

The role of vegetated areas on fish assemblage of the Paraná River floodplain: effects of different hydrological conditions

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In this paper, we analyze the changes in composition and abundance of fish assemblages in seven vegetated floodplain wetlands with different connectivity across different hydrologic conditions: after a prolonged connection of the floodplain with the main channel, during receding water, and after a prolonged isolation. We also investigated the size and abundance of large-sized migratory species found in these wetlands and the food resources exploited by the dominant fish. Fishes were captured by diurnal seining (8.0 m x 1.50 m, 5 mm mesh) along macrophyte banks. Despite the high total number of species registered (100), sample species richness varied between 7 and 31, depending on the sampling site and the sampling date. Cluster analysis indicated low similarity between sites during both the isolation and the prolonged connection. Species turnover decreased from high water ($\beta = 40.33$) to low water ($\beta = 33.83$), with the minimum value of beta diversity index obtained during the isolation of the floodplain wetlands ($\beta = 26.83$). Our results indicated that different dominant populations of fish occur in different hydrological conditions, even though high water and isolation phases occur in the same season of different years. The ordination (NMDS) indicated the importance of hydrologic conditions in structuring fish assemblages in the studied floodplain. Small-sized characids, typically associated with macrophytes, dominated the fish assemblages, whereas the younger stages of large sized migratory species were found in low abundance. The maximum standard length of the fish captured was 28 cm and for large migratory fish, standard length varied between 1.6 and 25.0 cm. The dominant fish used several food resources, but littoral macrophytes-associated organisms had a high frequency of occurrence in the three hydrologic conditions. The high species richness of fish in the small, vegetated lakes was related to the high spatial heterogeneity during different hydrological conditions. Disturbances in the hydrological pulses could reduce the biodiversity by modifying the connectivity of the floodplain with the river channel. Conservation of these vegetated wetlands requires maintenance of actual width range of connectivity that provide diverse habitat along the time.

Neste artigo analisamos as mudanças na composição e abundância das assembléias de peixes de sete áreas úmidas de planície de inundação com vegetação e com diferentes conectividades e em diferentes condições hidrológicas: depois de uma conexão prolongada da planície de inundação com o canal principal, durante o recuo das águas e após um isolamento prolongado. Nós também investigamos o tamanho e abundância das espécies migratórias de grande tamanho encontradas nestas áreas úmidas e os recursos alimentares explorados pelas espécies dominantes. Os peixes foram capturados com rede durante o dia (8.0 m x 1.50 m, malha de 5 mm) nos bancos de macrófitas. Apesar do alto número de espécies registradas (100), a riqueza de espécies nas amostras variou entre 7 e 31, de acordo com o local e data de coleta. A análise de cluster indicou uma baixa similaridade entre os locais tanto durante o período de isolamento como no de conexão prolongada. A substituição de espécies decresceu do período de cheia ($\beta = 40.33$) a vazante ($\beta = 33.83$), com o valor mínimo de índice de diversidade beta obtido durante o isolamento das áreas úmidas da planície de inundação ($\beta = 26.83$). Os resultados indicaram que diferentes populações dominantes de peixes ocorrem em condições hidrológicas diferentes, mesmo quando fases de cheia e de isolamento ocorreram na mesma estação em anos diferentes. A ordenação (NMDS) indicou a importância das condições hidrológicas na estruturação das assembléias de peixes na planície de inundação estudada. Caracídeos de pequeno tamanho, tipicamente associados à macrófitas, dominaram a assembléia de peixes, enquanto que indivíduos jovens de espécies de maior porte e migratórias foram encontradas em baixa abundância. O comprimento padrão máximo dos peixes capturados foi de 28 cm; para espécies migratórias de maior porte o comprimento padrão variou de 1,6 a 25 cm. Os peixes dominantes utilizaram vários recursos alimentares, mas organismos associados às macrófitas litorâneas apresentaram uma alta frequência de ocorrência nas três condições hidrológicas. A alta riqueza de espécies de peixes nos pequenos lagos com vegetação foi relacionado à alta heterogeneidade espacial durante as diferentes condições hidrológicas. Distúrbios nos pulsos hidrológicos podem reduzir a biodiversidade pela modificação da conectividade da área de inundação com o canal principal do rio. A conservação das áreas úmidas com vegetação requer a manutenção da variação de conectividade a fim de proporcionar a diversidade de habitats ao longo do tempo.

Key words: Fish diversity, Fish diet, Floodplain wetlands, Aquatic plants.

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Introduction

Hydrological regime is considered the key factor driving biodiversity pattern in riverine tropical and subtropical wetlands (Junk *et al.*, 1989; Neiff, 1990). Floodplains of large rivers encompass an array of ecosystem types and flooding regimes, which are characterized by high levels of habitat diversity and biotic spatial gradients in relation to the connectivity of different patches across the riverine landscape (Welcomme, 1985; Ward *et al.*, 1999; Neiff, 2001). Comparisons between the main channel and the floodplain indicated that the number of individuals caught per unit effort is lower in the rivers and channels than the lagoons, but species richness is higher (Agostinho *et al.*, 2000). Although floods seem to have a homogenization effect on the aquatic environments of the floodplain (Thomaz *et al.*, 2007), the consequences for fish assemblages are poorly understood. This is primarily because of the importance of local process operating at the habitat scale during low water (Rodríguez & Lewis, 1994). Information on Paraná River fishes, accumulated during the last decade, demonstrates distinct ecological responses to the annual pattern of flooding (Agostinho *et al.*, 2000).

The principal characteristic distinguishing the extended floodplain of the Paraná River, downstream from its confluence with the Paraguay River, is the quantity of many small, shallow, and densely vegetated lakes (Carignan & Neiff, 1992). These lakes are periodically connected to the river during high water, but the frequency, duration, and timing of the connections vary with river stage and with the topographic position of the lakes in relation to the main channel (Neiff, 1990). Thus, both spatial and temporal pattern associated with seasonal changes in the water level are important factor in this subtropical floodplain.

The importance of vegetated floodplain lakes as sites for development of young migratory fish, as well as refuge and feeding areas, has been indicated by several investigations (Bonetto, 1986; Agostinho *et al.*, 2000; Canón Verón, 2005). However, fish communities associated with macrophytes are composed of small sized species, typical of lentic environments, and a few juveniles of large sized migratory species (Cordiviola de Yuan *et al.*, 1984; Delariva *et al.*, 1994; Meschiatti *et al.*, 2000). Difficulties associated with sampling methods may be the reason for the scarcity of studies on fish assemblages in small, vegetated lagoons (Meschiatti *et al.*, 2000). Despite the importance of the area covered by small water bodies at a global-scale, studies on these aquatic systems have been under-emphasized (Downing *et al.*, 2006).

