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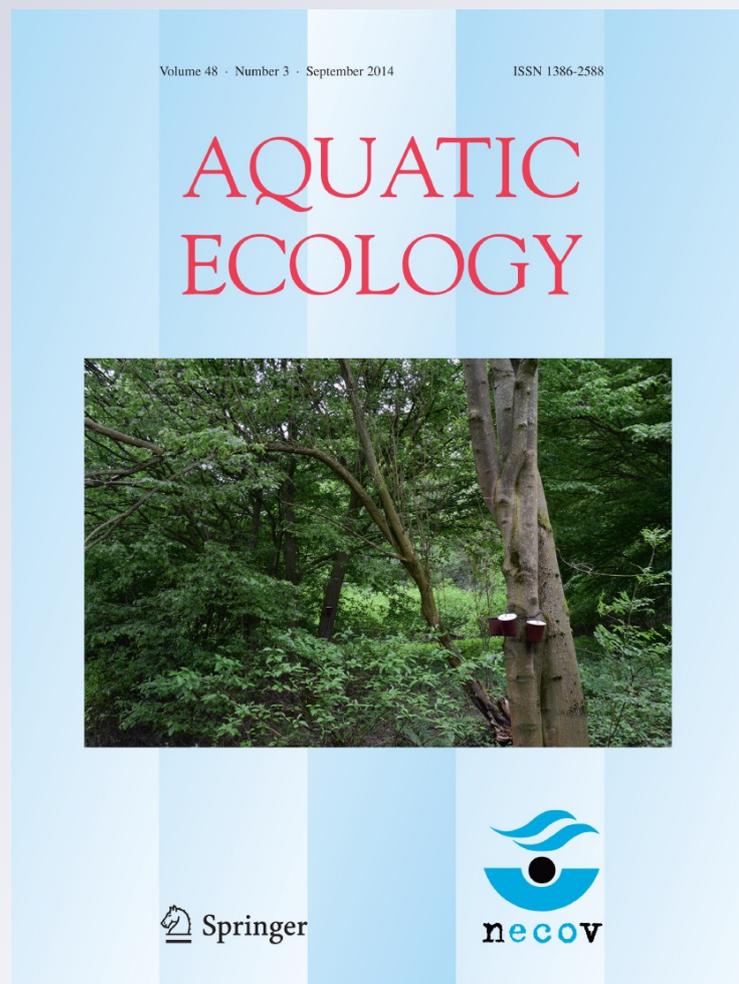
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Influence of hydrological changes on the fish community in two lotic environments of the Middle Paraná Floodplain, Argentina

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Abstract Temporal variations of fish abundance and species richness in two sites of a secondary channel of the Middle Paraná Floodplain (Argentina) have been analyzed from 2010 to 2012. Relationships of these ecological attributes with alternations of floods and dry periods were appraised. Permutational analyses of variance were applied to determine significance in temporal changes of the fish community, taking into account catch per unit effort and species richness of the whole community, by groups of distinct reproductive strategy and considering fish sizes. The results reveal significant differences in structure and composition of fish assemblages at distinct stages of the hydrological regime. Those temporal differences are associated with changes in timing, duration, and magnitude of floods since the three groups have shown distinct responses to the hydrological variations. Long-distance migrants depend on major inundations for a successful reproduction, short-distance migrants seem to have distinct responses to floods according to the kind of species, and sedentary fish-

developing parental care essentially needs high floodplain connectivity for juvenile development.

Keywords Flood pulse · Fish abundance · Species richness · Reproductive strategy · Middle Paraná Floodplain

Introduction

Natural river floodplains are among the most productive and diverse freshwater ecosystems in the world (Tockner and Stanford 2002). Until the 1970s, floodplains were studied separately by different disciplines, such as hydrology, ecology, or limnology. From then on, some authors started to study river–floodplain systems with an integrated approach, describing floodplains as specific ecosystems and pointing out the interactions between biogeochemical components and physical variables (e.g., Lowe-McConnell 1975, 1987; Welcomme 1979; Junk 1980). This new approach led to the formulation of the flood pulse concept (Junk et al. 1989), which describes how seasonal flooding increases the connectivity among water bodies, interfering in such aspects like limnological characteristics, the balance of production and respiration processes, the pattern of nutrient cycling, and the structuring of aquatic communities. Therefore, the alternating periods of floods and droughts were considered to be the principal driving force in the functioning of river–floodplain systems.

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Regarding fish, the effect of changing hydrology has been well documented in the large tropical and subtropical rivers of South America. Back in 1979, Welcomme summarized data on floodplain fishery, limnology, and hydrology and coupled fish production with the nutrient status of the parent rivers and the extent of flooding. The consequences of the fluctuating water level for fish were also summarized by Lowe-McConnell (1975, 1987). Later, various studies reported the crucial importance of connectivity among floodplain habitats for all kinds of fish species since it increases the number of natural nurseries and produces a diversity of highly productive environments, whereas a low connection between floodplain habitats increases the stressing environmental conditions (e.g., Junk et al. 1989; Winemiller and Jepsen 1998; Agostinho et al. 2003). Among the pioneers who studied fish migrations, Bonetto et al. (1971) gave precise descriptions of the upstream and downstream movements using the technique of tagging for two large migrators—*Salminus brasiliensis* and *Prochilodus lineatus*—in the middle and lower reaches of the Paraná River. After that, longitudinal migrations were well described: Rising waters at the beginning of floods coupled with high temperatures triggered the migratory movements of most long-distance migrants that spawned upstream in the main channels; then, hydrated eggs drifted along the river and spilt over alluvial plains where they completed their larvae development (Godoy 1975; Oldani 1990; Baigun et al. 2003; Agostinho et al. 2004). Fish movements between lentic–lotic environments of floodplains were also documented—mostly in the central part of the Amazon River—and the relationships were established between fish displacements and rising- and falling water periods (Goulding 1980; Fernandes 1997). Note also that fish disassemblage and reassemblage may occur in a few days as a response to rapid water fluctuations (Arrington et al. 2005), and the reproductive strategy is closely related to variations of water levels for many species (Gomes and Agostinho 1997). This last point was particularly well researched in the upper part of the Paraná River (Agostinho et al. 2001, 2003, 2004; Suzuki et al. 2002; Fernandes et al. 2009). These authors noted that the migration trigger for reproduction of most species precedes flood peaks and added that the association of reproduction with the beginning of rising waters is a common pattern for the majority of species, whereas the peak level might

