

ORIGINAL ARTICLE

Short-term dynamics in fish assemblage structure on a sheltered sandy beach in Guanabara Bay, Southeastern Brazil

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Keywords

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Abstract

Short-term dynamics in juvenile fish assemblage structure were studied to test whether the most abundant species show temporal segregation, in order to assess whether selected environmental variables could predict species groupings, and to examine the stability of sunset–day–sunrise–night differences. Samplings were collected at 3-h intervals over 48 h on a seasonal basis between spring 2005 and winter 2006. Fish species richness and abundance were higher in spring, and the lowest values occurred in winter. *Harengula clupeola* occurred mainly in spring, whereas *Atherinella brasiliensis* peaked in summer and autumn. On the other hand, *Trachinotus carolinus*, *Umbrina coroides* and *Mugil liza* were abundant in winter. Although temperature, salinity and dissolved oxygen were not found to have a strong effect on the abundance patterns of most species, they did appear to have a significant influence on assemblage groupings, according to canonical correspondence analysis and Spearman rank correlation. There is no consistency of diel usage patterns by a given species across seasons. The relative abundance differed between the time of day, which differed among the seasons; this further complicates an understanding of the dynamics of an assemblage. Studies of diel changes that pooled the sampling period as day or night can miss important changes that occur in a short time scale, such as a 3-h period.

Fishes inhabiting sandy beaches show seasonal variations (McFarland 1963), mostly due to movements into and out of such areas (Ross 1986; Ross *et al.* 1987; Gibson *et al.* 1993; Lamberth *et al.* 1995; Potter *et al.* 2001). Seasonal reproduction cycles of coastal fish species are adapted to maximize the use of available resources (Vazzoler 1996) and fluctuation in fish abundance throughout the year has been commonly attributed to shifts in recruitment peaks (Reina-Hervas & Serrano 1987; Gibson *et al.* 1993; Lazzari *et al.* 1999; Mariani 2001), or to species interacting with environmental variables (Ayvazian & Hyndes 1995; Potter *et al.* 2001).

In sandy beaches there is usually a distinct periodicity to the catch rate over 24-h periods (Lasiak 1984; Wright 1989; Nash & Santos 1998). Only a limited number of studies to date have examined the day/night catches for a 24-h period, and no information is available for a complete 48-h period, when one can better assess the degree of short-term stability in assemblage structure. Most studies generally involved discontinuous or spot observation/sampling rather than quantitative observation over continuous diel cycles. Therefore, there is a dearth of information on the dynamics of sandy beach fish assemblages on the temporal scale of 3 h. Complex environment

constraints and biotic interaction can result in changes in the structure of fish assemblages throughout the diel cycle (Allen *et al.* 1983). Some species appear to undergo a change in capture rate depending on the period of the day and analyses of photoperiod day *versus* night can miss important variations that occur over a shorter time, such as the sunset or sunrise or even shorter time scale (Eriksson 1978; Muller 1978).

Spatial and temporal variability in water variables, such as temperature, salinity and dissolved oxygen, can directly influence fish abundance, distribution/migration, and species composition, while indirectly affecting them through modifications of prey–predator relationships and competition (Jung & Houde 2003). It seems likely that temperature either directly or indirectly (*i.e.* by influencing the timing of spawning), is a major factor of seasonal surf-zone dynamics in temperate zones (Layman 2000). Decreases in salinity can increase fish density, as small amounts of estuarine water entering the surf zone can attract estuary-dependent larval and early juvenile fishes (Blaber 2000). Dissolved oxygen affects species distribution, with many marine fish becoming stressed at dissolved oxygen levels of $<4.5 \text{ mg}\cdot\text{l}^{-1}$ (Davis 1975; Poxton & Allouse 1982). Thus, low levels of dissolved oxygen will affect the species composition through the tolerance limits of the different species, although the synergistic effects of other variables, *e.g.* high temperature, will influence those tolerance limits.

The objective of this work is to describe the composition and structure of fish assemblage at Flamengo beach and to test the hypothesis that the most abundant species show temporal segregation throughout the year. Additionally, we examine the variability of fish community over a 48-h period to assess diel stability in the assemblage and changes in the catch rates of individual species that contribute to change in structure. Specifically, this study aims to determine: (i) the patterns of species composition, species richness, abundance and biomass of the fish assemblage on a tropical sandy beach throughout the year; (ii) whether the species composition and/or relative abundance of members of this fish assemblage differ on a short time scale (3-h) over a 48-h period; (iii) whether selected environmental variables may be used to predict species groupings.

Materials and Methods

Study area

Guanabara Bay (Fig. 1) is located on the coast of the state of Rio de Janeiro ($22^{\circ}50' \text{ S}$, $43^{\circ}10' \text{ W}$). The bay is 36 km long, with a mean depth of 7.6 m, reaching 30 m in the entrance channel; the total water volume is $3 \times 10^9 \text{ m}^3$

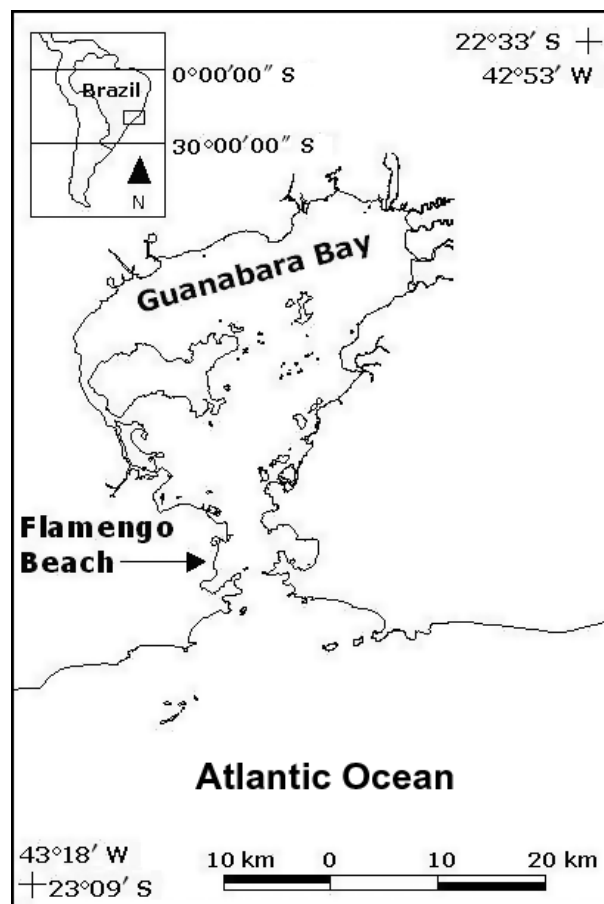


Fig. 1. Map of the Guanabara Bay, Brazil, with location of the study area, Flamengo beach.

(Amador 1997). Substrate is predominantly muddy. The estimated renewal time of 50% of the bay water volume is 11.4 days (Kjerfve *et al.* 1997). The region has a microtidal regime and semi-diurnal tides, with low amplitude and 0.7 m of mean variation. Tidal currents account for most circulation within Guanabara Bay with maximum currents attaining $1.6 \text{ m}\cdot\text{s}^{-1}$ (FEEMA/JICA 1994). The climate is humid-tropical (Kjerfve *et al.* 1997) with a warm rainy season (December–March) and a cool dry season (July–August) (Mayr *et al.* 1989; Paranhos & Mayr 1993). The mean annual air temperature is $23.7 \text{ }^{\circ}\text{C}$ and the salinity ranges from 21.0 to 34.5 (Kjerfve *et al.* 1997). The bay is surrounded by one of the largest metropolitan areas in Brazil, with more than 11 million inhabitants. The degraded bay environment can be divided into five sectors according to water quality, determined by pollution foci and circulation patterns (Villac *et al.* 1991). Water quality is poorest towards the inner bay, while the well-mixed channel area, where sampling was conducted, has the best water quality.

Field sampling

Sampling was performed at Flamengo beach (22°55' S, 43°10' W) on a seasonal basis (*i.e.* October 2005, January 2006, April 2006 and July 2006) (Fig. 1). The fish assemblages were sampled using a beach seine net (10.0 × 2.0 m; 7-mm mesh size). The net was fitted with 30-m hauling ropes and set perpendicular to the shore at approximately 1.5 m depth. Seine hauls were performed by two persons, one on each end of the rope, covering an extension of approximately 30 m; hauling lasted an average of 10 min. The distance seined and the time required for each haul were standardized, thus allowing comparison among collections. The total sampled area was taken to be the distance the net was laid offshore multiplied by the mean width of the haul, resulting in an effective fishing area of approximately 300 m². This procedure was replicated three times during each 3-h interval throughout the 48-h period, each separated by at least 50 m and no more than 100 m. Samples were collected at eight periods of the day: before/after sunrise; before/after noon; before/after sunset; and before/after midnight. This design resulted in 192 samples: two days, eight samples per day, and three replicates for each of four seasons. All samples were taken during spring tide, near to the full moon. Seine operations were conducted taking care not to repeat coverage of the same area. This sampling strategy, which covered all tidal states and two complete diel cycles, provides an adequate description of the fish assemblage and their short-term changes.

