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Response of fish assemblage structure to changing flood and flow pulses in a large subtropical river

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Abstract. Fish assemblages recorded from August 2010 to July 2013 in two lotic and lentic environments of the Middle Paraná River floodplain were studied in the light of flood and flow pulse variations. Three flood pulses occurred during the period of study, each with a different magnitude, duration and timing. Instead four flow pulses were recorded during this period. The varied hydrological conditions had an influence on the ichthyofauna. The fish species richness in both lentic and lotic habitat was negatively correlated with the maximum water level and fish assemblages were spatially and temporally structured according to their different reproductive strategies. Long- and short-distance migratory species were dominant after the flood pulse of the highest intensity and longest duration, whereas sedentary fish and internal fertilisation prevailed during flow pulses and lower flood pulses. Fish assemblage similarity was generally low between habitats during flood and flow pulses, but increased after those events depending on their magnitude, duration and timing. Apparently, flow pulses would also function like floods, as mechanisms of spatio-temporal structuring of fish assemblages.

Additional keywords: floodplain, ichthyofauna, Paraná River, temporal–spatial effects.

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Introduction

Several mechanisms have been mentioned so as to understand and predict the structure of communities and their spatio-temporal changes in different ecosystems, which are ranked as the most important issues in the study of community ecology (Hutchinson 1959; Gaston 2003). In this regard, the structure of fish community in a large river–floodplain system is a topic that deserves attention, considering that only limited studies have performed in this macro scale that includes highly heterogeneous and dynamic ecosystems.

Floodplains are essential components where the alternancy of seasonal periods between floods and low water play an essential role (Junk *et al.* 1989; Neiff 1990; Bayley 1995; Bunn and Arthington 2002; Junk and Wantzen 2004).

Some researchers have stated that the low-water phase (called limnophase) is as important as the flood phase (or potamophase) for the general functioning of river floodplains (Neiff 1990). During low-water phases, several aquatic bodies (i.e. floodplain lakes, swamps, abandoned channels) are separated from main river courses, giving rise to an increasing habitat heterogeneity with more diverse biotic communities and abiotic conditions (Neiff 1990; Humphries and Baldwin 2003; Agostinho *et al.* 2004*b*; Thomaz *et al.* 2007). Fish assemblage similarity decreases with increasing disconnection among floodplain habitats (Junk and Wantzen 2004). Oliveira *et al.* (2001) recorded low similarity among fish assemblages after a long period of low water and reduced connectivity. Ward *et al.* (1999) referred to this period as a ‘biological interaction phase’ because space (i.e. size and number of habitats) decreases while density of individuals and species increases. Thus, inter- and intra-specific interactions become stronger. Abiotic variables such as pH, conductivity and temperature also contribute to raise physiological stress in fish along this phase and play a critical role for juvenile survival and recruitment success (Nunn *et al.* 2007).

Hydrological connectivity increases during high-water phases and the different habitats (fluvial lakes with or without connection, canals and bogs) become more homogeneous with an increase of food and refuge resources.

Diversity of aquatic fauna, especially fish, benefits during these stages since flood phases favour their reproduction and recruitment (Junk 1999; Agostinho *et al.* 2004*a*; Thomaz *et al.* 2007). The dispersion and migration process of fish is favoured due to exchange of individuals within the hydrological system

(Michels *et al.* 2001), keeping diversity synchronism between the different habitats for the maintenance of regional diversity.

Agostinho *et al.* (2001) recorded that number of juveniles of migratory fish, such as *Prochilodus lineatus*, increased significantly in different habitats (canals, fluvial lakes and rivers) of the Upper Parana River, when large floods occurred. Thomaz *et al.* (2007) advanced the idea that floods increase biotic and environmental similarity among aquatics bodies of a river floodplain, which seems to be a frequent pattern observed in others floodplains.

Between floods and low water levels, exists water fluctuation, which apparently has an ecological relevance. Puckridge *et al.* (1998) referred to it as a low magnitude variation of the hydrometric level within the channel banks, i.e. without overflowing. Tockner *et al.* (2000) used the term 'flow pulses' to identify these hydrological events. The phenomenon is little treated in literature, so consistent data about the influence of flow pulses on the structure of aquatic communities are not available yet.

The Paraná River is a large river–floodplain system ranked ninth among the largest rivers in the world according to its mean annual discharge into the ocean (18 000 $m^3 s^{-1}$; Latrubesse 2008). In Argentina, it flows along 2000 undammed kilometres with very good water-quality conditions (Hammerly 2011). Samplings were performed at a sector of the floodplain in its middle reaches during 3 years. All the hydrological changes (flood and flow pulses of certain amplitude and low water levels) were recorded to study their influence on similarity and dissimilarity of fish assemblages associated with lentic–lotic floodplain environments. Life strategies of the different fish species were also taken into account in the study.

Materials and methods

Study area

The present study analyses fish assemblages in lotic and lentic environments of Catarata Brook, a secondary channel of the Middle Paraná floodplain located at the south of Santa Fe city (Fig. 1). This minor channel is ~50 m wide, with an average depth of 5 m, and has its origin on the left bank of the Coronda River, downward at the Salado del Norte mouth. This area of the alluvial plain has an anastomosed pattern, with an intricate lotic–lentic drainage network of high connectivity, comprising a complex mosaic of minor channels, fluvial lakes and swamps that covers a high percentage of this surface.

Two sample sites in the lotic environment were located 1.5 km apart from each other in the Catarata brook, and another two sample sites in lentic environment were placed in the closest fluvial lakes connected with the brook.

In low-water periods (August–September), most of the fluvial lakes in this area have no connection with the main channel, when the hydrological level is below 2.30 m (Paira and Drago 2007). For these habitats, the highest levels of hydrological connection occur during the flood period (February–March), when the hydrological level attains or surpasses 4.50 m. The alluvial plain is completely flooded when the hydrological level reaches 5 m (Bonetto *et al.* 1969; García and Vargas 1998).