signal the cessation of spawning. However, Bailly et al. (2008) observed that according to their reproductive strategy, species seem to respond differently when they face hydrological fluctuations; long-distance migrants clearly show the need of inundations to reproduce, whereas this pattern was not so evident for species embarking on short lateral migrations between floodplain lakes and channels or spending their whole life in the same area. Going back to the middle part of the Paraná River, ecological aspects such as fish reproductive strategies linked to hydrology have been dealt within few studies. Research efforts have been only made on high-value species, mainly large fish carrying out long upstream migrations to reproduce (Bonetto et al. 1971; Baigun et al. 2003).

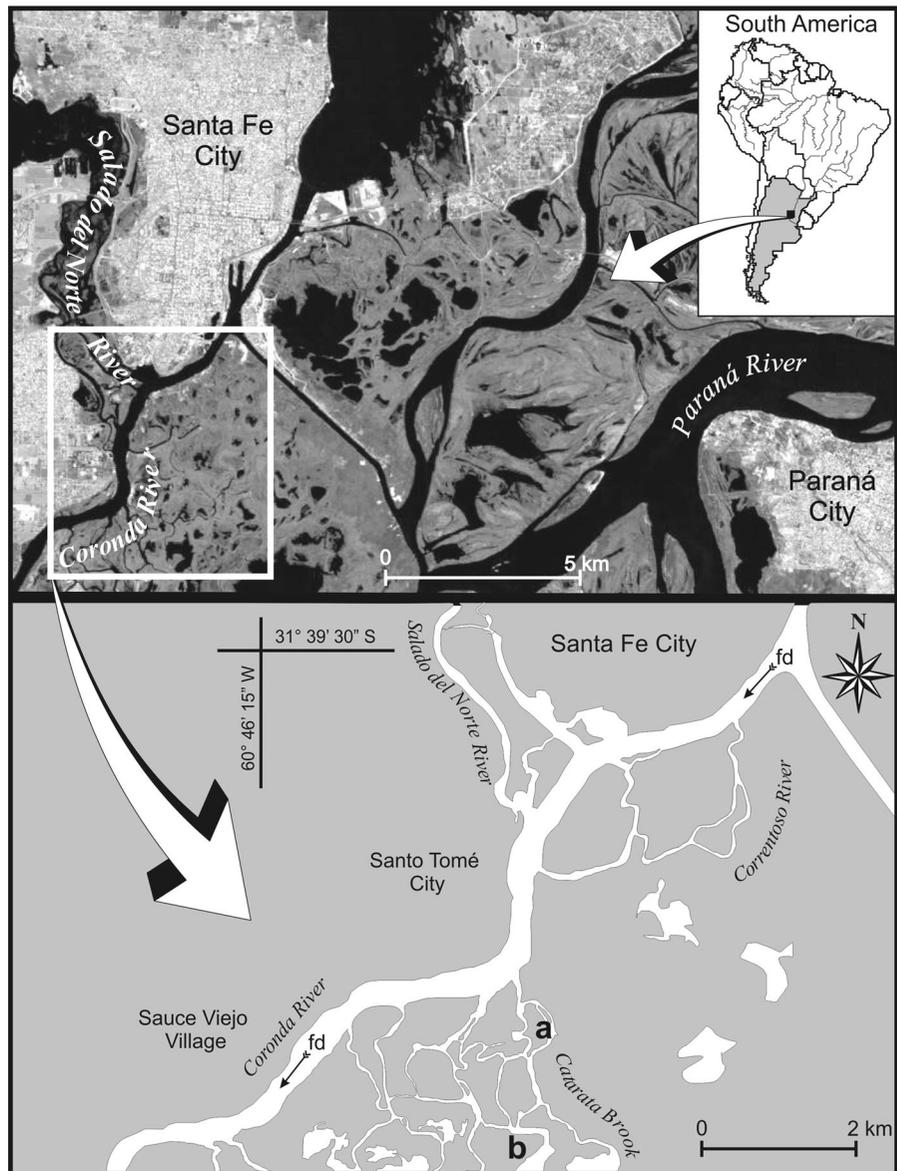
Based on the hypothesis that intensity, duration, and seasonality of floods are the main driving forces in structuring fish assemblages, we predict that composition and structure of fish assemblages will change with different hydrological conditions in the Middle Paraná Floodplain. We also expect that according to their reproductive strategy, fish will respond in different ways when faced with a changing hydrology.

Materials and methods

Study area

This study was conducted in the Paraná River, which ranks ninth among the largest rivers in the world according to its mean annual discharge into the ocean ($18,000 \text{ m}^3 \text{ s}^{-1}$; Latrubesse 2008). The field measurements were performed in its floodplain, in the south of Santa Fe City, Argentina. This area is characterized by an intricate lotic/lentic drainage network of high connectivity—i.e., a high percentage of its surface is covered by minor channels, lakes, and swamps almost permanently connected (Fig. 1). During large floods, they tend to merge into a continuous sheet of water that covers the whole floodplain (Paira and Drago 2007). The typical hydrometric regime is characterized by a high-water period in summer–autumn (December–April), and a low-water period in early spring (September–October) (Giacosa et al. 2000). The highest water temperatures are recorded in December–March, and the lowest ones in June–August (Drago 1984). This study aims to analyze fish assemblages in two sites, 1.5 km apart from each

Fig. 1 Study area in the alluvial plain of the Paraná River and sampling sites (*a*, *b*) located in the Catarata brook (modified from Espínola et al. 2014); *fd* flow direction



other, located in the Catarata brook. This minor channel is about 50 m wide, with an average depth of 5 m, and the discharges measured during the period studied ranged from 50 (December 2010) to 300 m³ s⁻¹ (April 2011) (Fig. 1).