Water temperature, dissolved oxygen and salinity were measured at every seine haul at approximately 0.5 m below surface water using a Horiba W-21 multiparametric probe. Fish were fixed in 10% formalin (in the field), and subsequently identified to the species level, counted, measured (total length in millimeters) and weighed (g) in the laboratory.

Data analysis

Logarithmic transformations [$\log_{10}(x + 1)$] of both environmental variables and fish abundance (number and biomass) data were performed to meet assumptions of normality and homoscedasticity for statistical tests and to reduce the bias of abundant species. Analyses of variance (ANOVA) were used to test for differences in the number of individuals and biomass, species richness and environmental variables among seasons. ANOVA was also used to test for differences in densities of selected fish species among the periods of the day for each season. An *a posteriori* comparison of means was performed using the Tukey test. Principal components analysis (PCA) was applied on environmental parameters.

A bi-plot of component scores was performed to detect patterns.

Multivariate analyses of fish community data were performed using the ANOSIM, MDS and SIMPER procedures in the PRIMER software package, version 5.2 (Field *et al.* 1982; Clarke 1993). Briefly, the numerical abundance data were root–root transformed and converted into a triangular matrix of similarities between all seasons, using the Bray–Curtis similarity coefficient. The results of this procedure were displayed on an ordination plot, generated by a non-metric multidimensional scaling procedure to assess seasonal variation. The degree of diel stability in assemblage structure was examined using ANOSIM and SIMPER procedures to compare adjacent periods of the day for each season. The principal species responsible for the sample groupings, and for the discrimination between specified groupings in these analyses, were identified using the SIMPER routine (Clarke 1993); those that showed a significant difference according to the period of the day, according to ANOVA, were analysed.

The influences of environmental factors on the characteristics of the fish assemblage were analysed using canonical correspondence analysis (ter Braak & Verdonschot 1995) and Spearman rank correlation. Rare species, *e.g.* those that constituted a low percentage of the fish assemblage (<0.1% of the total number) were not considered in this multivariate analyses.

Results

Environmental variables

Seawater temperatures showed a clear annual cycle, ranging from a minimum of 20.5 °C in winter to a maximum of 26.0 °C in summer (Fig. 2). Significant differences were detected among seasons, with higher values in summer–autumn and lower values in winter ($F = 105.44$; $P < 0.001$). Salinity varied between a minimum of 30 and a maximum of 35. Significant differences were detected among seasons, with higher values in autumn and lower values in spring ($F = 450.4$; $P < 0.001$) (Fig. 2). Dissolved oxygen ranged from 2.01 to 9.93 mg·l⁻¹ and significant differences were detected among seasons ($F = 41.44$; $P < 0.001$), with the highest values recorded in spring and winter and the lowest values in summer (Fig. 2).

PCA revealed two components obtained by the analysis of the three environmental variables, with eigenvalues exceeding 1.0, explaining 86.91% of the total variance. Component I (Env I) presented negative weight for dissolved oxygen. Component II (Env II) presented positive weight for temperature and negative weight for salinity. When plotting the sample scores, PCA produced

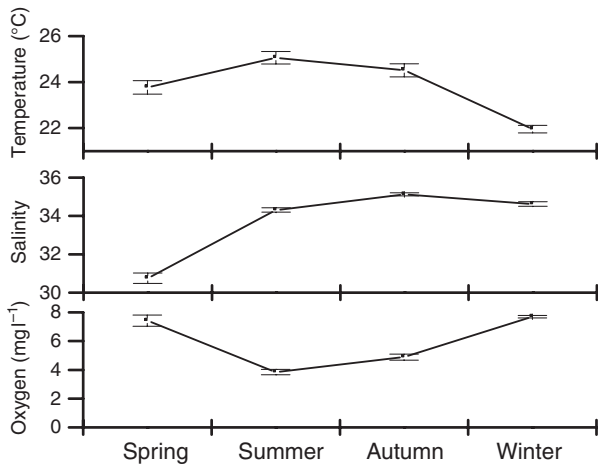


Fig. 2. Mean seasonal variation of the three selected environmental variables (vertical bars represent standard errors).

a distinctive clockwise spread pattern for the seasonal series (Fig. 3). A cycle was indicated, beginning with spring samples on the upper side (lower salinity levels) running across to the right with summer samples (high temperature and salinity and low dissolved oxygen), and then to the lower middle with autumn samples (high salinity and low dissolved oxygen). The cycle was completed with winter samples on the lower left side (low temperature and high dissolved oxygen).

Species composition and abundance

Sixty-three species were caught, yielding 25,788 fish or 78,008.9 g (Table 1) in the 192 beach-seine hauls. *Harengula clupeola*, *Atherinella brasiliensis*, *Pomatomus saltatrix*, *Trachinotus carolinus*, *Umbrina coroides*, *Sardinella janeiro* and *Anchoa lyoleps* were the seven most abundant species, accounting for 96.07% and 90.52% of the total number and biomass, respectively, with a clear dominance of

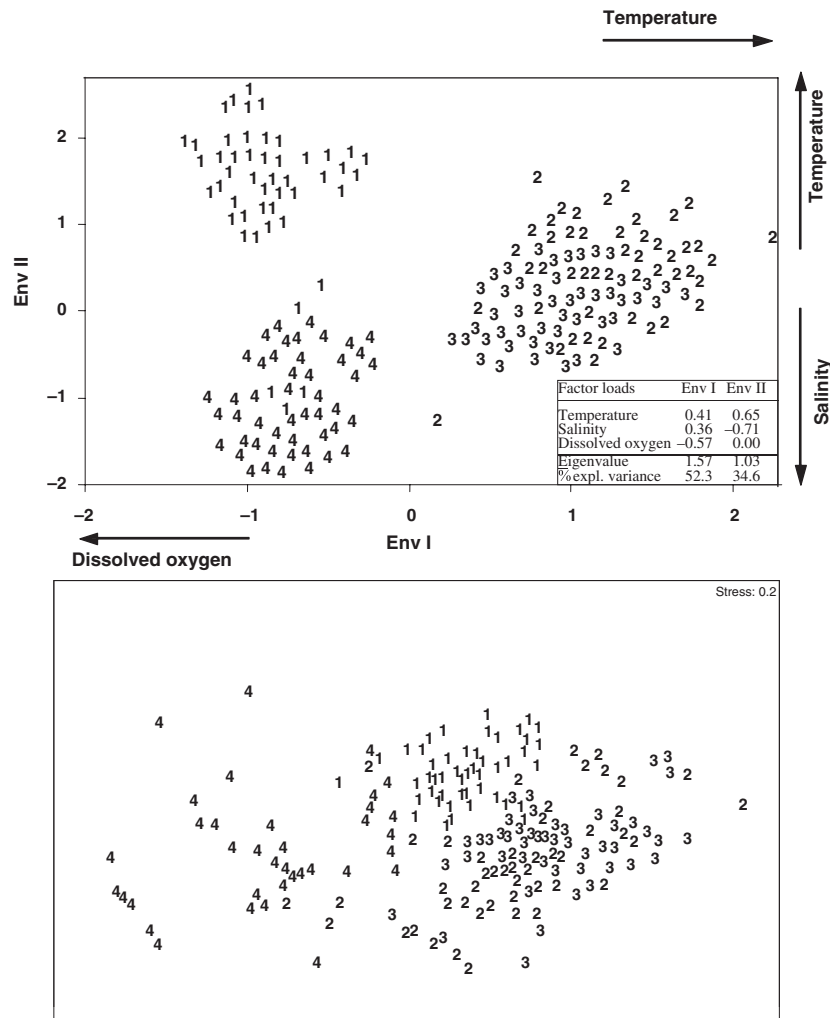


Fig. 3. Ordination diagram for principal components analysis on environmental variables (above) and non-metric dimensional scaling (n-MDS) ordination of fish assemblage structure based on similarity matrix among seasons (below). Seasons: 1 – spring; 2 – summer; 3 – autumn; 4 – winter.

Table 1. Species composition, number of individuals, biomass, frequency of occurrence (FO) and size of fishes collected at Flamengo beach from October 2005 to July 2006.

