reef; WC, water column; ?, information not available; number of
exclusive species and families between parentheses). Species are ordered alphabetically.

Species	Beaches				FR (%)	Estuary association	Preferential habitat				
	EU	PI	IC	СО	BR	EN	Total				
Achirus lineatus (Linnaeus, 1758)			2				2	0.0108	ME	S	
Albula vulpes (Linaeus, 1758)			1	1	12	1	15	0.0812	ME	S	
Anchoa lyolepis (Everman & Marsh, 1902)	155	1					156	0.845	ME	WC	
Anchoa parva (Valenciennes, 1848)	508	200	533	35	1	2	1279	6.9277	ME	WC	
Anchoa tricolor (Spix & Agassiz, 1829)*	274	80	148	3	37	39	581	3.147	ME	WC	
Archosargus rhomboidalis (Linnaeus, 1758)			1	2			3	0.0162	ME	S/RR	
Astroscopus ygraecum (Cuvier, 1829)			1			1	2	0.0108	ME	S	
Atherinella brasiliensis (Quoy & Gaimard, 1825)*	352	2807	1121	567	613	1698	7158	38.7715	Е	S	
Bairdiella ronchus (Cuvier, 1830)		5	5	3			13	0.0704	ME	S	
Bathygobius soporator (Valenciennes, 1837)			3				3	0.0162	ME	S/RR	
Caranx hippos (Linnaeus, 1766)	1						1	0.0054	ME	S/WC	
Caranx latus (Agassiz, 1831)					1		1	0.0054	М	S/WC	
Cathorops spixii (Agassiz, 1829)	38						38	0.2058	Е	?	
Centropomus parallelus (Poey, 1860)	4						4	0.0217	ME	S	
Centropomus undecimalis (Bloch, 1792)		1					1	0.0054	ME	?	
Cetengraulis edentulus (Cuvier, 1829)	1955	115	9	2	15		2096	11.353	ME	WC	
Chaetodipterus faber (Broussonet, 1782)			6	7	10	1	24	0.13	ME	WC	
Chloroscombrus chrysurus (Linnaeus, 1766)			6	90		5	101	0.5471	ME	WC	
Citharichthys arenaceus (Evermann & Marsh, 1900)	17	2	10	1	4		34	0.1842	ME	S	
Citharichthys spilopterus (Günther, 1822)	24	8	4	7	7		50	0.2708	Е	S	
Ctenogobius shufeldti (Jordan & Eigenmann, 1887)		1		,	,		1	0.0054	Е	?	
Cyclichthys spinosus (Linnaeus, 1758)	3	8	3	5	3		22	0.1192	ME	RR	
Diapterus rhombeus (Valenciennes, 1830)	8		3	3		1	15	0.0812	ME	S	
Engraulidae juveniles*	62	124	158	10	36	1	391	2.1179	-	-	
Etropus crossotus (Jordan & Gilbert, 1882)			3	1	8	4	16	0.0867	ME	S	
Eucinostomus argenteus (Baird & Girard, 1855*)	81	34	297	43	107	26	588	3.1849	ME	S	
Eucinostomus melanopterus (Bleeker, 1863)		167	8	1	28	13	217	0.5687	ME	S	
Eucinostomus sp.		4	7			-	11	1.1754	-	-	
Fistularia tabacaria (Linnaeus, 1758)			3				3	0.0162	М	RR	
Genidens genidens (Valenciennes, 1829)	14		2				16	0.0867	Е	?	
Harengula clupeola (Cuvier, 1829)*	35	12	357	344	52	416	1216	6.5865	ME	S	
Hyporhamphus unifasciatus (Ranzani, 1842)	9	4	4		10	86	113	0.6121	ME	WC	
Lagocephalus laevigatus (Linnaeus, 1766)	-		1				1	0.0054	ME	S	
Lycengraulis grossidens (Agassiz, 1829)	15	2	2	3	15		37	0.2004	ME	WC	
Menticirrhus americanus (Linnaeus, 1758)	4	34	16	4	2	8	68	0.3683	ME	S	
Menticirrhus littoralis (Holbrook, 1847)	•	5	2	21	4	25	57	0.3087	М	S	
Microgobius meeki (Evermann & Marsh, 1899)		9	2			2	11	0.0596	E	S	
Microgobius sp.		1					1	0.0054	_	_	
Micropogonias furnieri (Desmaresti, 1823)	2	8	1				11	0.0596	ME	S	

