Seasonal and diel variation in the fish assemblage of a Neotropical delta in southern Brazil

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ABSTRACT. The objective of this study was to identify the patterns of seasonal and diel variation and the most important abiotic factors that influence variation in the fish assemblage of the Delta of the Jacuí River in southern Brazil. Seventy-two samples were collected over a one year period. Water temperature was the abiotic factor with the greatest influence on the distribution of the assemblage. The structure of the assemblage exhibited significant changes in terms of species abundance and biomass during the year, with the greatest abundance and biomass being observed during the autumn. There was no significant difference between day and night in terms of abundance, but biomass was significantly greater during the night than during the day.

KEYWORDS. Fish ecology, freshwater fish, biological rhythm, circadian rhythm, Patos Lagoon.

RESUMO. Variação sazonal e circadiana na assembleia de peixes em delta Neotropical no sul do Brasil. O objetivo deste estudo foi identificar o padrão de variação sazonal e circadiana e os principais fatores abióticos que influenciam a estrutura da assembleia de peixes do delta do rio Jacuí, região sul do Brasil. Foram realizadas 72 amostragens durante o período de um ano. A distribuição da assembleia foi influenciada principalmente pela temperatura da água. A estrutura da assembleia apresentou diferenças significativas na abundância e biomassa das espécies entre as estações do ano e as maiores abundância e biomassa foram apresentadas no outono. Quando os resultados do dia e da noite foram comparados, a abundância não apresentou diferença significativa, entretanto a biomassa da noite foi significativamente maior que a do dia.

PALAVRAS-CHAVE. Ecologia de peixes, peixes de água doce, ritmo biológico, ritmo circadiano, laguna dos Patos.

The temporal and spatial variations of fish assemblages are influenced by both biotic and abiotic factors. Even in adjacent biotopes, these assemblages exhibit a high degree of variation which is dependent upon the relationships between each species intrinsic characteristics and environmental variables such as resource accessibility and availability (JACKSON *et al.*, 2001; OKADA *et al.*, 2003).

Several authors have emphasized the importance of studying the structure of fish assemblages as a tool for understanding the environment and for establishing relationships between their structures and environmental factors (RICKLEFS, 1987; JUNK *et al.*, 1989; TEJERINA-GARRO *et al.*, 1998; LOREAU *et al.*, 2001; GRANADO-LORENCIO *et al.*, 2005; PIANA *et al.*, 2006). These studies have investigated ecological mechanisms that act on assemblages (*e.g.* competition, reproduction, parasitism and predation) and evaluated interactions with environmental variables (*e.g.* dissolved oxygen, temperature and seasonality). It is therefore evident that the question of which environmental and ecological factors have a significant influence on the structure of the assemblage in a given location is considered important within the field of ecology (WELCOMME, 1979; SCHLOSSER, 1982; TOWNSEND & HILDREW, 1994; BROWN, 2000; SCHEINER & WILLIG, 2008).

The structure of a local assemblage may undergo seasonal and diel variations. In a considerable part of the Neotropical region, seasonal variation has been described in studies investigating the differences between flood and dry periods. These studies have demonstrated that there is greater availability of food and increased species abundance during flood periods, leading them to consider this seasonal phenomenon to be the main modulating the structure of the biota (AGOSTINHO *et al.*, 1995; MATTHEWS, 1998; LAKE, 2003; FREITAS & GARCEZ, 2004; MAGALHÃES *et al.*, 2007; SOUSA & FREITAS, 2008).

However, no studies could be located that have focused on the structure of the fish assemblage in Neotropical environments exhibiting both periods of high and low rainfall and strong temperature variations. Temperature is a limiting factor and higher or lower temperatures can favour the presence or absence of certain species, affecting the distribution and composition of the community (MAGNUSON *et al.*, 1979; JAUREGUIZAR *et al.*, 2003; WOLTER, 2007; CUSSAC *et al.*, 2009).

Furthermore, species-specific diel variations can mean that the abundance of individuals and species in a given habitat changes over the course of 24-hours, as determined by feeding activities (ROOKER & DENNIS, 1991; PIET & GURUGE, 1997), predation and the need to escape from predators (WRIGHT, 1989; COPP & JURAJDA, 1993; BURROWS *et al.*, 1994; GIBSON *et al.*, 1998; GROSSMAN *et al.*, 1998). According to LOWE-MCCONNELL (1999) the presence of predators and large species at night, while small species protect themselves in the vegetation, is a common observation in Neotropical rivers.

This article describes a study in which fishes were sampled systematically in a Delta located in the

Neotropical region of southern Brazil with the objective to investigate whether seasonal and diel variation is related to abiotic factors (pH; Secchi transparency; dissolved oxygen; air and water temperature; rainfall and water column depth).

MATERIAL AND METHODS

Study area. The Jacuí River Delta is located in southern Brazil and receives water from the Jacuí, Gravataí, Caí and Sinos rivers, forming a flooded freshwater area of approximately 22 thousand hectares comprising several islands and a network of channels and wetlands that provide the inflow to the Guaíba Lake, which itself flows out to the Patos Lagoon and on to the Atlantic Ocean (Fig. 1). The Delta is located in a region with a subtropical humid climate and has water temperature that varies from 11°C to 24°C over the course of the year, and a mean air temperature of 19.5°C, which can vary by up to 9°C during daylight hours (MALUF, 2000; FARIA & LERSCH, 2001). Annual rainfall is less than 1500 mm and the lowest rainfall is observed between December and February (MALUF, 2000).

