Master Sciences de la Terre, de l'Eau et de l'Environnement

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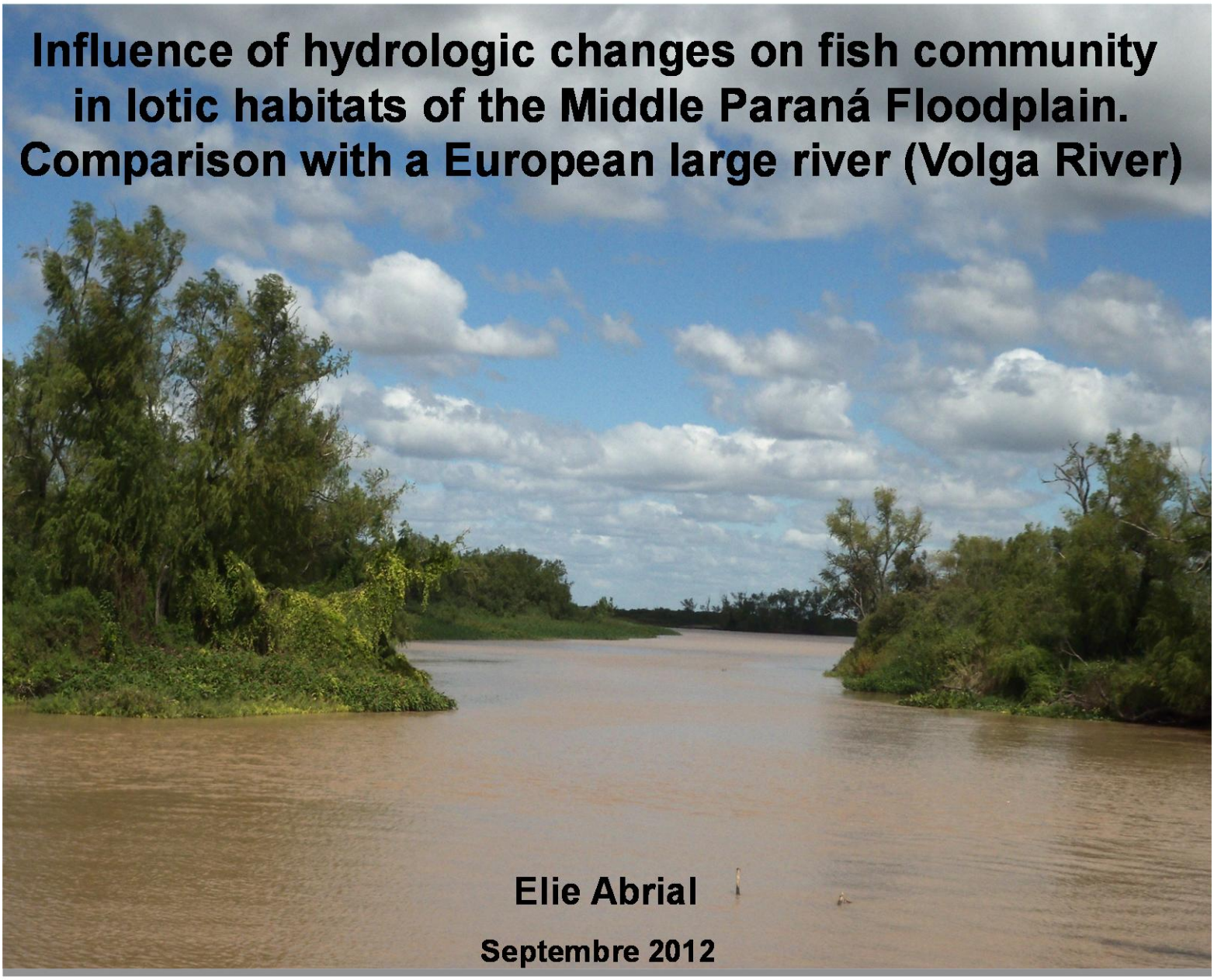
Rapport de stage pour l'obtention de la 2ème année de Master

Influence of hydrologic changes on fish community in lotic habitats of the Middle Paraná Floodplain. Comparison with a European large river (Volga River)



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Acknowledgments

Muchas gracias a ustedes, amigos del INALI.

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Y ojalá que esta experiencia es el comienzo de una historia que se va a seguir en el tiempo.

Summary

Spatial and temporal variations in diversity (species richness) and abundance (indexed by the capture per unit effort - CPUE) of fish into a circular meander pool and a confluence scour hole located in the floodplain of the Middle Paraná River are analyzed from 2009 to 2012. The relationships of these ecological attributes with alternations of floods and dry periods are evaluated. Annual variations of the hydrologic regime are known on the base of hydrometric levels recorded in the Santa Fe Port gauge (data supplied by the National Directorate of Waterways of Argentina). Canonical analysis on the principal coordinates based on any symmetric distance matrix is applied to determine eventual significant differences of spatial and temporal repartition of fish community between both environments. Analyses of variance enable to study relationships of three groups of species (sedentary, short and long-distance migratory fish) with the hydrologic regime.

No significant difference exists between the fish community recorded in the circular meander pool and the confluence scour hole but significant variations occur along time at the different stages of the hydrologic regime. The differences are associated to the changes in timing, duration and magnitude of floods of the floodplain. Diversity and abundance of long-distance migrants are closely related to the major pulse whereas short-distance migratory fish show a lower dependence to floods and seem to have distinct responses according to the kind of species. Sedentary fish also react positively to floods and seem to show a better persistence in abundance and diversity than for the migratory fish after inundations of the alluvial plain. The comparative study with the Volga-Akhtuba floodplain supports various conclusions enounced in this work and confirms that the integrity of the annual flood pulse is primordial for fish recruitment in floodplains, either in temperate or subtropical zone.

Preamble

The Paraná River is the second longest of South America after the Amazon River. It is among these mega-rivers of the world draining gigantesque areas in which inhabits a multitude of animals and plants either terrestrial or aquatic. Those large rivers present generally flat or nearly flat extended areas – known as floodplains – along their middle and lower courses periodically inundated by floods. The alternation of drought and inundation is crucial in those environments and generates highly rich ecosystems both in quantity and diversity.

Along its middle reach, the Paraná River builds a large floodplain forming a labyrinth of minor channels and lakes almost permanently connected. In 1999, some investigators of the INALI – National Institute of Limnology based in Santa Fe City – have observed with echo sounder a high density of fish in the deeper parts of those channels, located in confluences or in meander curves. Those particular geomorphological formations originated by erosion processes are known as scour holes. The comportment of fish is relatively well known in subtropical floodplains but it is not the case of those particular sites. The INALI has therefore established a Project of Investigation Pluri-annual (PIP 2010-2012) to study the eventual influence of scour holes on fish communities.

The present study responds to one of the specific objectives of the PIP 2010-2012 project. It analyzes the spatiotemporal variation of fish assemblages in a circular meander pool and a confluence scour hole located within the alluvial plain of the middle part of the Paraná River south of Santa Fe City. Fish community is analyzed as a whole and by group of species showing similar comportments of reproduction and migration. The aim of the present study is to analyze the possible distinct comportment of fish in those particular sites. To respond to the objective, the variations of water levels have been studied and associated with changes in fish population, confronted with existing knowledge on large floodplains and specifically compared with analyses of fish community done in the Volga River floodplain (Russia).