Sampling

Sampling was conducted in August 2010, August 2011, and August 2012. Fish were caught using gillnets of different mesh sizes (from 3 to 16 cm

between opposite knots), with sampling effort standardized. Gillnets were set out for a 24-h period at each sampling site and checked every 8 h. All individuals were identified at species level, and common biometric data were processed in the field [total length (Lt; cm), standard length (Ls; cm), total weight (Wt; g)]. No species caught was either endemic or classified as threatened (Liotta 2005). Physico-chemical parameters (pH, dissolved oxygen, conductivity, and water temperature) were analyzed in laboratory, and no significant correlations were established with biological data.

Hydrological regime

Water levels as recorded by the Santa Fe Port gauge (data supplied by the National Directorate of Waterways of Argentina) were used to characterize the changing hydrology. Within the study area, the height of 4.50 m is defined as the reference level when flow begins to flood the adjacent plain—considered as the overflow level—and the height of 2.30 m when the disconnection of most lakes starts (Paira 2003). Hydrological changes in a given year were considered through some hydrometric attributes, such as days of potamophase/limnophase (number of days above/under the overflow level) and connectivity (ratio between the number of days of potamophase and limnophase), which were computed with the fFITRAS function of the PULSO software (Neiff and Neiff 2003).

Analysis of fish assemblages

Species richness (number of species caught) and fish abundance calculated by the catch per unit effort (CPUE: number of individuals/1,000 m² of gillnets in 24 h) were used to characterize fish assemblages. We applied a canonical analysis of the principal coordinates (Anderson and Willis 2003) based on a discriminant analysis to see the temporal difference in the composition and structure of fish assemblages. We utilized one-way permutational analysis of variance (Anderson 2001) to determine differences in CPUE between sampling periods. The Bray–Curtis dissimilarity index was used (Bray and Curtis 1957) together with 1,000 random permutations without restrictions (Manly 1997).

Analysis by reproductive strategy

Fish species were classified into groups according to their strategy of reproduction and migration in line with the existing knowledge available about the Paraná River (e.g., Bonetto et al. 1971; Vazzoler 1996; Agostinho et al. 2004; Suzuki et al. 2002; Bailly et al. 2008). With respect to some species, strategies have not been found at species level and are based on genus or subfamily level (Table 1). This classification includes the following: (LM) long-distance migratory fish with external fertilization and without parental care: Those species carry out upstream longitudinal

Table 1 Abundance, size and reproductive strategy of the 48 species caught in the two studied sites from August 2010 to August 2012. Ls range (standard length range in cm), *N* (total number of fish), RS (reproductive strategy)

Order family species	Name abbrev.	Ls range	<i>N</i>	RS
Atheriniformes				
Atherinopsidae				
<i>Odontesthes bonariensis</i> (Valenciennes 1835)	<i>O bon</i>	21.5–33	3	SM
Characiformes				
Acestrorhynchidae				
<i>Acestrorhynchus pantaneiro</i> (Menezes 1992)	<i>A pan</i>	18.5–30	45	SM
Anostomidae				
<i>Leponirus obtusidens</i> (Valenciennes 1837)	<i>L obt</i>	7.4–40.1	157	LM
<i>Schizodon borellii</i> (Boulenger 1900)*	<i>S bor</i>	14.5–35	54	SM
<i>Schizodon platae</i> (Garman 1890)*	<i>S pla</i>	13.4–38.4	205	SM
Characidae				
<i>Astyanax abramis</i> (Jenyns 1842)*	<i>A abr</i>	6.7–13.5	132	SM
<i>Astyanax asuncionensis</i> (Géry 1972)*	<i>A asu</i>	6.7–17.5	71	SM
<i>Astyanax fasciatus</i> (Cuvier 1818)	<i>A fas</i>	8–9.5	9	SM
<i>Brycon orbignyanus</i> (Valenciennes 1850)	<i>B orb</i>	20.5–25.3	9	LM
<i>Cynopotamus argenteus</i> (Valenciennes 1836)*	<i>C arg</i>	9.5–21.9	59	SM
<i>Galeocharax humeralis</i> (Valenciennes 1834)	<i>G hum</i>	13.8	1	SM
<i>Mylossoma duriventre</i> (Cuvier 1818)	<i>M dur</i>	10.5–22.1	3	SM
<i>Oligosarcus jenynsii</i> (Günther 1864)	<i>O jen</i>	9.5	1	SD
<i>Pygocentrus nattereri</i> (Kner 1858)	<i>P nat</i>	12.5–31	18	PC
<i>Salminus brasiliensis</i> (Cuvier 1816)	<i>S bra</i>	18.4–54.5	57	LM
<i>Serrasalmus maculatus</i> (Kner 1858)	<i>S mac</i>	11.4–16.5	8	PC
<i>Serrasalmus marginatus</i> (Valenciennes 1837)	<i>S mar</i>	9.1–22	26	PC
<i>Triportheus nematurus</i> (Kner 1858)	<i>T nem</i>	20.5–27.5	7	SM
Cynodontidae				
<i>Rhaphiodon vulpinus</i> (Spix & Agassiz 1829)	<i>R vul</i>	14.1–43.5	29	LM