Field sampling. Sampling was carried out monthly from October 2004 to September 2005, at three locations that were considered replicates of each other: Saco da Alemoa (SA) (29º59’56.5’’S, 51º14’53.4’’W), Saco do Quilombo (SQ) (29º58’31’’S, 51º15’53.2’’W), and Saco do Ferraz (SF) (30º00’34.8’’S, 51º14’41.3’’W) (Fig. 1). All of these sampling stations are bays with a depth of more than 1.2 m, bushy vegetation, grass, and macrophytes (*Eichhornia* spp.) growing along the banks (OLIVEIRA & PORTO, 1999).

The following physical and chemical measurements were taken monthly at each sampling area: pH, Secchi transparency, dissolved oxygen and air and water temperature. Additionally, monthly data on rainfall and water column depth were obtained from the eighth district of the Instituto Nacional de Meteorologia and from the Superintendência de Portos e Hidrovias, respectively. We used several gillnets for each sampling area, with mesh sizes of 1.5, 2.5, 3.5, 4.5 and 6.0 cm between adjacent knots and with dimensions of 20 x 1.5 m, making a total area of 150 m^2. The nets were arranged in sequence, perpendicular to the shore for a period of 24 hours. Nets were set at 6pm and were checked at 6am on the following day. All individuals collected during this period were considered nocturnal, while individuals collected between 6am and 6pm were considered diurnal. Environmental data was used to define the seasons as follows, spring: September, October and November; summer: December, January and February, autumn: March, April and May and winter: June, July and August.

The individuals collected were classified according to taxonomic keys and were measured (mm), and weighed (g). Voucher species were deposited in the ichthyologic collection of the Laboratório de Ictiologia, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Brazil, under the following accession numbers: UFRGS 0088, 0188, 4190, 5059, 5172, 5838, 6366, 6707, 6727, 6989, 7114, 7576-7585, 7588-7590, 7592-7594, 7595, 7656, 8190, 8259, 8643, 8916, 8917.

Data analysis. In order to describe the main species distribution tendencies and to relate them to environmental factors, monthly means were calculated from the absolute numbers of individuals captured at the three sampling areas and, independent of diel variation, correlated with the abiotic data using canonical correspondence analysis (CCA), performed with CANOCO version 4.5 software (TER BRAAK, 1995).

The data were natural log-transformed (Ay + B) and the “downweighting of rare species” option was selected in order to ensure that where few individuals of a given species had been collected, this would not affect the final result. The significance of environmental factors was estimated using the “vif” function (variance inflation factor), which detects co-linearity between variables,

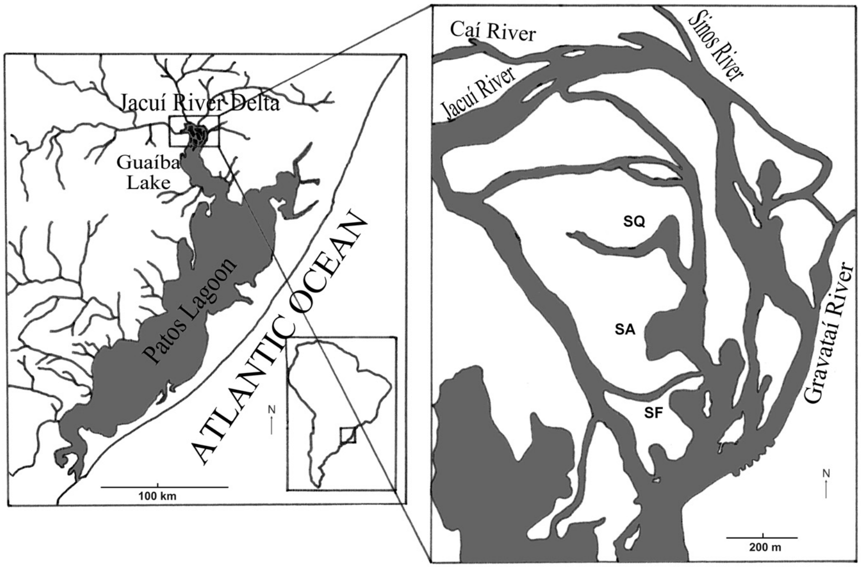

Figure 1. Location of the Jacuí River Delta, southern Brazil, with sample areas: Saco do Quilombo (SQ), Saco da Alemoa (SA) and Saco do Ferraz (SF).

where variables whose vif > 20 were defined as redundant and removed from the analysis (Myers, 1990; Hair *et al.*, 1998). Statistical significance was estimated using the Monte Carlo permutation test (10^4 unrestricted permutations) with the significance level set at $P \leq 0.05$. The null hypothesis was that species abundance did not correlate with environmental variables.

Principal coordinates analysis (PCA, ter Braak, 1995) was performed using a matrix of abundance data for each species, for each season, and for the day and night periods, in order to represent the pattern of associations between species composition and seasons and day/night. Data were natural log-transformed (Ay + B) and the downweighting rare species option was once more selected in order to avoid the influence of rare species leading to biased results. Detrended correspondence analyses (DCA, ter Braak, 1995) was performed in order to verify the length of the gradient (< 3 SD) and, on the basis of the DCA results, a linear PCA model was selected, in line with standard practice (ter Braak, 1995). Ordination analyses were carried out using the computer program CANOCO version 4.5.