Analyses on the field

The field investigations were led twice a year from 2009 to 2012 in the two selected sites in periods of high and low water level. Fish are captured using gillnets of different mesh size

during 24 h in the two environments. Easy-to-identify specimens are processed on the field. They are measured and weighed, the species level is checked and sex and maturate state is identified. The other fish are preserved in 10% formalin and transported to laboratory and determined following the available keys for fish of the Paraná River basin. The water Temperature, concentration in oxygen, pH and conductivity are measured in each patch to characterize environmental quality.

Results and discussion

Analysis of the hydrological regime

The analysis of the hydrological regime shows distinct mean water levels. A long-dry period occurred until the end of 2009, then followed a period of higher waters with two floods: the first one happened in summer-autumn 2010 and is characterized by a long duration and high magnitude. The second one occurred at the beginning of autumn 2011 and presents lower intensity and duration.

Spatial and temporal repartition of fish community

Fish community is firstly analyzed without distinction of strategies of reproduction and migration of species. The results do not show significant differences of the spatial repartition of fish assemblages within the circular meander pool and the confluence scour hole. It is mainly explained by the short distance of 1,600 m between the two sites permanently connected, thus no distinction between both environments are done in the following analyses.

Significant differences in temporal repartition of fish assemblages exist and are principally correlated with the influence of flood regime. With alternating periods of flood and drought, it is indeed recognized as the most important environmental factor in fish community structuring river-floodplain systems.

The highest abundances and diversities were observed in 2010 and are associated with the first flood carrying really good conditions for fish communities as well as for the reproduction of genitors, the development of larvae and the juvenile growth. Lower

abundances and diversities were described in August 2011, in comparison to the sampling of August 2010. It is associated with the minor duration and intensity of the second flood inducing lower connectivity between habitats in the alluvial plain and likewise with its occurrence at the beginning of autumn, which does not coincide with the high water temperatures. Consequently, that leads to conditions of reproduction and enlargement not as good as those of the first flood. Low values of abundance and diversity of fish species were recorded at the end of a long-dry period and when the inundation of the alluvial plain does not occur during the preceding summer-autumn season. It is explained by the negative effect of the lack of flood on fish populations.

Temporal repartition of fish species with distinct strategies of migration and reproduction

The long-distance migratory fish show a close dependence on the characteristics of flood regime in both the sites studied. High diversity and abundance were observed after the first flood, yet not after the second and even less in period of low water level. Those temporal differences in abundance and diversity are associated with the strategy of reproduction of those fish species. They principally need long duration of floods that must coincide to the temperature and to the time of spawning which occurs in summer-autumn.

The short-distance migratory fish demonstrate a lower dependence on the flood characteristics. No significant difference in abundance and diversity were observed after each flood. However, the features of floods appear to have a distinct influence according to the species. Some species seem to be affected by delayed floods of minor intensity and duration whereas others are found for each period. The heterogeneity of that group could explain why it is difficult to define common pattern related to flood regime. Species respond differently to the characteristics of flood and some of them have very distinct period of reproduction. Consequently, an analysis per species or genus should give more relevant results on the comportment of short-distant migratory fish under the influence of the hydrological variations.

The sedentary species show a significant increment in abundance and diversity after the first flood pulse – clearly revealing its positive influence. However, no significant difference in fish abundance has been found between the two floods, but higher abundances and species

richness were recorded after the major inundation of the alluvial plain. We would conclude that better conditions for the survival of juvenile forms occurred after the flood of higher magnitude and longer duration but sedentary fish do not present a dependence on flood as clear as long-distance migratory species. Moreover, a persistence of those species after floods has occurred but differs compared to the migratory species which decreased after the water went down. It is mainly associated with the sedentary strategy that does not imply significant displacements within the Middle Paraná floodplain.

Conclusion

The circular meander pool and the confluence scour hole do not present significant difference of fish abundance and richness species, but significant temporal differences occur along the period studied from 2009 to 2012 in the two lotic environments of the Middle Paraná floodplain.

The long-lasting pulse of major extent and coinciding with high temperatures has conduced to the highest abundances and diversities of fish. The delayed pulse of minor magnitude and duration does not present the same positive effect on fish recruitment; both of fish abundance and species richness are lower. In floodless years, the fish population is considerably reduced.

The influence of floods varies according to the reproductive strategy of fish species. Long-distance migrants are closely dependent to the flood pulse of major extent occurring in summer; short-distance migratory fish show a lower dependence to the characteristics of floods and seem to have distinct responses according to the kind of species; sedentary fish depend equally to floods and demonstrate a better persistence in abundance and diversity during the low water levels following the inundation of the alluvial plain.

In spite of the differences in migrations between species of the Paraná River and the Volga River, the comparative study supports various conclusions enounced in this work and confirms that the integrity of annual flood pulses, considering its timing, duration and magnitude, is very important for fish recruitment in floodplains, either in temperate or subtropical zone.

Contents

Introduction

The hydrological regime, with alternating periods of floods and droughts, is the most important environmental factor in the functioning of river-floodplain systems (Lowe McConnell, 1987; Junk et al., 1989; Neiff, 1990; Winemiller, 1996). Seasonal flooding increases the connectivity among water bodies, allowing: changes in limnological characteristics, balance of production and respiration processes, patterns of nutrient cycling (Thomaz et al., 2004), structuring of the aquatic communities (Junk, 1980) and increase in availability of food resources for aquatic communities. In brief, the flood pulses are highly important for the integrity of the floodplains (Junk, 1980; Lowe-McConnell, 1999).

Regarding fish, implicit relationships correlating hydrological and biological parameters are well known in large tropical and subtropical rivers (Junk et al., 1989; Machado-Allison, 1990; Vazzoler, 1996). Fish disassemblage and reassemblage may occur in a few days as a response to rapid water fluctuations (Arrington et al., 2005), reproductive strategy is closely related to the fluctuations of the hydrometric level for many species (Godoy, 1975; Gomes and Agostinho, 1997; Fernandes, 1997) and floods appear to affect the reproduction and recruitment of species of different reproductive strategies in various ways (Agostinho et al., 2004; Bailly et al., 2008). The dependence on floods of long-distance migrants for reproduction has been clearly observed (Godoy, 1975; Bonetto, 1971; Agostinho et al., 2004, Suzuki et al., 2009). However the dependence on water level variations of species doing short migration or not migrating at all is not as clear as for large migrators (Agostinho et al., 2003; Bailly et al., 2008). Different species can respond to distinct flow variables (Lamouroux & Souchon, 2002) because of their preferences for specific physical variables of a given environment (Lamouroux et al., 1999) such as depth, flow hydrodynamic features and connections with the nearby wetlands (Moyle and Baltz, 1985).

According to studies performed in the middle reach of the Paraná River, migrations of fish are observed between lentic and lotic environments when floods overflow the alluvial valley, and mortalities are associated to the frequent complete drying up of floodplain ponds during low water levels (Bonetto et al., 1969). Precise descriptions of the up and downstream movements using the technique of tagging for two large migrators – *Salminus brasiliensis* and *Prochilodus lineatus* – have been recorded in different branches and main tributaries of

the middle and lower reaches of the Paraná River basin (Bonetto et al., 1971). Transversal migrations of fish have been related to physical variables such as water temperature and variation of connectivity between lentic and lotic environments of the alluvial plain (Cordiviola de Yuan et al., 1984; Tablado et al., 1988). In the late 90s, high concentrations of fish have been identified in different type of scour holes (meander, confluence and levee toe) in the floodplain of the Paraná River (Drago et al., 1999). Espínola et al. (unpublished) report larger densities of fish at those holes during "normal" periods of flood pulses than during "long" periods of very low water levels. The 10 years long periods differ each in the magnitude and frequency of floods. The difference was associated to climate fluctuations.