Table 1 continued

Order family species	Name abbrev.	Ls range	N	RS
Curimatidae				
<i>Cyphocharax platanus</i> (Günther 1880)*	<i>C pla</i>	8.5–15.5	43	SM
<i>Cyphocharax voga</i> (Hensel 1870)*	<i>C vog</i>	7.8–25.5	34	SM
<i>Steindachnerina brevipinna</i> (Eigenmann & Eigenmann 1889)	<i>S bre</i>	8	1	SM
Erythrinidae				
<i>Hoplias malabaricus</i> (Bloch 1794)	<i>H mal</i>	18.5–44.5	21	PC
Gasteropelecidae				
<i>Thoracocharax stellatus</i> (Kner 1858)	<i>T ste</i>	15.3–16.5	2	PC
Parodontidae				
<i>Apareiodon affinis</i> (Steindachner 1879)	<i>A aff</i>	8.7	1	SM
Prochilodontidae				
<i>Prochilodus lineatus</i> (Valenciennes 1837)	<i>P lin</i>	11.7–43.5	558	LM
Clupeiformes				
Engraulidae				
<i>Lycengraulis grossidens</i> (Spix & Agassiz 1829)	<i>L gro</i>	11.5–20	10	LM
Gymnotiformes				
Sternopygidae				
<i>Eigenmannia trilineata</i> (López & Castello 1966)	<i>E tri</i>	20–39.5	5	SM
Perciformes				
Sciaenidae				
<i>Pachyurus bonariensis</i> (Steindachner 1879)	<i>P bon</i>	9.2–20.5	14	SM
Pleuronectiformes				
Achiridae				
<i>Catathyridium jenynsii</i> (Günther 1862)	<i>C jen</i>	18.5	1	SM
Siluriformes				
Auchenipteridae				
<i>Ageneiosus inermis</i> (Linnaeus 1766)	<i>A ine</i>	25.5–40.5	4	IF
<i>Ageneiosus militaris</i> (Valenciennes 1835)	<i>A mil</i>	23.8–34.1	14	IF
<i>Auchenipterus nigripinnis</i> (Boulenger 1895)	<i>A nig</i>	15.5–17.4	7	IF

Table 1 continued

Order family species	Name abbrev.	Ls range	N	RS
<i>Auchenipterus osteomystax</i> (Miranda-Ribeiro 1918)	<i>A ost</i>	15.9–17.2	3	IF
<i>Trachelyopterus lucenai</i> (Bertoletti, Pezzi da Silva & Pereira 1995)	<i>T luc</i>	7.8–19.4	23	IF
<i>Trachelyopterus striatulus</i> (Steindachner 1877)	<i>T str</i>	14.5–18.5	20	IF
Callichthyidae				
<i>Hoplosternum littorale</i> (Hancock 1828)	<i>H lit</i>	15.8	1	PC
Doradidae				
<i>Oxydoras kneri</i> (Bleeker 1862)	<i>O kne</i>	13.5–50.5	4	LM
<i>Pterodoras granulosus</i> (Valenciennes 1821)	<i>P gra</i>	9.8–28.5	61	LM
<i>Rhinodoras dorbignyi</i> (Kner 1855)	<i>R dor</i>	21.1	1	SM
Heptapteridae				
<i>Pimelodella gracilis</i> (Valenciennes 1835)	<i>Pi gra</i>	10.4–12.5	2	SM
Loricariidae				
<i>Brochiloricaria chauliodon</i> (Isbrücker 1979)**	<i>B cha</i>	35.4	1	PC
<i>Hypostomus commersoni</i> (Valenciennes 1836)*	<i>H com</i>	9.6–48.5	19	PC
<i>Loricaria simillima</i> (Regan 1904)*	<i>L sim</i>	12.8–37.5	11	PC
<i>Loricariichthys melanocheilus</i> (Reis & Pereira 2000)*	<i>L mel</i>	15.8–39.5	24	PC
<i>Loricariichthys platymetopon</i> (Isbrücker & Nijssen 1979)	<i>L pla</i>	14.5–37.5	20	PC
<i>Paraloricaria agastor</i> (Isbrücker 1979)**	<i>P aga</i>	30.5–38.3	7	PC
<i>Pterygoplichthys anisitsi</i> (Eigenmann & Kennedy 1903)	<i>P ani</i>	10.4–14.2	5	PC
<i>Ricola macrops</i> (Regan 1904)	<i>R mac</i>	26–36.8	8	PC
Pimelodidae				
<i>Iheringichthys labrosus</i> (Lütken 1874)	<i>I lab</i>	13	1	SM
<i>Luciopimelodus pati</i> (Valenciennes 1835)	<i>L pat</i>	29.7–32.1	2	LM

Table 1 continued

Order family species	Name abbrev.	Ls range	N	RS
<i>Parapimelodus valenciennis</i> (Lütken 1874)**	<i>P val</i>	10.5–21.5	18	SM
<i>Pimelodus albicans</i> (Valenciennes 1840)	<i>P alb</i>	11.1–20.9	3	LM
<i>Pimelodus maculatus</i> (Lacepède 1803)	<i>P mac</i>	8.5–23.7	50	LM
<i>Pseudoplatystoma corruscans</i> (Spix & Agassiz 1829)	<i>P cor</i>	28.4–47.1	8	LM
<i>Pseudoplatystoma reticulatum</i> (Eigenmann & Eigenmann 1889)	<i>P ret</i>	35.5–36.6	2	LM

* Reproductive strategy based on genus level

** Reproductive strategy based on subfamily level

migrations which extend for more than 100 km and spawn mainly during the summer; (SM) short-distance migratory fish with external fertilization and without parental care: They migrate less than 100 km with primarily lateral movements. Their reproductive period may extend over several months: (PC) sedentary fish with parental care and external fertilization. Those species predominantly spawn many times over a long period: (IF) sedentary or short-distance migratory fish with internal fertilization and without parental care. They show sexual dimorphism and/or mating rituals associated with reproductive behavior. The IF group was not taken into account because neither its abundance nor the number of species was statistically representative. We applied another one-way permutational analysis of variance to determine temporal differences in total abundance, species richness, and mean abundance for each group. We also used this statistical analysis to check differences in fish sizes in the three reproductive groups and between each sampling period. The analysis was also run with 1,000 random permutations without restrictions. Eventually, we performed a principal component analysis using the Hellinger standardization method (Oksanen 2013) to identify the relationships between fish sizes and selected periods. According to the Kaiser–Guttman criterion (Jackson 1993), only axes with eigenvalues >1 were retained for interpretation.

