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Research Article

Diel and tidal variation in surf zone fish assemblages of a sheltered beach in southern Brazil

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ABSTRACT. Diel and tidal variations of fish assemblages were assessed at Pontal beach, southern Brazil, using a seine net. Species richness was greater at night, whereas fish number, weight, and richness (community indicators) were all influenced by the tidal state. Samples from rising tides were more representative, probably due to onshore fish movements for feeding purposes. However, lower catches were associated with high tides, mainly through net avoidance, indicating that sampling in these conditions is not highly informative. Clupeoids exhibited greater variation in a 24 h period, and the night occurrence of *A. tricolor* and daylight shoaling of *Harengula clupeola*, *Anchoa parva* and *Sardinella brasiliensis* suggested distinct strategies for avoiding daylight predators. In some species, this behaviour may have been induced by the bottom morphology and tidal state, facilitating nearshore grouping. In addition to being caught at night, the occurrences of *Menticirrhus littoralis, Pomadasys corvinaeformis*, *Umbrina coroides* and *Hyporhamphus unifasciatus* indicated a spatial niche partition according to tidal state. Although not evaluated properly, temporal fluctuations could reflect species recruitment patterns. Seasonal fluctuations have to be considered when analysing short-term changes in the community as such fluctuations are synchronized with the natural history of the species, making it difficult to interpret short-term variations in isolation.

Keywords: diel cycle, tidal dynamics, species pattern, predators, shoals, southern Brazil.

Variación diaria y mareal de ensambles de peces en la zona de surf de una playa protegida en el sur de Brasil

RESUMEN. Se utilizó una red de arrastre para evaluar la variación diaria y mareal del ensamble de peces en la playa de Pontal, sur de Brasil. Se encontró la mayor riqueza de especies durante la noche mientras que la abundancia, peso y riqueza (indicadores de la comunidad) fueron influenciados por la marea. Las muestras de marea creciente fueron las más representativas debido probablemente a los movimientos costeros con fines alimentarios; sin embargo, las menores capturas estuvieron asociadas a pleamares debido a la evasión a la red, indicando que los muestreos en estas condiciones son poco informativos. Los clupeidos fueron los peces que más variaron durante un periodo de 24 h; la ocurrencia nocturna de *A. tricolor* y el agrupamiento matutino de *Harengula clupeola*, *Anchoa parva* and *Sardinella brasiliensis* sugieren distintas estrategias en la evasión de los depredadores diurnos. La morfología del fondo asociada con la marea, puede haber influenciado el comportamiento de algunas especies, facilitándoles el agrupamiento costero. Además de haber sido capturadas por la noche, la ocurrencia de *Menticirrhus littoralis, Pomadasys corvinaeformis*, *Umbrina coroides* and *Hyporhamphus unifasciatus* indicó la repartición espacial del nicho según el estado de la marea. Aunque no evaluadas correctamente, las fluctuaciones temporales pueden reflejar los patrones específicos de reclutamiento; la estacionalidad debe ser incluida cuando se estudian desplazamientos de corto plazo en la comunidad debido a su sincronización con la historia natural de las especies, haciendo que las variaciones de corto plazo sean difíciles de interpretar por sí solas.

Palabras clave: ciclo diario, dinámica mareal, patrones específicos, depredadores, cardúmenes, sur de Brasil.

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INTRODUCTION

Studies of fish assemblages in surf zones can provide not only information of the temporal structure of populations on both seasonal and diel basis, but also of the life-history phases that occupy the surf zone habitats. However, in such dynamic environment it is difficult to compare studies due to possible seasonal and diel differences in sampling effort, or gear susceptibility of different life stages (Ross, 1983). In general, seasonal changes in surf zone ichthyofaunas are characterised by low abundance and diversity during winter and the opposite pattern during warmer months (Fox & Mack, 1968; Naughton & Saloman, 1978; Modde & Ross, 1981; Allen, 1982; Ross, 1983; Lasiak, 1984b). These trends suggest that surf zone habitats may be briefly used by fish moving along the coast through passes into more protected waters, or by species that remain in the outer beach system for longer periods (Ross, 1983).

Short-term changes in abundance occur mainly due to the tidal cycle, moon phase, and alternation of night and day (Oliveira-Neto *et al.*, 2004). Many studies have found different patterns of fish habitat use, with greater daytime catches (Allen, 1982; Nash & Santos, 1998; Rooker & Dennis, 1991) and higher number of species and diversity during the night (Livingston, 1976; Nash & Santos, 1998; Lin & Shao, 1999). Nash (1986) and Gibson *et al.* (1996) concluded that community structure variation is strongly influenced by the dominant species peculiarities and as a consequence, failed to find a clear periodic pattern.

In this context, the present work aims to investigate the diel variability of the structure of a surf-zone fish community on a sheltered beach in southern Brazil. The study was carried out over a one-year period and emphasized the description of the patterns of variation of the most abundant species.

MATERIAL AND METHODS

Study site

Pontal do Sul is a sheltered sandy beach that is influenced by Ilha do Mel (island), which is located at Paranaguá estuary mouth. In addition, submerged channels created by ebb and flood tides reduce the incidental wave energy (Fig. 1). The beach is microtidal with two ebb tides per day. According to Godefroid *et al.* (1997) who investigated surf zone fishes on the same beach using different fishing gears, this beach is classified as dissipative due to the fine to medium sediment grain sizes, flat slope and medium wave heights. The weather is classified as subtropical humid with a warm and wet summer (December to February) and an undefined dry season (Maack, 1981), usually considered winter (June to August). Furthermore, spring and autumn months are defined as from September to November and March to May, respectively.

Sampling

The surf zone of Pontal beach, Paraná, Brazil, was extensively studied from August 2004 to June 2005. Bimonthly over a period of six months, three seine hauls were performed at 3 h intervals for 24 h on each sampling date. Due to weather conditions, April samples were postponed to the following month, May. Sampling occurred during spring tides at 8, 11, 14, 17, 20, 23, 2 and 5 h, in order to coincide with high, mid-falling, low and mid-rising tides, but this pattern could not always be followed. According to the day length, four samples were collected in daylight and other four at night-time during the entire studied period. All these samplings were considered replicates.