Though the role of hydrological variations that drive life history of fish is relatively well understood in lotic-lentic habitats of large tropical and subtropical rivers – including the Paraná River –, studies associating fish assemblages with morphological units as confluence and meander scour holes of large floodplain secondary channels are not common. To the author's knowledge, only Poddubnyi et al. (1981) report data recorded in the main channel of the Paraná River concerning certain species that linger a rather long time around the deep slopes of the bottom areas.

This study was performed at the National Institute of Limnology (INALI, Santa Fe, Argentina). Created in 1962 by the National Council of Scientific and Technical Investigations (CONICET), it is the most ancient institute of investigation of Argentina. Investigations on the continental aquatic ecosystems of Argentina regarding the biodiversity of invertebrates and vertebrates are currently performed at the Institute. Topics related with physical and chemical limnology, bacteriology, phytoplankton, zooplankton, zoobenthos, communities associated with aquatic vegetation, fish, amphibious, reptiles and birds are investigated in a number of projects. Nearly all of them focus in the study of the Paraná River and its alluvial plain, though other natural areas of the Neotropical region contaminated by the anthropogenic action are also of interest with objectives of management and conservation of biodiversity.

The project PIP 2010-2012 (Project of Investigation Pluri-annual) carried in the Physic Laboratory of the INALI aimed to clarify the observations concerning the scour holes. Specifically the influence on fish and benthos of hydrology, hydraulics and geomorphology of those particular lotic habitats of the alluvial plain of the middle Paraná River is investigated.

This study is framed by that project and focuses on one of its objectives, i.e. the spatiotemporal variations of fish community in a circular meander pool and a confluence scour hole of a secondary channel in the floodplain of the Middle Paraná River. The answer to changing hydrology of species with distinct reproductive strategies was of major interest. The results are confronted to available knowledge on fish assemblages in large floodplains, including a specific comparison with a large European river (Volga River, Russia).

1. Methods

1.1. Study area

The Paraná is the second largest river in South America in terms of catchment area (1.51 million km²), the second longest (4,400 km from the headwaters of Grande River in Brazil to the Río de la Plata estuary), and the third in terms of discharge (about 470 km^3 of freshwater carried to the sea annually). This hydrosystem drains nearly 32 % of Argentina, 100 % of Paraguay, 8 % of Bolivia and half the catchment area is within southern Brazil (Figure 1). The reach between its confluence with the Paraguay River and Diamante City is known as the Middle Paraná River and is 707 km long (Figure 2). At this place, the main channel typically braided shows a sequence of wide segments characterized by one or more anabranches with unstable sand bars and islands. Width varies from broad enlargements (over 8 km wide) to narrowings of only 400 m; depths can exceed 40 m and be limited as well to shallows of only a few meters. Current velocity varies from less than 0.2 ms^{-1} in sluggish stretches to more than 2 ms^{-1} at node points. The annual average discharge is 16,000 m^3s^{-1}.

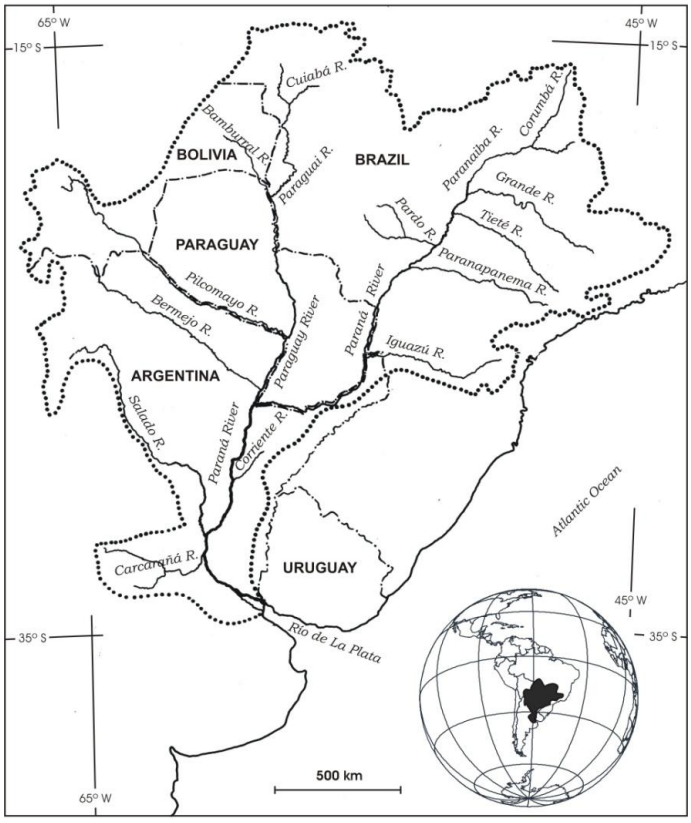

Figure 1: Paraná River basin including the Paraguay River and the Uruguay River, its two main tributaries (from the International Research Institute for Climate and Society)

Along its middle reach, the Paraná River builds a composite fringing floodplain covering an area of 13,063 km^2 with width ranging from 6 to 40 km (Drago, 1989). This alluvial plain has 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. At large floods, they tend to merge into a continuous sheet of water that covers the whole floodplain (Paira & Drago, 2007). Channel networks are characterised by sandy beds where prevail fine and medium grain sizes – transported principally by saltation and suspension (Drago & Amsler, 1998) – and high water turbidity mainly due to the elevated concentrations of suspended sediments from the Andean Cordillera through the Bermejo River (Drago & Amsler, 1988). Hydrometric regime is characterized by a high water period occurring in summer and autumn (December-April), and a low water period at the beginning of spring (September-October) (Giacosa et al., 2000). The water level is strongly influenced by that of the Paraná River, with mean seasonal variation of about 2 m. The region receives an annual rainfall of 1,000 mm concentrated essentially in summer and autumn. Mean daily temperature varies from 10°C in winter to 25°C in summer.

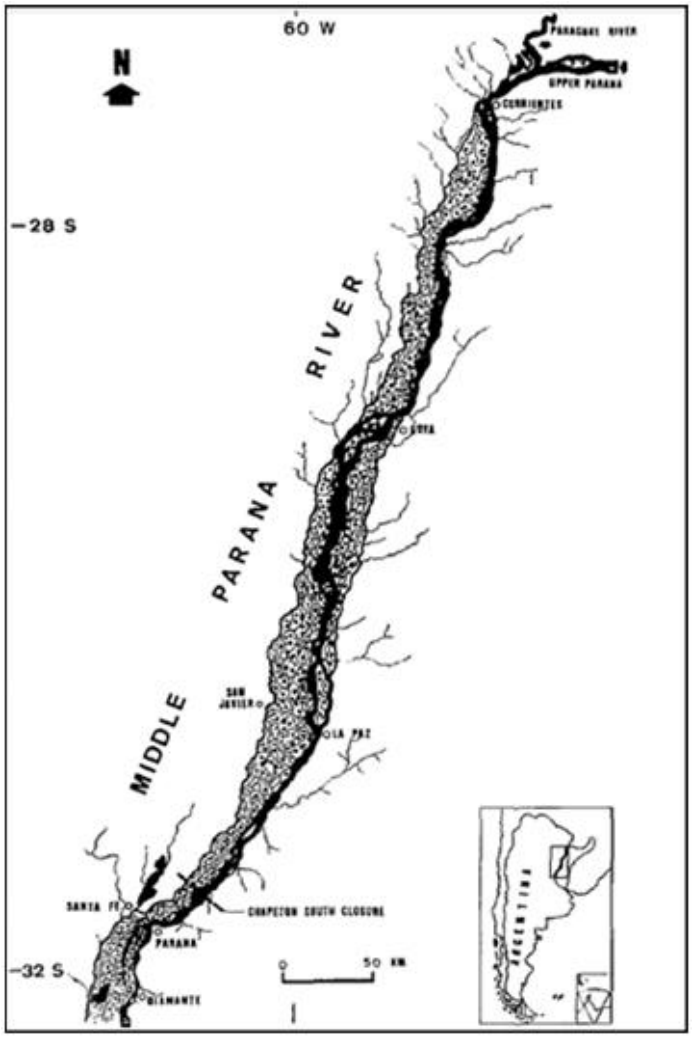

Figure 2 Middle Paraná River and its alluvial plain (modified from Drago 1989)