A significance level of $p < 0.05$ was accepted to indicate significance for every computation.

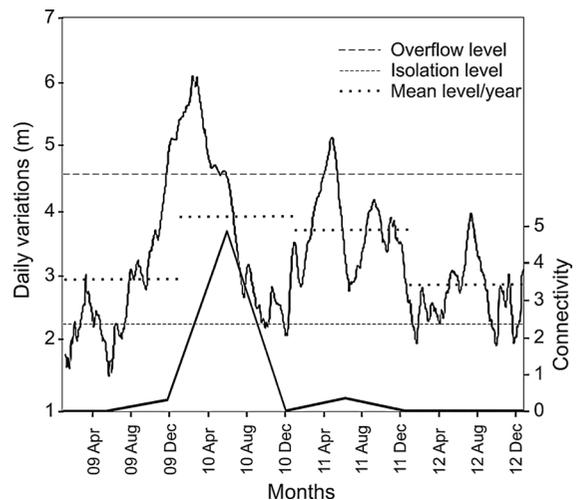


Fig. 2 Variations in water levels and connectivity in the Middle Paraná Floodplain

Permutational analyses of variance were done with the statistical software MULTIV version 2.4 (Pillar 2004), and all the other analyses were carried out with the R-statistical software (R Development Core Team 2011).

Results

Hydrological fluctuations

The hydrological regime can be approached from three different phases along the period studied (Fig. 2). First of all, the greatest flood pulse appeared in mid-2009 and ended in early December 2010. Characterized by a peak of 6.02 m on February 10, 2010, it exceeded the level of overflow on November 18, 2009, and connected the entire alluvial plain for 195 days. The following year, a lower inundation happened. Waters remained above the overflow level for only 47 days from early April until mid-May 2011, and its peak just went over 5 m high. The last phase occurred in the year 2012 and was characterized as a dry period. Waters stayed under the isolation level several times, and the only marked water rise occurred in July and did not exceed a threshold of 4 m; consequently, connections between floodplain environments remained low during that year. The connectivity recorded every 6 months from 2009 to 2012 clearly showed the three hydrological phases. A high rise in the period ranging from mid-2009 to mid-2010

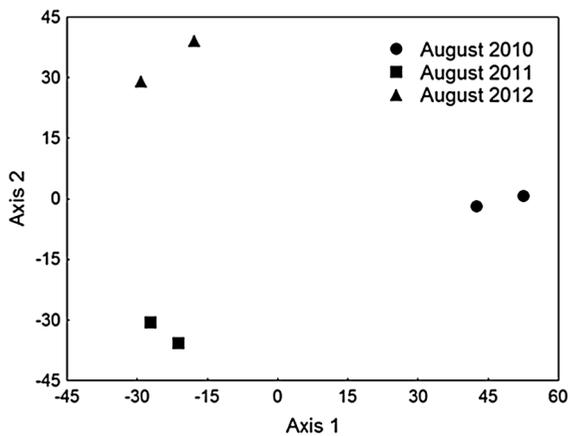


Fig. 3 Principal coordinate plot showing the repartition of fish assemblages (structure and composition) recorded in the two studied sites during August 2010, 2011, and 2012

to be followed by a decrease until the end of 2010; in 2011, a new but smaller rise happened, and 2012 was marked by a period of low connections between floodplain environments.

Characterization of the fish community

A total of 1,506 fish belonging to 48 species of 18 families and 6 orders were caught (Table 1). Characiformes (24) and Siluriformes (20) dominated in species richness; however, Characiformes largely dominated in the number of individuals with 82 % of total abundance. *P. lineatus* was the most abundant species with 494 individuals, or 33 % of the total abundance. Other species, such as *Leporinus obtusidens*, *Schizodon plataea*, and *Astyanax abramis*, reached an abundance of more than 100 individuals.

Temporal variation of fish assemblages

The structure and composition of fish assemblages were significantly different between each sampling period ($\text{tr} = 1.966$, $p = 0.033$; Fig. 3). In August 2010, the most representative species was *P. lineatus* (42 % of the total abundance) and *S. plataea*, *L. obtusidens*, *Pterodoras granulosus*, *Astyanax asuncionensis*, *Pimelodus maculatus*, and *Cynopotamus argenteus* presented a high abundance too. In August 2011, the most representative species was *A. abramis* (51 %) and *L. obtusidens*, *S. plataea*, *Cyphocharax platanus* and *A. asuncionensis* were also well represented. In August 2012, *Acestrorhynchus pantaneiro*,

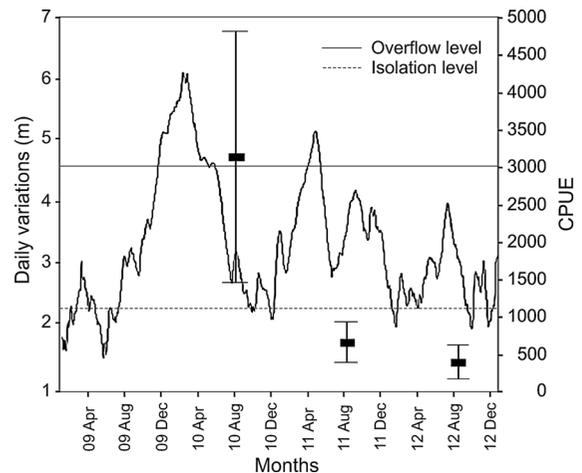


Fig. 4 Variations of CPUE in the studied sites in August 2010, 2011, and 2012

Loricariichthys melanocheilus, *P. lineatus*, and *Trachelyopterus striatulus* stood for more than 50 % of the catch.