All hauls covered a 30 m extension and were separated by 5 m to minimize the influence on the subsequent haul. A 15 m x 2.6 m seine net, with 2 m^2 bag and 0.5 cm^2 mesh throughout was used to collect the ichthyofauna. The net was laid parallel to the shore at approximately 1.5 m depth of water between 10 and 30 m offshore, and was hauled by two people, one on each end of the net, following the direction of the current.

All fish collected were identified to species level following Fischer (1978), Figueiredo & Menezes (1978, 1980, 2000), Menezes & Figueiredo (1980, 1985) and Barletta & Corrêa (1992). These fishes were then weighted (g) and measured to the nearest 1 mm (total length and standard length), except when samples were very large. In these occasions, measurements were restricted to a sub-sample of 30 individuals per species. The excess was weighted, counted and incorporated as weight and number counts. In addition, sex (male, female or not identified) and maturity stages were documented for the sub-sample through direct observation, according

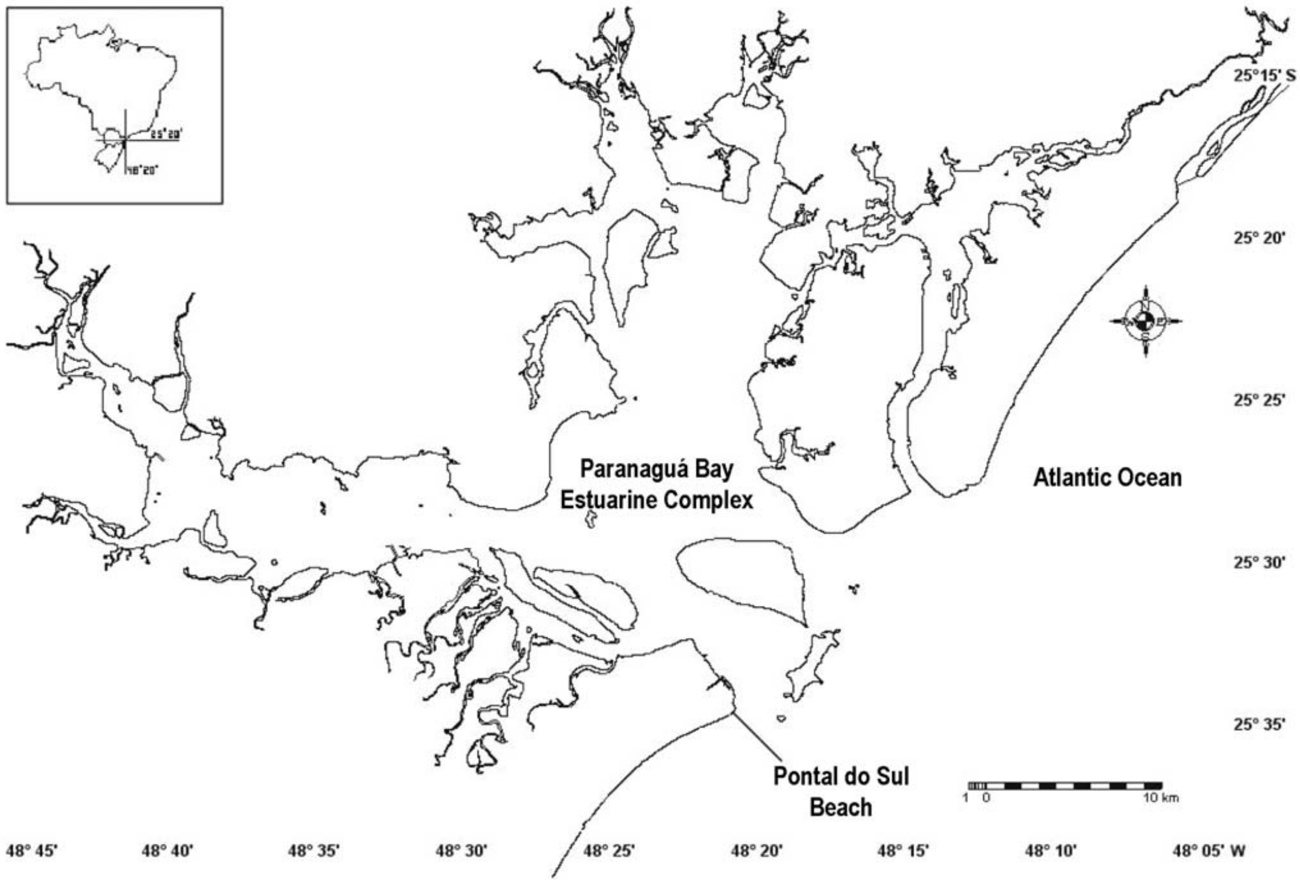

Figure 1. Location of Pontal do Sul beach, Brazil.

Figura 1. Localización de la playa de Pontal del Sur, Brasil.

to the macroscopic scale of gonadal maturation by Vazzoler (1981) (See Félix *et al.* 2007b for more information and results).

Environmental parameters such as surf zone water temperature (°C), salinity (Practical Salinity Scale-PSS), wave height (m) and period (s) were measured concomitantly at each sampling period. 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 sec) 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.