Sampling data

At each sampling site, fish were captured in different hydrological phases two or three times a year in the 2010–2013 period (August and December 2010; April and August 2011; March, August and December 2012; April and July 2013). Gill-nets with different mesh sizes (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm between opposite knots) were used for fish surveys, totalling an area of 180.9 m^2. Gill-nets were combined in groups of three or four according to the hydrological characteristics of the sampling. These gill-nets were exposed for 24 h and checked every 8 h. The fish sampling effort was the same in each period and environment, so as to avoid any bias and compare the fish assemblages. Additionally, temperature (T, °C), conductivity (K, $\mu S\ cm^{-1}$), surface dissolved oxygen (SDO, $mg\ L^{-1}$) and secchi depth (Sec, m) were recorded at each sampling site.

Easy-to-identify specimens were processed in the field (species determination, standard length (Ls, cm) and bodyweight (Wt, g) were recorded). Other fish were preserved in 10% formalin and transferred to laboratory where they were measured and identified following fish keys of the Paraná River Basin (e.g. Ringuelet *et al.* 1967, López *et al.* 2003; Rodriguez 2005).

All fish species were classified into groups according to their migratory strategy on the basis of the existing knowledge available about the Paraná River (e.g. Bonetto *et al.* 1970; Vazzoler 1996; Bailly *et al.* 2008). This classification includes the following categories: long-distance migratory fish with external fertilisation and without parental care (LM), short-distance migratory fish with external fertilisation and without parental care (SM), sedentary fish with parental care and external fertilisation (PC) and sedentary or short-distance migratory fish with internal fertilisation and without parental care (IF).

The permission for the fish sampling was granted by Dirección General de Manejo Sustentable de los Recursos Pesqueros, dependent on the Secretaría de Medio Ambiente de la Provincia de Santa Fe, Argentina.

Variation of the hydrological regime

To understand annual changes of the hydrological regime (2010–2013) at a short-term scale, water-level data were analysed from 2008 to 2014. These data were obtained from the Secretaria de Puertos y Vías Navegables recorded at the Santa Fe Port. A level of 4.50 m at the Santa Fe port gauge was used as a reference level (bankfull) when the flow begins to flood the adjacent plain in the studied area. A level of 2.30 m at the same gauge was used as the reference disconnection level of most fluvial lakes (Drago 1980; Paira 2003). Only the hydrological variations between 3 and 4 m were considered as 'flow pulses' in the present study. Annual hydrological changes were described and measured by means of some hydrometric attributes such as days of potamophase (i.e. number of days of high water levels as from 4.5 m), days of limnophase (i.e. number of days of low water levels, below 4.5 m) and connectivity (i.e. ratio between the number of days of potamophase and the number of days of limnophase, in our case, one value for each year). Analyses were computed with the *f*FITRAS function of the PULSO software (J. J. Neiff and M. Neiff, see www.neiff.com.ar, accessed 17 March 2016), which is broadly applied to study recurring phenomena with a sigmoidal function over long periods, such as the seasonal fluctuations of water level in rivers.

Data analysis

Principal component analysis (PCA) was used to analyse the spatial and temporal environmental features and to understand

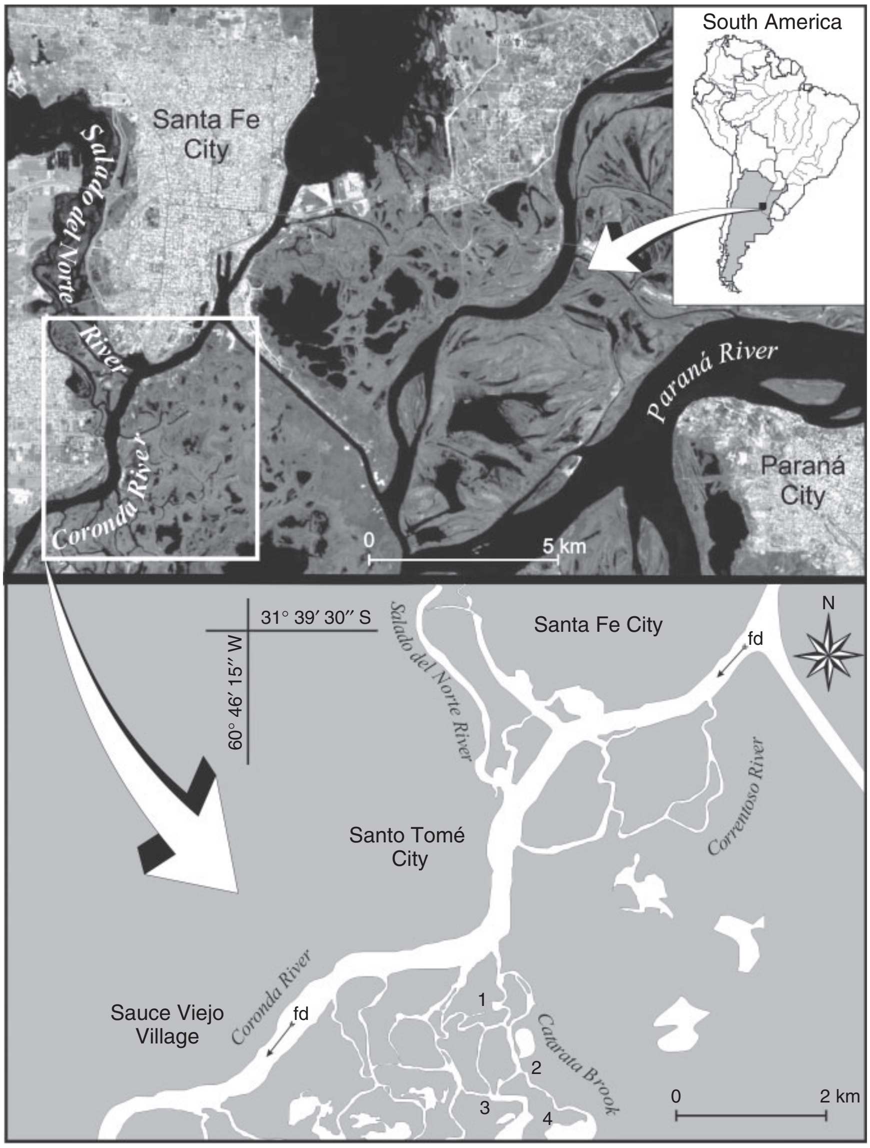

Fig. 1. Study area in the floodplain of the Paraná River, showing the sampling sites. Numbers specify type of environment: 1 and 3, lotic; 2 and 4, lentic. fd, flow direction.