Even if the difference was not statistically significant, we observe in Fig. 4 that mean CPUE was largely higher after the highest flood pulse (August 2010) than after the lowest flood pulse (August 2011) or the year with no floods (August 2012). Species richness was also higher in August 2010 (33 sp.) than in August 2011 or in 2012 (25; 21 sp.).

Responses of different reproductive strategies of fish to hydrological events

Short-distance migrants (SM) were greater in number of species (19 sp.) followed by long-distance migrants (LM) (13 sp.) and sedentary fish with parental care (PC) (12 sp.). Whichever may be the reproductive strategies of the species, the greater the connectivity, the richer and more abundant the species were (Fig. 5). LM were significantly more abundant when the connectivity was at its highest point; PC and SM had also a greater abundance when the connectivity was higher though no significant differences were observed. Species richness of the LM group significantly decreased when the connectivity was at its lowest point, the SM group did not show any significant differences during the changing connectivity, and the PC group was significantly higher during the highest floodplain connectivity (compare Table 2 for statistical relevance).

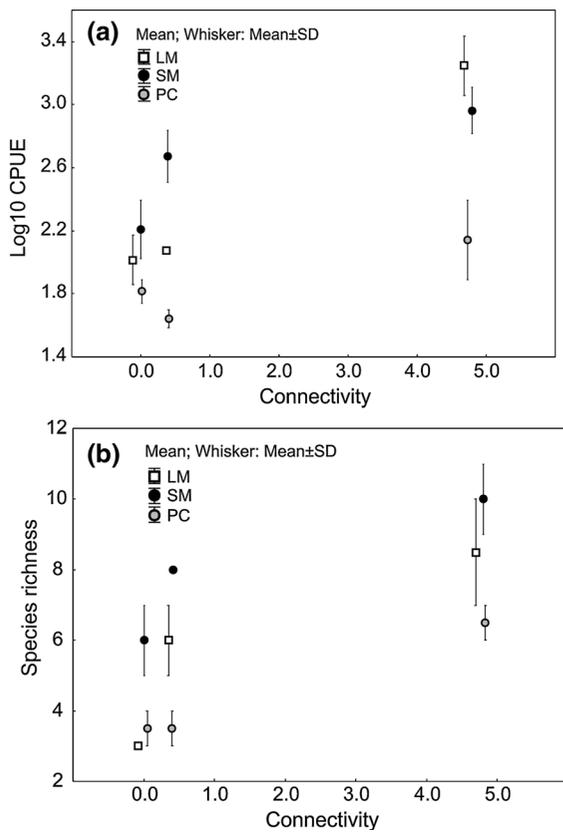


Fig. 5 Fish abundance (a) and species richness (b) of LM, SM, and PC in the studied sites after periods of distinct half-yearly connectivity. August 2010 (connectivity = 4.84), August 2011 (connectivity = 0.35), August 2012 (connectivity = 0). Values of connectivity from January to June of every year were used, covering each flood effect

Results of PERMANOVA revealed significant differences in the mean abundance of LM species between the three periods ($F = 0.618$, $p = 0.015$), but no significant differences of SM species ($F = 0.245$, $p = 0.54$) from PC species ($F = 0.401$, $p = 0.28$) were observed. The mean abundance of LM species in 2010 was significantly different to that of 2011 ($F = 0.424$, $p = 0.025$) and 2012 ($F = 0.283$, $p = 0.034$) both showed a similar mean abundance. The reduction of connectivity in 2011 did not affect the abundance of SM species; the mean abundance after the two pulses did not show significant differences. In 2012, the mean abundance of SM seemed to be different to that of 2010 and 2011; however, neither of them was significant. Apparently, PC species reacted in a way similar to LM species. Even if the difference was not significant for this reproductive

group, the mean abundance recorded in 2010 seemed to differentiate from that of 2011 and 2012 (Fig. 6).

Results of PERMANOVA (Table 3) revealed significant differences in fish sizes between the three distinct hydrological phases. Sizes of LM and SM were significantly different between each period, and sizes of PC were significantly different after the great flood compared to the two other periods, which showed similar sizes. Figure 7 shows the associations of the three periods with fish sizes. Only the first axis of PCA was significant and retained for the interpretation. We observed mainly juvenile LM of about 10–20 cm in length after the great flood pulse, whereas LM were strongly associated with larger sizes further to the lower flood pulse; note also the presence of juvenile LM in 2011 (5–10 cm of Ls), but this size range is of little significance. Larger LM, mostly those ranging from 25 to 35 cm in length, were also related to the year with no floods. After the great flood pulse, SM were mostly linked to sizes from 10 to 20 cm of Ls. We observed small-sized SM (5–10 cm of Ls) after the shorter pulse, and also some associations with larger sizes. In the year when there were no floods, SM of disparate sizes were caught (mostly from 20 to 30 cm of Ls). PC were associated with small sizes after the great flood (5–20 cm of Ls), whereas larger sizes were found during the two other periods (20–35 cm of Ls).

Discussion

Water levels recorded for the middle part of the Paraná River revealed years of very distinct flood intensity such as the period ranging from 2009 to 2012; in December 2009, a severe flood occurred producing high connectivity in the alluvial plain for more than 6 months; a smaller one in autumn 2011 gave rise to a short-time connection of lotic and lentic floodplain environments, and the 2012 year was marked by low-water levels. The structure and composition of fish assemblages recorded in the two lotic sites of the Middle Paraná Floodplain have significantly changed alongside these three different hydrological conditions.