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Species	Beaches								Estuary association	Preferential habita	
	EU	PI	IC	СО	BR	EN	Total				
Mugil spp.*	434	1529	188	434	11	17	2613	14.1534	_	_	
Mycteroperca sp.			1				1	0.0108	-	-	
Oligoplites saliens (Bloch, 1793)	8	9	7	53			77	0.4171	ME	S/WC	
Oligoplites saurus (Bloch & Schnider, 1801)	6	3	8	1	6	4	28	0.1517	ME	WC	
Ophichthus gomesii (Castelnau, 1855)			1				1	0.0054	М	S/RR	
Ophistonema oglinum (Lesueur, 1818)	3	1	1		1		6	0.0325	М	S/WC	
Paralichthys orbignyanus (Valenciennes, 1842)			1				1	0.0054	ME	S	
Platanichthys platana (Regan, 1917)					5		5	0.0271	Е	?	
Pomadasys corvinaeformis (Steindachner, 1868)		3	5	1	7	3	19	0.1029	ME	S/RR	
Pomadasys ramosus (Steindachner, 1868)			2				2	0.0108	ME	S/RR	
Prionotus nudigula (Ginsburg, 1950)			2		1		3	0.0162	М	S	
Rhinobatos percellens (Walbaum, 1792)			1				1	0.0054	М	S	
Sardinella brasiliensis (Steindachner, 1879)		3		233			236	1.2783	М	WC	
Scomberomorus sp.		2					2	0.0108	-	_	
Selene vomer (Linnaeus, 1758)			3	1			4	0.0217	ME	S/WC	
Sparidae juveniles			0			47	47	0.2546	-	_	
Sphoeroides greeleyi (Gilbert, 1900*)	4	41	128	21	40	3	237	1.2837	ME	S/RR	
Sphoeroides testudineus (Linnaeus, 1758)	14	. 9	4	55	7	1	90	0.4875	Е	S	
Sphyraena tome (Fowler, 1903)		2	·	1	,		1	0.0054	М	WC	
Stellifer brasiliensis (Schultz, 1945)	3						3	0.0162	ME	S	
Stellifer rastrifer (Jordan, 1889)	2		3				5	0.0271	ME	S	
Stellifer stellifer (Bloch, 1790)	17		5				17	0.0921	ME	S	
Stephanolepis hispidus (Linnaeus, 1766)	,		3				3	0.0162	М	S/RR	
Strongylura marina (Walbaum, 1792)	5	2	5			1	13	0.0704	ME	RR	
Strongylura sp.	7	3	,		2	6	18	0.0975	-	_	
Strongylura timucu (Walbaum, 1792)	/	1	1		-	9	11	0.0596	ME	RR	
Symphurus tesselatus (Quoy & Gaimard, 1824)	1	-	-			,	2	0.0108	ME	S	
Syngnathus elucens (Poey, 1868)	-		1				1	0.0054	M	RR	
Syngnathus folletti (Herald, 1942)		1	2				3	0.0162	M	RR	
Syngnatus pelagicus (Linnaeus, 1758)		2	5		1		8	0.0433	M	RR	
Synodus foetens (Linnaeus, 1766)		5	4	4	43	4	60	0.325	M	RR	
Trachinotus carolinus (Linnaeus, 1766)*		17	76	4 84	43 29	136	342	1.8525	ME	S	
Trachinotus falcatus (Linnaeus, 1758)	2	16	29	17	11	26	101	0.5471	ME	S	
Trachinotus goodei (Jordan & Evermann, 1896)	2	10	-9	1	11	26	27	0.1462	M	s/wc	
Ulaema lefroyi (Goode, 1874)			102	1		20	105	0.0596	M	S	
Umbrina canosai (Berg, 1895)		2	102	1		2	4	0.0390	M	S	
Umbrina coroides (Cuvier, 1830)		2				8	4 8	0.0433	ME	S	
Total catch	4067	5281	3303	2060	1129	2622	18462	100	11111	0	
Number of families	16 (0)	19 (1)	30 (6)	16 (1)	19 (0)	18 (0)	32				
Number of species	34 (5)	42 (4)	58 (11)	36 (1)	33 (2)	33 (2)	76				
Catch weight (Kg)	15.44	9.78	13.02	11.37	7.16	15.60	72.37				