Species	Number				Total number		Biomass		FO	Size range (mm)
	Spring	Summer	Autumn	Winter	(N)	N %	(g)	(g%)		
<i>Harengula clupeola</i>	9073	2406	6226	234	17939	69.56	47537.8	60.94	78.12	27–198
<i>Atherinella brasiliensis</i>	67	1644	1288	0	2999	11.63	30.5	3.91	48.43	21–149
<i>Pomatomus saltatrix</i>	1516	2	0	23	1541	5.98	12580.3	16.13	34.37	4–155
<i>Trachinotus carolinus</i>	338	536	160	179	1213	4.70	4446.5	5.70	95.31	16–119
<i>Umbrina coroides</i>	306	15	18	62	401	1.55	699.3	0.90	62.55	13–200
<i>Sardinella janeiro</i>	96	80	0	213	389	1.51	1879.7	2.41	25.00	30–129
<i>Anchoa lyoleps</i>	26	217	51	0	294	1.14	411.7	0.53	32.81	17–125
<i>Menticirrhus littoralis</i>	19	30	10	91	150	0.58	268.4	0.34	59.37	4–160
<i>Diplodus argenteus</i>	1	90	39	0	130	0.50	664.9	0.85	28.12	25–119
<i>Mugil liza</i>	80	2	0	45	127	0.49	253.9	0.33	28.12	21–240
<i>Trachinotus goodei</i>	25	51	23	11	110	0.43	451.4	0.58	54.68	16–143
<i>Eucinostomus argenteus</i>	5	73	15	0	93	0.36	1284.9	1.65	35.93	112–160
<i>Trachinotus falcatus</i>	0	36	23	0	59	0.23	123.3	0.16	23.43	27–69
<i>Orthopristis ruber</i>	1	6	28	0	35	0.14	334.1	0.43	20.31	50–200
<i>Sphoeroides greeleyi</i>	5	1	13	16	35	0.14	263.7	0.34	20.31	13–95
<i>Caranx latus</i>	0	19	14	0	33	0.13	578.9	0.74	23.43	70–182
<i>Syngnathus pelagicus</i>	26	0	1	0	27	0.10	8.9	0.01	9.37	40–95
<i>Cosmocampus elucens</i>	16	0	4	0	20	0.08	14.2	0.02	15.62	45–100
<i>Chaetodipterus faber</i>	5	0	12	0	17	0.07	34.7	0.04	15.62	21–50
<i>Eucinostomus gula</i>	0	9	4	0	13	0.05	274.8	0.35	9.37	95–147
<i>Dactyloscopus crossotus</i>	1	2	3	4	10	0.04	6.3	0.01	15.62	40–69
<i>Anchoa tricolor</i>	2	1	6	0	9	0.03	23.2	0.03	6.25	62–110
<i>Synodus foetens</i>	1	4	3	1	9	0.03	54.2	0.07	14.06	55–166
<i>Elops saurus</i>	7	0	0	1	8	0.03	2.0	<0.01	4.68	41–65
<i>Fistularia tabacaria</i>	5	3	0	0	8	0.03	54.6	0.07	9.37	172–414
<i>Genyatremus luteus</i>	0	8	0	0	8	0.03	20.9	0.03	6.25	50–70
<i>Astroscopus y-graecum</i>	2	1	1	3	7	0.03	109.7	0.14	10.93	35–160
<i>Selene vomer</i>	2	1	4	0	7	0.03	60.8	0.08	9.37	51–99
<i>Sphoeroides tyleri</i>	0	0	0	7	7	0.03	81.2	0.10	7.81	75–97
<i>Trichiurus lepturus</i>	1	6	0	0	7	0.03	895.5	1.15	7.81	590–690
<i>Fistularia petimba</i>	5	0	1	0	6	0.02	32.8	0.04	7.81	12–290
<i>Lagocephalus lagocephalus</i>	4	1	0	1	6	0.02	120.4	0.15	7.81	35–175
<i>Cantherines pullus</i>	5	0	0	0	5	0.02	6.1	0.01	4.68	25–38
<i>Carangoides bartholomaei</i>	0	0	5	0	5	0.02	126.2	0.16	3.12	112–124
<i>Polydactylus virginicus</i>	0	1	4	0	5	0.02	51.9	0.07	3.12	96–120
<i>Boridia grossidens</i>	4	0	0	0	4	0.02	8.8	0.01	3.12	18–67
<i>Chilomycterus spinosus</i>	0	0	2	2	4	0.02	413.3	0.53	4.68	43–170
<i>Pomadasys corvinaeformis</i>	1	2	1	0	4	0.02	5.7	0.01	4.68	23–58
<i>Dactylopetrus volitans</i>	0	2	1	0	3	0.01	23.3	0.03	4.68	85–92
<i>Epinephelus itajara</i>	3	0	0	0	3	0.01	0.8	<0.01	3.12	20–30
<i>Polydactylus oligodon</i>	0	2	1	0	3	0.01	20.2	0.03	4.68	36–125
<i>Sphoeroides testudineus</i>	1	0	2	0	3	0.01	3.5	<0.01	4.68	20–55
<i>Sphyraena tome</i>	3	0	0	0	3	0.01	19.5	0.03	3.12	120–132
<i>Trachurus lathami</i>	2	0	1	0	3	0.01	6.2	0.01	3.12	35–87
<i>Bryx dunkeri</i>	0	2	0	0	2	0.01	0.1	<0.01	3.12	44–50
<i>Canthidermis sufflamen</i>	0	0	0	2	2	0.01	0.1	<0.01	1.56	16–32
<i>Eucinostomus lefroyi</i>	0	1	1	0	2	0.01	1.5	<0.01	3.12	34–45
<i>Lagocephalus laevigatus</i>	2	0	0	0	2	0.01	6.7	0.01	3.12	50–59
<i>Menticirrhus americanus</i>	0	0	0	2	2	0.01	9.0	0.01	3.12	36–112
<i>Micropogonias furnieri</i>	0	2	0	0	2	0.01	574.4	0.74	3.12	185–375
<i>Prionotus punctatus</i>	1	1	0	0	2	0.01	51.6	0.07	3.12	38–160
<i>Anchoa januaria</i>	1	0	0	0	1	<0.01	2.4	<0.01	1.56	76
<i>Canthigaster rostrata</i>	1	0	0	0	1	<0.01	0.4	<0.01	1.56	26
<i>Cetengraulis edentulus</i>	1	0	0	0	1	<0.01	11.4	0.01	1.56	109

Table 1. (Continued.)

Species	Number				Total number		Biomass		FO	Size range (mm)
	Spring	Summer	Autumn	Winter	(N)	N %	(g)	(g%)		
<i>Citharichtys macrops</i>	0	0	1	0	1	<0.01	1.7	<0.01	1.56	53
<i>Epinephelus morio</i>	1	0	0	0	1	<0.01	0.5	<0.01	1.56	344
<i>Hemicaranx amblyrhynchus</i>	0	1	0	0	1	<0.01	7.9	0.01	1.56	85
<i>Mugil curema</i>	1	0	0	0	1	<0.01	0.2	<0.01	1.56	30
<i>Mugil platanus</i>	1	0	0	0	1	<0.01	0.1	<0.01	1.56	30
<i>Rachycentron canadum</i>	0	1	0	0	1	<0.01	14.3	0.02	1.56	165
<i>Scartella cristata</i>	0	0	1	0	1	<0.01	6.9	0.01	1.56	85
<i>Selene setapinnis</i>	1	0	0	0	1	<0.01	7.1	0.01	1.56	84
<i>Stellifer rastrifer</i>	1	0	0	0	1	<0.01	0.5	<0.01	1.56	35
TOTAL (63 species)	11,665	5,259	7,967	897	25,788		78008.9			

herring *H. clupeiola* (Table 1). Most fish were juveniles, mainly young-of-the-year. Individuals of a wide range of sizes from 4 to 690 mm total length (TL), consisting of postlarval to adult stages, were collected. Nevertheless, the majority collected were smaller than 100 mm TL.

There was a distinct temporal trend in species richness and abundance (Fig. 4). Most fish were collected in spring (number: $F = 69.3$; $P < 0.001$; biomass: $F = 59.2$; $P < 0.001$) and the lowest values occurred in winter. The mean species richness was highest in spring–summer–autumn and lowest in winter ($F = 18.4$; $P < 0.001$), with the total species richness decreasing from a maximum of 44 in spring to a minimum of 18 in winter (Fig. 4).

The nMDS ordination plot (Fig. 3) revealed distinct groupings of fish samples. Summer and autumn samples are in close proximity in ordination space because each of these seasons was characterized by intermediate fish abundance (number and biomass). On the other hand, the spring and winter samples were differentiated in

ordination space because of the higher richness and abundance in spring and the reverse in winter.

The fish community structure differed across seasons according to ANOSIM with R-values ranging from 0.48 to 0.64 ($P < 0.001$), although differences between summer and autumn were negligible due to a comparatively lower R-value ($R = 0.12$; $P = 0.009$). Results of SIMPER analysis (Table S1) indicated that *H. clupeiola* provided the greatest contribution to similarities for spring, summer and autumn. *Trachinotus carolinus*, *Menticirrhus littoralis* and *Umbrina coroides* were the major species responsible for the similarity of winter. *Trachinotus carolinus*, although providing the greatest contribution to winter similarity, showed a higher abundance in spring and summer, whereas *Atherinella brasiliensis* was abundant in summer and autumn. *Pomatomus saltatrix* occurred mainly in spring.