The present study is conducted in the middle Paraná River floodplain between the main channel and the Coronda River, south of the Salado del Norte River mouth and downstream Santa Fe City, Argentina. The minor channels such as the Catarata brook are formed by breaching the Coronda River levees and characterized by steep transversal slopes within the alluvial plain. These phenomena explain strong hydraulic processes during floods producing

significant changes in the drainage pattern, through silting and/or avulsion of channels and changes in shape and depth of lakes (Paira & Drago, 2007). Deep holes may be found along the minor channels – consequence of erosive processes derived from the interaction of morphology with the high turbulence and kinetic energy of water. This study aids to analyze fish assemblages in two of those holes located downstream to the confluence of two minor channels and at a meander curve (Figure 3).

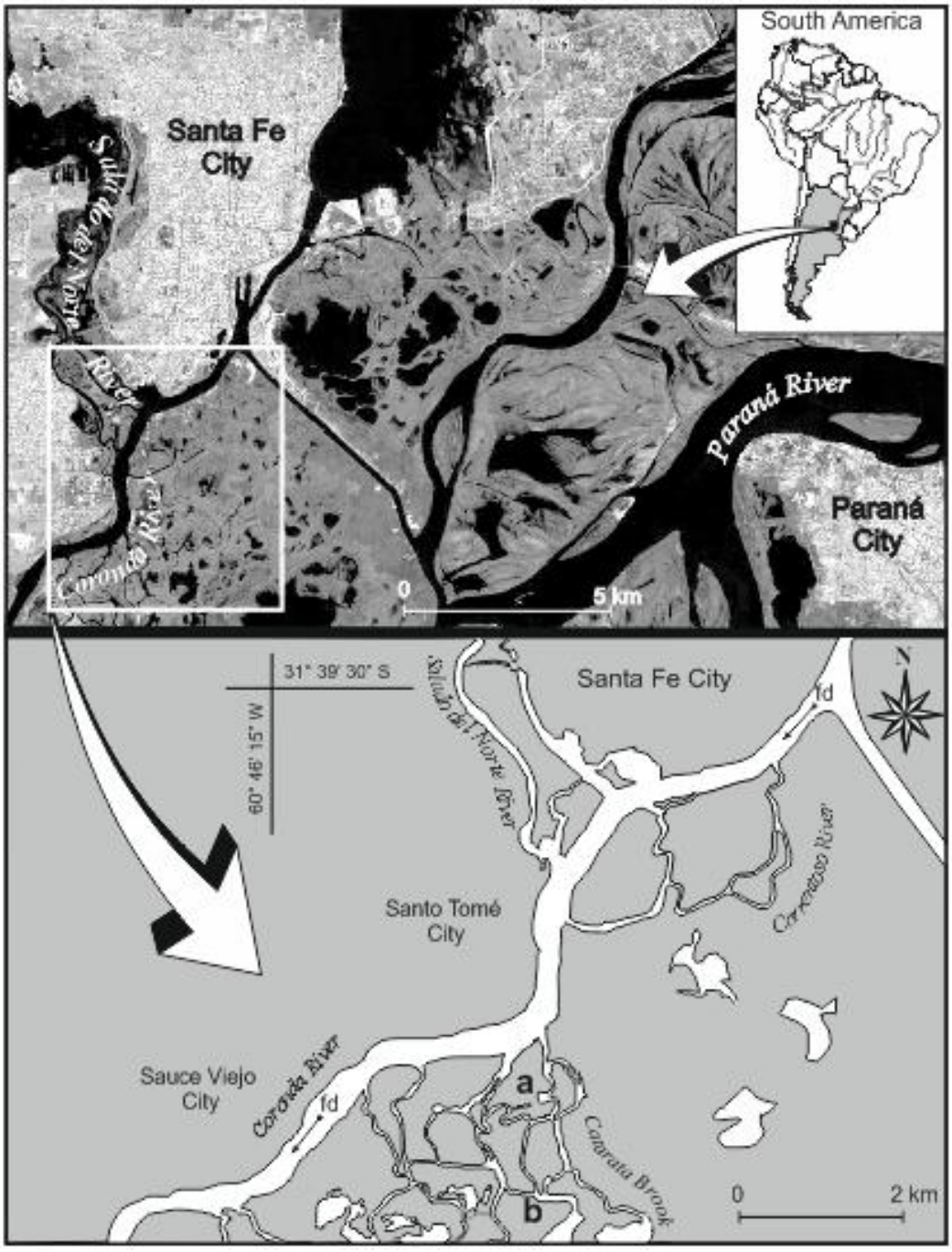

Figure 3: Study area in the alluvial plain of the Paraná River showing the sampling sites located in the Catarata brook. (a). Circular meander pool; (b). Confluence scour hole (modified from Espinola et al., in revision).

The meander studied (Figure 4a), similar to the "circular meander pool" described firstly by Andrle (1994), presents a large countercurrent occupying approximately half the pool towards the concave bank of the bend. This feature differs greatly from the typical river bend in which flow is generally subparallel to the channel banks throughout the bend with the largest depths located near the curve apex. Erosion is concentrated on the convex bank of the meander studied – with big depths approaching 15 m. Scour holes in channel confluences are more common in the Middle Paraná floodplain and have been described by Drago et al (2003). The confluence studied (Figure 4b) shows a maximum depth of 18 m located where flows merge generating a highly turbulent zone. The hydraulic characteristics of this confluence can be found in Szupiany et al (2011) and Herrero et al (2011). These authors have recorded large temporal fluctuations of flow velocity and secondary flow cells during high water levels within the scour hole of this confluence.

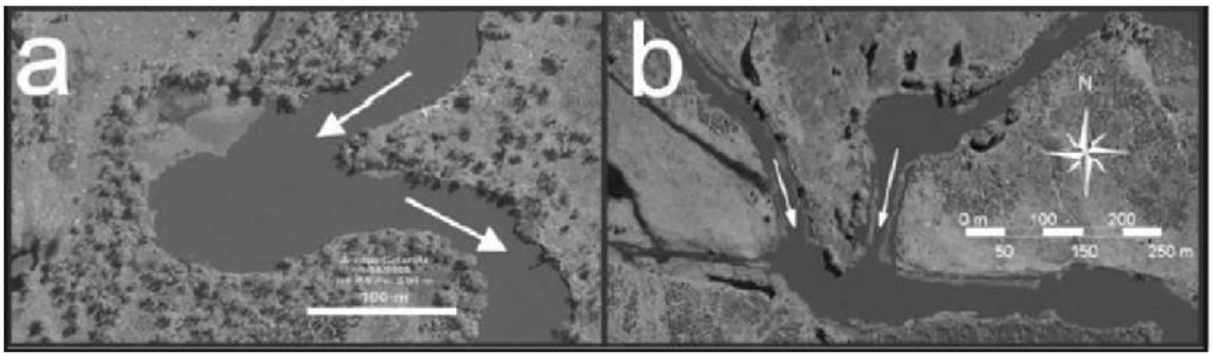

Figure 4: Aerial view of the two studied areas. (a). Circular meander pool, (b). Confluence scour hole (from google earth)

1.2. Sampling

Sampling was conducted twice a year from 2009 to 2012 in both the sites selected. 2012 has been sampled only once until now. No sampling was done in the confluence zone during 2009. Fish were captured using gillnets of different mesh size (ranging from 3 to 16 cm opposite knots) and trammel nets (internal mesh of 6, 7 and 8 cm opposite knots). Stationary and trawl nets were used for the fish catches, with a standardized effort exerted for each type of fishing gear. Easy-to-identify specimens were processed on the field (species determination, standard and total length, weight and identification of sex and maturate state). The other fish were preserved in 10% formalin and transported to laboratory and identified following the available keys for fish of the Paraná River basin. Temperature (°C), oxygen ($mg.L^{-1}$), pH and conductivity ($\mu S.cm^{-1}$) were measured in each patch to characterize environmental quality.