Data analysis

Homogeneity and normality of abiotic monthly means and biotic (diel and tidal) means were tested using Bartlett chi-square test and Kolmogorov-Smirnov test, respectively (Sokal & Rohlf, 1995). Number of individuals, species number and weight were log-transformed to comply with Anova and t-test assumptions. Environmental and diel biotic data were submitted to one-way and nested Anova, respectively, to test for differences on the abiotic variables and the influence of light (diel) on the surf zone catches (number, weight and number of species) between the sampling periods (time). Due to unequal tidal effort along the sampling period, Anova tests could not be conducted and t-test was used to evaluate tidal influence on catch number, weight and number of species. For the significant results ($P < 0.05$), Newman-Keuls *post-hoc* tests were performed to evaluate which means differed from each other. To evaluate individual occurrence pattern, and diel and tidal influence, these factors were tested for each of the 14 most abundant species, but as Engraulidae juveniles (10^{th}) and Mugilidae juveniles (11^{th}) are taxonomic categories they were not considered in the analysis, resulting in only 12 species. These analyses were performed with Anovas (diel and time nested in diel) and t-tests (tidal).

For operational purposes some abbreviations were adopted to distinguished between two different species: *S. brasiliensis* 1 is *Sardinella brasiliensis* Eigenmann, to separate from *Scomberomorus* *brasiliensis* Collette, Russo and Zavalla-Camin, abbreviation (*S. brasiliensis* 2) (ICZN, 2000). Additionally, *Mugil* sp. is the species once named *Mugil gaimardianus* Desmarest that no longer exists (Menezes *et al.*, 2003).

RESULTS

Abiotic data

Salinity (Anova, $F_{5,42} = 11.813$; $P < 0.05$) and temperature (Anova, $F_{5,42} = 10.783$; $P < 0.05$) were statistically significant during the evaluated months, particularly in February when high temperatures and low values of salinity were recorded, and in October which showed an unexpected low salinity value (Figs. 2a-2b). Wave height (Anova, $F_{5,41} = 0.931$; $P > 0.05$) and period (Anova, $F_{5,41} = 4.809$; $P < 0.05$) showed both a similar fluctuation pattern, with increasing values up to summer, and significant differences in wave period values of May and June compared to the other months (Figs. 2c-2d).

Fish composition

A total of 9,502 individuals was captured in 144 seine hauls, representing 25 families and 55 taxa, which weighted 39,017 g. Clupeidae (45.6%), Carangidae (23.2%), Sciaenidae (8.7%), Engraulidae (7.3%) and Atherinopsidae (6.1%) represented more than 90% of the total catch in numbers. *Harengula clupeola* Cuvier (34.4%), *Trachinotus carolinus* Linnaeus (14.7%), *S. brasiliensis* 1 (10.8%), *Oligoplites saliens* (Bloch) (7.82%) and *Odontesthes bonariensis* (Valenciennes) (6.10%) were the five most numerous species in the samples, representing 73.8% of the total catch in numbers (Table 1).

Night-time *versus* daylight captures

The species *Chloroscombrus chrysurus* (Linnaeus), *Sphoeroides greeleyi* (Gilbert), *Eucinostomus melanopterus* (Bleeker), *S. brasiliensis* 2, *Isopisthus parvipinnis* (Cuvier), *Oligoplites saurus* (Bloch and Schneider) and the *taxon* Clupeidae juveniles were captured only in daylight samples, whilst *Mugil platanus* Günther, *Chirocentrodum bleekerianus* (Poey), *Pomadasys ramosus* (Poey), *Cynoscion leiarchus* (Cuvier), *Stellifer rastrifer* (Jordan), *Sphoeroides testudineus* (Linnaeus), *Pelona harroweri* (Fowler), *Mugil* sp., *Conodon nobilis* (Linnaeus), *Prionotus nudigula* Ginsburg and *Synodus foetens* (Linnaeus) were captured exclusively at night-time (Table 1).

Fish numbers and weights of daylight catches were higher (58.6% of total capture and 25 kg) than bimonthly nocturnal catches (41.4% and 13 kg) but no statistical differences were found between photo-periods (Numbers: Anova, $F_{1,132} = 0.542$; $P > 0.05$ nor weights: Anova, $F_{1,132} = 0.029$; $P > 0.05$). Significant differences in the number of individuals were only found between February and December night catches when the factor time was nested in diel factor (Anova, $F_{10,132} = 2.588$; $P < 0.05$). Species number was influenced by both factors, diel (Anova, $F_{1,10} = 3.934$; $P < 0.05$) and time-diel interaction (Anova, $F_{10,132} = 4.713$; $P < 0.05$), with absolute nocturnal captures (48 species) higher than diurnal (44 species). August catches (both photoperiods) were both statistically distinct from February, May and June (Table 2).

Tidal captures

Only two species were caught exclusively at one specific tidal state. *Centropomus parallelus* Poey occurred only at mid-rising tides on both diurnal and nocturnal periods, and the *Mycteroperca* sp. followed the same pattern, occurring exclusively at low tides on both periods (Table 1).

Increasing number of individuals, species and weights were registered across tidal states as follows, high tide < mid-falling < low < mid-rising. According to t-tests, high tides were almost always distinct from other tidal states in respect to all variables evaluated (fish number and species and weight). The exceptions occurred for species number, when high tides were not distinct from mid-rising tides and for weight, in which high tides were not statistically different from low tides (Table 3).

Species pattern

The twelve most abundant species, which together contributed with 95.13% of the total catch in numbers, were studied in detail. All species were significantly influenced by one or both of the factors analysed. *H. clupeola*, *Menticirrhus littoralis* (Holbrook), *Pomadasys corvinaeformis* (Steindachner), *Umbrina coroides* Cuvier, *Hyporhamphus unifasciatus* Ranzani and *Anchoa parva* (Meek and Hildebrand) were statistically distinct for both factors. From the six species mentioned above *H. clupeola* was the only one in which day catches exceeded night ones; the remainder species showed major nocturnal captures (Table 1). These species were also influenced by temporal fluctuations, exhibited by an elevated number of fishes during specific months. Daytime captures in August, December and May, as well as in February samples (both periods) showed greater *H. clupeola* counts, differing from all other month captures (Fig 3a). For *A. parva* and *M. littoralis*, differences were found between October night catches