Short-term variation

There were changes in structure of the fish assemblages between the periods of the day for each season (Fig. 5). We have included an electronic attachment (Table S2) with the results of one-way ANOSIM (R values and significance levels) and SIMPER for comparisons of fish assemblages between the periods of the day for each season. In spring, there were major changes in the structure during the morning (after sunrise/before noon) due to the appearance of *Atherinella brasiliensis* in large numbers. There was also a change in the structure during the afternoon (after noon/before sunset) due to the appearance of *Mugil liza*, and at the sunset (before/after sunset) caused by appearance of *Umbrina coroides* and disappearance of *Mugil liza*. Another change in structure occurred before dawn (after midnight/before sunrise) with increasing numbers of *Harengula clupeiola* and *Pomatomus saltatrix* and the disappearance of *Umbrina coroides*.

In summer, *Atherinella brasiliensis* and *Diplodus argenteus* were common during the day and decreased sharply

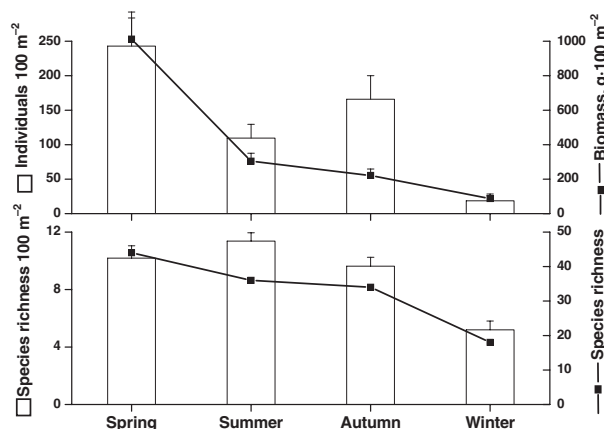


Fig. 4. Seasonal variations (means + 1 SE) of the abundance, biomass and the number of species.

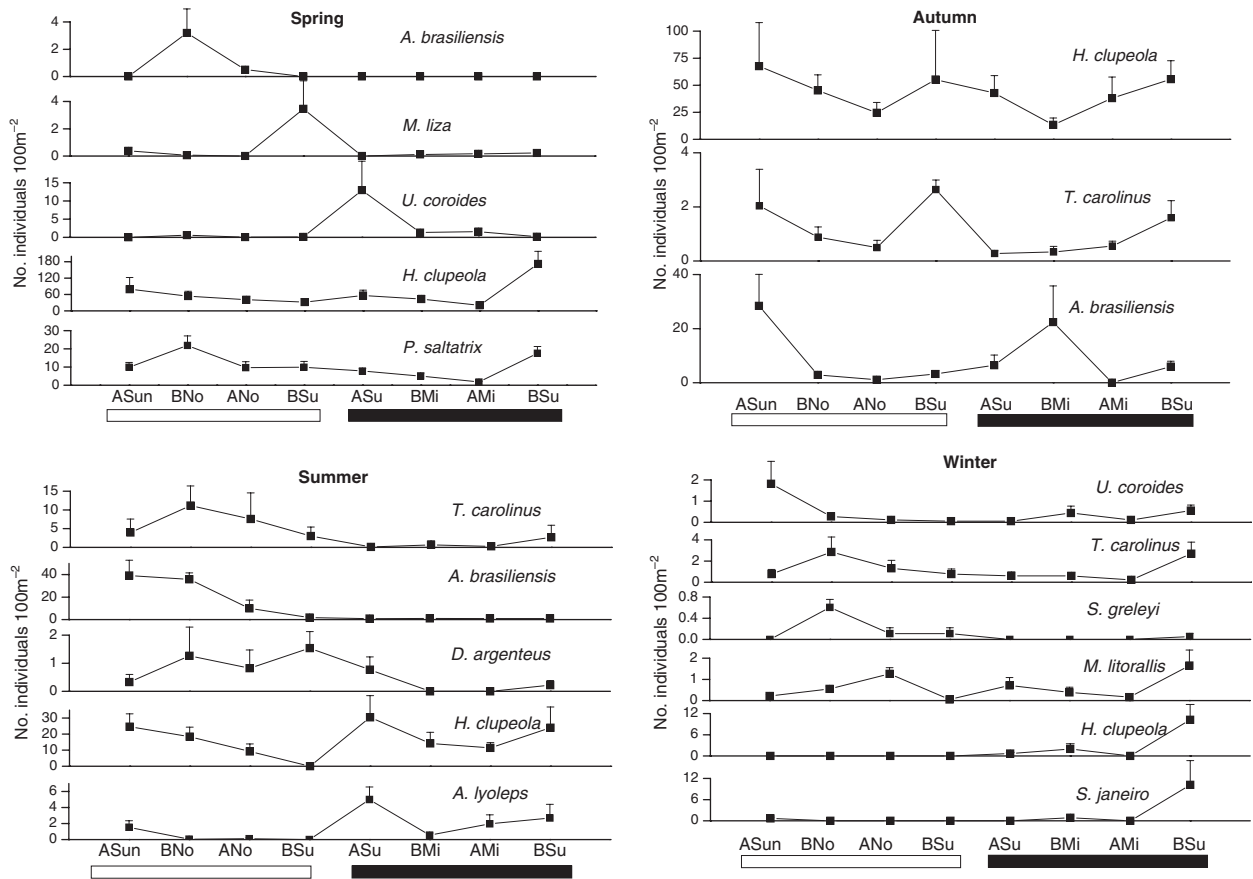


Fig. 5. Diel changes of fish densities that differed among the period of the day for each season. ASun, after sunrise; BNo, before noon; ANo, after noon; BSu, before sunset; ASu, after sunset; BMi, before midnight; AMi, after midnight; BSu, before sunrise; black bar, night; white bars, day.

during the night (Fig. 5). Changes in structure occurred at the end of the day (after noon/before sunset), with the disappearance of *Harengula clupeola* before the sunset. After sunset, the main change in structure occurred due to the disappearance of *T. carolinus* and appearance in large numbers of *Anchoa lyoleps*. At sunrise (before sunrise/after sunrise), the community was dominated by *A. brasiliensis*, *A. lyoleps* and *H. clupeola*.

Harengula clupeola, *A. brasiliensis* and *Trachinotus carolinus* were common and showed only slight changes throughout the day periods during autumn (Fig. 5). The major change in structure occurred before sunset due to the largest number of *T. carolinus*, and after midnight due to decreased number of *A. brasiliensis*.

During winter, changes in structure of fish assemblage occurred between midnight and the morning (Fig. 5). Abundances of *H. clupeola*, *Sardinella janeiro* and *M. littoralis* were at the highest before sunrise, with changes occurring after sunrise due to a higher abundance of *U. coroides*, and before noon due to increased numbers of *Sphoeroides greeleyi* and *T. carolinus*. *Atherinella*

brasiliensis, *A. lyoleps* and *D. argenteus* did not occur during winter.

Influences of environmental variables on fish abundance

The results of the Spearman correlation revealed that temperature, salinity and dissolved oxygen had significant effects on the occurrence of some species, although most values were comparatively low (<0.50) (Table 2). Species-environmental correlations from CCA were higher for the first (0.89) and second (0.60) axes (Table 3). The two vectors (temperature and salinity) crossed almost perpendicularly, indicating that the effects of those factors on fish assemblage were largely independent, whereas temperature and dissolved oxygen were almost inversely correlated (Fig. 6).

The Spearman coefficient and CCA revealed relationships among the 17 most abundant species and environmental variables. Three species (*Atherinella brasiliensis*, *Diplodus argenteus*, *Eucinostomus argenteus* and *Anchoa lyoleps*) occurred mainly in summer and autumn and

Table 2. Results of Spearman rank correlation analysis of selected environmental variables on the abundance of the 17 most abundant species. Correlations in bold are significant at $P < 0.01$ ($n = 192$).

Species	Temperature	Salinity	Dissolved oxygen
<i>T. goodei</i>	0.11	0.04	-0.27
<i>T. carolinus</i>	0.05	0.02	-0.17
<i>P. saltatrix</i>	-0.14	-0.70	0.45
<i>H. clupeiola</i>	0.24	-0.31	-0.11
<i>M. littoralis</i>	-0.22	0.13	0.12
<i>A. brasiliensis</i>	0.41	0.38	-0.47
<i>U. coroides</i>	-0.07	-0.19	0.26
<i>M. liza</i>	-0.26	-0.22	0.20
<i>D. argenteus</i>	0.24	0.19	-0.33
<i>E. argenteus</i>	0.36	0.02	-0.31
<i>A. lyoleps</i>	0.21	-0.10	-0.33
<i>T. falcatus</i>	0.11	0.13	-0.32
<i>O. ruber</i>	0.19	0.09	-0.11
<i>C. latus</i>	0.13	0.11	-0.27
<i>S. janeiro</i>	-0.18	-0.10	0.04
<i>S. greeleyi</i>	-0.09	-0.03	0.10
<i>S. pelagicus</i>	-0.09	-0.20	0.05

Table 3. Summary of the CCA performed on abundance of the 17 most numerous fish species at Flamengo beach.