In this paper, we compared the composition and abundance of fish assemblages in seven vegetated floodplain wetlands among different hydrological conditions: after a prolonged connection of the floodplain with the main channel, during receding water, and after a prolonged isolation. Beta diversity was measured for each hydrological condition as an integrator of habitat heterogeneity across a connectivity gradient within the floodplain. We also investigated the size and abundance of large sized migratory species found in the vegetated wetlands and the food resources exploited by the dominant fish.

We hypothesized that: 1- at each hydrological condition, the turnover in species richness exhibits a different pattern; 2-

different species of small sized fishes, either species typical of lentic environment or young individuals of large sized migratory species, dominate the vegetated floodplain lakes at different hydrological conditions; and 3- there are assemblages of ubiquitous species that use a broad spectrum of feeding resources in high water and low water.

Results of this paper were expected to elucidate the importance of spatial and seasonal changes associated with the hydrologic regime of the Paraná River for fish assemblages in small vegetated wetlands. The importance of vegetated areas as substrate for development of fish juveniles and feeding habitat are also discussed.

Material and Methods

Site description. The studied area is located on the west bank of the Paraná River, 30 km downstream from the confluence with the Paraguay River (Fig. 1) and within the RAMSAR Site Wetlands CHACO (Argentine). As area and connection of the floodplain lagoons affect fish assemblages (Welcomme, 1985), we chose seven adjacent sites (Fig. 1) distributed in 1458 ha that reflected different local habitat conditions (lotic and lentic; temporary and permanent) with different connectivity to the main channel.

Site 1 (27°25'42"S, 58°52'10"W) is a typical small stream that is 40 m wide, and its banks offer support for rooted aquatic plants dominated by *Panicum elephantipes* and *Polygonum acuminatum*. During high water, this channel transports water and material from the Paraná River to the floodplain at a mean velocity of 0.73 m.s⁻¹. During low water, current velocity becomes markedly reduced and in some situations, flow ceases producing temporary lentic characteristics. Site 2 (27°26'22"S, 58°51'13"W) and Site 3 (27°26'09"S, 58°51'28"W) are oxbow lakes, periodically connected to the Paraná River. Both lagoons sustain high amounts of biomass of the floating macrophyte *Eichhornia crassipes*, which covers less than 50% of Site 2 and nearly 95% of the lake surface at Site 3.

The other sites are small and very shallow (Table 1), remaining dry for more than six months in years with extremely low water levels. Different macrophytes: *Scirpus giganteus* (Site 4, 27°25'53"S 58°51'52"W), *Hymenachne amplexivaulis* (Site 5, 27°25'51"S 58°51'56"W), *Ludwigia peploides* (Site 6, 27°25'46"S 58°51'58"W), as well as *L. peploides* and *E. crassipes* (Site 7, 27°25'42"S 58°52'10"W) cover 40 - 50% of the area. During the prolonged isolation, sites 6 and 7 dried up completely.

The physical and chemical characteristics recorded in littoral areas of the study sites are shown in Table 1. Water temperatures were generally high and pH values were slightly acidic. Dissolved oxygen concentrations were usually lesser than 6.7 mg.l⁻¹. Low concentrations (0.5-0.9 mg.l⁻¹) were recorded in several sites during receding and isolation phases (Table 1).

Sampling. Fishes were sampled in the morning, during March 1999 (after a long lasting inundation phase of the Paraná River), September 1999 (at the beginning of a low water phase), and February 2000 (after a prolonged isolation) using a seine (8.0 m x 1.50 m, 5 mm mesh). At each site and each sampling date, 4 seine hauls, covering an area of 10 m² following the macro-

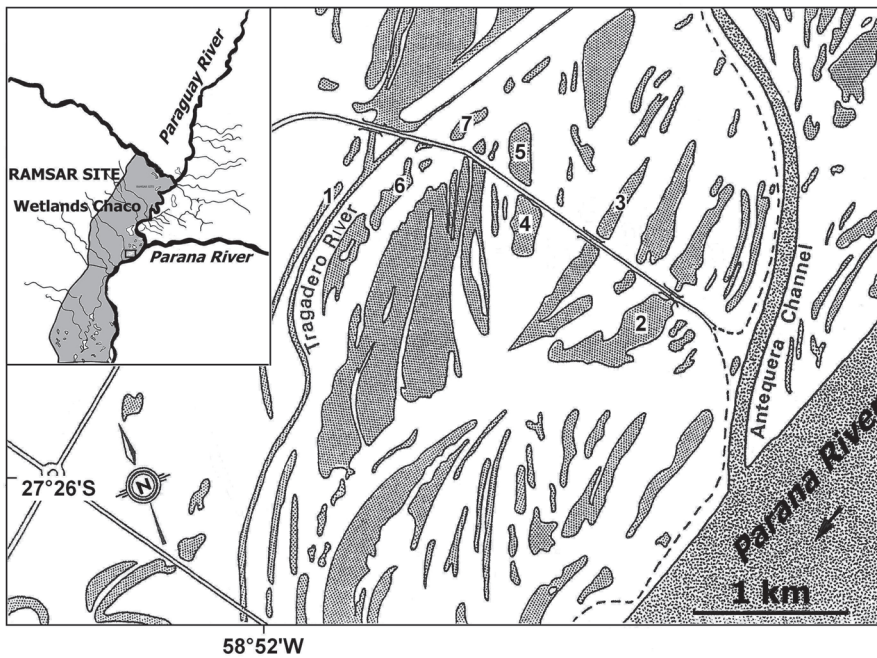


Fig. 1. Distribution of 7 vegetated wetlands across the studied alluvial floodplain.

phytes banks, were conducted (sampled area = 40 m²). Fishes were counted, identified according to Ringuet *et al.* (1967) and López *et al.* (2003), and standard length was measured. Voucher specimens were deposited in the Ichthyological Collection of Centro de Ecología Aplicada del Litoral (CECOAL-CONICET). The scientific names of species listed in Table II and III were reviewed according the Catalog of fishes, On-Line Version (<http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html>). In laboratory, gut content of the dominant fish was analyzed under a microscope; all plants and animals were identified to the lowest possible taxonomic level. We examined more than 20 stomachs with identifiable food items for each species, totaling 760 stomachs for the floodplain.