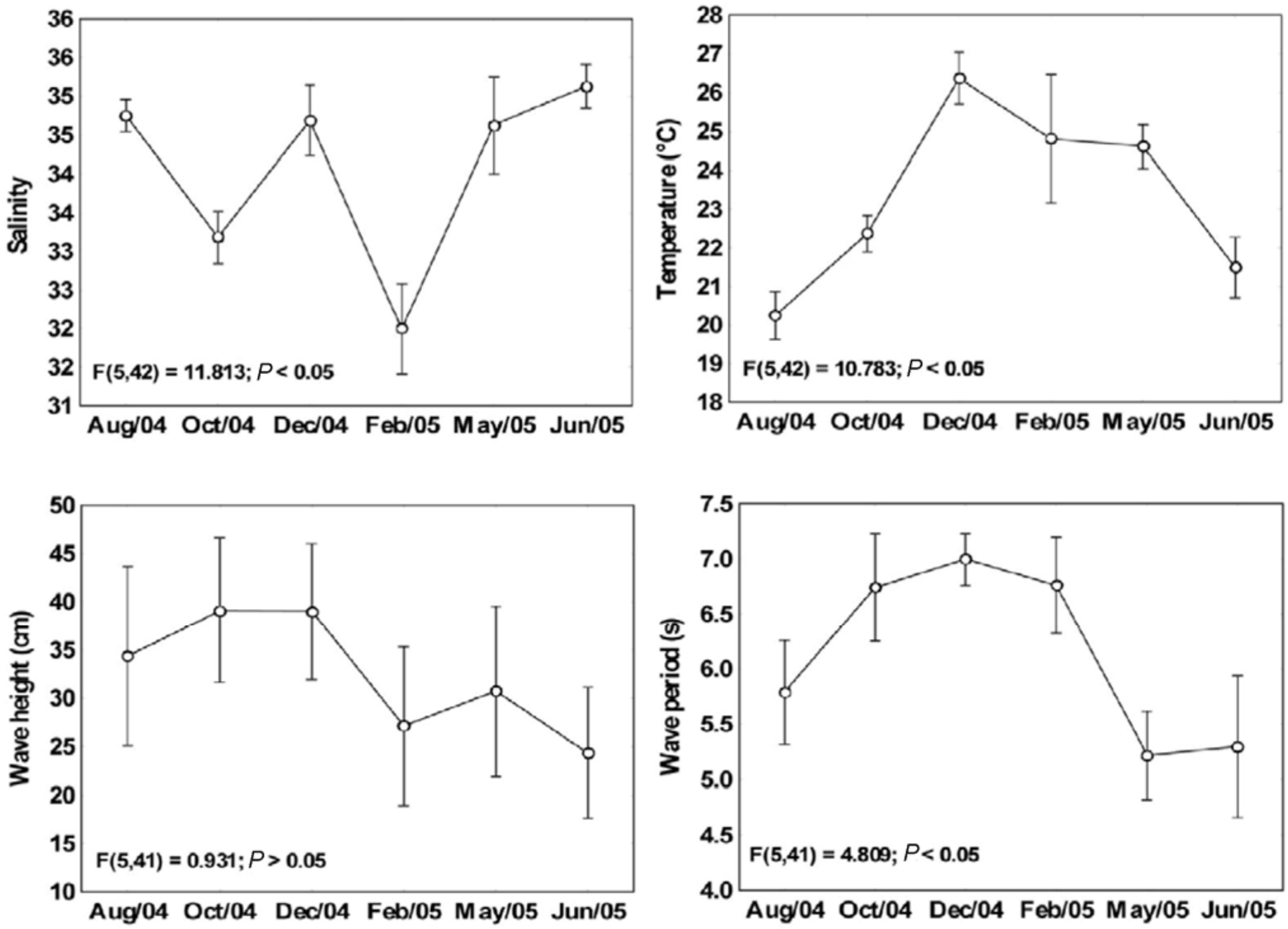

Figure 2. Analysis of variance of the temporal variation of the environmental parameters. a) salinity, b) temperature, c) wave height, and d) wave period of a sheltered beach in southern Brazil (means and standard deviation).

Figura 2. Análisis de varianza de la variación temporal de los parámetros ambientales. a) salinidad, b) temperatura, c) altura y d) periodo de las olas de una playa protegida en el sur de Brasil (media y desviación estándar).

and, respectively, all months and between night periods of other months (fig 3b,c). For the species *P. corvinaeformis, H. unifasciatus* and *U. coroides*, high abundances during the night in February contributed to the significant differences observed amongst the sampling periods (Figs. 3d-3f).

The same pattern of temporal variation occurred for the other five species, *O. bonariensis*, *T. carolinus*, *O. saliens*, *P. virginicus* and *S. brasiliensis* 1, who showed significant differences only for the interaction of factor time nested in diel. Similarly to *H. clupeola*, the great occurrence of *O. bonariensis* in August samples were distinct from the other months, whilst for *O. saliens* only the night period of the same month was significantly different (Figs. 3g, 3h). No differences were found amongst August (day and night), October and December diurnal period in regard to *T. carolinus* occurrence, however, these months and periods were statistically distinct from the remaining ones (Fig. 3i). *P. virginicus* showed statistical differences across night captures of May and other months (Fig. 3j), whilst *S. brasiliensis* 1 was significantly different comparing February night to the remaining months (Fig. 3k).

Anchoa tricolor (Agassiz) was the only species who has not been influenced by the interaction between time and diel factors; only diel was significantly different, with higher day catches compared to night ones (Fig. 3l).

Although common during all tidal states, several species were significantly different in some tidal comparisons. Low abundance of *O. bonariensis* at low water caused a difference from both mid-rising and mid-falling tides; on the other hand, high occurrence of *S. brasiliensis* 1 at mid-falling tides differed from the other states (Table 4). Catches of *H. unifasciatus*, *P. corvinaeformis* and *U. coroides* were similar according to the tidal states; low catches at high tides

Table 1. Total catch (absolute and relative) during diel and tidal samplings for each species captured in Pontal do Sul, Brazil.