	Axes			
	1	2	3	4
Correlation of environmental variables				
Temperature	0.43	-0.39	-0.22	0.00
Salinity	-0.73	0.12	-0.21	0.00
Dissolved oxygen	0.73	0.33	-0.03	0.00
Summary statistics for ordination axes				
Eigenvalues	0.28	0.09	0.02	0.24
Species – environment correlations	0.89	0.60	0.40	0.00
Cumulative percentage of variance				
of species data	12.8	16.7	17.8	28.7
of species-environmental correlations	71.7	93.8	100.0	0.0
Sum of all unconstrained eigenvalues				2.230
Sum of all canonical eigenvalues				0.397

were associated with higher temperatures, whereas *Sardinella janeiro*, *Menticirrhus littoralis* and *Mugil liza* were more abundant in winter and were associated with low temperatures, with the latter also being abundant in spring. *Atherinella brasiliensis* and *D. argenteus* were associated with high salinity in autumn, in contrast to *Pomatomus saltatrix*, *Harengula clupeiola*, *Umbrina coroides*, *M. liza* and *Syngnathus pelagicus*, which were related to low salinity in spring. *Mugil liza*, *P. saltatrix* and *U. coroides* were associated with high dissolved oxygen in spring and winter. *Trachinotus goodei*, *Trachinotus falcatus*, *A. brasiliensis*, *D. argenteus*, *A. lyoleps*, *Caranx latus* and

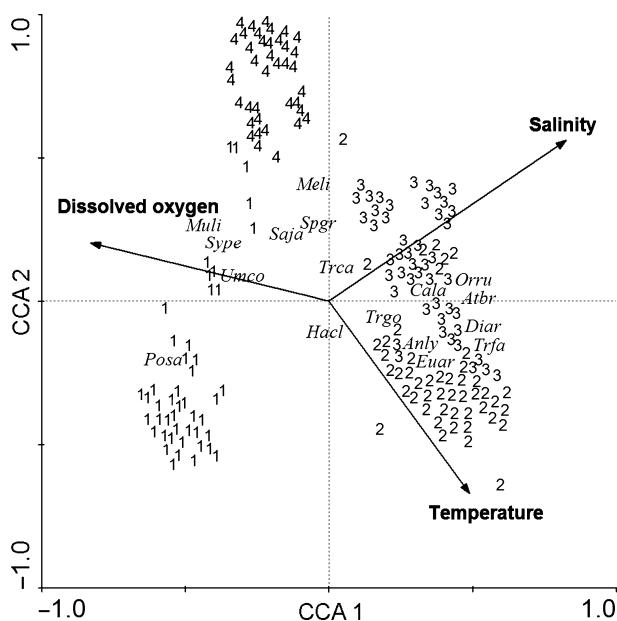


Fig. 6. Ordination diagram (triplet) from canonical correspondence analysis, including fish species, environmental variables and seasons. Species coded by the two first words of the genus and species scientific names. *Muli* – *M. liza*; *Sype* – *S. pelagicus*; *Umco* – *Umbrina coroides*; *Posal* – *Pomatomus saltatrix*; *Hacl* – *Harengula clupeiola*; *Meli* – *Menticirrhus littoralis*; *Spgr* – *Sphoeroides greeleyi*; *Saja* – *Sardinella janeiro*; *Trca* – *Trachinotus carolinus*; *Trfa* – *Trachinotus falcatus*; *Atbr* – *Atherinella brasiliensis*; *Cala* – *Caranx latus*; *Orru* – *Orthopristis ruber*; *Trgo* – *Trachinotus goodie*; *Diar* – *Diplodus argenteus*; *Euar* – *Eucinostomus argenteus*; *Anly* – *Anchoa lyoleps*.

E. argenteus occurred mainly in low dissolved oxygen concentration in summer and autumn (Fig. 6).

Discussion

Although seasonal differences in fish assemblage structure were not tested in this study, as only 1 year was sampled, some trends can be outlined from our findings. Seasonality seems to play a role in structuring the fish assemblage at Flamengo beach, with composition and structure shifting among seasons. Higher abundance, biomass and species richness occurred in spring and the reverse occurred in winter.

In tropical areas, seasonal variation in fish assemblages exhibits different patterns from temperate areas. Temperature in such areas is unlikely to be the main driving force determining peaks of fish species abundance in sandy beaches. Furthermore, the range of temperature change found in this study was only 5.5 °C, which is very small compared to temperate areas, which may experience greater ranges of temperature, such as 23.2 °C on the Virginia coast, USA (Layman 2000) or 16 °C on the

Kashimanada coast, Japan (Nanami & Endo 2007). In temperate areas, it seems likely that temperature is the major factor of seasonal surf-zone dynamics (Poxton & Allouse 1982; Layman 2000). Fish richness and density are generally highest between late spring and summer (Lasiak 1984; Ayvazian *et al.* 1992; Santos & Nash 1995; Clark *et al.* 1996) due to the influx of juveniles of both resident and transient species following their breeding seasons (Gibson *et al.* 1993; Gibson & Yoshiyama 1999), although the exact timing of these peaks in abundance varies considerably. Low abundances in winter are typical of many temperate shallow-water fish assemblages (Lasiak 1986; Nash 1988; Wright 1989). On the other hand, in tropical and subtropical areas, abundances of juvenile fishes on sand beaches vary irrespective of season. According to Barreiros *et al.* (2004), the total number of individuals and total biomass were lowest in December and highest in February on a sandy beach in Southern Brazil (27° S). Vasconcellos *et al.* (2007) found higher abundances in spring/summer and lowest abundances in autumn/winter on sandy beaches in Rio de Janeiro Municipality (22°30'S). Gaelzer & Zalmon (2008) found differences in fish abundances between two proximate beaches in Southeastern Brazil (latitude 23° S, *c.* 4 km apart) which had different environmental characteristics such as wave exposure and morphodynamics.

In Sepetiba Bay, a nearby area in Rio de Janeiro State, Pessanha *et al.* (2000) found higher fish abundance in summer and autumn (1983–84) at beaches sampled during the day. Ten years later (1993–1994), Araújo *et al.* (1997) carried out a similar fish sampling program and did not find a clear seasonal pattern of abundance of fish in the same area. On the other hand, Pessanha & Araújo (2003) found the highest fish density in winter between 1998 and 1999, sampling at 3-h intervals throughout a 24-h period. The present study, carried out throughout a 48-h period, found the highest fish abundance in spring, which does not coincide with the findings of Pessanha & Araújo (2003). Therefore, we conclude that temperature is not a primary factor dictating recruitment peaks in shallow areas in tropical beaches.

The peak in fish density in spring recorded in this work was due to high abundance of *Harengula clupeiola*, *Umbrina coroides* and *Pomatomus saltatrix*. *Pomatomus saltatrix* spawns in the South Atlantic Bight during spring (Kendall & Walford 1979; Collins & Stender 1987) with larval development occurring near the surface. The young are dispersed by prevailing currents, and perhaps perform active migration to the sandy beaches. This piscivorous fish seems to utilize the area for feeding and growth, probably taking advantage of the abundant food resources provided by many shoals of Clupeiformes. According to Juanes & Conover (1994), young-of-the-year bluefish

(*P. saltatrix*) undergo a habitat shift from offshore waters to inshore nursery areas at about 40–70 mm total length, which coincides with an increased growth rate and a dietary shift from planktivory to piscivory. Variability in the use of estuarine beaches by young-of-the-year *P. saltatrix* was found by Taylor *et al.* (2007), who considered the occurrence of this species in beaches to be a response to prey composition dynamics. Therefore, it is reasonable to suppose that high abundance of *P. saltatrix* (a typical spring species) at Flamengo beach is due to high abundance of Clupeiformes such as *H. clupeiola*, which likely is a prey of the former species. A preliminary investigation to assess the diet of *P. saltatrix* was carried out to corroborate this hypothesis. Of 40 examined stomachs, 15 were empty, 25 mostly contained Clupeiformes (13 cases), and some contained other teleosts (5 cases) and invertebrates such as Mysidacea (5 cases), Isopoda and Brachyura (1 case).