1.3. Data analysis

1.3.1. Hydrological regime

Water levels as recorded in the Santa Fe Port gauge (data supplied by the National Directorate of Waterways of Argentina) are used to characterize the changing hydrology. The height of 4.50 m in the Santa Fe port gauge has been defined as the reference level when flow begins to flood the adjacent plain of the area studied (Drago, 1980; Paira, 2003). A water level of 2.30 m when begins disconnection of most lakes in the study area has been fixed through specific topographic measurements.

The annual change of the hydrologic is known through some of the hydrometric attributes such as: days of potamophase, limnophase and connectivity (Table 1), and comforted with the fFITRAS function of the PULSO software (Neiff and Neiff, 2003). This software is used to study phenomena that repeat according to a sigmoidal function over long periods, such as seasonal fluctuations in river levels.

Table 1: Definitions of the hydrologic attributes considered in the study

Variables	Definitions
Days of potamophase	Number of days of high water levels
Days of limnophase	Number of days of low water levels
Connectivity	Ratio between the number of days of potamophase and the number of days of limnophase (in our case, two values for each year).

1.3.2. Characterisation of fish assemblages

Species richness (number of species captured) and abundance (capture per unit effort (CPUE): number of individuals/1000 m² of gill nets in 24 hours) is used to characterize fish assemblages. Reproductive and migrating strategies of fish species are defined according to the existing knowledge available on the Paraná River (e.g. Bonetto et al., 1971; Tablado et al., 1988; Vazzoler, 1996; Agostinho et al., 2004; Suzuki et al., 2005; Rossi et al., 2007; Bailly et al., 2008). For a few species, strategies have not been found at species level and are thus based in genus or sub-family level (Table 3).

1.3.3. Statistical analysis

Significant differences of spatial and temporal composition (structure) of fish assemblages are analyzed with the CAP statistical software (Anderson, 2004) using the canonical analysis on principal coordinates based on any symmetric distance matrix and a permutation test. The non-metric Bray-Curtis dissimilarity (Bray & Curtis, 1957) delivers robust and reliable dissimilarity results for a wide range of applications. It is one of the most commonly applied measurements to express relationships in ecology, environmental sciences and related fields and has been chosen to conduct the analyses of spatial and temporal dissimilarities of abundance and species richness. The number of 999 for permutation test (Manly, 1997) and significance level of $p<0.05$ is used. Data of 2009 could not be used for the CAP analyses because no sampling had been done in the confluence scour hole during this period. In case of no significant difference of spatial composition of fish assemblages, data of abundance and species richness of both sites will be joined to analyze the temporal repartition of migratory and sedentary fish.

The analysis of Variance (ANOVA) is used to test differences in abundance and diversity of migratory and sedentary fish. We can apply this method because it complies to the assumptions of homoscedasticity and normality. The analysis of Variance (ANOVA) using the nonparametric Kruskal-Wallis test has been chosen to check the differences of size (median, standard deviation, non-outlier range) of short and long-distance migratory fish after periods of distinct extent floods. Tree samples have been selected for the reason that they happen at the same period each year and show the influence of floods of distinct extent: July 2009, 29th (after a long period without floods), August 2010, 11th (after a flood pulse of high magnitude and long duration), August 2011, 9th (after a flood pulse of lower magnitude and duration). Size of sedentary fish has not been analyzed because of their absence in July 2009 and for the significant differences of species length which did not permit to have relevant results. Those two analyses of Variance are realized with the Statistica 7.0 software (Statsoft, 2005). The significance level adopted for all analyses is $p < 0.05$.

2. Results

2.1. Variations of the hydrological regime

The water level fluctuations during the period studied are shown in Figure 5. No flooding occurred during 2008 and 2009 summer-autumn seasons and water levels were particularly low with annual averages less than 3 m high. According to Espínola et al. (unpublished), this period corresponds to the end of a long-dry period that begun in 2000. Then followed two years of higher levels (annual averages close to 4 m high), including two flood pulses of distinct extent. Sampling was done in different hydrological phases; sampling (1) was at the end of the long-dry period, with very low water levels (disconnection of most lakes of the adjacent floodplain); (2) and (5) were performed with high levels during the rising phase when flow inundates the adjacent plain; (3) and (6) were done in august after each flood pulse (2010, 2011); (4) in December 2010 during low levels and when the second pulse began. Finally, sampling (7) was done in March 2012 during a low water period.

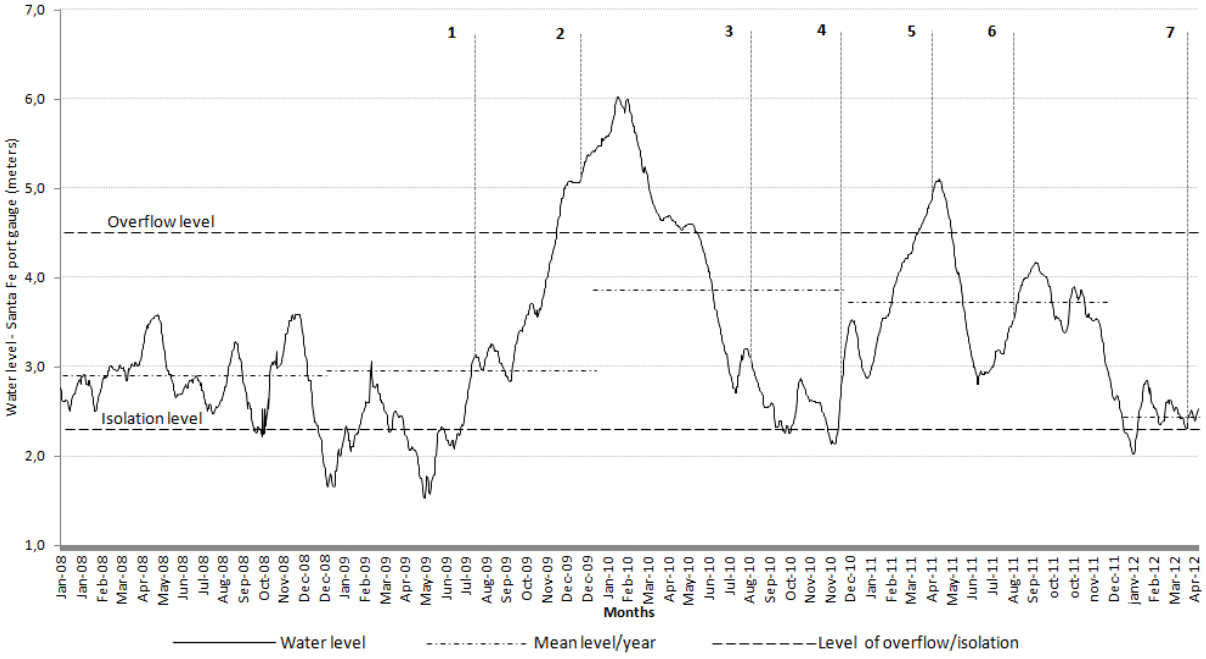

Figure 5: Hydrograph between January, 2008 and April, 2012 including the field surveys dates: (1). July-2009, 29th, WL=3,14m; (2). December-2009, 15th, WL=5,06m; (3). August-2010, 11th, WL=3,14m; (4). Dercember-2010, 13th, WL=2,55m; (5). April-2011, 13th, WL=4,74m; (6). August-2011, 9th, WL=3,49m; (7). March-2012, 29th, WL=2,42m.