Tabla 1. Captura total (absoluta y relativa) durante los muestreos diarios y mareales para cada una de las especies muestreadas en Pontal del Sur, Brasil.

Family	Species	Day tides						Night tides							
		High	Mid-falling	Low	Mid-rising	Sub-total	%	High	Mid-falling	Low	Mid-rising	Sub-total	%	Total	%
Albulidae	*Albula vulpes*				1	1	0.02			3	1	4	0.10	5	0.05
Atherinopsidae	*Odontesthes bonariensis*	108		3	355	466	8.36	7	44	12	51	114	2.90	580	6.10
Belonidae	*Strongylura marina*				5	5	0.09	1		1	1	3	0.08	8	0.08
	Strongylura timucu				6	6	0.11		1	6		7	0.18	13	0.14
Carangidae	*Chloroscombrus chrysurus*		1	2		3	0.05						0.00	7	0.03
	Oligoplites saliens	15	33	82	200	330	5.92		18	84	311	413	10.51	1400	7.82
	Oligoplites saurus				1	1	0.02						0.00	16	0.01
	Selene vomer				6	6	0.11				1	1	0.03	3	0.07
	Trachinotus carolinus	135	52	289	240	716	12.85	137	145	225	177	684	17.40	36	14.73
	Trachinotus falcatus	5		1		6	0.11	2	6	1	1	10	0.25	743	0.17
	Trachinotus goodei	4	8	3	6	21	0.38	6	4	1	4	15	0.38	1	0.38
Centropomidae	*Centropomus parallelus*				1	1	0.02				2	2	0.05	3	0.03
Clupeidae	Clupeidae juveniles			5	4	9	0.16						0.00	9	0.09
	Harengula clupeola	251	180	441	2048	2920	52.40	68	110	164	5	347	8.83	3267	34.38
	Ophistonema oglinum	11	8	1	3	23	0.41			1		1	0.03	24	0.25
	Sardinella brasiliensis	7	4	5	36	52	0.93		974	1		975	24.80	1027	10.81
Engraulidae	*Anchoa lyolepis*		1		2	3	0.05		1	4	1	6	0.15	9	0.09
	Anchoa parva		11	9	14	34	0.61	1		2		3	0.08	37	0.83
	Anchoa tricolor		36	202	110	348	6.25	24	2	4	1	31	0.79	379	3.99
	Cetengraulis edentulus	2			6	8	0.14	7	1	62	1	71	1.81	79	0.19
	Engraulidae juveniles		3	8	152	163	2.93	2	1			3	0.08	166	1.75
	Lycengraulis grossidens				5	5	0.09			14		14	0.36	19	0.39
Ephipidae	*Chaetodipterus faber*				1	1	0.02		1		1	2	0.05	3	0.03
Gerreidae	*Diapterus rhombeus*			4	2	6	0.11		1	2		3	0.08	9	0.09
	Eucinostomus argenteus		5	2	2	9	0.16		1	3	1	5	0.13	14	0.15
	Eucinostomus gula				2	2	0.04			2		2	0.05	4	0.04
	Eucinostomus lefroyi	1		21	12	34	0.61			4		4	0.10	38	0.40
	Eucinostomus melanopterus		2			2	0.04						0.00	2	0.02
	Eucinostomus sp.			1	12	13	0.23			1		1	0.03	14	0.15
Haemulidae	*Conodon nobilis*						0.00			10	4	14	0.36	14	0.15
	Pomadasys corvinaeformis	3	1	1	1	6	0.11	1	220	78	42	341	8.67	347	3.65
	Pomadasys ramosus						0.00		4		2	6	0.15	6	0.06

Family	Species	Day tides						Night tides							
		High	Mid-falling	Low	Mid-rising	Sub-total	%	High	Mid-falling	Low	Mid-rising	Sub-total	%	Total	%
Hemiramphidae	*Hyporhamphus unifasciatus*		5		3	8	0.14	1	4	19	24	48	1.22	56	0.59
Mugilidae	Mugilidae juveniles	8	1	23	42	74	1.33	4	5	53	6	68	1.73	142	1.49
	Mugil sp.						0.00	2	1	1	1	5	0.13	5	0.05
	Mugil platanus						0.00			2		2	0.05	2	0.02
Paralichthyidae	*Citarichthys arenaceus*		1	1	3	5	0.09		5	9	3	17	0.43	22	0.23
	Etropus crossotus	1	1	1	4	7	0.13	3	6	15	1	25	0.64	32	0.34
Polynemidae	*Polydactylus virginicus*	42				42	0.75	2	1	11	13	27	0.69	69	0.73
Pomatomidae	*Pomatomus saltatrix*	2	13	1	3	19	0.34	7	3	3	1	14	0.36	33	0.35
Pristigasteridae	*Chirocentrodon bleekerianus*						0.00			8		8	0.20	8	0.08
	Pellona harroweri						0.00			6	1	7	0.18	7	0.07
Sciaenidae	*Ctenosciaena gracilicirrhus*				1	1	0.02	5		11	4	20	0.51	21	0.22
	Cynoscion leiarchus						0.00		1			1	0.03	1	0.01
	Isopisthus parvipinnis				2	2	0.04						0.00	2	0.02
	Menticirrhus americanus	1				1	0.02	3	1	4	1	9	0.23	10	0.11
	Menticirrhus littoralis	49	22	16	47	134	2.40	76	45	91	183	395	10.05	529	5.57
	Stellifer rastrifer						0.00			2	1	3	0.08	3	0.03
	Umbrina coroides	16	12	19	25	72	1.29	16	9	81	81	187	4.76	259	2.73
Scombridae	*Scomberomorus brasiliensis*				5	5	0.09						0.00	5	0.05
Serranidae	*Mycteroperca* sp.			1		1	0.02			2		2	0.05	3	0.03
Synodontidae	*Synodus foetens*						0.00			1		1	0.03	1	0.01
Tetraodontidae	*Sphoeroides greeleyi*				1	1	0.02	2				2	0.05	3	0.03
	Sphoeroides testudineus						0.00				1	1	0.03	1	0.01
Triglidae	*Prionotus nudigula*						0.00	1	5	1		7	0.18	7	0.07

Table 2. Analysis of variance of the factors diel (day and night) and time (months nested in diel) on fish number, weight and species number of fish caught in Pontal do Sul, Brazil. (* significant values at $P < 0.05$; SS: sum of squares; df: degrees of freedom; MS: mean squares, F statistic and P value).