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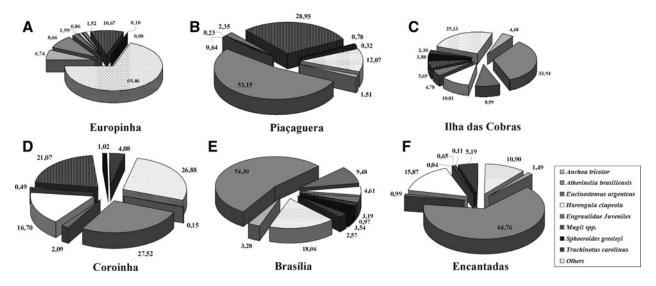


Fig. 3. Dominant species proportion in each of the six beaches studied at Paranaguá Bay, Paraná, Brazil.

*Eucinostomus argenteus, Sphoeroides greeleyi* and *Hyporhamphus unifasciatus* were the species that most contributed to this pattern (Table 4).

In contrast to summer, autumn was the season when grouping of the beaches was more pronounced and a distinction between internal and external beaches could be noted.

Table 2. Analysis of variance of factors influencing the biotic variables. Factors analysed: months, sites and factor interaction. ns, non-significant.

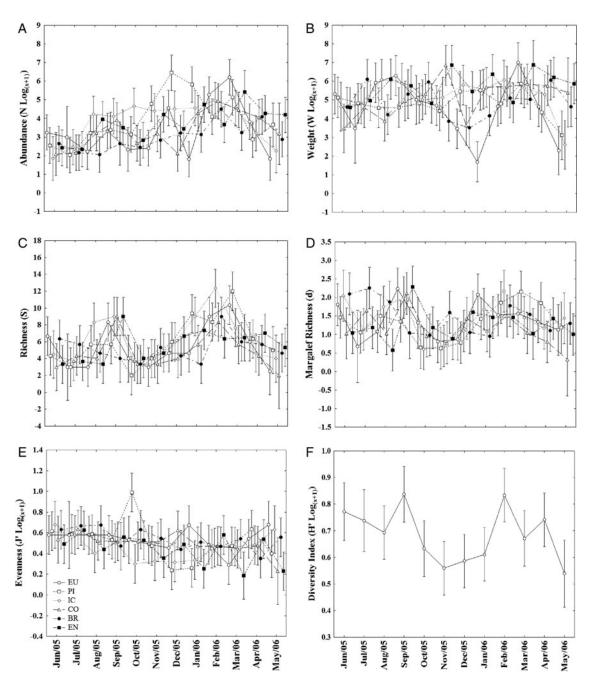
Factors	df	SS	MS	F	Р
Abundance (N Log <sub>(x+1)</sub> )					
Months	11	104.24	9.48	13.59	P < 0.05
Sites	5	22.13	4.43	6.34	P < 0.05
Months $\times$ sites	55	116.23	2.11	3.03	P < 0.05
Error	132	92.06	0.70		
Weight (W Log <sub>(x+1)</sub> )					
Months	11	44.95	4.09	4.72	P < 0.05
Sites	5	27.85	5.57	6.43	P < 0.05
Months $\times$ sites	55	142.15	2.58	2.98	P < 0.05
Error	132	114.37	0.87		
Richness (S)					
Months	11	589.72	53.61	13.53	P < 0.05
Sites	5	54.12	10.83	2.73	P < 0.05
Months $\times$ sites	55	416.70	7.58	1.91	P < 0.05
Error	132	522.83	3.96		
Margalef richness (d)					
Months	11	15.75	1.43	5.90	P < 0.05
Sites	5	2.25	0.45	1.85	ns
Months $\times$ sites	55	24.71	0.45	1.85	P < 0.05
Error	132	32.02	0.24		
Pielou evenness $(J' \text{ Log}_{(x+1)})$					
Months	11	0.89	0.08	3.04	P < 0.05
Sites	5	0.30	0.06	2.27	ns
Months $\times$ sites	55	2.26	0.04	1.54	P < 0.05
Error	132	3.51	0.03		
Shannon–Wiener diversity index $(H' Log_{(x+1)})$					
Months	11	1.844	0.168	3.603	P < 0.05
Sites	5	0.310	0.062	1.333	ns
Months $\times$ sites	55	3.618	0.062	1.414	ns
Error	132	6.140	0.047		