the correlation pattern of the environmental variables. Axes with eigenvalues higher than 1 were retained for interpretation (Kaiser–Guttman criterion; Jackson 1993). To identify the attributes that greatly contributed to the retained axes, we conducted Pearson correlations between the scores of the PCA axis and the original data matrix. Higher correlations ($r > 0.60$) indicated the importance of an attribute over the ordination.

Fish abundance was calculated by catch per unit effort (CPUE: number of individuals per 1000 m^2 of gill-nets per 24 h), which was used to characterise fish assemblages. Species richness (number of species caught) was calculated to evaluate the temporal variation in fish assemblages that could account for patterns; a Spearman's correlation between the hydrometric levels versus species richness was also performed.

De Oliveira *et al.* (2005) recommended excluding rare species from the analysis, because it is not possible to determine whether this rarity alters the analysis and also, because rare species could underestimate pattern occurrence. Therefore, those species with less than 1% of the total CPUE (sum of the CPUE for all species, sampling sites and sampling dates) were excluded. Rare species (20) were excluded from the all (uni and multivariate) analyses, compiling a final matrix of 60 from the 80 species.

To test spatial and temporal patterns in fish assemblages, non-parametric multivariate analyses were used. The canonical analysis of principal coordinates (CAP software v1.0; Anderson 2004) was used to find spatio-temporal patterns of similarity in the structure of fish assemblage. This analysis is a constrained ordination procedure that initially calculates unconstrained principal coordinate axes, followed by canonical discriminant analysis on the principal coordinates to maximise the separation between predefined groups (Anderson and Willis 2003). CAP is

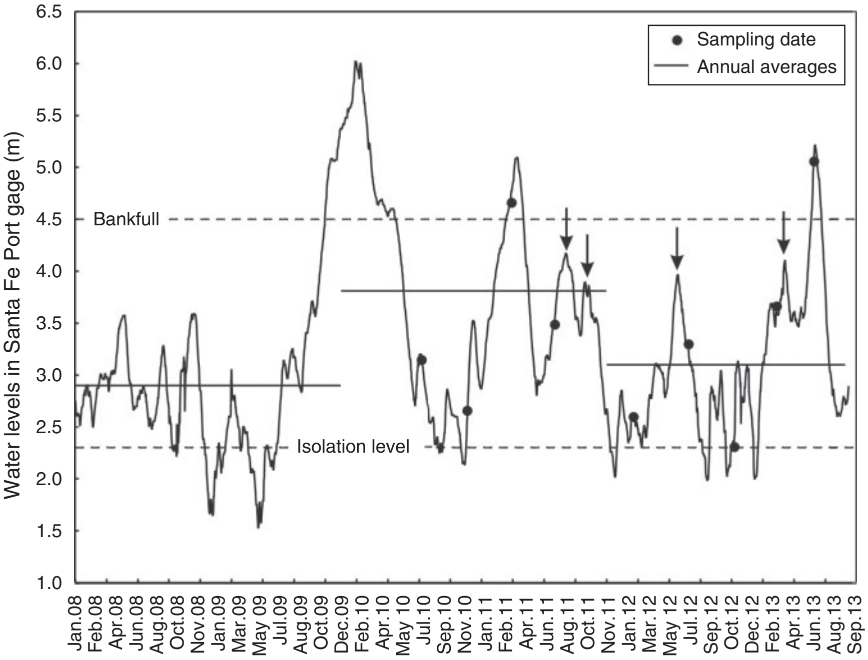

Fig. 2. Daily variations of water level between January 2008 and September 2013. Fish surveys (closed circles) started in August 2010 and finished in July 2013. Dashed lines show the threshold mean values for riverbanks overflowing (bankfull level: 4.50 m) and isolation of floodplain lakes (isolation level: 2.30 m). Horizontal full lines are annual averaged water levels in 2008–2009, 2010–2011 and 2012–2013. Arrows show periods with flow pulses in 2011, 2012 and 2013.

considered more flexible than direct canonical discriminant analysis because any dissimilarity measure can be utilised.

In addition, a two-way permutational ANOVA (PERMANOVA software v.1.6; Anderson 2001) was used to test for the abundance of fish groups per month and aquatic environments. Bray–Curtis dissimilarity index (Bray and Curtis 1957) and 999 permutations (Manly 1997) were the parameters selected in both CAP and PERMANOVA analyses.

The homogenising effect of flood pulse on fish assemblages was analysed on the basis of the dissimilarity among habitats (β diversity). On this basis, the effect of the different phases of the hydrological cycle on fish turnover between lotic and lentic environments was studied. At each sampled time, a multiple dissimilarity index was used as a measure of β diversity (Baselga 2010) so as to encompass the average rate of species replacement between sites. Accordingly, to describe spatial–temporal turnover without the influence of richness gradients, the Simpson dissimilarity index was used, as follows:

$$\beta_{\mathrm{sim}} = \frac{\left[\sum_{i<j} \min\left(b_{ij}, b_{ji}\right)\right]}{\left[\sum_i S_i - S_t\right] + \left[\sum_{i<j} \min\left(b_{ij}, b_{ji}\right)\right]}$$

where S_i is the number of species at Site i, S_t is the total number of species at all sites considered together, and b_{ij} and b_{ji} are the number of species exclusive to Sites i and j respectively. β_{sim} ranges from zero to one, with values near zero indicating the highest similarity and values near one indicating the lowest similarity.