The two flood pulses occurred in this period with distinct timing, duration and intensity (Table 2). The first one shows the typical timing of flooding in the Paraná River with a higher intensity and a longer duration than the second which began to flood the plain on April, 1st.

Low water levels occurred during the first months of 2012, contrary to the normal tendency for that period (January-April).

Table 2 : Flood pulses characteristics during the studied period: duration, intensity and timing of flooding.

Flood pulses' characteristics	**Flood pulse 1**	**Flood pulse 2**
Beginning of overflow	18/11/2009	01/04/2011
End of overflow	30/05/2010	17/05/2011
Duration of flood plain inundation (days)	195	47
Peak level (m)	6.02	5.1
Date of the peak	10/02/2010	30/04/2012

Values of connectivity calculated every six months from 2008 to April 2012 are shown in Figure 6. From 2008 to June 2009, the connectivity was zero – indicating a really low connection of lotic and lentic environments into the floodplain. The increment of connectivity from June to December 2009 (0.31) and the highest value at summer-autumn 2010 (4.84) reveal a progressive high connection of floodplain habitats during the first flood pulse. Between both floods, a period of low connectivity occurred (zero connectivity from Jun.10 to Dec.10); then followed a new increment of connectivity of lower extent during the second flood pulse (0.35 from January to June 2011). A new episode of zero connectivity finally happened until June 2012 – a period representative of a few connections between floodplain habitats.

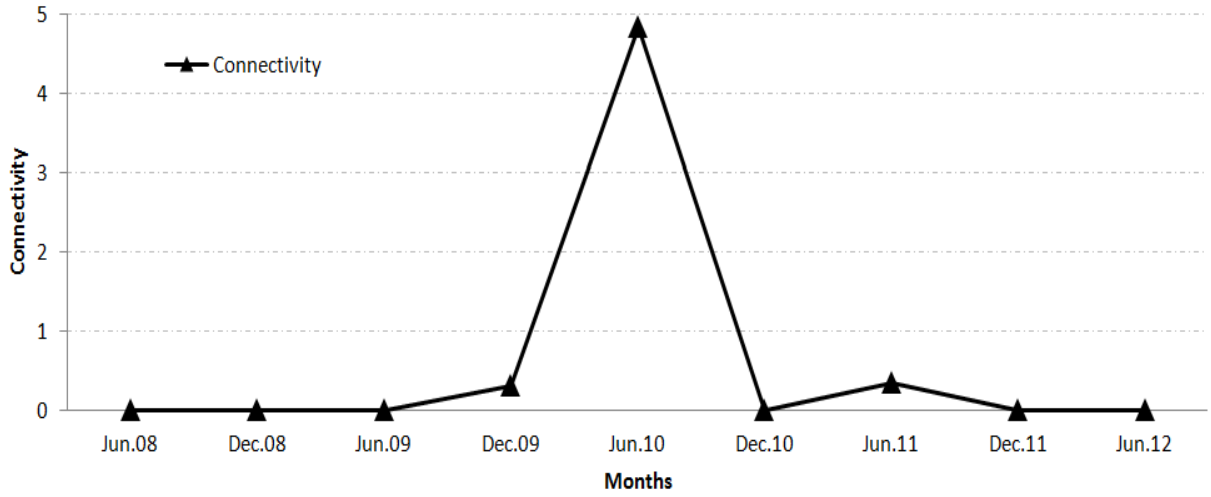

Figure 6: Biannual values of connectivity of the floodplain during the period studied (values of connectivity were calculated from January 1st to June 30th and from July 1st to December 31st for each year).

2.2. Characterization of fish assemblage

2.2.1. Details of species caught during the period studied

A total of 2,113 individuals belonging to 52 fish species of 20 families and 7 orders have been caught (Table 3). Siluriforms (25 species) and characiforms (22 species) dominate in diversity of species, however characiforms largely dominate in term of abundance with 83.5 % of total abundance. *Prochilodus lineatus* is the most abundant species (653 individuals, 30.9 % of total abundance). Other species such as *Leporinus obtusidens, Schizodon platae, Astyanax asuncionensis* and *Astyanax abramis,* show abundances higher than 100 individuals. Size range demonstrates presence of juveniles and adults for many species.

Fish species have been classified into four groups according to their strategy of migration and reproduction:

- Long-distance migrators (LM) group – with external fertilization, without parental care; those species carry out extensive longitudinal migrations (more than 100 km), using more than one habitat during their life cycle and migrating upstream to spawn in specific sites. Juveniles use the lower parts of the basin, especially lakes, for their initial development. They have seasonal and total spawning, high fecundity, small oocytes, rapid embryonic development and a passive egg transport to nursery areas;
- Short-distance migrators (SM) group – with external fertilization, without parental care; they carry out migrations of less than 100 km, with primarily lateral movements, have relatively high fecundity and small oocytes. Spawning may be total or partial, and the reproductive period may extend over several months;
- Parental care (PC) group – sedentary, with external fertilization; fish in this category predominantly spawn many times over a long period, have low fecundity and large adhesive eggs with prolonged embryogenesis. Parental care is well developed – including the construction of nests and transport of eggs stuck to the body;
- Internal fertilization (IF) group – sedentary or short-distance migrators, without parental care; they may show sexual dimorphism and mating rituals associated with reproductive behaviour. Fecundity is relatively low, with medium-sized eggs, and they generally conceal their offspring.

Species of the short-distance migratory group (SM: 19 species) are the most abundant, followed by the group of parental care (PC: 14 species) and long-distance migratory group

(LM: 13 species). Only 6 species of the group of internal fecundation (IF) were caught during the sampling period.

Table 3: Abundance, size and reproductive/migrating strategy of the 52 species caught in the study from July 2009 to March 2012. Standard length (SL) range in cm, total number (N) of fish and reproductive/migrating strategy (RMS) shown.