Hypotheses were tested using analysis of variance with randomization (Manly, 1991) in order to verify whether there were significant diel differences between species abundance at seasonal stations. A multivariate analysis based on randomization and bootstrap non-parametric re-sampling methods was performed (Manly, 1991; Crowley, 1992; Podani, 1994; Pillar, 1998; 1999). Data were transformed [log (x+1)], and the Euclidian distance was used as measure of similarity. The randomization test was performed through 1000 interactions and the main criterion adopted was the sum of the square of the distances between groups. The significance level used for all analyses was $P \leq 0.05$ and the null hypothesis tested was that the composition of these species does not change in relation to seasonal variations and is independent of day or night. The MULTIV computer program, version 2.4.2 (Pillar, 2006), was used to transform the data and perform the similarity measurements and randomization tests.

The constancy (*c*) for each species was calculated using the number of months and the period (day/night) during which the species was collected. Each species were classified as frequent ($c > 50\%$), accessory ($25\% \leq c \leq 50\%$), or accidental ($c < 25\%$) (Dajoz, 1983).

Indices of richness (Margalef, 1951), diversity *H'* (ln), and evenness *J'* (Pielou, 1966, 1975) were calculated using the Divers computer program (Perez-Lopez & Sola-Fernandez, 1993). MULTIV version 2.4.2 (Pillar, 2006) was used to compare results with analysis of variance (one-way ANOVA), by season and sampling period (day/night).

RESULTS

A total of 3862 individuals were collected, distributed across 34 species (Tab. I). *Cyphocharax voga* (Hensel, 1870), *Astyanax fasciatus* (Cuvier, 1819), *Parapimelodus nigribarbis* (Boulenger, 1889), *Pachyurus bonariensis* Steindachner, 1879, *Corydoras paleatus* (Jenyns, 1842), *Loricariichthys anus* (Valenciennes, 1835), *Pimelodus maculatus* Lacepède, 1803 and *Hoplosternum littorale* (Hancock, 1828) accounted for 80% of the total catch in terms of number of individuals, while *C. voga*, *L. anus*, *P. bonariensis*, *P. maculatus*, *Hoplias malabaricus* (Bloch, 1794) and *H. littorale* accounted for 80% of the total biomass (Tab. II).

With relation to the significance of the environmental factors, the variables "air temperature" and "depth of the water column" were considered redundant (vif > 20) and were removed from the analysis. The environmental variable measurements are given in table III and the results of the canonical correspondence analysis (Tab. IV; Fig. 2) based on these measurements demonstrated that water temperature was the environmental variable with the greatest influence on the distribution of species. The results of this analysis were significant and the environmental factors measured explained 59.2% of the variation in abundance. The first and second ordination axes were predominantly correlated with the variables "water temperature" and "rainfall" (Tab. V).

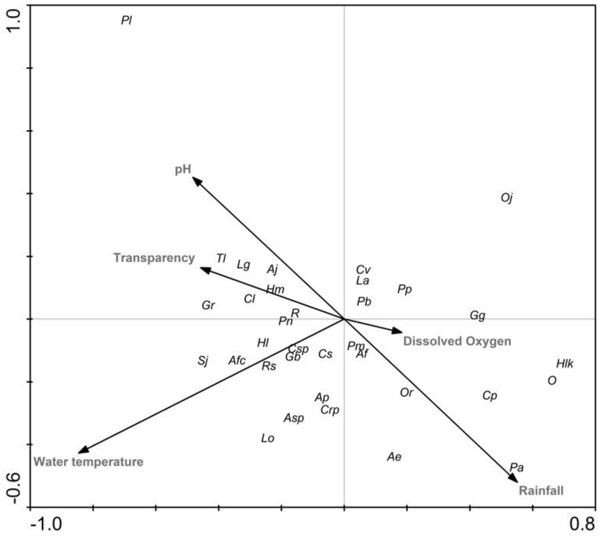

Figure 2. Pattern in fish assemblages distribution among environmental variables based on canonical correspondence analysis (CCA) in the Jacuí River Delta, RS, Brazil, from October 2004 to September 2005 (Ap, *Acestrorhyncus pantaneiro*; Ae, *Astyanax eigenmanniorum*; Af, *Astyanax fasciatus*; Aj, *Astyanax jacuhiensis*; Asp, *Astyanax* sp.; Afc, *Australoheros facetus*; Cs, *Charax stenopterus*; Cp, *Corydoras paleatus*; Cl, *Crenicichla lepidota*; Crp, *Crenicichla punctata*; Cv, *Cyphocharax voga*; Csp, *Cyphocharax spilotus*; Gb, *Geophagus brasiliensis*; Gg, *Gymnogeophagus gymnogenys*; Gr, *Gymnogeophagus rhabdotus*; Hm, *Hoplias malabaricus*; Hl, *Hoplosternum littorale*; Hlk, *Hyphessobrycon luetkenii*; Lo, *Leporinus obtusidens*; La, *Loricariichthys anus*; Lg, *Lycengraulis grossidens*; O, *Odontesthes* sp.; Oj, *Oligosarcus jenynsii*; Or, *Oligosarcus robustus*; Pb, *Pachyurus bonariensis*; Pn, *Parapimelodus nigribarbis*; Pa, *Pimelodella australis*; Pm, *Pimelodus maculatus*; Pp, *Platanichthys platana*; Pl, *Prochilodus lineatus*; R, *Rhamdia*; Rs, *Rineloricaria strigilata*; Sj, *Schizodon jacuiensis*; Tl, *Trachelyopterus lucenai*).

Table I. Individuals (n) collected in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005 in every season and day period and their respective ecological indices.