Harengula clupeiola was the most abundant species, being recorded all year round, but showing higher densities from spring to autumn. Notably, the other member of Clupeidae, *Sardinella janeiro* was more abundant in winter, a possible strategy to avoid competition with *H. clupeiola*. Similar to the findings in the present work, peaks of *Atherinella brasiliensis* have been consistently recorded in summer/autumn (Araújo *et al.* 1997; Pessanha *et al.* 2000, 2003; Pessanha & Araújo 2001; Neves *et al.* 2006). This may indicate a more defined spawning period and the ability of this species to colonize different habitats, mainly in summer/autumn. *Atherinella brasiliensis* is highly dominant in mangrove areas in Sepetiba Bay, where it constitutes more than 50% of all fish (Neves *et al.* 2006). *Trachinotus carolinus* occurred throughout the year, peaking in spring/summer, whereas *Anchoa lyoleps* was more abundant in summer/autumn and absent in winter. *Umbrina coroides* occurred mainly in spring and winter. As such, the most numerous fish species in Flamengo beach show temporal segregation throughout the year. Competitive interaction may be a dominant feature shaping the juvenile fish assemblage at Flamengo beach. Resource partitioning describes the limits that interspecific competition imposes on species richness that can stably coexist (MacArthur 1965; Schoener 1974; Roughgarden 1976, 1983).

The most distinct fish assemblages were recorded in winter with low abundance and richness, whereas summer and autumn had the most similar fish assemblages. Spring, summer and autumn had as typical species *H. clupeiola* (mainly in spring) and *A. brasiliensis* (mainly in summer and autumn), both planktophagous, feeding on Copepoda and Diatomacea (Ortiz *et al.* 1996; Chaves & Vendel 2008). During this period, high temperatures favor phytoplankton production and, consequently, the

zooplankton (Félix *et al.* 2007), which increases the survival chances for larval and juvenile fish. On the other hand, winter is dominated by *T. carolinus*, *M. littoralis* and *U. coroides*, species that are more closely associated with the substrate (Finucane 1969; Zahorcsak *et al.* 2000). Hence, food availability also plays an important role in juvenile fish distribution at this sandy beach.

Changes in fish assemblage structure over the studied 48-h period were due to variation in abundance of some individual species, which differed among the seasons. As seen here, some abundant species were absent from catches in one or other periods of the day. The relative abundance can also differ between the periods of the day, with many species occurring in the whole time period but especially abundant in a single one. *Harengula clupeola* occurred in high abundance throughout the whole time period in spring, summer and autumn but only before sunrise in winter. On the other hand, *A. brasiliensis* changed in abundance according to time of the day, occurring mainly during the day period (after sunrise to before sunset) in summer, and during the day and the night in autumn. *Pomatomus saltatrix* occurred only in spring but was abundant in the whole time period (day and night). Overall, there is no consistency of diel usage patterns at sandy beaches by a given species across seasons. This raises some concerns about studies assessing diel variation of fish communities at sandy beaches. Most studies on this subject are based only on 1-month sampling throughout a 1-year cycle and the period of sampling is pooled in either day or night. This procedure can miss important changes that occur in a shorter time scale (such as a 3-h period), as was observed in this study. Additionally, there is no available information based on two 24-h cycles, such as the present study, which could assess the degree of diel stability in assemblage structure at beaches.

Short-term variation in species abundance is an indicator of species separation and a partitioning of the habitat along a time axis. The selective advantage of such a partitioning can be manifold, including reductions in competition for food and/or space and avoidance of predation (Ross 1986). The fish assemblage structures in each period of the day at Flamengo beach did differ to a certain extent. However, several non-significant dissimilarities between adjacent time periods suggest that several species occur in both periods. Some species appear to switch over the year (seasons) from a time period (for example *A. brasiliensis*), which further complicates the dynamics. Care must be taken when describing assemblage dynamics to include diel variation if only one time frame is being considered. As seen here, abundance fluctuations may not be as severe as at first perceived because species switch behavioural habits.

It is reasonable to suppose that the diel activity is strongly influenced by the local habitat constraints. Habitat structure, which is unique to each beach, as well as biotic interactions, could be the underlying factors influencing the use of the tropical beaches by juvenile fishes. Additionally, competitive interactions may be a dominant feature shaping juvenile fish assemblages, as resource partitioning describes the limits that interspecific competition imposes on the species richness that can stably coexist (MacArthur 1965; Schoener 1974; Roughgarden 1976, 1983). According to Vinagre *et al.* (2006), some species may avoid foraging in some periods of the day of high predation pressure and take advantage of periods of lower predation pressure to forage, regardless of their endogenous diel rhythm. Prey abundance can also play an important role in the cost–benefit relation underlying foraging behaviour.

Environmental factors such as temperature and salinity are known to influence changes in fish community structure and the colonization capacity of species, especially in shallow habitats such as surf zones, where physical parameters are extremely variable, causing dramatic seasonal and diurnal shifts in the composition of fish assemblages (Haedrich 1983; Thorman 1986; Kneib 1997; Akin *et al.* 2003). Unlike temperate areas, where temperature and salinity are positively correlated because freshwater flow increases in winter months and heating and evaporation increase salinity in the warmer months, tropical areas show an inverse correlation between these two variables, as the rainfall is more intense during summer. In the present study, the three environmental variables examined (temperature, salinity and dissolved oxygen) were significantly associated with some fish species. The lowest temperature and highest salinity were associated with the highest abundance of *M. littoralis* and *U. coroides*, with the reverse (high temperature and low salinity) associated with the highest abundances of *H. clupeola*, *P. saltatrix* and *T. carolinus*. *Pomatomus saltatrix* showed a trend for a seasonal change in abundance and was recorded mainly when salinity was at the lowest levels. The three environmental CCA vectors are located in different parts of the diagram (quadrants) and show similar size, suggesting that each factor independently affected species occurrence. The results of Spearman correlation and CCA suggested that three species (*Eucinostomus argenteus*, *Diplodus argenteus* and *A. lyoleps*) preferred high temperatures, in contrast to *M. littoralis* and *M. liza*, which were found mainly at low temperatures. The seasonal effects and variability of migration, spawning and recruitment patterns within the area (Wheeler 1969; Elliott *et al.* 1990) may well also be embedded within the temperature relationship and are likely to be the dominant factors influencing the observed distributions.

The lowest salinities coincided with highest abundances of *P. saltatrix*, *H. clupeiola*, *U. coroides*, *M. liza* and *Syngnathus pelagicus*. On the other hand, the highest salinity coincided with high abundances of *A. brasiliensis* and *D. argenteus*. Salinity has been cited as the environmental variable that predominantly influences the distribution of estuarine species (Wagner & Austin 1999; Whitfield 1999). However, Attrill *et al.* (1999) warned against over-interpreting the role of salinity because of its multi-co-variation with other environmental variables. Whitfield (1999) determined that salinity, temperature and the synergy between these two variables were most important in structuring assemblages in a number of South African estuaries. In this study, temperature and salinity appeared to play a role in shaping fish assemblages; however, none of these measures was able completely to predict the groupings of species, as most species–salinity correlations were low.

Dissolved oxygen is hardly a factor limiting fish distribution in sandy beaches due to hydrodynamics of such areas. High dissolved oxygen was directly associated with *M. liza*, *P. saltatrix* and *U. coroides* abundances. The lowest values were associated with high abundances of *Trachinotus goodei*, *Trachinotus falcatus*, *A. brasiliensis*, *D. argenteus*, *A. lyoleps*, *Caranx latus* and *E. argenteus*. This environmental parameter is important to the distribution of fish species, with many marine fish becoming stressed at dissolved oxygen levels of $<4.5 \text{ mg l}^{-1}$ (Poxton & Allouse 1982). A consideration of oxygen as a resource suggests that net oxygen gain per unit of energy expenditure will be the most useful currency for ecological models of breathing. Fish should choose whichever combination of responses minimizes the costs of meeting their oxygen demands. The most stressful conditions at Flamengo beach occur in summer as a result of high temperatures and relatively low dissolved oxygen. This situation can eventually lead to deterioration of water quality, which is most likely to occur during this season.

In general, the timing of seasonal patterns in fish abundance, biomass, richness and composition have previously been attributed primarily to abiotic influences. Temperature is often cited as a major factor determining timing of reproduction, immigration, and emigration (Livingston 1976; Marshall & Elliott 1998; Witting *et al.* 1999). However, co-varying factors, such as salinity, dissolved oxygen, nutrient input and freshwater discharge often contribute, and make it difficult to determine a main driving factor (Potter *et al.* 1986; Morin *et al.* 1992; Valiela 1995; Fraser 1997). Other factors can also affect fish recruitment in shallow areas, including biotic interactions, such as the presence of feeding resources, predator avoidance and adults spawning, as well as coastal currents, winds and tides, which bring eggs and larvae to

sandy beaches. Habitat structure, which is unique to each beach, as well as biotic interactions, could be the underlying factors influencing the use of the tropical beaches by juvenile fishes. In spring on the Rio de Janeiro coast, predominant southwestern winds (Barbière & Kronemberger 1994; Camargo *et al.* 2004) bring eggs and larvae into bay areas, favoring recruitment. It can be concluded that in spring the majority of coastal fish concentrate spawning efforts to use phytoplankton and zooplankton resources and to take advantage of the winds and currents. This may result in the peaks of fish recruitment in spring.