All statistical analyses (except for multivariate ones) were performed with the R 3.1 software (R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org, accessed August 2015). For all the analyses, the statistical significance level was $P < 0.05$.

Results

During the 2008–2013 period, three flood pulses were recorded; one was extremely large and extended with respect to magnitude and duration, and two were smaller with a shorter duration (Fig. 2).

No flood pulses occurred during the 2008–2009 period; however, the hydrometric level began to rise from November 2009, reaching its highest level (6.20 m) in February 2010 and recording a total of 194 days of high water levels (above 4.5 m)., Another flood pulse was recorded in April 2011. It peaked 5.1 m, and had a duration of 47 days. Two shorter water rises (flow pulses) occurred following this flood. The first was higher than the second one (4.3 and 3.9 m respectively). No flood pulses occurred in 2012, but there was a flow pulse that did not exceed 4 m. Consequently, there were 366 days of low water and the lowest disconnection value (1.98 m) was attained during this year. At the beginning of 2013, a flow pulse rose until 4.2 m, with variations between 3 and 3.5 m. This year a new flood pulse, which was as large as that of April 2011, but with a shorter duration (29 days), occurred in July.

Two axes of the PCA were retained for interpretation, accounting for 65.1% of data variability. The first axis (PCA1) represented a temporal dynamic of connectivity

Table 1. Pearson's correlations between abiotic variables and the two first principal component axes (PCA 1 and PCA 2)

Abiotic variable	PC1	PC2
Connectivity (CON)	0.61	0.35
Hydrometric level (HL, m)	0.65	−0.23
Water temperature (T, °C)	−0.83	−0.06
Conductivity (K, μS cm^{-1})	−0.84	0.32
Transparency (Sec, m)	0.18	−0.79
Surface dissolved oxygen (SDO, mg L^{-1})	0.38	0.79

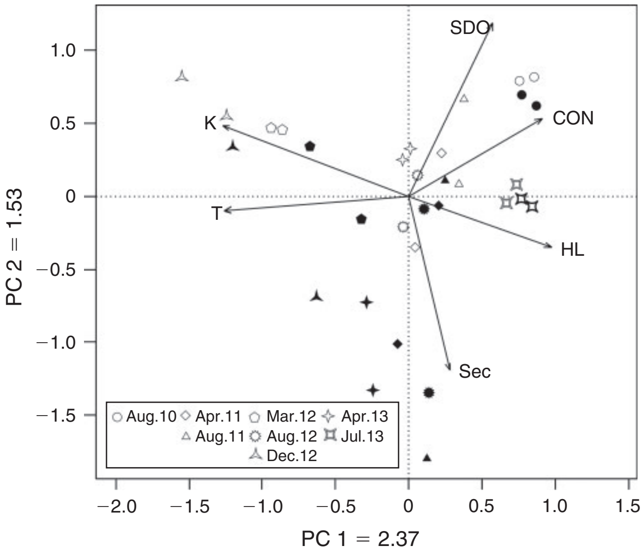

Fig. 3. Principal component analysis (PCA) of abiotic variables. Lentic environments (closed symbols); lotic environments (open symbols). Each symbol type indicates a different sampling month. HL, hydrometric level (m); CON, connectivity; T, water temperature (°C); K, conductivity (μS cm^{-1}); Sec, transparency (Secchi disc) (m); SDO, surface dissolved oxygen (mg L^{-1}). No abiotic data were obtained in December 2010 because of equipment malfunction.

(Con), hydrometric level (HL, m), temperature (T, °C) and conductivity (K, μS cm^{-1}) (Table 1, Fig. 3). The first two variables were positively correlated with the periods of August 2010 and July 2013 respectively, both in lotic and lentic environments. There was a great connectivity in 2010 because of the flood pulse, which was not only long (194 days), but higher (6.20 m) as well. The hydrometric level correlated significantly with the pulse that occurred in July 2013 in both types of environments, whereas temperature and conductivity correlated positively with March and December 2012 in those habitats. Furthermore, no flood pulses were recorded for that year, although there was an increase in the hydrometric level, which reached almost 4-m height. The second axis (PCA2) followed a temporal dynamic of SDO and transparency. Oxygen correlated positively with both lotic and lentic environments in 2010. Although fluvial lakes presented a negative correlation, they showed a tendency of increasing transparency values during low waters rather than in lotic environments (Table 1, Fig. 3).

Fish assemblage

In total, of 4585 fish belonging to 60 species of 23 families and six orders were caught (Table 2). Characiformes ($n = 29$ species) and Siluriformes ($n = 31$) dominated in species richness. However, Characiformes largely dominated in the number of individuals, accounting for 75 % of total abundance. *Prochilodus lineatus* was the most abundant species ($n = 1412$), accounting for 25.18 % of the total abundance. Other species, such as *Leporinus obtusidens*, *Schizodon platae* and *Hoplias malabaricus*, reached or surpassed 300 individuals in abundance. Species richness was correlated with hydrometric levels and was lower during periods of high water levels in both lotic ($r_s = -0.54$, $P = 0.02$) and lentic habitats ($r_s = -0.052$, $P = 0.03$; Fig. 4).

Spatio-temporal variation of fish assemblages

Canonical analysis of principal coordinates (CAP) showed significant spatio-temporal differences ($\mathrm{tr}(Qm'HQm) = 6.55$, $P = 0.001$) for the structure of fish assemblages in the Middle Paraná River floodplain. There was a significant interaction between months and habitat type (PERMANOVA, $F = 1.69$, $P = 0.001$). This interaction was characterised by high similarity in fish structure between lotic and lentic environments during low-water periods (December 2010, March 2012, August 2012 and December 2012). Even though the same species were present in lentic habitat and lotic environment even during flood pulses (April 2011 and July 2013) and a flow pulse (April 2013); however, the structure of the lotic environment was different from that of lentic environment during high-water periods (April 2011 and July 2013) as well as during the flow pulse of April 2013 (Fig. 5).