Taxa	Abbrev.	Spring		Summer		Autumn		Winter		Constancy (%)	
		Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
ATHERINIFORMES											
Atherinopsidae											
Odontesthes sp.	*O*	3						1			16.7
CHARACIFORMES											
Acestrorhynchidae											
Acestrorhynchus pantaneiro Menezes, 1992	*Ap*	2		2		2	2			50	16.7
Anostomidae											
Leporinus obtusidens Valenciennes, 1837	*Lo*				1	4	1			16.7	16.7
Schizodon jacuiensis Bergmann, 1988	*Sj*	1	2	3	2	4	1			33.3	25
Characidae											
Astyanax eigenmanniorum (Cope, 1894)	*Ae*	1	1	1		5	1			41.7	8.3
Astyanax fasciatus (Cuvier, 1819)	*Af*	43	56	66	41	198	36	20	12	100	100
Astyanax jacuhiensis (Cope, 1894)	*Aj*	7		10	7	2		1		50	25
Astyanax sp.	*Asp*	1		2		7				33.3	
Charax stenopterus (Cope, 1894)	*Cs*			2	4	1	3	1	1	25	25
Hyphessobrycon luetkenii (Boulenger, 1887)	*Hlk*	3	5						4	8.3	16.7
Oligosarcus jenynsii (Günther, 1864)	*Oj*	1	1			21	3	15	43	33.3	50
Oligosarcus robustus Menezes, 1969	*Or*	3	3	2	3	12	21		6	33.3	50
Curimatidae											
Cyphocharax spilotus (Vari, 1987)	*Csp*	22	4	16	4	8		3	1	91.6	50
Cyphocharax voga (Hensel, 1870)	*Cv*	103	79	139	20	244	264	110	203	100	91.6
Erythrinidae											
Hoplias malabaricus (Bloch, 1794)	*Hm*	12	11	10	26	3	13	1	6	66.7	91.6
Prochilodontidae											
Prochilodus lineatus (Valenciennes, 1837)	*Pl*	1								8.3	
CLUPEIFORMES											
Engraulidae											
Lycengraulis grossidens (Agassiz, 1829)	*Lg*	6	2	2	4	3		2		66.7	33.3
Clupeidae											
Platanichthys platana (Regan, 1917)	*Pp*	2	1					1		16.7	16.7
PERCIFORMES											
Cichlidae											
Australoheros facetus (Jenyns, 1842)	*Afc*			1		1				16.7	
Geophagus brasiliensis (Quoy & Gaimard, 1824)	*Gb*	4	1	16	2	19	4	2	4	66.7	58.3
Gymnogeophagus gymnogenys Hensel, 1870	*Gg*	4	3			8	3	7	3	58.3	33.3
Gymnogeophagus rhabdotus Hensel, 1870	*Gr*	3	1	4	4	8	1			41.7	25
Crenicichla lepidota Heckel, 1840	*Cl*	4	1	12						41.7	8.3
Crenicichla punctata Hensel, 1870	*Crp*	5				3	2			33.3	16.7
Sciaenidae											
Pachyurus bonariensis Steindachner, 1879	*Pb*	15	9	25	11	117	42	51	45	91.6	100
SILURIFORMES											
Auchenipteridae											
Trachelyopterus lucenai Bertoletti, Pezzi da Silva & Pereira, 1995	*Tl*	3	10		2		3			8.3	41.7
Callichthyidae											
Corydoras paleatus (Jenyns, 1842)	*Cp*	2	9			95	66	15	109	41.7	50
Hoplosternum littorale (Hancock, 1828)	*Hl*	10	12	11	58	14	39		4	66.7	91.6
Loricariidae											
Loricariichthys anus (Valenciennes, 1835)	*La*	14	28	47	44	29	24	23	57	100	91.6
Rineloricaria strigilata (Hensel, 1868)	*Rs*				2				1		8.3
Heptapteridae											
Rhamdia spp.	*R*		1	7	13	2	2	3	4	33.3	66.7
Pimelodella australis Eigenmann, 1917	*Pa*					1				8.3	
Pimelodidae											
Parapimelodus nigribarbis (Boulenger, 1889)	*Pn*	22	57	66	14	150	41	18	7	91.6	83.3
Pimelodus maculatus LaCepède, 1803	*Pm*	31	36	44	13	58	28	10	25	91.6	91.6
Total		328	333	488	275	1019	600	284	535		
No. of species		28	23	22	20	27	22	18	18		
Diversity		2.45	2.27	2.29	2.4	2.25	2.01	1.92	1.92		
Richness		4.66	3.78	3.39	3.38	3.75	3.28	3	2.7		
Eveness		0.73	0.72	0.74	0.8	0.68	0.65	0.68	0.66		
No. of samples		9	9	9	9	9	9	9	9		

Table II. Biomass (g) of individuals collected in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005 in each season (day and night).