Conclusions

The present study reports on the dynamics of fish assemblage structure over a 1-year period at a relatively well-protected subtropical sandy beach. Changes in fish assemblage structure over the 48-h period studied were due to variation in abundance of some individual species, which differed among the seasons. Concerns must be raised when pooling fish samples as either day or night, as this can miss important changes that occur in a shorter time scale (such as a 3-h period), as was observed in this study. The fish assemblage structures in each time period differed to a certain extent, however, abundance fluctuations may not be as severe as at first perceived because species switch behavioural habits.

We also found changes in assemblage structure throughout the four examined seasons. Water temperature, salinity and dissolved oxygen independently influenced the occurrence of a few species. The surf zone probably functions as a nursery area for *Harengula clupeiola*, *Atherinella brasiliensis*, *Pomatomus saltatrix*, *Trachinotus carolinus*, *Umbrina coroides*, *Sardinella janeiro* and *Anchoa lyoleps*. Because numerous studies have demonstrated that surf zones are refuges against predators, as well as feeding places for juvenile fishes, more detailed studies on the nursery function of sheltered sandy beaches would be worthwhile.

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References

- Akin S., Winemiller K.O., Gelwick F.P. (2003) Seasonal and spatial variations in fish and macrocrustacean assemblage

- structure in Mad Island Marsh estuary, Texas. *Estuarine, Coastal and Shelf Science*, **57**, 269–282.
- Allen L.G., Horn M.H., Edmonds F.A., Usui C.A. (1983) Structure and seasonal dynamics of the fish assemblages in the Cabrillo beach area of Los Angeles harbor, California. *Bulletin of the South California Academy of Science*, **82**, 47–70.
- Amador E.S. (1997) *Baía de Guanabara e Ecossistemas Periféricos: Homem e Natureza*. Reproarte Gráfica e Editora Ltda, Rio de Janeiro.
- Araújo F.G., Cruz Filho A.G., Azevedo M.C.C., Santos A.C.A., Fernandes L.A.M. (1997) Estrutura da Comunidade de Peixes Jovens da Margem Continental da Baía de Sepetiba, RJ. *Acta Biológica Leopoldensia*, **19**, 61–83.
- Atrill M.J., Power M., Thomas R.M. (1999) Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends. *Marine Ecology Progress Series*, **178**, 89–99.
- Ayvazian S.G., Hyndes G.A. (1995) Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leewin Current influence the characteristics of the fish fauna? *Marine Biology*, **122**, 527–536.
- Ayvazian S.G., Deegan L.A., Finn J.T. (1992) Comparison of habitat use by estuarine fish assemblages in the Acadian and Virginian zoogeographic provinces. *Estuaries*, **15**, 368–383.
- Barbière E.B., Kronemberger D.M.P. (1994) Climatologia do litoral Sul-Sudeste do Estado do Rio de Janeiro. *Caderno de Geociências*, **12**, 57–73.
- Barreiros J.P., Figna V., Hostim-Silva M., Santos R.S. (2004) Seasonal changes in a sandy beach fish assemblage at Canto Grande, Santa Catarina, South Brazil. *Journal of Coastal Research*, **20**, 862–870.
- Blaber S.J.M. (2000) *Tropical Estuarine Fishes: Ecology, Exploration and Conservation*. Wiley-Blackwell, Oxford: 372 pp.
- ter Braak C.J.F., Verdonschot P.F.M. (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, **57**, 255–289.
- Camargo J.M.R., Guerra J.V., Patchineelam S.M. (2004) Variações das forças hidrodinâmicas junto a um campo de dunas Subaquáticas na baía da Guanabara – RJ. *Atlântica*, **26**, 5–15.
- Chaves P.T., Vendel A.L. (2008) Análise comparativa da alimentação de peixes (Teleostei) entre ambientes de marisma e de manguezal num estuário do sul do Brasil (Baía de Guaratuba, Paraná). *Revista Brasileira de Zoologia*, **25**, 10–15.
- Clark B.M., Bennett B.A., Lamberth S.J. (1996) Factors affecting spatial variability in seine net catches of fishes in the surf-zone of False Bay, South Africa. *Marine Ecology Progress Series*, **131**, 17–34.
- Clarke K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Collins M.R., Stender B.W. (1987) Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. *Bulletin of Marine Science*, **41**, 822–834.
- Davis J.C. (1975) Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *Journal of the Fisheries Research Board of Canada*, **32**, 2295–2332.
- Elliott M., O'Reilly M.G., Taylor C.J.L. (1990) The Forth estuary: a nursery and overwintering area for North Sea fishes. *Hydrobiologia*, **195**, 89–103.
- Eriksson L.O. (1978) Diurnalism versus nocturnalism – dualism within fish individuals. In: Thorpe J.E. (Ed.), *Rhythmic Activity of Fishes*. Academic Press, London: 69–89.
- FEEMA/JICA. (1994) *Fishes. The Study on Recuperation of the Guanabara bay Ecosystem*. Japan International Cooperation Agency and Kokusai Kogyo, Tokyo: 1–55.
- Félix F.C., Spach H.L., Moro P.S., Schwarz R. Jr, Santos C., Hackradt C.W., Hostim-Silva M. (2007) Utilization patterns of surf zone inhabiting fish from beaches in Southern Brazil. *Pan-American Journal of Aquatic Sciences*, **2**, 27–39.
- Field J.G., Clarke K.R., Warwick R.M. (1982) A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37–52.
- Finucane J.H. (1969) Ecology of the Pompano (*Trachinotus carolinus*) and the Permit (*T. falcatus*) in Florida. *Transactions of the American Fisheries Society*, **98**, 478–486.
- Fraser T.H. (1997) Abundance, seasonality, community indices, trends and relationships with physiochemical factors of trawled fish in upper Charlotte Harbor, Florida. *Bulletin of Marine Science*, **60**, 739–763.
- Gaelzer L.R., Zalmon I.R. (2008) Diel variation of fish community in sandy beaches of southeastern Brazil. *Brazilian Journal of Oceanography*, **56**, 23–39.
- Gibson R.N., Yoshiyama R.M. (1999) Intertidal fish communities. In: Horn M.H., Martin K.L.M., Chotkowski M.A. (Eds), *Intertidal Fishes: Life in Two Worlds*. Academic Press, New York: 264–296.
- Gibson R.N., Ansell D.A., Robb L. (1993) Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Marine Ecology Progress Series*, **98**, 89–105.
- Haedrich R.L. (1983) Estuarine fishes. In: Ketchum B. (Ed.), *Estuaries and Enclosed Seas. Ecosystems of the World*. Elsevier, Amsterdam: 183–207.
- Juanes F., Conover D.O. (1994) Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1752–1761.
- Jung S., Houde E.D. (2003) Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. *Estuarine, Coastal and Shelf Science*, **58**, 335–351.
- Kendall A.W. Jr, Walford L.A. (1979) Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the