In August 2010 (after the first flood pulse of high intensity and amplitude), the structure was similar among fish assemblages in both environments. However, after the flood pulses of low intensity and short duration of April 2011 and July 2013, even if the two lotic habitats were similar, the composition was different between lotic and lentic sites. In short, in contrast to August 2010, the similarity in April 2011 and July 2013 was low between the environments. As shown in Fig. 5, species composition in lotic sites is similar during periods of floods (April 2011, July 2013) and during the water rise of April 2013; patterns of similarity during periods of high water seem to show the same trend. However, species composition in lotic sites was different during the descending phase of the flow pulse, which took place in August 2012, but the similarity of the lentic environments increased during the low-water period.

It is important to highlight that the short-distance migrants (*C vog*, *C pla*, *P val*, *S pla*, *S bor*, *C arg*, *A asu* and *T nem*; see Table 2 for explanation of abbreviations) and the long-distance migrants (*P lin, L obt, S bra, B orb, P mac, R vul, P cor, P alb* and *O kne*) were dominant in both environments only after the flood pulse of high intensity and duration. In contrast, the parental-care species (*L sim*, *L apl*), and internal-fertilisation species (*A nig, A ost* and *A mil*) were dominant in the lotic environment during high water levels and during the flow pulse of April 2013. Other less-abundant species of the short-distance migrants and parental-care groups were dominant during months of low water levels, both in lotic and lentic environments.

Table 2. Abundance of 60 fish species caught in lotic and lentic habitats of the Paraná River floodplain from August 2010 to July 2013

Species name abbreviations (see Fig. 5), capture per unit effort (CPUE) and reproductive strategy (RS) are shown. Categories of reproductive strategy (RS): LM, long-distance migratory fish with external fertilisation and without parental care; SM, short-distance migratory fish with external fertilisation and without parental care; PC, sedentary fish with parental care and external fertilisation; and IF, sedentary or short-distance migratory fish with internal fertilisation and without parental care

Order, family, species, author	Name abbreviation	CPUE	RS
Characiformes			
Acestrorynchidae			
Acestrorhynchus pantaneiro (Menezes, 1992)	*A pan*	558.32	SM
Anostomidae			
Leporinus obtusidens (Valenciennes, 1837)	*L obt*	2448.87	LM
Schizodon borellii (Boulenger, 1900)	*S bor*	403.54	SM
Schizodon platae (Garman, 1890)	*S pla*	1592.04	SM
Characidae			
Astyanax abramis (Jenyns, 1842)	*A bra*	1011.61	SM
Astyanax asuncionensis (Géry, 1972)	*A asu*	447.76	SM
Astyanax rutilus (Jenyns, 1842)	*A rut*	105.03	SM
Charax stenopterus (Cope, 1894)	*C ste*	16.58	SM
Roeboides microlepis (Reinhardt, 1851)	*R mic*	11.06	SM
Salminus brasiliensis (Cuvier, 1816)	*S bra*	873.41	LM
Cynopotamus argenteus (Valenciennes, 1836)	*C arg*	370.37	SM
Astyanax erythropterus (Holmberg, 1891)	*A ery*	16.58	SM
Galeocharax humeralis (Valenciennes, 1834)	*G hum*	11.06	SM
Triportheidae			
Triportheus nematurus (Kner, 1858)	*T nem*	44.22	SM
Triportheus paranensis (Günther, 1874)	*T par*	11.06	SM
Bryconidae			
Brycon orbignyanus (Valenciennes, 1850)	*B org*	60.81	LM
Curimatidae			
Cyphocharax platanus (Günther, 1880)	*C pla*	1238.25	SM
Cyphocharax spilotus (Vari, 1987)	*S spi*	60.81	SM
Cyphocharax voga (Hensel, 1870)	*C vog*	685.46	SM
Potamorhina squamoralevis (Braga & Azpelicueta, 1983)	*P squ*	16.58	SM
Steindachnerina brevipinna (Eigenmann & Eigenmann 1889)	*S bre*	11.06	SM
Cynodontidae			
Rhaphiodon vulpinus (Spix & Agassiz 1829)	*R vul*	248.76	LM
Erythrinidae			
Hoplias malabaricus (Bloch, 1794)	*H mal*	1597.57	PC
Prochilodontidae			
Prochilodus lineatus (Valenciennes, 1837)	*P lin*	6965.17	LM
Gasteropelecidae			
Thoracocharax stellatus (Kner, 1858)	*T ste*	11.06	PC
Serrasalmidae			
Mylossoma duriventre (Cuvier, 1818)	*M dur*	16.58	SM
Pygocentrus nattereri (Kner, 1858)	*P nat*	182.42	PC
Serrasalmus maculatus (Kner, 1858)	*S mac*	326.15	PC
Serrasalmus marginatus (Valenciennes, 1837)	*S mar*	187.95	PC
Siluriformes			
Heptapteridae			
Pimelodella gracilis (Valenciennes, 1835)	*P grc*	16.58	SM
Pimelodidae			
Luciopimelodus pati (Valenciennes, 1835)	*L pat*	11.06	LM
Parapimelodus valenciennis (Lüken, 1874)	*P val*	221.12	SM
Pimelodus albicans (Valenciennes, 1840)	*P alb*	22.11	LM
Pimelodus maculatus (Lacepède, 1803)	*P mac*	724.16	LM
Pseudoplatystoma corruscans (Spix & Agassiz 1829)	*P cor*	77.39	LM
Auchenipteridae			
Ageneiosus inermis (Linnaeus, 1766)	*A ine*	49.75	IF

(*Continued*)

Table 2. (Continued)