King et al. (2003) stated that optimum flood conditions for success in fish recruitment had to fulfill the following recruitments: coincidence with high temperatures, predictability, slow rise and fall of the

Table 2 Results of one-way permutational analyze of variance conducted on CPUE and species richness for LM, SM, and PC. *F* (distance-based *F*-statistic), *t* (distance-based *t*-statistic),

*P*_{MC} (Monte Carlo asymptotic *p* value), *df* (degrees of freedom), *SS* (sums of squares)

Variables	Source	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i> _{MC}
<i>CPUE and species richness of species groups of distinct reproductive strategies</i>						
CPUE	Connectivity	2	815.9	407.9	18.31	<0.001
Sp. richness	Connectivity	2	3,257	1,628	20.44	<0.001
Variables	Levels compared	<i>t</i>	<i>P</i> _{MC}			
<i>Pair-wise comparisons: tests among levels of the factor “connectivity”</i>						
CPUE of LM	(0; 0.35)	0.417	0.732			
	(0; 4.84)	4.740	0.047			
	(0.35; 4.84)	7.523	0.015			
CPUE of SM	(0; 0.35)	1.815	0.213			
	(0; 4.84)	2.998	0.087			
	(0.35; 4.84)	1.305	0.330			
CPUE of PC	(0; 0.35)	1.961	0.200			
	(0; 4.84)	1.262	0.344			
	(0.35; 4.84)	2.103	0.169			
Sp. richness of LM	(0; 0.35)	3.875	0.044			
	(0; 4.84)	5.281	0.030			
	(0.35; 4.84)	1.373	0.291			
Sp. richness of SM	(0; 0.35)	1.776	0.218			
	(0; 4.84)	2.569	0.119			
	(0.35; 4.84)	2.162	0.174			
Sp. richness of PC	(0; 0.35)	<0.001	>0.999			
	(0; 4.84)	3.693	0.046			
	(0.35; 4.84)	3.693	0.048			

Significant results of pair-wise comparisons are in bold

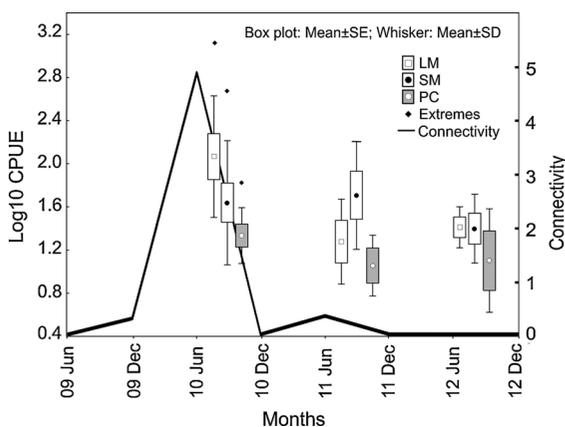


Fig. 6 Mean abundances of LM, SM, and PC species recorded in the studied sites in August of 2010, 2011, and 2012 and half-yearly connectivity. Species whose abundance is lower than three individuals were not considered in the analysis

river level, duration, lasting from several weeks to a few months, and covering an extensive floodplain area. In 2010, the flood pulse presented the features described above. Moreover, Agostinho et al. (2001) associated the higher values of species richness and fish abundance with years of longer floods and greater connectivity in the Upper Paraná River. We noted the same pattern in August 2010. Irrespective of the reproductive strategy, fish abundance and species richness were higher after the inundation and individuals were mainly small in size.

On the one hand, the summer water rise coinciding with high temperatures might have triggered the reproductive processes of most migratory species. This could account for the dominance of LM, being them 10–20 cm in standard length in August 2010. Such small sizes, mainly individuals of *P. lineatus*, *L.*

Table 3 Results of PERMANOVA showing the differences on standard lengths of LM, SM, and PC after three distinct hydrological phases. z' (distance value), p (significance value), August 10 (after a great flood pulse), August 11 (after a smaller flood pulse), August 12 (without floods)

Fish groups	Levels compared	SS	p
LM	Between groups	7.288	0.001
	(Aug. 2010; Aug. 2011)	1.815	0.001
	(Aug. 2010; Aug. 2012)	5.766	0.001
	(Aug. 2011; Aug. 2012)	1.179	0.001
SM	Between groups	29.33	0.001
	(Aug. 2010; Aug. 2011)	26.98	0.001
	(Aug. 2010; Aug. 2012)	0.833	0.003
	(Aug. 2011; Aug. 2012)	11.31	0.001
PC	Between groups	5.574	0.001
	(Aug. 2010; Aug. 2011)	2.965	0.001
	(Aug. 2010; Aug. 2012)	3.968	0.001
	(Aug. 2011; Aug. 2012)	<0.001	0.974

obtusidens, *P. maculatus*, or *P. granulosus*, corresponded to juvenile LM that were most likely to be born during the rising period of the flood. In the upper part of the Paraná River, high-water levels during the summer were clearly associated with the migration and reproduction success of LM species (Agostinho et al. 1993; Vazzoler 1996). Our results show that long-distance migratory fish followed the same pattern in the middle part of the Paraná River. The other more representative species caught in August 2010 were SM species, such as *A. asuncionensis*, *C. argenteus*, and *S. platae*. When the period of rising water begins, mature SM start a lateral migration from the floodplain lakes up to the rivers apparently related to spawning (Fernandes 1997) and show an intense reproductive activity between October and March (Agostinho et al. 2003). In all likelihood, the summer water rise also triggered SM lateral migrations to spawn and could explain the high abundance of small-in-size SM in August 2010.