Data analysis. The connectivity of the wetlands was defined by determining the date for initial connection to the river in relation to the water level of the Parana River in the gauge located near the study sites (Neiff & Poi de Neiff, 2003). Due to disparities in the slopes of the study floodplain, topographic position of each site, rather than distances from the river, indicated the connectivity of each site. The number of flooding days (potamophase) for each site was calculated for the period from January 1997-January 2001 with the Software Pulse (Neiff & Neiff 2003). The elasticity of the floodplain allows us to determine the variability in the habitat for fish, birds, and other organisms (Neiff *et al.*, 1994). This index was calculated for the studied area, as the quotient between the maximum surface of water during the prolonged flooding and the minimum area occupied after the prolonged drought using LANDSAT 7 TM images representing May 1998 and January 2001, respectively.

Temporal variation in assemblage attributes (species richness and abundance) was analyzed with Kruskal Wallis test. The software EstiMates (Colwell, 1997) was used to calculate the Shannon-Wiener diversity index for each site and the simi-

larity among fish assemblages from different sites, based on Jaccard distance (UPGMA method). The total species richness found in each hydrological condition was compared with the estimated species richness given by the second-order jackknife estimator, considering each site as unit (n=7). Beta diversity was estimated for each hydrological condition as an integrator of habitat heterogeneity across the floodplain using the Whittaker index with the modification introduced by Harrison (Magurran, 2004): $\beta_w = \{(S/\alpha) - 1\} / (N - 1) \cdot 100$, where: S = total number of species, α = mean species richness, and N = number of sites. The measure ranges from 0 (no turnover) to 100 (every sample has a unique set of species).

To examine spatial patterns in fish assemblages, the abundance of the 10 dominant species were ordered using non-metric multidimensional scaling (NMDS)

with a Bray-Curtis measure in PC-ORD (Version 4.17, 1999, MJM Software, Gleneden Beach, OR, U.S.A).

To express diet of the species, we used the frequency of occurrence of microcrustaceans, mollusks, terrestrial and aquatic insects, other invertebrates, fishes, algae, higher plants, and detritus. Results were ordered in a table and main trends were described.

Results

The hydrologic regime of the Parana River was irregular with floods of different intensities, recurrences, and amplitudes (Fig. 2). Between January 1998 and January 1999, there was a

Table 1. Physical and chemical characteristics recorded in littoral areas of the study sites during different hydrological conditions.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
High Water							
Temperature (°C)	20	23.3	22	24	24	24	24
Dissolved oxygen (mg.l ⁻¹)	6.3	6.7	3.3	1.2	1.7	1.9	1.6
pH	7.1	7.36	6.98	6.3	6.4	6.8	6.6
Conductivity (µS.cm ⁻¹)	102	155	190	190	140	122	122
Depth (m)	6	1.80	1.50	0.85	1.25	0.80	0.93
Secchi (cm)	69	45	37	60	30	31	22
Receding Water							
Temperature (°C)	18	18	18	23	23	18	23
Dissolved oxygen (mg.l ⁻¹)	3.3	3.7	2.4	0.9	1.2	0.9	2.2
pH	7.9	6.7	6.6	6.3	6.2	6.7	6.1
Conductivity (µS.cm ⁻¹)	150	230	260	390	340	305	150
Depth (m)	4.30	1.6	1.07	0.6	0.9	0.40	0.34
Secchi (cm)	24	65	67	15	19	14	19
Isolation							
Temperature (°C)	25	27	26	29	31		
Dissolved oxygen (mg.l ⁻¹)	2.2	2.5	0.5	0.6	0.75		
pH	7.32	6.8	6.6	6.3	6.5		
Conductivity (µS.cm ⁻¹)	205	245	340	418	360		
Depth (m)	1.3	1.2	0.75	0.4	0.60		
Secchi (cm)	13	26	19	15	11		

long lasting hydrologic phase of the Paraná River, whereas between January 1999 and January 2000 there was a prolonged isolation phase. The sites were connected to the river above the hydrometric level, as indicated in Fig. 1. Scores from 1 to 7 indicate the decreasing order in connectivity according the number of days in which sites were connected to the river channel. The elasticity quotient for the studied area was 7.1.

Spatial and temporal pattern in assemblages attributes. A total of 100 species were captured in the 7 studied sites during low and high water phases, belonging to 8 orders, 26 families, and 70 genera (Table 2). Representatives from the order Characiformes, mainly comprised of small-sized species, dominated the samplings. Seventy species were recorded during the prolonged connection of the sites with the river, 58 during receding water and 33 during the isolation of the floodplain (Table 2). There were 33 species exclusive to the high water condition, whereas only 12 species were common amongst the three hydrological conditions (Table 2). The estimated species richness with the second order jackknife technique decreased from 106.8 and 98.8 (high and receding water, respectively) to 48.6 (isolation).

Despite the high total number of species registered, the number of species found in a particular site (sample species richness, Table 3) varied between 7 and 31 depending on the sampling site and the sampling date. During high water, sites that were more connected (1, 2 and 3) presented higher values of density and species richness than sites less connected, but this pattern changed over receding water (Table 3). Thus, no significant differences in the abundance (Kruskal Wallis = 3.87, $P = 0.1445$) or sample species richness (Kruskal Wallis = 3.92, $P = 0.1386$) were observed among different hydrological conditions. Species turnover decreased from high water ($\beta = 40.33$) to receding water ($\beta = 33.83$), with the minimum value of beta diversity index obtaining during the isolation of the floodplain ($\beta = 26.83$). Shannon-Wiener specific diversity varied site from site between 1.99 and 4.1 (Table 3).

Cluster analysis, based on presence-absence analysis, indicated low similarity (less than 35%) among sites during both the isolation and the prolonged connection (Fig. 3 A, C). At high water, the three sites that were more connected were grouped and separated from others. During the receding water period, the similarity increases slightly and sites 1 and 3 were associated by 39.28% (Fig. 3B).

After the connection with the main channel, 8 species (*Roeboides microlepis*, *Triportheus nematurus*, *Prionobrama paraguayensis*, *Moenkhausia dichroua*, *Moenkhausia sanctaefilomenae*, *Odontostilbe paraguayensis*, *Pimelodus maculatus* and *Gymnogeophagus balzanii*) were relatively abundant and frequent (Table 2). *Odontostilbe paraguayensis* and *Cyphocharax voga* had high relative frequency (Table 2), while *Prochilodus lineatus* was the only species found in all sites (relative frequency = 100%, Table 2). Other long distance migratory species (*Pseudoplatystoma corruscans*, *Sorubim lima*, *Schizodon borellii* and *Raphiodon vulpinus*) were found in low relative abundance during this hydrologic condition, whereas *Pimelodus maculatus* reached up to 4.29% of the captures.