Tabla 2. Influencia de la variación diaria (día y noche) y el tiempo (meses) sobre el número de peces, peso y número de especies capturadas en Pontal del Sur, Brasil. (* valores significativos a nivel de $P < 0.05$, SS: suma de cuadrados, df: grados de libertad, MS: promedio de los cuadrados, estadístico F, valor de P).

Variable	Factor	SS	df	MS	F	*P*
Fish number	Diel	0.566	1	0.566	0.542	0.463 ^{ns}
	Time (diel)	26.991	10	2.699	2.588	0.007*
	Error	137.675	132	1.043		
Weight	Diel	0.045	1	0.045	0.029	0.865 ^{ns}
	Time (diel)	13.429	10	1.343	0.873	0.560 ^{ns}
	Error	203.063	132	1.538		
Species number	Diel	0.8292	1	0.829	4.713	0.032*
	Time (diel)	6.9214	10	0.692	3.934	0.000*
	Error	23.2228	132	0.176		

All tests are ANOVAs

Table 3. Tidal influence on fish number, weight and number of species caught at Pontal do Sul, Brazil. (L: low; MF: mid-falling, H: high, MR: mid-rising; df: degrees of freedom, P value).

Tabla 3. Influencia de la marea sobre el número de peces, peso y número de especies capturadas en Pontal del Sur, Brasil. (L: bajamar; MF: vaciante, H: pleamar, MR: llenante; df: grados de libertad, valor de P).

Variable	Factor	t-value	df	*P*
Fish number	H – MF	-2.019	55	0.048*
	H – L	-2.877	73	0.005*
	H – MR	-2.423	82	0.018*
	MF – L	-0.168	58	0.868 ^{ns}
	MF - MR	-0.026	67	0.980 ^{ns}
	L - MR	0.164	85	0.870 ^{ns}
Weight	H – MF	-2.139	55	0.037*
	H – L	-1.811	73	0.074 ^{ns}
	H – MR	-2.400	82	0.019*
	MF – L	0.631	58	0.530 ^{ns}
	MF - MR	0.106	67	0.916 ^{ns}
	L - MR	-0.610	85	0.544 ^{ns}
Species number	H – MF	-3.061	55	0.003*
	H – L	-3.108	73	0.003*
	H – MR	-1.612	82	0.111 ^{ns}
	MF – L	0.195	58	0.846 ^{ns}
	MF - MR	1.858	67	0.068 ^{ns}
	L - MR	1.841	85	0.069 ^{ns}

All tests are paired t-tests

were responsible for the differences in the comparisons with both mid-falling and low tides for all three species, and compared to mid-rising only for *H. unifasciatus* (Table 4).

DISCUSSION

The lack of diel correspondence with community descriptors agrees with other studies (Lasiak, 1984b;