Order, family, species, author	Name abbreviation	CPUE	RS
Ageneiosus militaris (Valenciennes, 1835)	*A mil*	105.03	IF
Auchenipterus nigripinnis (Boulenger, 1895)	*A nig*	99.50	IF
Auchenipterus osteomystax (Miranda-Ribeiro, 1918)	*A ost*	27.64	IF
Trachelyopterus lucenai (Pezzi da Silva & Pereira 1995)	*T luc*	320.62	IF
Trachelyopterus striatulus (Steindachner, 1877)	*T str*	983.97	IF
Loricariidae			
Hypostomus commersoni (Valenciennes, 1836)	*H com*	403.54	PC
Loricaria apeltogaster Boulenger, 1895	*L ape*	16.58	PC
Loricaria simillima (Regan, 1904)	*L sim*	77.39	PC
Loricariichthys anus (Valenciennes, 1835)	*L anu*	110.56	PC
Loricariichthys melanocheilus (Reis & Pereira, 2000)	*L mel*	281.92	PC
Loricariichthys platymetopon (Isbrücker & Nijssen, 1979)	*L pla*	950.80	PC
Paraloricaria agastor (Isbrücker, 1979)	*P aga*	154.78	PC
Pterygoplichthys anisitsi (Eigenmann & Kennedy, 1903)	*P ani*	127.14	PC
Ricola macrops (Regan, 1904)	*R mac*	88.45	PC
Doradidae			
Oxydoras kneri (Bleeker, 1862)	*O kne*	22.11	LM
Pterodoras granulosus (Valenciennes, 1821)	*P gra*	370.37	LM
Callichthyidae			
Hoplosternum littorale (Hancock, 1828)	*H lit*	121.61	PC
Perciformes			
Sciaenidae			
Pachyurus bonariensis (Steindachner, 1879)	*P bon*	99.50	SM
Crenicichla lepidota (Heckel, 1840)	*C lep*	110.56	PC
Crenicichla vittata (Heckel, 1840)	*C vit*	11.06	PC
Atheriniformes			
Atherinopsidae			
Odontesthes bonariensis (Valenciennes, 1835)	*O bon*	33.17	SM
Clupeiformes			
Pristigasteridae			
Pellona flavipinis (Valenciennes, 1836)	*P fla*	77.39	SM
Engraulidae			
Lycengraulis grossidens (Agassiz, 1829)	*L gro*	60.81	LM
Gymnotiformes			
Sternopygidae			
Eigenmannia trilineata López & Castello, 1966	*E tri*	55.28	SM

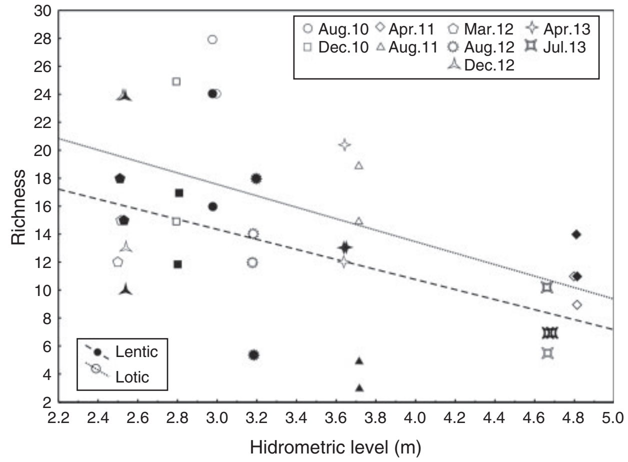

Fig. 4. Correlation between fish species richness and water level during the sampling period. Lentic habitat (closed symbols); lotic habitat (open symbols).

In general, β diversity values for fish assemblages in lotic–lentic habitats of the Middle Paraná followed the pattern of water-level fluctuations (Fig. 6). During floods (April 2011, July 2013) and the flow pulse of April 2013, values of β diversity were higher, showing a low similarity of species between both habitat types. After the flood pulses (August 2010, December 2010, August 2011), values β of diversity were low, showing a high assemblage similarity between the habitats. Before and after the flow pulse (March 2012, December 2012), values of β diversity were lower than those of the descending phase of this hydrologic event (August 2012). We also note that the species turnover in 2012 was not so intense as when flood pulses occurred.

Discussion

It is well known that the interaction of water levels with the river landscapes largely controls the degree of spatial heterogeneity between the different environments of a floodplain. Similarities among aquatic habitats increase during floods in these ecosystem