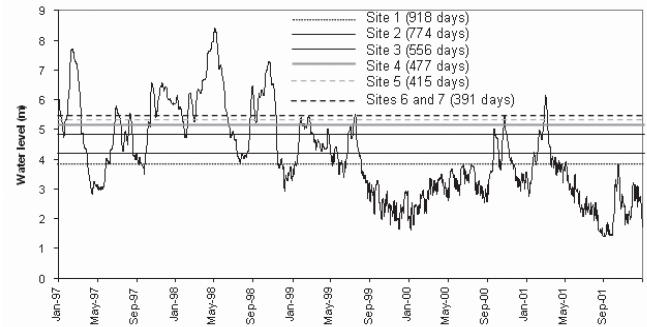


Fig. 2. Water level fluctuations of the Paraná River at Corrientes between 1997 and 2001. The Sites were connected with the Paraná River above the hydrological level indicated by the horizontal lines. The number of flooding days (in parentheses) indicates the connectivity between the floodplain and the river channel.

During receding water, the most frequent species (found in more than 85% of the sites, Table 2) were *Cyphocharax voga*, *Odontostilbe pequirá*, *Astyanax bimaculatus*, *Hyphessobrycon eques*, and *Hoplias malabaricus*. The first of these, with 12.99% of the captures, was the most abundant. The migratory fish species registered during receding water were *P. lineatus*, *Leporinus obtusidens*, *Leporinus acutidens*, *Leporinus octofasciatus*, and *Pimelodus albicans*, which had low relative abundance (<1%, Table 2).

After the prolonged isolation, 6 species (*Astyanax bimaculatus*, *Serrapinnus calliurus*, *Diapoma terofali*, *Parodon suborbitalis*, *Gymnogeophagus balzanii*, and *Moenkhausia intermedia*) accounted for 80% of the total abundance. *Serrapinnus calliurus* and *D. terofali* had a high frequency (71%, Table 2). Juveniles of three migratory species (*Leporinus acutidens*, *Schizodon borellii*, and *Raphiodon vulpinus*) were registered in this condition, but with low abundance. The rarest species was the lungfish *Lepidosiren paradoxa*, which can live buried in holes during the unfavorable period when the lagoons dry out.

The ordination (NMDS) had a relatively high final stress (16.30%) and low instability (<0.00005). The two-dimensional solution explained 0.58 of the total variation in the data set, with 0.291 (50.5%) of the variation loaded on Axis 1 and 0.285 (49%) loaded on axis 2 (Fig. 4). The axes explained significantly more variance than would be expected by chance based on the Monte Carlo permutation test ($p = 0.03$). The ordination showed good separation of taxa and hydrological conditions (Fig. 4) in both axes, without clumping of points. Sites at high water showed separation from those at receding water and isolation and were grouped on the lower left quadrant. The ordination indicated that differences in the abundance of dominant species were more important across hydrological conditions than across sites with different connectivity (spatial pattern). Axis 1 was driven primarily by the abundance of *Moenkhausia dichroua* ($r = -0.612$), *Gymnogeophagus balzanii* ($r = -0.443$), *Roeboides microlepis* ($r = -0.455$), *Serrapinnus calliurus* ($r = -0.529$) and *Astyanax bimaculatus* ($r = -0.443$). Axis 2 was driven primarily by the abundance of *Odontostilbe pequirá* ($r = 0.617$), *Cyphocharax voga*, ($r = 0.530$) and *Odontostilbe paraguayensis* ($r = -0.503$).

Table 2. Relative abundance of the total number of individuals represented by each species (RA), range of standard length (SL, cm) and relative frequency which each was collected (RF) in different hydrological conditions.