Taxa	Abbrev.	Spring		Summer		Autumn		Winter	
		Day	Night	Day	Night	Day	Night	Day	Night
ATHERINIFORMES									
Atherinopsidae									
Odontesthes sp.	*O*	173.9						20.42	
CHARACIFORMES									
Acestrorhynchidae									
Acestrorhyncus pantaneiro Menezes, 1992	*Ap*	151.3		154.79		38.0	242.0		
Anostomidae									
Leporinus obtusidens Valenciennes, 1837	*Lo*			91.6		642.0	268.0		
Schizodon jacuiensis Bergmann, 1988	*Sj*	19.2	149.7	230.2	205.0	514.0	155.0		
Characidae									
Astyanax eigenmanniorum (Cope, 1894)	*Ae*	6.6	9.3	10.0		60.0	8.0		
Astyanax fasciatus (Cuvier, 1819)	*Af*	519.8	598.8	790.6	518.9	2278.0	441.0	223.01	133.21
Astyanax jacuhiensis (Cope, 1894)	*Aj*	86.8		375.0	68.3	54.0		6.8	
Astyanax sp.	*Asp*	9.8		24.2		85.0			
Charax stenopterus (Cope, 1894)	*Cs*			13.0	29.0	6.0	19.0	7.0	8.0
Hyphessobrycon luetkenii (Boulenger, 1887)	*Hlk*	22.3	30.1						27.63
Oligosarcus jenynsii (Günther, 1864)	*Oj*	42.0	55.0			1643.0	231.0	1075.0	3085.0
Oligosarcus robustus Menezes, 1969	*Or*	169.6	293.0	39.0	272.0	1645.0	1701.0		684.0
Curimatidae									
Cyphocharax spilotus (Vari, 1987)	*Csp*	266.1	60.1	213.2	68.6	158.0		45.35	10.8
Cyphocharax voga (Hensel, 1870)	*Cv*	8359.9	8269.9	16695.9	2192.3	30308.5	35001.8	13076.0	27845.98
Erythrinidae									
Hoplias malabaricus (Bloch, 1794)	*Hm*	2372.2	3286.00	1911.2	8490.3	688.0	3958.0	321.0	2076.0
Prochilodontidae									
Prochilodus lineatus (Valenciennes, 1837)	*Pl*	250.0							
CLUPEIFORMES									
Engraulidae									
Lycengraulis grossidens (Agassiz, 1829)	*Lg*	304.4	78.4	57.6	89.1	165.0		75.0	
Clupeidae									
Platanichthys platana (Regan, 1917)	*Pp*	10.2	10.3					7.47	
PERCIFORMES									
Cichlidae									
Australoheros facetus (Jenyns, 1842)	*Afc*			84.9		80.0			
Geophagus brasiliensis (Quoy & Gaimard, 1824)	*Gb*	258.6	98.0	1073.0	244.0	1012.0	245.0	136.0	342.0
Gymnogeophagus gymnogenys Hensel, 1870	*Gg*	95.2	58.0			193.0	94.0	235.0	97.0
Gymnogeophagus rhabdotus Hensel, 1870	*Gr*	156.0	41.9	111.2	104.4	545.0	41.0		
Crenicichla lepidota Heckel, 1840	*Cl*	410.1	26.4	382.3					
Crenicichla punctata Hensel, 1870	*Crp*	442.1				255.0	116.0		
Sciaenidae									
Pachyurus bonariensis Steindachner, 1879	*Pb*	1223.9	652.2	1803.1	894.0	9809.0	3947.0	6024.0	5209.5
SILURIFORMES									
Auchenipteridae									
Trachelyopterus lucenai Bertoletti, Pezzi da Silva & Pereira 1995	*Tl*	326.0	676.9		164.6		257.0		
Callichthyidae									
Corydoras paleatus (Jenyns, 1842)	*Cp*	20.0	78.0			829.0	578.0	129.0	825.0
Hoplosternum littorale (Hancock, 1828)	*Hl*	709.3	1570.5	1548.4	6691.1	1398.0	4589.0		563.0
Loricariidae									
Loricariichthys anus (Valenciennes, 1835)	*La*	1763.0	3710.5	5028.37	5390.5	3633.0	3492.0	2959.0	7944.0
Rineloricaria strigilata (Hensel, 1868)	*Rs*				18.0				20.0
Heptapteridae									
Rhamdia spp.	*R*		456.0	2089.4	3238.5	563.0	760.0	1600.0	1286.0
Pimelodella australis Eigenmann, 1917	*Pa*					11.0			
Pimelodidae									
Parapimelodus nigribarbis (Boulenger, 1889)	*Pn*	376.7	1004.5	1076.5	290.4	3168.0	825.0	357.0	95.0
Pimelodus maculatus LaCepède, 1803	*Pm*	3984.0	3620.9	4006.7	1318.6	6799.0	2663.0	920.0	2918.0
Total		22529.1	24834.4	37718.5	30379.2	66579.5	59631.8	27217.0	53170.1
No. of species		28	23	22	20	27	22	18	18
No. of samples		9	9	9	9	9	9	9	9

In contrast with the majority of species observed, the overall tendency of the species *Oligosarcus jenynsii* (Günther, 1864), *C. paleatus* and *L. anus* was to exhibit increased abundance during the winter, particularly during the night. Conversely, *Acestrorhynchus pantaneiro* Menezes, 1992, *Schizodon jacuiensis* Bergmann, 1988, *Astyanax eigenmanniorum* (Cope, 1894), *Gymnogeophagus rhabdotus* Hensel, 1870 and *Trachelyopterus lucenai* Bertoletti, Pezzi da Silva & Pereira, 1995 were all caught during the other three seasons, but not during winter, leading to lower species richness in the winter.

The number of individuals observed increased during the autumn; in particular, there were greater numbers of *A. fasciatus*, *P. bonariensis* and *P. nigribarbis* during the daytime, while high frequencies of predator species such as *Oligosarcus robustus* Menezes, 1969, *H. malabaricus*, *T. lucenai*, *H. littorale* and *Rhamdia* spp. were observed during the nocturnal period (Tab. I).

Abundance and biomass were significantly higher during the winter (Tab. II) than during the summer and the lowest abundance and biomass were observed during the spring.