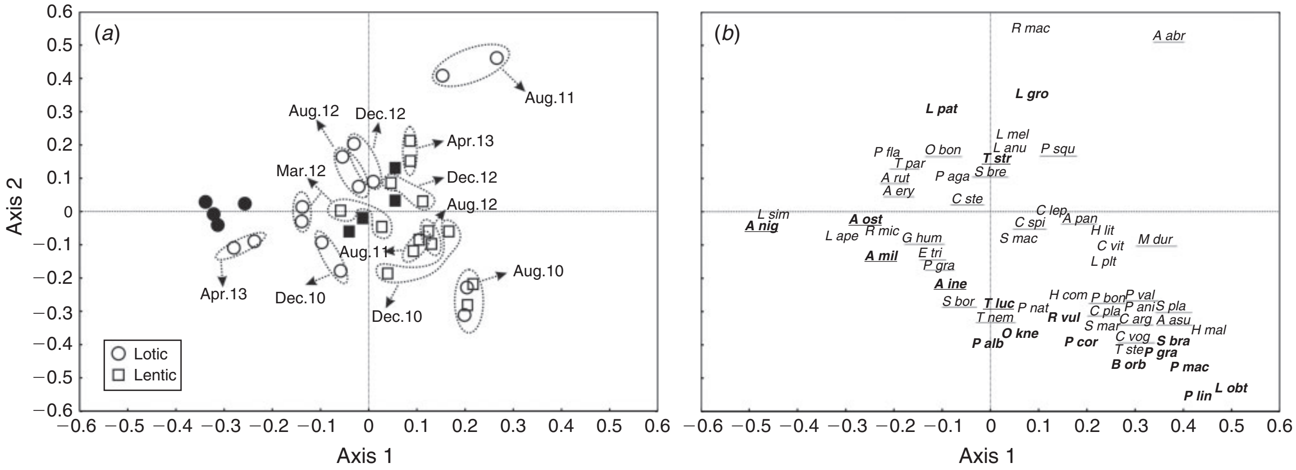

Fig. 5. Spatio-temporal variation of fish assemblages structure in lotic and lentic environments of the Middle Paraná River floodplain during the studied 2010–2013 period. (*a*) Lotic and lentic habitat: high-water levels (closed symbols); low-water levels (open symbols). (*b*) Species structure: short-distance migratory fish (SM, underlined and italic); long-distance migratory fish (LM, bold and italic); internal fertilisation (IF, bold, underlined and italic); parental care (PC, italic). See Table 2 for fish species abbreviations.

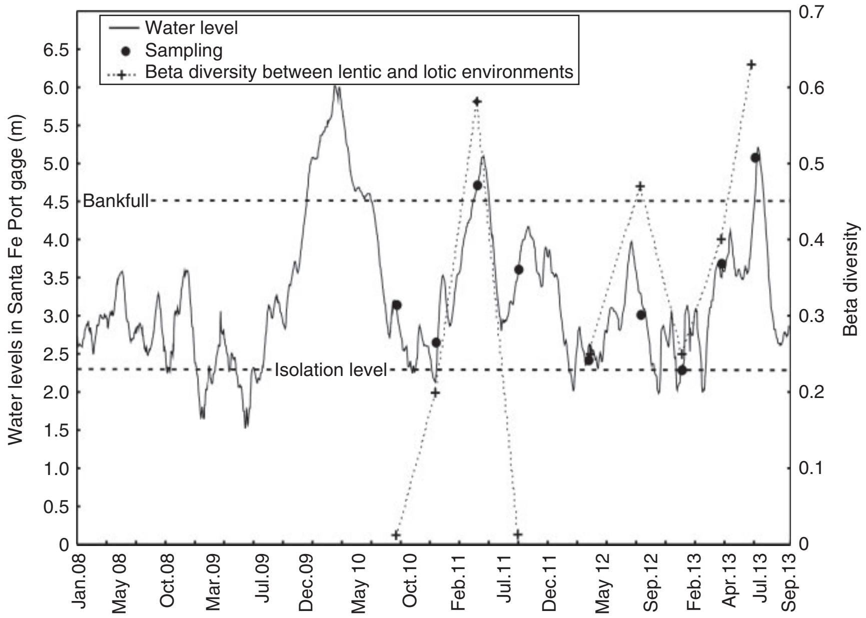

Fig. 6. Temporal change in β diversity of fish assemblages between lotic and lentic habitats in the Middle Paraná River floodplain during 2010–2013. Dotted line shows the variation in the β diversity tendency, according to the hydrological fluctuations.

types (Escalera-Vázquez and Zambrano 2010). Thus, more homogeneous fish assemblages between lotic and lentic environments would be expected after a large flood (Depetris 2007), such as the one in August 2010. This homogeneity was first described as a high similarity in physical, chemical or biological features between the main river and the fluvial lakes of its floodplain (e.g. Junk and Furch 1985, in the Amazonian floodplain; Hamilton and Lewis 1990, in the Orinoco River floodplain; Bozelli 1992, in the Trombetas River floodplain and Scarabotti *et al.* 2011, in the Parana River floodplain). Amoros and Bornette (2002) remarked that changes in fish assemblage cannot be produced only by the effects of chemical and physical water variables and biotic factors, but also by the variation of the hydrological attributes.

Thomaz *et al.* (1997) and Agostinho *et al.* (2000) were the first to recognise and quantify the 'homogenisation effect of floods' on fish assemblages in the Upper Paraná River floodplain. This finding was further confirmed by Agostinho *et al.* (2001) and Fernandes *et al.* (2009). Thomaz *et al.* (2007) advanced the concept by recognising that the seasonal dynamics of hydrometric levels work as a regional factor that increases physical, chemical and biological similarities in floodplains 'after' a high-water period.

In Argentina, the responses of fish assemblages to hydrological variations are barely known. Our results showed that the concept of the homogenisation effect of floods could be also extended to the Paraná River floodplain in its middle reach. However, our findings about habitat homogeneity were not exactly similar to those obtained in previous studies. Data showed that similarity in fish structure between lotic and lentic habitats increased noticeably not only after each flood, but also after each flow pulse. Apparently the increment depended on the characteristics of the flood and flow pulses. This was evident when the 2011–2013 flow pulses were compared with the 2010, 2011 and 2013 floods. Two of the flow pulses occurred in winter and spring 2011 and the third in winter 2012, lasting ~77 days with water levels ranging between 3 and 4 m. The fourth one peaked in autumn 2013 (see Fig. 2). The homogenisation effect between lotic and lentic environments was recorded during low-water periods, a time lapse after flood and flow pulses in all cases (see Figs 5, 6). Although not included in Fig. 6, the β diversity decreased (0.34) in December 2013, after the winter flood of that year. Thomaz *et al.* (2007) called this delay a 'time lag', which will depend, among other factors, on the intensity of the drought when the water level decreases, and on the species composition of the assemblages during the previous high-water period. With rising waters, the lag will depend on the intensity of floods and on the dispersion and migration rate of the different species.