	Isolation			Receding water			High water		
	RA	SL	RF	RA	SL	RF	RA	SL	RF
LEPIDOSIRENIFORMES									
Lepidosirenidae									
<i>Lepidosiren paradoxa</i>	<1	10	14.3						
CHARACIFORMES									
Parodontidae									
<i>Apareiodon affinis</i>				<1	5.5-6.3	14.3	<1	8.0-9.5	28.6
<i>Parodon suborbitalis</i>	8.66	2.3-2.5	14.3				<1	2.0-2.9	14.3
<i>Parodon</i> sp.							<1	2.0-2.9	14.3
Curimatidae									
<i>Steindachnerina brevipinna</i>				<1	9.5	14.3	<1	5.0-11.0	28.6
<i>Steindachnerina</i> sp.	<1	6.5-6.7	14.3	<1	5.5-10.0	28.6	<1	10.0-11.0	28.6
<i>Cyphocharax voga</i>	<1	2.5-5.5	28.6	12.99	2.8-3.5	85.7	<1	4.1-11.0	71.4
<i>Cyphocharax saladensis</i>				0.46	2.8-3.5	14.3			
<i>Potamorhina squamoralevis</i>							<1	2.9-5.0	42.8
<i>Psectrogaster curviventris</i>				<1	5.5	14.3			
Prochilodontidae									
<i>Prochilodus lineatus</i>				<1	9.0-25.0	71.4	1.86	1.6-25.0	100
Anostomidae									
<i>Leporinus acutidens</i>	<1	8-17.2	28.6	<1	9-20.5	14.3			
<i>Leporinus octofasciatus</i>				<1	9	14.3			
<i>Leporinus obtusidens</i>				<1	5.0-5.8	14.3			
<i>Schizodon borellii</i>	<1	1.7-2.0	14.3				<1	1.7-6.0	42.8
Crenuchidae									
<i>Characidium rachovii</i>	2.78	3.7-4.5	42.8	2.03	2.5-5.0	28.6			
Gasteropelecidae									
<i>Thoracocharax stellatus</i>							<1	2.7-13.0	42.8
Characidae									
<i>Charax leticiae</i>				<1	2.5-8.9	28.6	1.24	3.2-4.0	14.3
<i>Charax stenopterus</i>	<1	5.8-7.0	28.6	<1	2.0-3.4	57.1			
<i>Roebooides microlepis</i>							22.12	5.5-17.0	42.8
<i>Roebooides descavadensis</i>				<1	5.5-7.2	14.3	<1	5.5-16.2	14.3
<i>Roebooides affinis</i>				<1	4.0-6.2	14.3			
<i>Cynopotamus argenteus</i>	<1	6.0-10.0	14.3						
<i>Triporthus nematurus</i>	<1	1.8-5.0	14.3	<1	6.6	14.3	6.52	1.6-10.0	42.8
<i>Prionobrama paraguayensis</i>	1.19	2.0-4.8	28.6	<1	3.0-4.2	71.3	3.27	4.0-9.0	42.8
<i>Aphyocharax anisitsi</i>	2.78	3.0-3.5	14.3	2.65	2.5-4.0	42.8			
<i>Aphyocharax rathbuni</i>				1.08	2.5-5.5	42.8	<1	2.7-4.0	28.6
<i>Diapoma terofali</i>	10.89	3.5-5.0	71.4	1.39	3.9-5.0	42.8	2.93	2.5-5	57.1
<i>Pseudocorynopoma doriae</i>	2.37	2.0-4.2	28.6				<1	1.5-3.5	42.8
<i>Poptella paraguayensis</i>				<1	8.7-10.5	14.3	<1	6.2-9.0	28.6
<i>Astyanax abramis</i>							<1	2.8-9.2	28.6
<i>Astyanax bimaculatus</i>	22.89	2.6-11.0	57.1	5.04	3.2-8.2	85.7			
<i>Astyanax fasciatus</i>				4.05	2.5-5.5	42.8	2.54	2.0-5.5	57.1
<i>Astyanax eigenmaniorum</i>				<1	4.5-6.4	14.3			
<i>Astyanax lineatus</i>				3.34	3.5-7.0	57.1	1.13	1.5-8.0	57.1
<i>Astyanax pellegrini</i>				<1	9	14.3			
<i>Astyanax taeniatus</i>							<1	2.5-3.0	28.6
<i>Ctenobrycon alleni</i>				<1	3.7-6.0	28.6	<1	2.0-4.0	28.6
<i>Hyphessobrycon eques</i>	1.35	3.5-5.0	28.6	2.95	1.5-8.5	87.7	<1	2.4-2.7	28.6
<i>Hyphessobrycon luetkenii</i>				<1	3.9-4.2	14.3			
<i>Hyphessobrycon</i> sp.							<1	2.1-2.5	14.3
<i>Moenkhausia dichroua</i>				<1	2.0-7.0	28.6	3.64	3.1-5.0	57.1
<i>Moenkhausia intermedia</i>	8.74	3.0-4.0	28.6	<1	3.0-3.5	28.6			
<i>Moenkhausia sanctaefilomenae</i>	<1	4.2-5.0	28.6	<1	3.0-4.5	42.6	8.47	1.7-2.5	14.3
<i>Psellogrammus kennedyi</i>	<1	3.0-5.4	14.3	6.06	2.5-5.3	42.8	<1	3.2-4.5	14.3
<i>Tetragonopterus argenteus</i>				<1	6	14.3	<1	8.0-9.0	28.6
<i>Cheirodon interruptus</i>				7.76	2.1-4.2	28.6			
<i>Serrapinnus calliurus</i>	14.78	2.6-3.1	71.4	10.31	2.0-5.3	71.4	<1	2.0-3.0	14.3
<i>Odontostilbe</i> sp.	6.20	3.0-6.0	28.6						
<i>Odontostilbe paraguayensis</i>							8.78	1.2-5.2	71.4
<i>Odontostilbe pequirá</i>	1.42	2.5-4.0	28.6	30.24	2.0-4.7	85.7			
<i>Pygocentrus nattereri</i>	1.19	3.0-3.5	14.3				<1	3.2	14.3
<i>Serrasalmus maculatus</i>							<1	2.5-24	28.6
<i>Mylossoma duriventre</i>	<1	10.0-18.1	14.3				<1	19.3	14.3
Acestrotrichidae									
<i>Acestrotrichus pantaneiro</i>							<1	14.7-19.0	28.6
Cynodontidae									
<i>Raphiodon vulpinus</i>	<1	8.0-19.3	14.3				<1	5.8-24.5	28.6

Table 2. Cont.

	Isolation			Receding water			High water		
	RA	SL	RF	RA	SL	RF	RA	SL	RF
Erythrinidae									
<i>Hoplerythrinus unitaeniatus</i>							<1	17.5	14.3
<i>Hoplias malabaricus</i>	<1	3.2-11.5	28.6	<1	5.8-26.0	85.7	<1	4.0-28	57.1
Lebiasinidae									
<i>Pyrrhulina australis</i>	<1	3.0-3.5	14.3	<1	2.0-3.8	42.8	<1	3.3-4.0	14.3
SILURIFORMES									
Callichthyidae									
<i>Corydoras hastatus</i>	<1	1.9-3.0	14.3	2.00	1.7-3.0	57.1			
<i>Hoplosternum littorale</i>				<1	12.0-15.5	14.3			
Loricariidae									
<i>Hypostomus commersoni</i>				<1	16.5	14.3	<1	3	14.3
<i>Otocinclus vittatus</i>				<1	2.1-3.0	14.3	<1	19	14.3
<i>Loricariichthys anus</i>				<1			<1	3.0-7.3	14.3
<i>Loricariichthys platymetopon</i>				<1	4.0-8.6	14.3	<1	9.2-24.5	14.3
<i>Pseudohemiodon platycephalus</i>				<1	8.6	14.3			
<i>Rhinelepis aspera</i>	<1	3.5	42.8	<1	3.7	14.3			
<i>Ricola macrops</i>							<1	22.0-24.5	42.8
Auchenipteridae									
<i>Trachelyopterus striatulus</i>							<1	3.2-15.0	28.5
Pimelodidae									
<i>Hypophthalmus edentatus</i>							<1	3.2-8.0	28.6
<i>Microglanis cottoides</i>							<1	3.0-5.0	14.3
<i>Pimelodella cristata</i>							1.27	6.0-15.0	28.6
<i>Pimelodella gracilis</i>				<1	6.9	14.3			
<i>Pimelodella howesi</i>				<1	10.2	14.3	<1	13	14.3
<i>Pimelodella laticeps</i>							<1	13.2-17.0	28.6
<i>Pimelodus albicans</i>				<1	5.0-8.5	14.3	<1	9.0-11.0	14.3
<i>Pimelodus argenteus</i>							<1	3.0-5.0	14.3
<i>Pimelodus maculatus</i>							4.29	2.7-7.0	14.3
<i>Pseudoplatystoma corruscans</i>							<1	6.3	14.3
<i>Sorubim lima</i>							<1	4.5-12.0	14.3
Aspredinidae									
<i>Bunocephalus doriae</i>							<1	3.5-4.0	14.3
GYMNOTIFORMES									
Hypopomidae									
<i>Brachyhypopomus brevirostris</i>				<1	8.5-9.5	14.3	1.24	7.0-16.0	42.8
Sternopygidae									
<i>Eigenmannia virescens</i>	<1	5.5-6.0	14.3	<1	2.8-12.0	14.3	<1	17.7	14.3
CYPRINODONTIFORMES									
Rivulidae									
<i>Rivulus punctatus</i>							<1	2.2	14.3
Anablepidae									
<i>Jenynsia multidentata</i>							<1	3.5	
Poeciliidae									
<i>Phalloceros</i> sp.				<1	2.5	14.3			
SYNBRANCHIFORMES									
Synbranchidae									
<i>Synbranchus marmoratus</i>				<1	14.0-21.5	14.3			
PERCIFORMES									
Sciaenidae									
<i>Pachyurus bonariensis</i>							<1	8.0-12.0	14.3
<i>Plagioscion ternetzi</i>							<1	2.7-24.0	57.1
Cichlidae									
<i>Apistogramma borellii</i>				<1	1.7-4.0	57.1			
<i>Apistogramma commbrae</i>	3.40	2.0-4.0	42.8						
<i>Australoheros facetus</i>							<1	3.0. 5.0	14.3
<i>Bujurquina vittata</i>				<1	5	14.3			
<i>Cichlasoma dimerus</i>	3.17	5.3-6.0	42.8	<1	3.7-8.2	42.8			
<i>Crenicichla lepidota</i>				<1	8.2-15.0	14.3	<1	4.9-13.0	14.3
<i>Gymnogeophagus australis</i>				<1	4.6-5.6	71.4	<1	2.0-8	28.6
<i>Gymnogeophagus balzanii</i>	13.83	2.0-15	14.3				1.98	4.2-13	57.1
<i>Gymnogeophagus gymnogenys</i>							<1	4	14.3
<i>Laetacara dorsigera</i>							<1	2.0-6.5	28.6
PLEURONECTIFORMES									
Achiridae									
<i>Catathyridium jenynsii</i>							<1	2.5-4.0	14.3