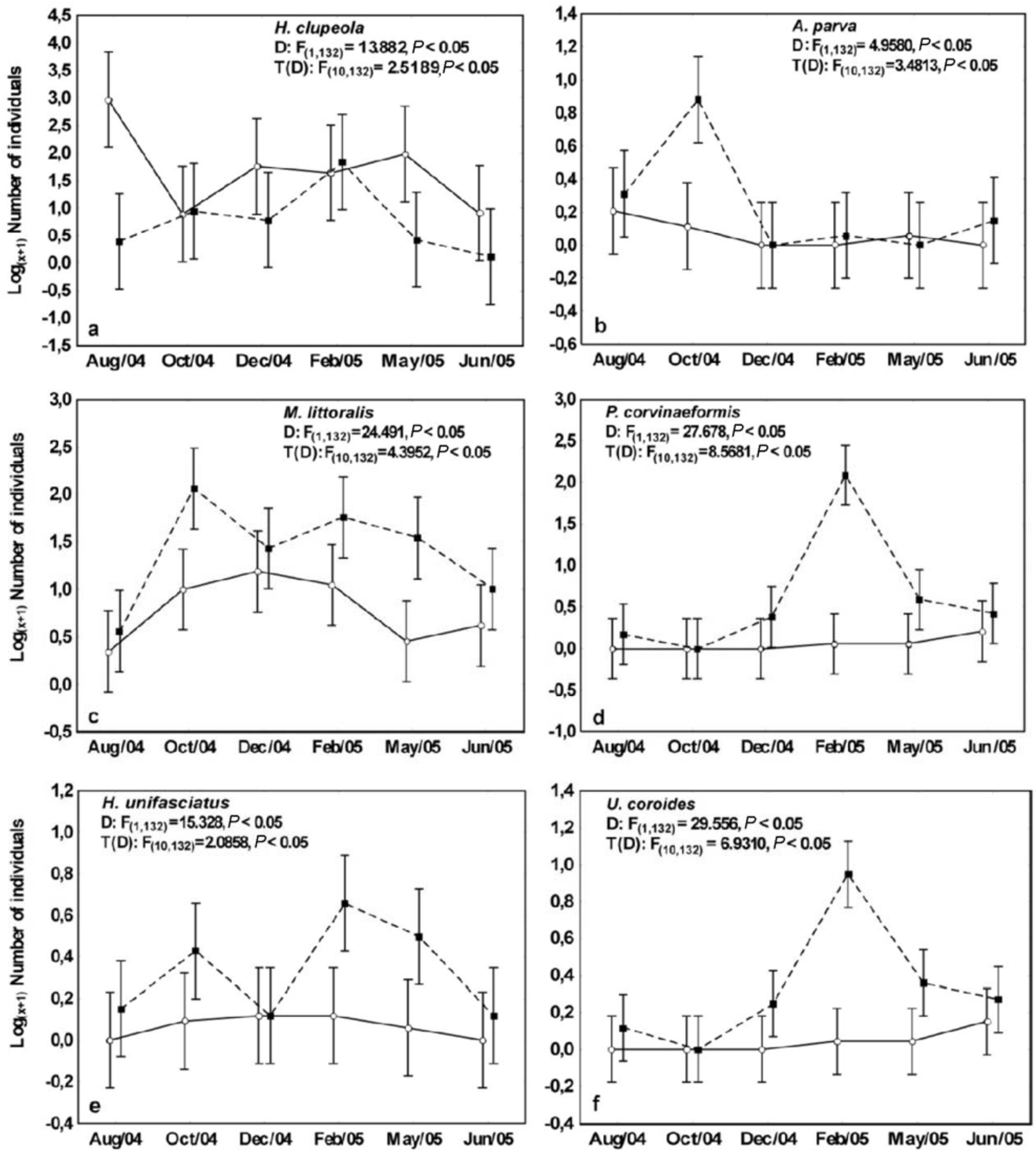

Figure 3. Influence of diel (D) and the interaction between time nested in diel (T(D) on mean number of fish caught for the 12 most abundant species in Pontal do Sul, Brazil. a) *Harengula clupeola*, b) *Anchoa parva*, c) *Menticirrhus littoralis*, d) *Pomadasys corvinaeformis*, e) *Hyporhamphus unifasciatus,* f) *Umbrina coroides*. (○: daylight means; ■: night-time means; I: confidence interval; F statistic (degrees of freedom, sample *n*) and *P* values for diel and time nested in diel factors).

Figura 3. Influencia del fotoperíodo (D) e interacción entre el tiempo anidado y fotoperíodo (T(D)) en el promedio del número de peces capturados pertenecientes a las 12 especies más numerosas en Pontal del Sur, Brasil. a) *Harengula clupeola*, b) *Anchoa parva*, c) *Menticirrhus littoralis*, d)*Pomadasys corvinaeformis*, e) *Hyporhamphus unifasciatus,* f) *Umbrina coroides*. (○: promedio día; ■: promedio noche; I: intervalo de confianza; estadístico F (grado de libertad, y *n* muestreal) y valor de *P* para los factores fotoperíodo y el tiempo anidado al fotoperíodo).

Table 4. Significant tidal influence for species caught at Pontal do Sul, Brazil. (L: low, MF: mid-falling, H: high, MR: mid-rising, df: degrees of freedom, *P* value).

Tabla 4. Influencias significativas de la marea sobre las especies capturadas en Pontal del Sur, Brasil. (L: bajamar; MF:vaciante, H: pleamar, MR: llenante, df: grados de libertad, valor de *P*).

Variable	Factor	*t*-value	df	*P*
O. bonariensis	L – MF	2.019	58	0.048
	L – MR	-2.376	85	0.019
S. brasiliensis	MF – H	-2.35	55	0.022
	MF – L	2.379	58	0.020
	MF – MR	2.003	67	0.049
H. unifasciatus	H – MF	-2.658	55	0.010
	H – L	-2.968	73	0.004
	H – MR	-2.708	82	0.008
P. corvinaeformis	H – MF	-2.323	55	0.023
	H – L	-2.65	73	0.009
U. coroides	H – MF	-2.235	55	0.029
	H – L	-2.675	73	0.009

All tests are paired t-tests.

Morrison *et al.*, 2002; Pessanha & Araújo, 2003), which showed no occurrence of strong changes in fish assemblage composition between day and night. An exception was observed for number of species, with richer fish assemblages occurring at night (Nash & Santos, 1998; Suda *et al.*, 2002).

The occurrence pattern of the abundant species may have masked real differences in a short-term perspective. Probably, the absence of diel periodicity of an assemblage is caused by changes in catches of individual species whose capture rate depends upon the prevailing photoperiod (Eriksson, 1978; Muller, 1978b; Nash, 1986). The main reasons for short-period changes in fish assemblages remain unclear, but may include processes such as displacement for feeding purposes (Helfman, 1978, 1993; Pessanha & Araújo, 2003), protection and predator avoidance (Morisson *et al.*, 2002) or annual spawning migrations (Harden-Jones, 1968).

On the opposite trend, tidal cycle had more effects on the number, weight and species richness. Significant differences between high tide and the other tidal states were attributed to low fish catches, which according to Morrison *et al.* (2002) could be related to net avoidance by most fish species or influenced by sea agitation. In such condition, breaking waves pushes the net shoreward to the beach face (pers. obs.) making hauls more difficult by limiting its speed. Although statistical differences were absent, highest catches in number of fishes, weight and species richness were attributed to mid-rising tides. Gibson (1982) suggests that fish can respond in two ways to tidal variation: (1) remaining under the low-tide mark and inhabiting tidal pools, (2) or moving across the intertidal zone and returning to the area during rising tides. Based on this hypothesis, higher catches at mid-rising tides could be attributed to returns of local fish as well as other onshore fish movement, such as during predator foraging. Gibson's work (1982) found that tidal movements are caused primarily by feeding migration and secondarily for predator avoidance, giving support to the proposed hypothesis.

Differences were found when diel, tidal and temporal occurrence of the most abundant species were analysed separately. Clupeiforms showed distinct temporal, diel and tidal patterns, which is consistent with Modde & Ross (1981) results showing that clupeoids vary more than percoids within 24 h period. *H. clupeola* and *A. tricolor* were significantly more numerous during the day (Allen & DeMartini, 1983; Godefroid *et al.*, 1998; Oliveira-Neto *et al.*, 2004). Probably, shoaling behaviour allowed them to occur in daylight since in this formation they are protected from visual predators, such as adult fish or shore birds. In contrast, major captures of *A. parva* in numbers occurred at night, whilst those of *S. brasiliensis*1 did not show any diel influence. The latter was, nevertheless, the only species whose occurrence was related to tidal states.