Furthermore, the extended floodplain inundation during the 2010 warm season enabled the interconnection of large areas in the floodplain. Larvae and juveniles accessed areas with important food supply and better conditions to reduce predation by piscivorous fish, reptiles, or birds; survival of young specimens could have been optimized during that period. Agostinho et al. (2003) reported the increment of

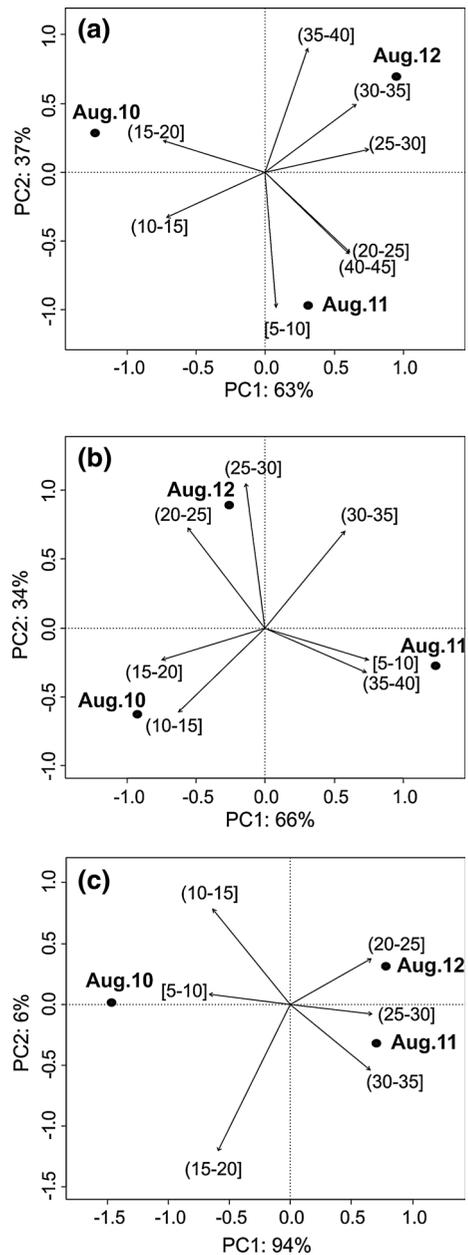


Fig. 7 Association of sizes of LM (a), SM (b), and PC (c) during three periods of different hydrological conditions recorded in the studied sites. August 2010 (after a great flood pulse), August 2011 (after a smaller flood pulse), August 2012 (without floods)

juvenile survival under similar conditions in the Upper Paraná River and associated that increase with the juvenile access to inundated areas rich in food and shelters. We consider that apart from the success of the

reproduction of migratory fish, the high richness and abundance observed in 2010 could also have been influenced by the better conditions for juvenile survival provided by the previous flood. Those favorable conditions were apparent at the community level, i.e., irrespective of the reproductive strategy of the fish caught in this part of the Paraná Floodplain.

In August 2011 and 2012, species richness and fish abundance were much lower compared to those of August 2010. That was particularly true for LM and PC species. Indeed, the difference was statistically significant for LM species, and even though PC species did not suffer such a marked decline, they showed a similar trend too. It was also remarkable that LM and PC fish were mainly associated with large sizes in those two sampling periods. It seems that hydrological conditions in 2011 and 2012 did not favor the reproduction or the juvenile survival of LM and PC species. Agostinho et al. (2004) noted in the upper part of the Paraná River that fish migrations are favored by annual floods with a duration longer than 75 days (beginning in early summer), and the failure of fish reproduction is reported to be a consequence of the absence of flooding during the spawning season. It is very likely that the shorter duration of the 2011 flood pulse—47 days—and its rising water period—February–April—(out of the spawning season) as well as the absence of inundation in 2012 did not bring about the necessary conditions for the successful reproduction of LM and caused the significant decline of this fish group.

On the other hand, PC species reproduce independently from the flood regime (Agostinho et al. 2004); however, their reproductive activity is greater during drought though abundance of juveniles is the lowest due to factors such as increased exposure to predation and the lost of habitat (Agostinho et al. 2003). So the decline of PC fish in 2011 and 2012 should be closely related to the low connectivity in the floodplain. Little access to breeding areas as well as lack of shelters together with exposure to predation might have been the main factors that caused the low abundance and the absence of juvenile PC in 2011 and 2012. With respect to LM and PC groups, we highlight that the species were not strongly favored when the flood was short, and out of the summer season or when no floods occurred. In both cases, we observed low species richness and fish abundance and the juveniles were almost absent.

Species richness and fish abundance of SM tended to be higher in 2011 than in 2012. The decrease of SM fish in 2012 was probably due to the absence of flood to trigger reproductive processes and to the few opportunities for fish to have access to areas rich in food and shelters, as it occurred with other reproductive groups. In addition, the genus *Astyanax*, characterized by individuals small and homogeneous in size, was dominant in August 2011. The other species caught—e.g., *S. platae* and *C. platanus*—were adult in size. It seems that *Astyanax* spp. found good conditions for recruitment, but the presence of the other species could be associated with the particular hydrology of that sampling period. Indeed, it coincided with a water rise, and it could be likely that those mature SM came from nearby lakes to accomplish their reproduction processes in the lotic environments. Bailly et al. (2008) noted that SM include a range of species from very short-to-moderate reproduction displacements and appear to be less dependent on flood for reproduction than LM. This may be the case for some species such as *Astyanax* spp., but the absence of young individuals for some species in August 2011 revealed that various species could not find the appropriate conditions for a successful reproduction during this period. An analysis at species or genus level might be a relevant approach to better understand the relation between SM species and hydrological variations.

Concluding remarks

Under distinct hydrological conditions, the structure and composition of fish assemblages significantly changed in lotic sites of the Middle Paraná Floodplain. High connectivity in the floodplain was essential for the recruitment of all kinds of fish; however, species responded differently to floods according to their reproductive strategies. Migratory fish saw their abundance greatly increased when came the extended summer flood. Richness and abundance of long-distance migratory fish and sedentary fish-developing parental care were affected by the small flood out of the summer season, and the same trend was observed for the year with no floods. Short-distance migratory species did not present a common pattern in relation to flood characteristics; some species seemed to be dependent on the extended summer floods, whereas

others appeared to have a more opportunistic reproductive strategy.

The findings of this study confirm well-known concepts of the ecology of fish assemblages in large river floodplains showing, in three consecutive years, the effects on species richness and fish abundance of different types of flood pulses followed by a period without floods. These results that had not been available for the Middle Paraná River before respond to the need for further research on the crucial role of changing hydrology in sustaining the ecosystems of large rivers.

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