Table 3. Variation in the fish assemblage attributes in the studied sites during different hydrologic conditions.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
March 1999							
Specific diversity	2.77	2.93	4.11	2.86	2.17	2.56	2.20
Species richness	31	25	29	13	13	14	18
Captures per 40 m ²	1728	288	242	132	329	322	504
September 1999							
Specific diversity	1.99	2.2	2.8	2.34	2.8	3.06	2.8
Species richness	19	20	19	15	15	21	25
Captures per 40 m ²	779	876	164	691	180	1342	1717
February 2000							
Specific diversity	3.19	2.92	2.30	2.24	2.12		
Species richness	17	16	15	8	7		
Captures per 40 m ²	173	415	502	73	161		

Variation in size. The maximum standard length of the fish captured in different sites and hydrological condition was 28 cm and the size of large migratory fish varied between 1.6 and 25.0 cm. (Table 2). During the isolation of the bodies of water, fish with size less than 5 cm of four species (*Serrapinnus calliurus*, *Diapoma terofali*, *Parodon suborbitalis*, and *Moenkhausia intermedia*) accounted for 43% of the total abundance (Table 2). During high water, there were small sized species (<5 cm) typical of lentic environments, even though the size of dominant species reached up to 17 cm (Table 2).

Diet. Our results suggest that most of the fish utilized several food resources (Table 4). The exception was *H. malabaricus*, which diet included only fish of small size (from 1.8 to 2.5 cm), but this species was found in low density in the vegetated areas. During analysis of the diet of other fish, we found terrestrial insects and vegetal debris in carnivorous fish. Molluscs were not found in the gut content of fish in the studied floodplain. Higher plants served as the intake for ten species and were the main resource for *Astyanax fasciatus* and *Diapoma terofali*. Other diets (*Gymnogeophagus balzanii* and *Triportheus nematurus*) included seeds of *Polygonum* and *Ludwigia*.

Based on the diet of 38 species, microcrustaceans appeared in the diet of 29 species (Table 4), but had a high frequency of occurrence only in the stomachs of *R. descalvadensis*, *B. brevirostris*, *P. doriae*, *T. nematurus*, *S. borellii*, and *M. sanctaefilomenae*. Their diets included cladocerans (mainly *Moina*, *Latonopsis*, *Leydigia*, *Bosmina*, *Ceriodaphnia* and *Chidoridae*) and conchostraceans (*Cyclestheria hislopai*). In the gut content of *Roeboides microlepis* we found fish scales.

Juveniles of *Prochilodus lineatus* included diatom algae and filamentous algae (*Eunotia*, *Nitzschia*, *Oedogonium*, *Gomphonema*, *Euglena*, and *Phacus*) in their diet. Other fish, which also ingested algae (Table 4), consumed *Navicula*, *Pinnularia*, *Spirogyra*, *Trachelomonas*, and *Aulacoseira distans* in addition to the mentioned genera.

Detritus were the main resource for 13 fishes in the studied floodplain (Table 4). Insects (mainly Chironomidae larvae) also constituted an important food resource consumed by 23 species, with a high frequency of occurrence in four species (Table 4). Other insects exploited by fish were mayflies (*Caenis* and *Callibaetis*), bugs (Corixidae and Belostomatidae), dragonflies, caddisflies, and beetles (adults and larvae of Helodidae,