Due to local strong tidal currents, troughs and ridges were found across submerged beach slopes, making some regions deeper than others. The elevated number of clupeoids found in the present work, which normally are found in shoals, could be related to this bottom morphological feature (Félix *et al.*, 2007). By using this troughs *S. brasiliensis*1 could easily be caught at mid-falling tidal conditions, rendering its capture statistically distinct from the other tidal states. This pattern was only found for *S. brasiliensis*1, probably due to a combination of tidal condition and its restricted occurrence period, mainly February, which is well known as part of the reproductive period of many species in the study area (Godefroid *et al.*, 2004; Spach *et al.*, 2004). Monthly differences in species catches indicated strong temporal influence, which may be a reflex of seasonal changes in abundance and diversity of surf zone fishes resulting from recruitment patterns (Ross *et al.*, 1987).

Benthic fishes such as *M. littoralis, U. coroides* and *P. corvinaeformis* and the planktophagic feeder *H. unifasciatus* were predominantly nocturnal (Godefroid *et al.*, 1998); coastal approximation during the night may be strategic to avoid daylight predators guided mainly by vision (Abou-Seedo *et al.*, 1990). Except for *M. littoralis* who did not show tidal influence and occurred every month, all species exhibited the same temporal and tidal occurrence patterns. Similarly to *S. brasiliensis*1, these species showed elevated catches in February, indicating reproductive period and lowest catches during high tides.

Amongst sciaenids, *M. littoralis* is the most extensive user of the surf zone (Teixeira *et al.*, 1992), showing peaks of abundances during spring months when recruitment probably occurs (Modde, 1980). Also, Modde & Ross (1983) studying the feeding ecology of surf zone species found that *M. littoralis* has different peaks of abundance and feeding activity during the day, with the best foraging period in the afternoon and at night, corroborating with the high nocturnal catches observed in the present study. Their bottom-associated behaviour allows the exploration of a variety of items such as macro- and meiofauna or zooplankton (Lasiak, 1986; Nelson, 1986), which is abundant in surf zone habitats and easily available through high-energy waves. This wide diet width may permit benthic fishes such as *H. unifasciatus* to share many characteristics involving diel, temporal and tidal occurrence by segregating niche spatially (vertical movements and zonation) and/or temporally (distinct month occurrence and abundance). Low high-tide catches of *P. corvinaeformis*, *U. coroides* and *H. unifasciatus* indicate that either these fishes were not caught or did not move forward to shallower waters to feed, remaining at deeper zones during this tidal period. Apparently, these species do not compete directly and may share resources by moving vertically in the water column (like *H. unifasciatus*) and/or feed on a variety of abundant items (*P. corvinaeformis* and *U. coroides*), whilst *M. littoralis* co-occurs by making extensive use of sandy beach bottoms. McPherson (1981) reported that competition is the most common behaviour amongst organisms with predominant benthic activity, thus, it may be inferred that sharing resources and space have to occur higher to favour the coexistence of these species.

P. virginicus was the only benthic species of those already cited who has not shown significant diel dissimilarities, but like *O. saliens*, it has been influenced by seasonal trends reflected on the monthly catches. *T. carolinus*, like *M. littoralis,* is a wide user of surf zone beaches (Modde & Ross, 1983) but, it did not show any diel variation in the present work, occurring at the same catch rates on both day and night. However, statistical differences between August, October and December and the remaining months may be attributed to the entrance of recruits after December, when night-time and daylight catches were higher and mean size of individuals smaller (*pers. obs.*; Félix *et al.* 2007b).

Despite tidal distinctiveness, high captures of *O. bonariensis* in August made temporal fluctuations a significant factor for the cited species. Monteiro-Neto *et al.* (1990) provided a hypothesis to explain this seasonal occurrence in northern beaches. The authors believe that this species opportunistically shift places from oceanic to coastal waters, probably occupying an unexplored niche due to low numbers of residents or exclusive species in the surf zone. In estuarine habitats, occupation is effective in cold months, differing from sandy beaches where fish reside during warmer months (Modde, 1980). Consequently, the higher competition in the estuary and its absence in coastal waters may have favoured *O. bonariensis* to migrate toward northern areas; however, this hypothesis is still unproven. Finally, as there is a need for a re-evaluation of this species and consequently, some doubts concerning the description of the species, this question will remain open.

CONCLUSIONS

Despite the larger number of species caught during night periods and the results found by several researchers (Abou Seedo *et al.*, 1990; Nash & Santos, 1998; Suda *et al.*, 2002), no great changes at community level were observed across the tidal and diel cycles. However, when species were analysed separately many differences were detected. This variability in fish assemblages caught in shallow waters may be related to tidal height and light level combination (Nash *et al.*, 1994), which has major implications on the feeding patterns and, according to

Gibson (1982), is the primary cause for fish movement across tidal zones.

Although seasonality was not evaluated in the present study, distinct monthly captures indicated that temporal variation was more important for some species than others. These variations reflected the recruitment patterns determined by reproductive activity and coastal circulation (Ross *et al.*, 1987; Gibson *et al.*, 1993, Lamberth *et al.*, 1995), either by adult emigration or by temporary exploration of adjacent high productivity areas (Allen, 1982).

This work has shown that methodological standardization is essential to obtain good and unequivocal results. Unfortunately, tides could not be standardized for every sampling occasion and were not evaluated properly; likewise, the missing seasonal replicates prevented more conclusions about fish community variation, indicating that further studies are required to solve the existent questions. More investments on basic fish biology studies have to be made, particularly in Brazil owing to its high diversity of species and because community patterns can provide important information on population behaviour of the studied species.

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