- East Coast of the United States. *Fishery Bulletin*, **77**, 213–227.
- Kjerfve B., Ribeiro C.H.A., Dias G.T.M., Filippo A.M., Quar-
esma V.S. (1997) Oceanographic characteristics of an
impacted coastal bay: Baía de Guanabara, Rio de Janeiro,
Brazil. *Continental Shelf Research*, **17**, 1–13.
- Kneib R.T. (1997) The role of tidal marshes in the ecology of
estuarine nekton. *Oceanography and Marine Biology an
annual review*, **35**, 163–220.
- Lamberth S.J., Clark B.M., Bennett B.A. (1995) Seasonality of
beach seine catches in False Bay, South Africa, and implica-
tions for management. *South African Journal of Marine
Science*, **15**, 157–167.
- Lasiak T.A. (1984) Structural aspects of the surf-zone fish
assemblage at King's beach, Algoa Bay, South Africa: long-
term fluctuations. *Estuarine, Coastal and Shelf Science*, **18**,
459–483.
- Lasiak T.A. (1986) Juveniles, food and the surf-zone fish habi-
tat: implications for teleost nursery areas. *South African
Journal of Zoology*, **21**, 51–56.
- Layman C.A. (2000) Fish assemblage structure of the shallow
ocean surf zone on the eastern shore of Virginia
Barrier Islands. *Estuarine, Coastal and Shelf Science*, **51**,
201–213.
- Lazzari M.A., Sherman S., Brown C.S., King J., Joule B.J.,
Chenoweth S.B., Langton R.W. (1999) Seasonal and annual
variations in abundance and species composition of two
near shore fish communities in Maine. *Estuaries*, **22**,
636–647.
- Livingston R.J. (1976) Diurnal and seasonal fluctuations of
organisms in a north Florida estuary. *Estuarine, Coastal and
Shelf Science*, **4**, 373–400.
- MacArthur R.H. (1965) Patterns of species diversity. *Biology
Reviews*, **40**, 510–533.
- Mariani S. (2001) Can spatial distribution of ichthyofauna
describe marine influence on coastal lagoons? A central
Mediterranean case study. *Estuarine, Coastal and Shelf
Science*, **52**, 261–267.
- Marshall S., Elliott M. (1998) Environmental influences on the
fish assemblage of the Humber estuary, U.K. *Estuarine,
Coastal and Shelf Science*, **46**, 175–184.
- Mayr L.M., Tenenbaum D.R., Villac M.C., Paranhos R.,
Nogueira C.R., Bonecker S.L.C., Bonecker A.C.T.
(1989) Hydrobiological characterization of Guanabara
Bay. In: Magoon O., Neves C. (Eds), *Coastlines of
Brazil*. American Society of Civil Engineers, New York:
124–138.
- McFarland W.N. (1963) Seasonal change in the number and
biomass of fishes from the surf at Mustang Island, Texas.
Public Institute of Marine Science University of Texas, **9**,
91–105.
- Morin B., Hudon C., Whoriskey F.G. (1992) Environmental
influences on seasonal distribution of coastal and estuarine
fish assemblages at Wemindji, eastern James Bay. *Environ-
mental Biology of Fishes*, **35**, 219–229.
- Muller K. (1978) Locomotor activity of fish and environmental
oscillations. In: Thorpe J.E. (Ed.), *Rhythmic Activity of
Fishes*. Academic Press, London: 1–9.
- Nanami A., Endo T. (2007) Seasonal dynamics of fish assem-
blage structures in a surf zone on an exposed sandy beach
in Japan. *Ichthyological Research*, **54**, 277–286.
- Nash R.D.M. (1988) The effects of disturbance and severe
seasonal fluctuations in environmental conditions on north
temperate shallow-water fish assemblages. *Estuarine, Coastal
and Shelf Science*, **26**, 123–135.
- Nash R.D.M., Santos R.S. (1998) Seasonality in diel catch rate
of small fishes in a shallow-water fish assemblage at Porto
Pim Bay, Faial, Azores. *Estuarine, Coastal and Shelf Science*,
47, 319–328.
- Neves L.M., Pereira H.H., Costa M.R., Araújo F.G. (2006) Uso
do manguezal de Guaratiba, Baía de Sepetiba, Rio de
Janeiro, pelo peixe-rei *Atherinella brasiliensis* (Quoy &
Gaimard) (Atheriniformes, Atherinopsidae). *Revista Brasile-
ira de Zoologia*, **23**, 421–428.
- Ortiz M., Rocha E., Posada J.M. (1996) Food habits of the
sympatric fishes *Harengula humeralis* and *H. clupeiola*
(Clupeidae) in the Archipelago de Los Roques
National Park, Venezuela. *Caribbean Journal of Science*, **32**,
26–32.
- Paranhos R., Mayr L.M. (1993) Seasonal patterns of tempera-
ture and salinity in Guanabara Bay, Brazil. *Fresenius Envi-
ronment Bulletin*, **2**, 647–652.
- Pessanha A.L.M., Araújo F.G. (2001) Recrutamento do
peixe-ei, *Atherinella brasiliensis* (Quoy & Gaimard)
(Atheriniformes, Atherinopsidae), na margem continental
da Baía de Sepetiba, Rio de Janeiro, Brasil. *Revista Brasileira
de Zoologia*, **18**, 1265–1274.
- Pessanha A.L.M., Araújo F.G. (2003) Spatial, temporal and diel
variation of fish assemblages at two sandy beaches in the Se-
petiba Bay, Rio de Janeiro, Brazil. *Estuarine, Coastal and
Shelf Science*, **57**, 817–828.
- Pessanha A.L.M., Araújo F.G., Azevedo M.C.C., Gomes I.D.
(2000) Variações temporais e espaciais na composição e
estrutura da comunidade de peixes jovens da Baía de Sepeti-
ba, RJ. *Revista Brasileira de Zoologia*, **17**, 251–261.
- Pessanha A.L.M., Araújo F.G., Azevedo M.C.C., Gomes I.D.
(2003) Diel and seasonal changes in the distribution of fish
on a southeast Brazil sandy beach. *Marine Biology*, **143**,
1047–1055.
- Potter I.C., Claridge P.N., Warwick R.M. (1986) Consistency
of seasonal changes in an estuarine fish assemblage. *Marine
Ecology Progress Series*, **32**, 217–228.
- Potter I.C., Bird D.J., Claridge P.N., Clarke K.R., Hyndes G.A.,
Newton L.C. (2001) Fish fauna of the Severn Estuary. Are
there long-term changes in abundance and species composi-
tion and are the recruitment patterns of the main species
correlated? *Journal of Experimental Marine Biology and
Ecology*, **258**, 15–37.
- Poxton M.G., Allouse S.B. (1982) Water quality criteria for
marine fisheries. *Aquacultural Engineering*, **1**, 153–191.

- Reina-Hervas J.A., Serrano P. (1987) Structural and seasonal variations in inshore fish populations in Malaga Bay, south-eastern Spain. *Marine Biology*, **95**, 501–508.
- Ross S.T. (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia*, **1986**, 352–388.
- Ross S.T., McMichael R.H., Ruple D.L. (1987) Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estuarine, Coastal and Shelf Science*, **25**, 391–412.
- Roughgarden J. (1976) Resource partitioning competing species – a coevolutionary approach. *Theoretical Population Biology*, **9**, 388–424.
- Roughgarden J. (1983) Competition and theory in community ecology. *The American Naturalist*, **122**, 583–601.
- Santos R.S., Nash R.D.M. (1995) Seasonal changes in a sandy beach fish assemblage at Porto Pim, Faial, Azores. *Estuarine, Coastal and Shelf Science*, **41**, 579–591.
- Schoener T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.
- Taylor L.D., Nichols R.S., Able K.W. (2007) Habitat selection and quality for multiple cohorts of young-of-the-year bluefish (*Pomatomus saltatrix*): comparisons between estuarine and ocean beaches in southern New Jersey. *Estuarine, Coastal and Shelf Science*, **73**, 667–679.
- Thorman S. (1986) Physical factors affecting the abundance and species richness of fishes in the shallow waters of the southern Bothnian Sea (Sweden). *Estuarine, Coastal and Shelf Science*, **22**, 357–369.
- Valiela I. (1995) *Marine Ecological Processes*. Springer, New York: 686 pp.
- Vasconcellos R.M., Santos J.N.S., Silva M.A., Araújo F.G. (2007) Efeito do grau de exposição às ondas sobre a comunidade de peixes juvenis em praias arenosas do Município do Rio de Janeiro, Brasil. *Biota Neotropica*, **7**, 93–100.
- Vazzoler A.E.M. (1996) *Biologia da reprodução de peixes Teleosteos: teoria e prática*. Eduem, Maringá: 169 pp.
- Villac M.C., Mayr L.M., Tenenbaum D.R., Paranhos R. (1991) Sampling strategies proposed to monitor Guanabara Bay, RJ, Brazil. In: Magoon O.T., Converse H.V., Tippie V., Tobin L.T., Clarck D. (Eds), *American Society of Civil Engineers*. Coastal Zone'91, New York: 1168–1182.
- Vinagre C., França S., Cabral H.N. (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. *Estuarine, Coastal and Shelf Science*, **69**, 246–254.
- Wagner C.M., Austin H.M. (1999) Correspondence between environmental gradients and summer littoral fish assemblages in low salinity reaches of the Chesapeake Bay, USA. *Marine Ecology Progress Series*, **177**, 197–212.
- Wheeler A. (1969) *The Fishes of the British Isles and North West Europe*. State University Press, East Lansing, MI: 613 pp.
- Whitfield A.K. (1999) Ichthyofaunal assemblages in estuaries: a South African case study. *Reviews in Fish Biology and Fisheries*, **9**, 151–186.
- Witting D.A., Able K.W., Fahay M.P. (1999) Larval fishes of a Middle Atlantic Bight estuary: assemblage structure and temporal stability. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 222–230.
- Wright J.M. (1989) Diel variation and seasonal consistency in the fish assemblage of the nonestuarine Sulaibikhat Bay, Kuwait. *Marine Biology*, **102**, 135–142.
- Zahorcsak P., Silvano R.A.M., Sazima I. (2000) Feeding biology of a guild of benthivorous fishes in a sandy shore on south-eastern Brazilian coast. *Revista Brasileira de Biologia*, **60**, 511–518.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Discriminating species of each season determined by SIMPER analysis. Only species contributing to 90% to the average similarity are listed. Av sim, average similarity.

Table S2 Results of one-way ANOSIM (R values and significance levels) and SIMPER for comparisons of fish assemblages between the periods of the day for each season.

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