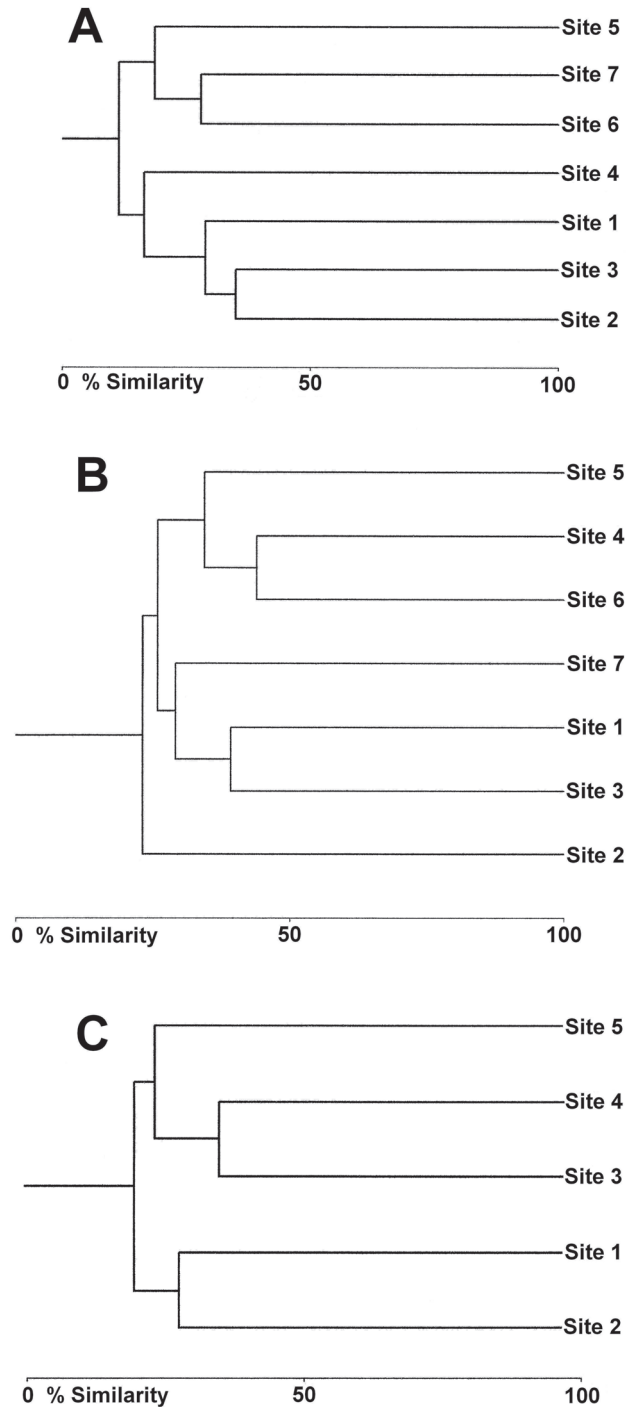


Fig. 3. Cluster analysis based on Jaccard distance (UPGMA method) of fish assemblages in the seven floodplain lakes. A. March 1999 (after a long lasting inundation phase of the Paraná River), B-September 1999 (at receding water) and C-February 2000 (during isolation).

Hydrophilidae, Dytiscidae and Curculionidae).

Dominant species during high water consumed microcrustaceans, diatoms, filamentous algae, and insects, whereas the dominant species in isolation conditions consumed aquatic plants, algae diatom and detritus.

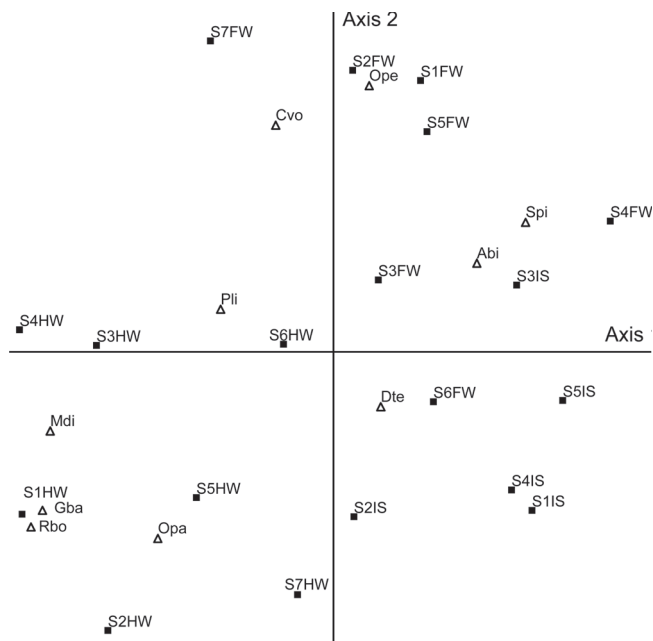


Fig. 4. NMDS ordination of dominant fish for different hydrologic condition (HW = high water, FW receding water, IS isolation) and sites (S). Ope = *Odontostilbe pequirá*, Cvo = *Cyphocharax voga*, Spi = *Serrapinnus calliurus*, Abi = *Astyanax bimaculatus*, Pli = *Prochilodus lineatus*, Mdi = *Moenkhausia dichrourea*, Gba = *Gymnogeophagus balzanii*, Rbo = *Roeboides microlepis*, Opa = *Odontostilbe paraguayensis*, Dte = *Diapoma terofali*.

Discussion

The number of species found in our studied area is high in comparison to the total species richness (216 species) reported for the middle Paraná River (Rossi *et al.*, 2007). For 15 floodplain lakes located in this stretch, Cordiviola (1980) mentioned a total of 85 species during an isolation period, whereas Bonetto *et al.* (1969) found 75 species in 18 temporary lakes of a Paraná River tributary after they were connected to the river. The estimated number of species by the jackknife 2, during high water, was very similar to the total species richness for the three sampling dates (100 species). In contrast, data from the isolation period underestimated the total number of fish species. The high total species richness and the low number of sample species richness are consistent with the high spatial species turnover found in the studied floodplain. This pattern has been reported by Agostinho *et al.* (2004) for the upper Paraná River. In our study, the high beta diversity was maintained in both high and receding water, but decreased during isolation. Based on the data of Bonetto *et al.* (1969), other authors suggest that the relative abundance of fish vary stochastically from pool to pool in the middle Paraná River (Lowe-McConnell, 1987), which reflects local habitat conditions (Robinson *et al.*, 2002) and the size of floodplain waterbodies (Welcomme, 1985). Our results indicated that different dominant populations occurred in different hydrological conditions, even though high water and isolation phases occur in the same season of different years.

The ordination (NMDS) indicates that species composition is not random and the importance of hydrological condition in structuring fish assemblages in the studied floodplain. The importance of rising and receding water has been recognized in stream ecology (Ward *et al.*, 1999; Tockner *et al.*, 2000), because wet areas can increase by several orders of magnitude during the annual floods. Highly variable assemblage composition within habitat types due to high spatial and temporal heterogeneity was found for large fish in a Venezuelan floodplain river (Layman & Winemiller, 2005). The role of connectivity on fish assemblages and the effect of extended absence of flooding have been mentioned for the floodplain of other large rivers (Petry *et al.*, 2003; Miranda, 2005; Pompeu & Godinho, 2006).

As in other vegetated areas of the Paraná River floodplain, (Cordiviola de Yuan *et al.*, 1984; Delariva *et al.*, 1994; Meschiatti *et al.*, 2000; Agostinho *et al.*, 2003; Casatti *et al.*, 2003), small sized characids, typical of lentic environments, dominated the fish assemblages, but with different fish composition. Although aquatic macrophytes has been indicated in the Paraná River as substrate for development of juveniles fish, refuge, feeding, and dispersion (Rossi *et al.*, 2007), we found low relative abundance of the young stages of large sized migratory species in vegetated areas. Our findings are in agreement with other results obtained in vegetated areas of the upper Paraná River floodplain (Delariva *et al.*, 1994; Meschiatti *et al.*, 2000). The reproduction of migrating fish occurs in the main channel and in the secondary channels (Nascimento & Nakatani, 2006), and is highly synchronized with the water level fluctuation of the Paraná River (Canon Verón, 2005). Spawning occurs at high water phase and, during the spring-summer peaks of ichthyoplankton, first development stages of *Prochilodus lineatus* and *Leporinus obtusidens* are abundant (Canon Verón, 2005). The lower stretch of the Paraná River is considered by Oldani & Oliveros (1984) as the spawning and breeding area for *P. lineatus*, *L. obtusidens*, *P. albicans*, and *S. lima*. In spite of the limitation imposed by our scale, it appears that the proportion of juveniles of large migratory fish is low in all sites at different hydrological conditions. Therefore, further investigation is necessary in vegetated habitat with permanent connection to the river channel, to proper evaluate the role of these areas for development of young migratory fish.