Analysis of variance with randomization demonstrated that, independent of diel variation, autumn was the season with the greatest abundance of species, significantly different from winter ($P = 0.03$), spring ($P = 0.04$) and summer ($P = 0.005$). Winter abundance was significantly greater than summer abundance ($P = 0.01$). No significant differences were detected in species abundance when the differences between numbers of individuals observed during the day and during the night were analyzed independent of season.

With relation to the differences in biomass between seasons, independent of diel variation, autumn exhibited the greatest biomass, with a statistically significant difference in relation to winter ($P = 0.007$), summer ($P = 0.006$), and spring ($P = 0.05$). Winter biomass was significantly greater than summer biomass ($P = 0.003$) and biomass was significantly lower during spring than during the summer ($P = 0.01$). When diurnal biomass was compared with nocturnal biomass, independent of season, the sum of the nocturnal individuals' mass was significantly greater ($P = 0.01$) than that of the diurnal individuals (Fig. 3).

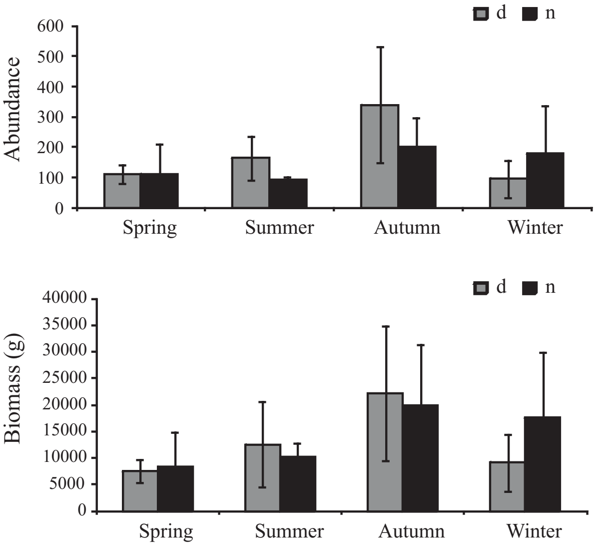

Figure 3. Seasonal abundance (n) and biomass (g) (mean ± SD) and period of collection (day/night) in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005.

Table III. Mean (±SD) of environmental variables in the sample areas (SA; SQ; SF) in the Jacuí River Delta, southern Brazil, from October/2004 to September/2005.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Water temperature	21.0±0.1	24.1±0.3	19.3±0.6	24.7±2.3	21.7±0.6	23.3±2.3	21.0±0.1	18.5±0.5	17.4±0.4	13.3±0.4	14.0±0.1	18.0±1.0
pH	7.16±0.1	7.2±0.1	6.6±0.4	6.7±0.5	6.7±0.6	6.9±0.7	6.7±0.1	6.5±0.2	6.9±0.1	6.9±0.1	6.8±0.1	6.4±0.1
Secchi transparency (cm)	53.6±4.9	33.6±16.8	25.0±4.5	20.3±7.6	7.7±2.5	24.7±6.6	38±3.6	15.3±1.5	14±2.6	20±0.1	20±0.1	0.3±9.4
Dissolved oxygen (mg/L)	3.7±0.4	6.4±2.0	9.0±1.7	8.0±0.1	8.6±0.1	9.0±1.7	8.0±0.1	7.3±1.1	9.3±2.8	7.1±1.6	11.0±0.1	5.0±1.7
Rainfall (mm)	76.2	117.6	33.7	28.8	41.0	141.3	145.8	153.7	15.2	57.7	155.9	164.3
Rainfall (mm) 1961-1992	114.3	104.2	101.2	100.1	108.6	104.4	86.1	94.6	132.7	121.7	140.0	139.5

Table IV. Summary of the results of canonical correspondence analysis (CCA) based on five environmental variables measures in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005 (* Global test).

	Axis 1	Axis 2
Eigenvalues (λ)	0.164	0.062
Pearson's correlations (species-environment)	0.964	0.972
Cumulative percentage variance of species data (%)	28.5	39.2
Cumulative percentage variance of species-environment relation (%)	48.1	66.2
Monte Carlo test		
F	2.387	1.741*
P	0.01	0.002*

The first two axes of the ordination analysis (PCA) explained 65.9% of seasonal species variability. Axis 1 (42.3%) demonstrated that, with the exception of diurnal winter data and nocturnal autumn data there was separation between the species collected during the day and during the night, with greater richness during the daytime (Fig. 4).

When species were arranged in order of biomass, the two first axes explained 52.7% of the observed variation, with 30.1% explained by axis 1. Although species richness was greater during the diurnal period when compared with the nocturnal period, the largest species, with the greatest biomass, were observed during the night, meaning that total biomass was greater at night (Fig. 5).

Table I lists the results of classifying the species by constancy of occurrence (*c*) and also gives the results for richness, diversity *H'* (ln) and evenness *J'*. Analysis of variance of the indices of richness, diversity *H'* and evenness *J'* did not detect significant seasonal variation (Tab. VI) or significant diel variation (diversity $P = 0.74$, evenness $P = 1$, richness $P = 0.38$).