Order Family Species	SL range	N	RMS
Atheriniformes			
Atherinopsidae			
Odontesthes bonariensis (Valenciennes, 1835)	20,6 - 40,5	36	SM
Characiformes			
Acestrorhynchidae			
Acestrorhynchus pantaneiro (Menezes, 1992)	19,5 - 28,7	15	SM
Anostomidae			
Leponirus obtusidens (Valenciennes, 1837)	7,4 - 40,1	148	LM
Schizodon borellii (Boulenger, 1900)	14,5 - 35	54	SM
Schizodon platae (Garman, 1890)*	13,4 - 38,4	196	SM
Characidae			
Astyanax abramis (Jenyns, 1842)*	6,7 - 13,5	132	SM
Astyanax asuncionensis (Géry, 1972)*	6,4 - 17,5	185	SM
Brycon orbignyanus (Valenciennes, 1850)	20,5 - 25,3	9	LM
Cynopotamus argenteus (Valenciennes, 1836)*	9,5 - 21,9	54	SM
Galeocharax humeralis (Valenciennes, 1834)	8 - 20,5	3	SM
Mylossoma duriventre (Cuvier, 1818)	10,5 - 22,1	3	SM
Pygocentrus nattereri (Kner, 1858)	12,5 - 24,5	16	PC
Salminus brasiliensis (Cuvier, 1816)	10 - 54,5	60	LM
Serrasalmus maculatus (Kner, 1858)	11,4 - 16,5	8	PC
Serrasalmus marginatus (Valenciennes, 1837)	9,1 - 22	26	PC
Triportheus nematurus (Kner, 1858)	14,2 -27,5	9	SM
Cynodontidae			
Rhaphiodon vulpinus (Spix & Agassiz, 1829)	9,4 - 43,5	36	LM
Curimatidae			
Cyphocharax platanus (Günther, 1880)	7,5 - 14,3	81	SM
Cyphocharax voga (Hensel, 1870)	7,5 - 25,5	53	SM
Erythrinidae			
Hoplias malabaricus (Bloch, 1794)	18,5 - 44,5	21	PC
Gasteropelecidae			
Thoracocharax stellatus (Kner, 1858)	15,3 - 16,5	2	PC
Parodontidae			
Apareiodon affinis (Steindachner, 1879)	8,7	1	SM
Prochilodontidae			
Prochilodus lineatus (Valenciennes, 1837)	6,4 - 43,5	653	LM
Clupeiformes			
Engraulidae			

Lycengraulis grossidens (Spix & Agassiz, 1829)	11,5 - 12,9	3	LM
Gymnotiformes			
Sternopygidae			
Eigenmannia trilineata (López & Castello, 1966)	20 - 39,5	5	SM
Perciformes			
Sciaenidae			
Pachyurus bonariensis (Steindachner, 1879)	11,3 - 24,5	10	SM
Pleuronectiformes			
Achiridae			
Catathyridium jenynsii (Günther, 1862)	18,5	1	SM
Siluriformes			
Auchenipteridae			
Ageneiosus inermis (Linnaeus, 1766)	25,5 - 40,5	5	IF
Ageneiosus militaris (Valenciennes, 1835)	23,8 - 34,1	14	IF
Auchenipterus nigripinnis (Boulenger, 1895)	15,5 - 17,4	7	IF
Auchenipterus osteomystax (Miranda-Ribeiro, 1918)	/	3	IF
Trachelyopterus lucenai (Bertoletti, Pezzi da Silva & Pereira, 1995)	7,8 - 19,4	24	IF
Trachelyopterus striatulus (Steindachner, 1877)	15,2 - 16,5	4	IF
Callichthyidae			
Hoplosternum littorale (Hancock, 1828)	15,8	1	PC
Doradidae			
Oxydoras kneri (Bleeker, 1862)	13,5 - 50,5	4	LM
Pterodoras granulosus (Valenciennes, 1821)	9,8 - 28,5	61	LM
Rhinodoras dorbignyi (Kner, 1855)	21,1	1	SM
Heptapteridae			
Pimelodella gracilis (Valenciennes, 1835)	10,4 - 12,5	2	SM
Loricariidae			
Brochiloricaria chauliodon (Isbrücker, 1979)**	35,4	1	PC
Hypostomus commersoni (Valenciennes, 1836)*	9,6 - 48,5	19	PC
Loricaria simillima (Regan, 1904)*	12,8 - 37,5	10	PC
Loricariichthys melanocheilus (Reis & Pereira, 2000)*	15,8 - 39,5	9	PC
Loricariichthys platymetopon (Isbrücker & Nijssen, 1979)*	14,5 - 37,5	17	PC
Paraloricaria agastor (Isbrücker, 1979)**	30,5 - 38,3	7	PC
Pterygoplichthys anisitsi (Eigenmann & Kennedy, 1903)	10,4 - 14,2	5	PC
Ricola macrops (Regan, 1904)	27,5 - 36,8	6	PC
Pimelodidae			
Luciopimelodus pati (Valenciennes, 1835)	29,7 - 32,1	2	LM
Parapimelodus valenciennis (Lütken, 1874)**	10,5 - 21,5	23	SM
Pimelodus albicans (Valenciennes, 1840)	11,1 - 20,9	5	LM
Pimelodus maculatus (Lacepède, 1803)	8,5 - 23,7	53	LM
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	28,4 - 47,1	8	LM

Pseudoplatystoma reticulatus (Eigenmann & Eigenmann, 1889)	35,5 - 36,6	2	LM

** Reproductive and migrating strategy based in genus level*

*** Reproductive and migrating strategy based in sub-family level*

2.2.2. Fish assemblages within the circular meander pool and the confluence scour hole

Species richness and abundance for both the sites sampled are presented in Table 4. Fish abundance and number of species within the circular meander were relatively low in July 2009 (10, 5.53) and higher in December 2009 (13, 14.21). Captures in August 2010 were the highest of the period studied (M: 29, 42.79; C: 24, 19.02). A progressive decrement was recorded from December 2010 (M: 15, 3.81; C: 27, 12.22) to April 2011 (M: 11, 1.66; C: 9, 0.66). A new increment occurred in August 2011 (M: 19, 8.62; C: 16, 4.75), followed by a decrement in March 2012 (M: 16, 1.82; C: 14, 1.77).

Table 4: Date, species richness and Catch Per Unit Effort for samplings done between 2009 and 2012; (M) circular meander pool; (C) confluence scour hole, (GL) hydrometric level of Santa Fe port Gauge, (T) water temperature, (K) conductivity, (SR) species richness, (CPUE) catch per unit effort.

Code	Zone	Date	GL (m)	T (°C)	K ($\mu S.cm^{-1}$)	pH	SR (nb. of sp.)	CPUE (ind/1000m²)
M1	M	01/06/2009	1.79	-	-	-	10	5.53
M2	M	15/12/2009	5.06	-	-	-	13	14.2
M3	M	11/08/2010	3.14	12.7	104	5.5	29	42.7
C3	C	11/08/2010	3.14	13.3	118	5.5	24	19.0
M4	M	13/12/2010	2.55	-	-	-	15	3.81
C4	C	13/12/2010	2.55	-	-	-	27	12.2
M5	M	13/04/2011	4.74	24.9	112	6	11	1.66
C5	C	13/04/2011	4.74	24.8	111	5.5	9	0.66
M6	M	09/08/2011	3.49	15.8	101	7.1	19	8.62
C6	C	09/08/2011	3.49	16.4	103	7.1	16	4.75
M7	M	29/03/2012	2.42	22.3	310	7.3	16	1.82
C7	C	29/03/2012	2.42	22.1	296	7.4	14	1.77

2.3. Changes of CPUE and species richness along the hydrologic regime

Figure 7a shows the temporal variation of fish abundance (log CPUE) measured in the circular meander pool and the confluence scour hole. An increase of captures, followed by a progressive fall, happened after both flood pulses (Aug.2010; Aug.2011). The abundance recorded after the largest and longest flood pulse (Aug.2010) is higher than the second one

(Aug.2011). Low abundances were identified after periods without floods (Jul.2009, Mar.2012) or when high waters occurred later during summer-autumn period (Apr.2011).

Figure 7b shows the temporal variation of richness measured at each site sampled. An increment of species richness was also observed after both flood pulses, with higher values after the first one. The lowest diversities were also recorded after periods relatively long without flood pulses (Jul.2009 and Mar.2012) and with high water levels during the second flood (Apr.2011).