Few species of Neotropical fish predominantly intake aquatic macrophytes as food, and many of these include other food resources in their diets (Agostinho *et al.*, 2003). Our findings are in agreement with these results. In spite of being abundant in the macrophytes of the study floodplain (Poi de Neiff & Carignan, 1997), snails are not prominent as a food resource for fish. The scarcity of molluscs in the diet of fish has been indicated for the upper Paraná River (Hahn *et al.*, 2004). As in other vegetated areas (Resende, 2000; Casatti *et al.*, 2003), most fish used several feeding resources, but littoral macrophyte-associated organisms had a high frequency of occurrence. The abundance of generalist species in floodplain rivers is another indicator of the adjustment of populations to variations in the hydrologic regime (Junk, 2000). Most of the dominant species collected at low water can be classified into algivore/detritivore whereas at high water the abundance of invertebrate feeders

Table 4 Frequency of occurrence (%) of food resources exploited by the dominant fish in the Paraná River floodplain: 1-microcrustaceans; 2-molluscs; 3-insects; 4-others invertebrates; 5-fishes; 6-algae; 7-higher plants; 8-detritus.

SPECIES	SITES							
	1	2	3	4	5	6	7	8
<i>Acestrorhynchus pantaneiro</i>	50	-	-	40	100	-	-	40
<i>Aphyocharax anisitsi</i>	50	-	-	25	-	50	50	-
<i>Astyanax fasciatus</i>	20	-	-	-	-	20	60	40
<i>Astyanax lineatus</i>	20	-	30	10	-	60	50	20
<i>Brachyhyopomus brevirostris</i>	100	-	60	20	-	-	-	60
<i>Crenicichla lepidota</i>	50	-	50	-	-	25	-	100
<i>Ctenobrycon alleni</i>	25	-	75	75	-	25	-	-
<i>Cyphocharax voga</i>	-	-	-	-	-	75	-	90
<i>Diapoma terofali</i>	50	-	-	-	-	50	80	-
<i>Gymnogeophagus balzanii</i>	15	-	65	-	15	15	60	40
<i>Hoplias malabaricus</i>	-	-	-	-	100	-	-	-
<i>Loricariichthys anus</i>	40	-	50	40	-	40	-	70
<i>Moenkhausia dichroura</i>	50	-	-	-	-	50	-	35
<i>Moenkhausia sanctaefilomenae</i>	70	-	-	-	-	70	-	70
<i>Odontostilbe paraguayensis</i>	40	-	-	-	-	80	-	100
<i>Otocinclus vittatus</i>	-	-	-	-	-	100	-	-
<i>Parodon suborbitalis</i>	30	-	-	-	-	100	-	100
<i>Pimelodella laticeps</i>	50	-	40	-	40	-	20	60
<i>Pimelodus maculatus</i>	-	-	-	40	50	-	-	100
<i>Plagioscion ternetzi</i>	-	-	-	80	50	-	-	100
<i>Poptella paraguayensis</i>	20	-	100	-	-	-	20	-
<i>Potamorhina squamoralevis</i>	20	-	30	-	-	100	-	20
<i>Prionobrama paraguayensis</i>	35	-	10	10	-	20	-	80
<i>Prochilodus lineatus</i>	20	-	5	-	-	100	-	100
<i>Psellogramus kennedyi</i>	50	-	25	50	-	25	-	25
<i>Pseudocorynopoma doriae</i>	100	-	20	-	-	80	-	20
<i>Pseudoplatystoma corruscans</i>	-	-	20	-	100	-	-	-
<i>Pygocentrus nattereri</i>	-	-	40	-	100	-	-	-
<i>Raphiodon vulpinus</i>	-	-	20	-	100	-	-	-
<i>Roebooides descavadensis</i>	60	-	40	20	10	-	10	20
<i>Roebooides microlepis</i>	40	-	60	10	30	-	-	25
<i>Schizodon borellii</i>	100	-	60	-	-	60	-	-
<i>Serrapinnus calliurus</i>	40	-	-	-	-	100	-	-
<i>Serrasalmus maculatus</i>	30	-	-	-	100	-	-	50
<i>Tetragonopterus argenteus</i>	45	-	25	10	20	10	-	90
<i>Thoracocharax stellatus</i>	50	-	50	-	-	30	-	60
<i>Trachelyopterus striatulus</i>	-	-	100	-	-	20	20	-
<i>Triportheus nematurus</i>	100	-	50	-	-	50	50	-

tended to increase. Retention of invertebrates by aquatic plants in the studied floodplain during high water (Poi de Neiff & Carignan, 1997) could be affecting trophic relations by increasing the food resources for invertebrate feeders. Restrictions on the efficacy of piscivorous fish are expected to be higher in dense vegetated areas.

The studied floodplain has a high geomorphological heterogeneity, as evidenced by the high variation in physicochemical conditions, concentrations of nutrients, and decomposition rate of organic matter (Poi de Neiff *et al.*, 2006), which is important for the fish diet. Also, the biomass of dominant aquatic plants (*i.e.* *E. crassipes*) is significantly different at different hydrological conditions (Neiff *et al.*, 2008). The seasonal variation in fish assemblage composition described in this study, could be explained by changes in factors such as wetlands size (indicated by the elasticity quotient), hydrological connectivity, food resources availability and dissolved oxygen concentration in the water column, all recognized as important for fish distribution in floodplain lakes (Miranda, 2005). During receding and isolation of the floodplain dominant spe-

cies at high water reduce its abundance and several species with adaptations to thrive in low oxygen conditions such as *Lepidosiren*, *Corydoras*, and *Hoplosternum* (Welcomme, 2000) were registered in some sites.

The high species richness of fish in the small, vegetated lakes is undoubtedly related to the high spatial and temporal heterogeneity. Disturbances in the hydrological regime of pulses could reduce the biodiversity by modifying the connectivity with the river channel and reducing the duration of the high water phase. Conservation of these vegetated wetlands requires maintenance of actual width range of connectivity that provide diverse habitat along time.

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