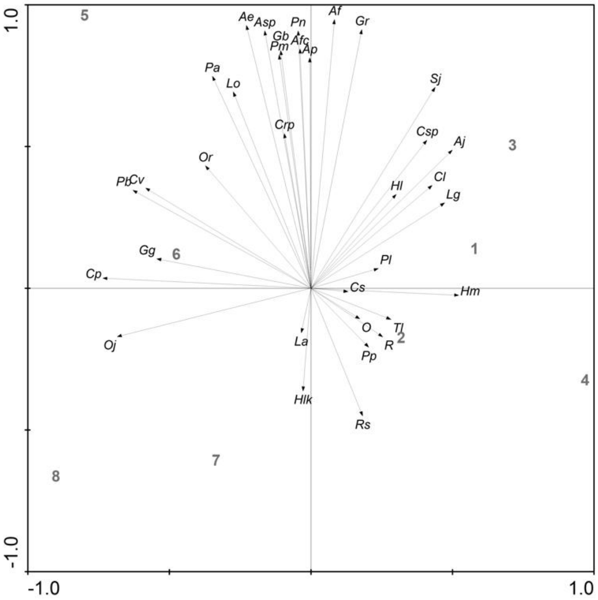

Figure 4. Ordination of the species (number of individuals) in relation to season (day/night) resulting from principal components analysis (PCA) applied to abundance (n) data matrix in the Jacuí River Delta, RS, Brazil, from October 2004 to September 2005 (1, spring day; 2, spring night; 3, summer day; 4, summer night; 5, autumn day; 6, autumn night; 7, winter day; 8, winter night; Ap, *Acestrorhyncus pantaneiro*; Ae, *Astyanax eigenmanniorum*; Af, *Astyanax fasciatus*; Aj, *Astyanax jacuhiensis*; Asp, *Astyanax* sp.; Afc, *Australoheros facetus*; Cs, *Charax stenopterus*; Cp, *Corydoras paleatus*; Cl, *Crenicichla lepidota*; Crp, *Crenicichla punctata*; Cv, *Cyphocharax voga*; Csp, *Cyphocharax spilotus*; Gb, *Geophagus brasiliensis*; Gg, *Gymnogeophagus gymnogenys*; Gr, *Gymnogeophagus rhabdotus*; Hm, *Hoplias malabaricus*; Hl, *Hoplosternum littorale*; Hlk, *Hyphessobrycon luetkenii*; Lo, *Leporinus obtusidens*; La, *Loricariichthys anus*; Lg, *Lycengraulis grossidens*; O, *Odontesthes* sp.; Oj, *Oligosarcus jenynsii*; Or, *Oligosarcus robustus*; Pb, *Pachyurus bonariensis*; Pn, *Parapimelodus nigribarbis*; Pa, *Pimelodella australis*; Pm, *Pimelodus maculatus*; Pp, *Platanichthys platana*; Pl, *Prochilodus lineatus*; R, *Rhamdia* spp.; Rs, *Rineloricaria strigilata*; Sj, *Schizodon jacuiensis*; Tl, *Trachelyopterus lucenai*).

Table V. Matrix of correlation among environmental variables measures and abundance of individuals collected in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005.

	Principal Components	
Variables	Axis 1	Axis 2
Water temperature (°C)	- 0.8150	- 0.4154
pH	- 0.4648	0.4391
Dissolved Oxygen (mg/L)	0.1769	- 0.0417
Secchi Transparency (cm)	- 0.4408	0.1588
Rainfall (mm)	0.5312	- 0.5051

Table VI. Ecological indexes between seasons in the Jacuí River Delta, southern Brazil, from October 2004 to September 2005.

Contrasts	Diversity	Evenness	Richness
	p	p	p
spring x summer	1	0.32	0.34
spring x autumn	0.41	0.30	0.34
spring x winter	0.32	0.32	0.33
summer x autumn	0.3	0.34	1
summer x winter	0.31	0.34	0.33
autumn x winter	0.34	1	0.32