Group A joined Encantadas (March and May); group B included samples of all beaches and both groups C and D aggregated Europinha in April and May, and Piaçaguera in March (Figure 5D). Lowest levels of significance (14%) and correlation (0.223) were found according to ANOSIM (Table 3). However, inner similarities and dissimilarities between groups were all around 60%, when occurrence and abundance of *Anchoa parva, Mugil* spp., *Anchoa tricolor, Eucinostomus argenteus, Atherinella brasiliensis, Harengula clupeola, Trachinotus falcatus, Trachinotus carolinus, Strongylura timucu, Trachinotus goodei* and *Cetengraulis edentulus* were responsible for the grouping (Table 4). The latter was particularly important due to a single catch with more than 1900 individuals at Europinha in March.

The BIOENV routine was used to compare environmental data with abundance and distribution of species at the beaches studied. Despite low correlation values displayed by the BIOENV results, the best variable that explained 21% of data variation was depth. Temperature was the second variable that might have influenced species pattern; other variables, when present, decreased the correlation value owing to their negative correlation with biotic data (Table 5).

## DISCUSSION

Romer (1990) showed that abundance and diversity are inversely proportional compared to beach exposure degree. However, other factors may affect the fish communities in shallow environments, for instance the availability of microhabitats (Clark *et al.*, 1996), e.g. leafy accumulation and submerged vegetation, which increase fish abundance. Cobras' Island beach provided the highest number of families and species. The most probable explanation for this pattern is the presence of distinct adjacent environments, such as rocky coastlines on both sides of the beach and a greater depth, which according to Suda *et al.* (2002) promote an increase in number of individuals and species. In addition, that beach presented the only record of typical rocky reef species such as *Fistularia tabacaria, Ophichthus gomesii, Mycteroperca* sp. and *Stephanolepis hispidus*, which



**Fig. 4.** Analysis of variance plots displaying only significant results for the variables studied. (A) Abundance (log transformed); (B) catch weight (log transformed); (C) number of species (richness) and the ecological indices; (D) Margalef richness; (E) Pielou eveness (log transformed); (F) Shannon–Wiener diversity index (log transformed).

corroborate the micro-habitat influence hypothesis. This influence is normally linked to small beach width, which attracts species from adjacent habitats, and to morphology, which in the case of Cobras' Island concentrates individuals in the centre of the bay as a result of the shape configuration (Gibson, 1973; Suda *et al.*, 2002).