Homogeneity and heterogeneity of aquatic habitats implies a spatial turnover of species, i.e. species replacement among different habitats, as a result of environment restructuring or spatial restrictions such as temporal disconnection between lotic and lentic environments (Gaston *et al.* 2007). According to our results, species turnover would be small during low-water periods after flood and flow pulses (Fig. 6). In contrast, high waters would be associated to varied levels of species interchanges between lotic and lentic habitats. The consequence would be an increasing turnover, prompting heterogeneity of habitats as water levels rise. The opposite would occur as water levels diminish because homogeneity increases, but with a certain delay depending on the peak levels. The result would be lower β diversities among habitats, with minimum values that would depend on attributes of the previous flood and flow pulses. Apparently, floods give rise to larger homogeneities than do flow pulses, according to data in Fig. 6.

Many environmental factors, such as temperature, hydrological connectivity and flood-pulse amplitude influence fish reproduction in river–floodplain systems. The last two closely linked variables are key factors (Gomes and Agostinho 1997) that facilitate the access to nurseries for rearing fish (Humphries *et al.* 1999; Janáč *et al.* 2010), thus favouring reproduction success and recruitment (Lytle and Poff 2004; Bailly *et al.* 2008; Nabout *et al.* 2009).

Agostinho *et al.* (2004*a*), Fernandes *et al.* (2009) and Suzuki *et al.* (2009) found the greatest fish richness, abundance and recruitment success in the Upper Paraná River floodplain, also after a very high-water phase that remained more than 50 consecutive days above the overflowing level. Agreeing with these authors, our study showed that the most abundant catch and the high fish species richness, recorded at both lentic and lotic habitats occurred in August 2010. This was after the largest flood (maximum level: 6.20 m; duration: 194 days above bankfull level) occurred during the spring of 2009 and the summer–autumn of 2010. A similar pattern was found in August 2011 (after the lower pulse of April 2011), although richness values were comparatively lower (see more details in Abrial *et al.* 2014).

Richness decreased in April 2011 and July 2013 during the high-water phase in both lentic and lotic habitats. These findings showed that the flood regime would increase the chance of species dispersion and would decrease richness, as also reported by Tablado *et al.* (1988) and Oldani (1990). Studies conducted in other river basins (Cinaruco River in Venezuela) have attained similar results (Arrington and Winemiller 2006).

Segregation patterns exist in the particular case of freshwater fish (de Oliveira *et al.* 2005), including functional groups such as the trophic or reproductive ones (Hoeinghaus *et al.* 2007). Fig. 5*a, b* shows that LM and SM species were dominant in August 2010 at both habitats, after the largest flood pulse in spring–summer. This result is not surprising because this type of hydrologic event in the adequate season triggers reproduction peaks of these two fish groups; the association between reproduction and the beginning of an increase in the hydrometric levels appears to be a common pattern (Paugy 2002; Agostinho *et al.* 2004*a*, 2004*b*). When the period of rising water begins in early November–December, mature SM start a lateral migration from the fluvial lakes up to the rivers, apparently related to spawning (Fernandes 1997), whereas LM species initiate large migrations (Godoy 1975; Bonetto *et al.* 1969; Agostinho *et al.* 2004*a*; Suzuki *et al.* 2009) to favourable zones for spawning.

The dominant species changed during the flood pulses of low intensity and short duration of April 2011 and July 2013 because PC and IF species prevailed. The same occurred with the flow pulses of August 2012 and April 2013. The results of the samplings of March 2012 and December 2012, after the flow pulses of September 2011 and August 2012, were similar, although some SM species may have also been associated with them.

In brief, and viewing the results of Fig. 5 as a whole, PC and IF species are little influenced by the hydrologic regime (flood and flow pulses of diverse attributes), as observed by Agostinho *et al.* (2004*a*, *b*). In contrast, SM and LM species are strongly associated with a flood pulse of proper intensity, duration and timing. Timing would be especially crucial for LM species, which need the rising of water levels at late spring in the Paraná River system, to begin their large migrations to the reproduction zones. Apparently, some SM species are also associated with flood and flow pulses despite their seasonality.

Conclusions

It is widely known that climatic seasonality, together with the characteristics of hydrometric-level fluctuations (amplitude, duration and timing), enables a differentiation of the fish assemblage structure in lotic as well as lentic environments (Junk and Wantzen 2004; Dudgeon *et al.* 2006).

Our results seem to show that, depending on the flood and flow pulse attributes, the structuring processes would vary according to the habitat type. Apparently, spatial and temporal variation of fish structure is more evident in lotic than in lentic environment.

It's important to remark that 'flow pulses', i.e. the water-level variations of certain magnitude (above 3.5 m) but below the bankfull level, would have a visible influence on the homogenisation of channels and the nearby floodplain habitats (Fig. 6). The similarities were high, with a certain lag depending on the peak water levels similar to what occurred with floods. High similarities after flood and flow pulses occurred with continuous diminutions of the water level, till near the isolation level. This result implies that flow pulses in river–floodplain ecosystems would function as mechanisms of spatial and temporal structuring of fish assemblages, which was previously attributed only to flood pulses. Their importance for the different species is not clear from the data of the present study (see Fig. 5).

It's clear that the conditions that trigger interchanges between habitats and their direction for the different species are all issues that still need more investigation. Sampling is required in lotic and lentic habitats with different degrees of connectivity and encompassing additional hydrological years with flood and flow pulses of diverse amplitude, duration and timing, so as to contextualise the findings of the present study.

In the light of the results presented herein, and those of the earlier work, hydrology and temperature would be overriding regional factors driving the structuring the fish assemblages in the middle reaches of the Paraná River, one of the largest river–floodplain systems in the world. Seasonality could be considered as a invariant factor compared with hydrology, characterised by highly variable fluctuations where stochastic phenomena play a crucial role, as suggested by Wu (1999). This last feature acquired particular relevance in the context of the present study, because flood and flow pulses of diverse magnitude (peak level and duration) and timing took place along the 3 years of sampling. Only one flood pulse conformed with the average regimen of the Paraná River in its middle reach, to which aquatic biota (fish community in this case) is adapted. Other important environmental variables influencing segregation and structure of fish community, as well as connectivity, are also closely dependent on hydrology.

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