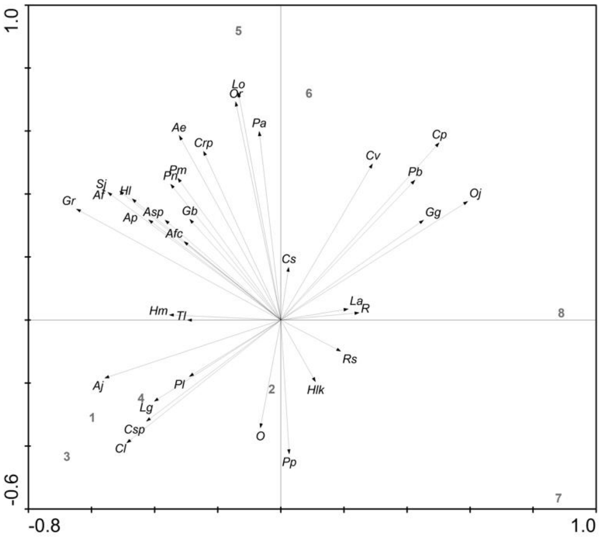

Figure 5. Ordination of the species (biomass) in relation to season (day/night) resulting from principal components analysis (PCA) applied to total biomass (g) data matrix in the Jacuí River Delta, RS, Brazil, from October 2004 to September 2005 (1, spring day; 2, spring night; 3, summer day; 4, summer night; 5, autumn day; 6, autumn night; 7, winter day; 8; winter night; Ap, *Acestrorhyncus pantaneiro*; Ae, *Astyanax eigenmanniorum*; Af, *Astyanax fasciatus*; Aj, *Astyanax jacuhiensis*; Asp, *Astyanax* sp.; Afc, *Australoheros facetus*; Cs, *Charax stenopterus*; Cp, *Corydoras paleatus*; Cl, *Crenicichla lepidota*; Crp, *Crenicichla punctata*; Cv, *Cyphocharax voga*; Csp, *Cyphocharax spilotus*; Gb, *Geophagus brasiliensis*; Gg, *Gymnogeophagus gymnogenys*; Gr, *Gymnogeophagus rhabdotus*; Hm, *Hoplias malabaricus*; Hl, *Hoplosternum littorale*; Hlk, *Hyphessobrycon luetkenii*; Lo, *Leporinus obtusidens*; La, *Loricariichthys anus*; Lg, *Lycengraulis grossidens*; O, *Odontesthes* sp.; Oj, *Oligosarcus jenynsii*; Or, *Oligosarcus robustus*; Pb, *Pachyurus bonariensis*; Pn, *Parapimelodus nigribarbis*; Pa, *Pimelodella australis*; Pm, *Pimelodus maculatus*; Pp, *Platanichthys platana*; Pl, *Prochilodus lineatus*; R, *Rhamdia* spp.; Rs, *Rineloricaria strigilata*; Sj, *Schizodon jacuiensis*; Tl, *Trachelyopterus lucenai*).

DISCUSSION

According to LOWE-MCCONNELL (1999), it is very common for Ostariophysi to dominate in Neotropical rivers, in particular Characiformes and Siluriformes, and this is what was observed in the Jacuí River Delta. *Cyphocharax voga* exhibited the greatest biomass and abundance during all periods, followed by *P. nigribarbis*, *C. paleatus*, *L. anus*, and *P. maculatus*. Overall, the fish that make up the assemblage in the Jacuí River Delta also occur frequently in the Patos Lagoon system (MALABARBA, 1989).

One factor that could contribute to the biomass and abundance of the species mentioned above is the fact that the Delta has a muddy bottom with large quantities of debris resulting from the confluence of rivers from different areas (FARIA & LERSCH, 2001). This feature would encourage a local increase in the abundance and biomass of detritivorous species such as *C. voga*, *P. nigribarbis*, *C. paleatus*, *L. anus,* and *P. maculatus* (HARTZ & BARBIERI, 1993; YOSSA & ARAÚJO-LIMA, 1998; DELARIVA & AGOSTINHO, 2001; FUGI *et al*., 2001; LIMA-JUNIOR & GOITEIN, 2004; GRANADO-LORENCIO *et al*., 2005; CARDONE *et al*., 2006). According to GRENOUILLET *et al.* (2002), species abundance is intimately related to the availability of food sources.

However, in common with the description of Patos Lagoon published by PEREIRA (1994), seasonal factors have a significant influence on the distribution of individuals in the Delta. During periods of heavy rain and higher water levels, an elevated abundance of freshwater fish was observed in Patos Lagoon, which led researchers to raise the hypothesis that some species may be being carried towards the lagoon (GARCIA & VIEIRA, 2001; GARCIA *et al*., 2003). Notwithstanding, abundance of species and biomass in the Delta also increased in line with rainfall. MACHADO-ALLISON (1990) made the observation that increases in the abundance of species are to be expected during periods with increased rainfall because of the greater availability of food sources.

In contrast with species in flooded areas, where the structure of the assemblage is mainly influenced by the flood pulse (WINEMILLER *et al*., 2000; SÚAREZ *et al*., 2001), variations in the ichthyofauna in the Delta were mainly influenced by water temperature. This pattern is similar to that observed in other areas with subtropical climates (JAUREGUIZAR *et al*., 2003; ADAMS *et al*., 2004).

Previous studies carried out with three different species of the genus *Astyanax* (BERTACO *et al*., 1998) and with *P. nigribarbis* (BERTACO & BECKER, 2000) in Guaíba Lake have reported low abundance during periods with low temperatures, and related this decrease to individuals seeking protected areas in deeper waters. Individuals engaging in such migration would avoid collection by gillnets, which may also have occurred in the study described here.

Alternatively, the largest number of individuals caught in autumn, resulting in greater abundance and biomass, could be a result of increasing movement and feeding activity of individuals in the period before the breeding season of most species. Furthermore, it has been demonstrated that many fish feed with greater intensity during the periods before and after their reproductive season (BARBIERI *et al*., 1982; SCHLOSSER, 1982; HARTZ *et al*., 1996; TRIPE & GUY, 1999).

The majority of species inhabiting the coastal regions of southern Brazil begin their reproductive cycles during the spring (FIALHO *et al*., 1996; NUNES *et al*., 2004; MARQUES *et al*., 2007; MILANI & FONTOURA, 2007) and the fact that the greatest richness and lowest abundance and biomass was observed during this period could be related to a high number of juveniles in species assemblages. These juveniles would not be collected by gillnets due to their small size.

In addition to seasonal influences, several fish exhibit diel variation in their habitat use, varying in biomass, richness and abundance when day and night are compared (LOWE-MCCONNELL, 1964; WINEMILLER, 1989; GAUDREAU & BOSCLAIR, 1998; YU & PETERS, 2003; WOLTER & FREYHOF, 2004; OKUN *et al*., 2005). Although the number of individuals did not significantly differ between day and night, biomass was significantly higher during the night, which is probably linked to frequent collection of large predator species such as *H. littorale*, *H. malabaricus*, *O. robustus*, *Rhamdia* spp. and *T. lucenai* at night. This result is in contrast with the abundance data, where a large number of small individuals were observed during the day.

Finally, in common with tropical regions, where fish assemblages are influenced mainly by rainfall, in this subtropical area rainfall also plays a role. However, this study supports the view that temperature-related seasonal and diel variation is the most important factor impacting the distribution of the fish assemblage in the Jacuí River Delta.

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