The species *Cathorops spixii* and *Centropomus undecimalis* (exclusively captured at Europinha beach), the large number of soles captured, *Citharichthys spilopterus* and *Citharichthys arenaceus*, and the additional records of *Genidens genidens*, *Stellifer rastrifer* and *Centropomus parallelus*, showed the influence of mudflats on this beach which was expressed by the presence of typical estuarine species (Gomes *et al.*, 2003). Despite the existence of mudflats on the other

beaches, its large extension and composition seem to have greater influence on species composition than beach profile alone.

Although captured on almost all beaches studied, the carangid species *Trachinotus carolinus* and *Trachinotus falcatus* were more abundant at Cobras' Island, Coroinha, Brasília and Encantadas, whilst *Trachinotus goodei* was only associated with Brasília and Encantadas. These are recognized as sandy beach species (Modde, 1980) and thus, beaches closer to the bay entrance show greater similarity with adjacent oceanic beaches. *Trachinotus falcatus* has already been recorded in the innermost areas of the estuarine complex, in the oligohaline sector of the Antonina Bay (Spach *et al.*, 2006), whilst the other species of the genus seem to be

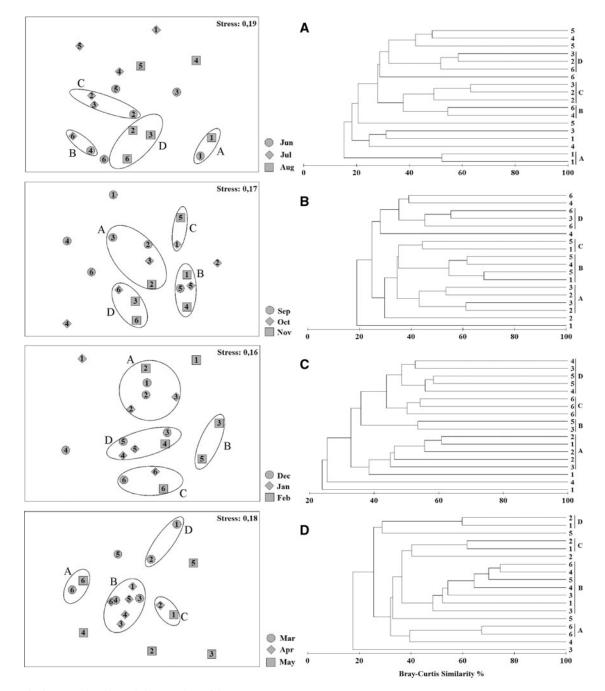


Fig. 5. Multi-dimensional scaling and cluster analysis of the seasons (A, winter; B, spring; C, summer; D, autumm).

restricted to the outermost areas (Vendel *et al.*, 2003; Spach *et al.*, 2004).

The beaches studied showed dominance of few species according to the criteria determined in this study, which is

 Table 3. Analysis of similarities results showing global R values and significance levels for each season.

	Global R	Significance level
Winter	0.207	48%
Spring	0.253	33%
Summer	0.449	60%
Autumn	0.223	14%

expected for beach environments (McFarland, 1963; Modde & Ross, 1981; Ross *et al.*, 1987; Santos & Nash, 1995; Godefroid *et al.*, 2004) and shallow estuarine areas (Kennish, 1986; Santos *et al.*, 2002). Worldwide studies on sandy beaches demonstrated that dominance increases proportionally with increases in exposure to energy gradient (Romer, 1990; Clark *et al.*, 1994; Clark, 1997; Gaelzer & Zalmon, 2003). This was evidenced by the increase in exposure levels towards beaches next to Paranaguá bay entrance and the concomitant dominance increase. Although Piaçaguera beach is located in front of Paranaguá harbour (and, therefore, in an intermediary position in relation to the degree of exposure) a high dominance was detected. This factor could be explained by

Season	Similarity %				Dissimila	arity %				
Winter	Α	В	С	D	$A \times B$	A × C	$A \times D$	$B \times C$	$B \times D$	C × D
	52.22	22.68	53.87	54.03	90.20	85.14	74.76	66.95	71.61	67.20
C. spixii	39.27				15.62	14.51	11.84			
A. parva	31.91				14.56	13.59				
S. greeleyi			38.90			12.07		16.72		
A. brasiliensis		100	36.61	34.41			13.43			
A. tricolor				20.08			12.35		15.49	14.99
H. clupeola				19.50			12.30		11.83	15.01
Spring	Α	В	С	D	$\mathbf{A} \times \mathbf{B}$	$A \times C$	$A \times D$	$B \times C$	$B \times D$	C × D
	47.85	58.02	44.34	48.63	65.20	65.93	65.12	64.85	66.77	71.48
Engraulidae juveniles			38.27			11.43		19.79		13.75
A. brasiliensis	43.42	55.47	23.46	37.01		15.19		10.71		
Mugil spp.	21.31		23.46		17.37	10.52	10.74	12.70		
S. greeleyi		23.11	14.80							
S. testudineus		12.85						11.06		
M. americanus	12.39									
H. clupeola				38.88			14.62		22.75	20.30
T. carolinus									11.11	10.47
Summer	Α	В	С	D	$\mathbf{A} \times \mathbf{B}$	$\mathbf{A} \times \mathbf{C}$	$A \times D$	$B \times C$	$B \times D$	C × D
	52.84	54.53	43.70	54.20	71.57	67.54	55.57	64.86	62.78	55.76
Mugil spp.	41.85			15.10	15.03	16.79	14.16			
A. brasiliensis	40.05	23.55	47.77	53.67						
T. carolinus			21.16	15.08		12.93	10.21			11.97
E. argenteus		31.63			14.43			13.84	16.89	
S. greeleyi		10.63								
H. unifasciatus			10.21							
Autumn	Α	В	С	D	$A \times B$	$\mathbf{A} \times \mathbf{C}$	$A \times D$	$B \times C$	$B \times D$	C × D
	67.24	55.97	61.63	59.72	63.36	79.42	79.83	59.91	71.54	65.28
A. parva			28.14	22.21			12.01	11.24	10.85	10.18
Mugil spp.			10.02	20.25						
A. tricolor				17.37						12.84
E. argenteus		13.59	20.05	10.92						
A. brasiliensis	49.93	35.47	25.91			17.49		11.33		
H. clupeola		34.50			16.40			21.96	10.15	
T. falcatus			15.89							
T. carolinus	12.52					10.15				
S. timucu	12.52									
T. goodei	12.52									
C. edentulus										11.16

 Table 4. Similarity percentage (SIMPER) analysis within and between groups formed by cluster and multidimensional scaling plots showing the species that most contributed to similarities and dissimilarities, and their respective proportions.

the removal of rare individuals from the population (Clarke & Warwick, 1994) due to stress resulting from harbour activities.

Table 5. BIOENV results showing the best variables that explain abundance and distribution of species caught at the six estuarine beaches studied.

Number of variables	Correlation	Selection variables
1	0.216	Depth
2	0.237	Temperature; depth
2	0.213	pH; depth
2	0.207	Salinity; depth
3	0.236	Temperature; pH; depth
3	0.230	Temperature; salinity; depth
3	0.208	Salinity; pH; depth
3	0.205	Temperature; wave period; depth
4	0.231	Temperature; salinity; pH; depth
4	0.202	Temperature; pH; wave period; depth

Analyses of weight, number of individuals and species and ecological indices data showed distinctions between the beaches in time and space. Notable differences occurred between the seasons, and summer showed the greatest captures in abundance and number of species. Such a pattern could be associated with the congruence of the reproductive period of many species and the great availability of food provided by an increase in the plankton (the base of the food chain), making more food available for plankton feeders (Kennish, 1986). Weight varied considerably due to the capture of large-sized samples at the deepest beaches and to the sporadic catch of large shoals. Margalef's richness and Pielou's evenness varied in temporal and spatial scales, owing to a greater heterogeneity in assemblage distribution during winter and spring (Nash & Santos, 1998). However, Shannon-Wiener diversity only displayed temporal differences due to the fluctuation in species number and abundance between the seasons. In fact, the dominant species are always the same, only alternating their rank position in frequency,

abundance and weight (Modde & Ross, 1981). As a result, the more stable an environment is the stronger the trend for higher values of diversity and evenness (Dexter, 1984).

Owing to ANOVA results, a multivariate analysis was conducted by grouping sampled months into seasons. Further evidence that corroborated the spatial variability amongst the beaches studied was from the multidimensional scaling analysis which revealed a general tendency in the beach groups. Europinha and Encantadas were distinct from the remaining beaches, with the former being more similar in species composition to other tidal flats studied throughout the estuary (Santos *et al.*, 2002; Vendel *et al.*, 2002) and the latter showing an ichthyofauna similar to those described on the adjacent oceanic beaches (Godefroid *et al.*, 2004; Félix *et al.*, 2007a).

In spite of the spatial and temporal distinctions in the two analyses conducted, one factor should be taken into consideration when interpreting these differences. The random catch of the fishing gear could influence the results of the uni- and multivariate analyses, reflecting in grouping of some hauls from different beaches in certain sampling months. A further interesting factor is the elevated stress observed in the ordination analysis, which suggests that the graphic distances may not adequately represent the original similarities. Due to data logarithmic transformations, the actual differences or the lack of them may have been further masked. ANOSIM has also shown low correlation values between formed groups, with summer being an exception. Nevertheless, even considering the factors mentioned above, the beaches behaved differently and they were distinct for most of the time.

Abrupt variations in salinity, temperature, oxygen and turbidity are common in estuarine regions and are caused by the influence of tides and mixture between fresh and seawater (Kennish, 1986). The rapid variations in physical, chemical and biological properties require a great demand of energy for biological components from these locations (Day et al., 1989). A tendency for higher values of the abiotic factors towards the bay entrance was observed in the studied areas. According to the results of the BIOENV analysis used to explain that the ichthyofaunal raise composition and distribution in relation to the environmental variables, we observed that amongst the variables analysed, those providing the most expressive contribution in small scale were depth and temperature. However, additional data on beach profile and its comparison to morphodynamic data are necessary to improve our understanding of the environmental influence on the ichthyofauna of low energy beaches.

In general, spatial differences found between beaches in this study could be explained by a sum of factors. The morphodynamic characteristics that figure as fundamental in fish community structure in oceanic beaches (Dye et al., 1981; Lasiak, 1984; Romer, 1990; Clark et al., 1994, 1996; Clark, 1997) may be considered secondary in estuarine beaches. Nonetheless, these characteristics should not be disregarded since beaches displayed differences in species occurrence and occupation patterns, and the factors describing beach environments may have influenced that variation. Factors such as high wave heights and periods on external beaches (Romer, 1990; Gaelzer & Zalmon, 2003; Félix et al., 2007b) may create an energy-gradient, which increases towards the bay entrance direction (Lana et al., 2001). However, differences on beach features seem to be the main factors influencing the ichthyofauna, because the energy of oligohaline and mesohaline regions has shown limited influence. Moreover, depth showed significant differences on species distribution.

Another factor that might be influencing is the presence of adjacent habitats like rocky coasts and muddy flats (Clark *et al.*, 1996; Suda *et al.*, 2002). Different features like adjacent habitat influence, distinct substrate composition and human activities appear to have a great potential to influence the beaches studied. However, to make any conclusion on which factors truly determine the observed patterns and how much they influence, sampling schemes designed to solve the influence of factors must be properly planned and the use of spatial replicates should be emphasized (Underwood, 1997).

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