Summarizing, changes of CPUE and richness follow the same tendency of water level fluctuations with a certain time lag in both habitats. Apparently the magnitude of floods would be directly correlated with the maximum values of catches and richness. Moreover, a tendency of higher abundance and diversity in the circular meander pool would exist. The values of December 2010 are the exception.

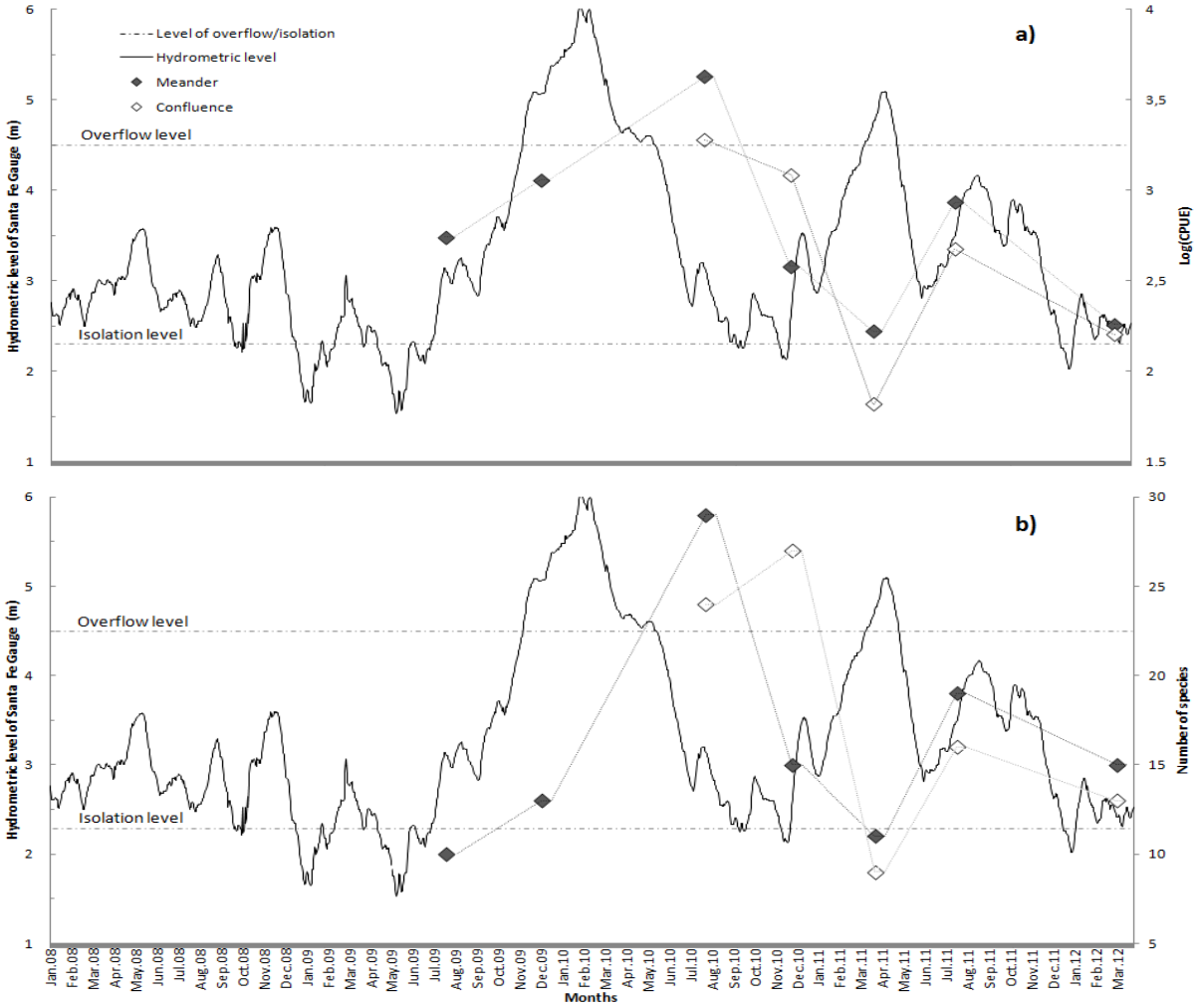

Figure 7: Temporal variations of fish abundance (a) and species richness (b) in the circular meander pool and the confluence scour hole of the Middle Paraná floodplain according to the hydrological regime recorded from January 2008 to April 2012.

2.4. Significance of spatial and temporal differences in fish assemblages

The overall differences of CPUE and richness between the two habitats are not significant (CAP: 0.040790; p= 0.925). However, they are significant between each sampling period (CAP: 2.753270; p= 0.002). The analysis by scatterplot using the first two canonical axes shows the temporal repartition of fish assemblages (Figure 8). The point data scatter forming three groups according to the similarity gradient of abundances and species richness. Fish assemblage structure in August 2011 seems to be distinct compared to the other groups. Fish abundance and species richness of August 2010/December 2010 and of April 2011/March 2012 show similarities. This statement seems to be more justifiable for the data of August 2010/December 2010 since fish assemblages appear to be closer.

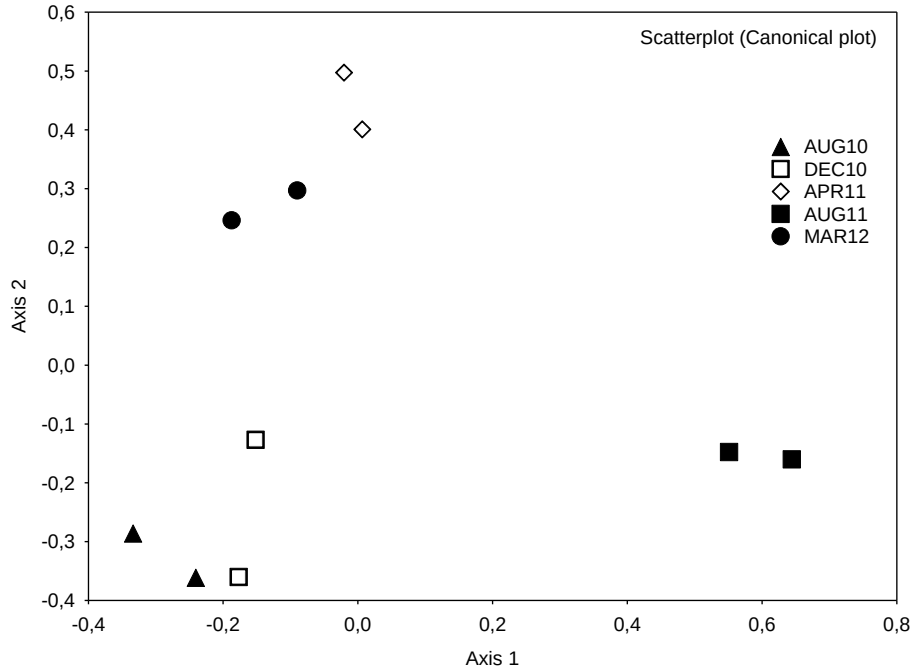

Figure 8: Canonical plot using abundance and species richness variables showing the temporal repartition of fish assemblages From August 2010 to March 2012.

2.5. Temporal distribution of three species groups of distinct migrating and reproductive strategies

2.5.1. Analysis of diversity and abundance of long and short-distance migrants and sedentary fish

Species diversity of sedentary fish (PC), short-distance migrants (SM) and long-distance migrants (LM) is represented in Figure 9. No sedentary fish and few migratory species were caught within both environments in July 2009. During the rising water period of the first

flood pulse (December 2009), the number of LM species increased (LM: 6). The highest diversities for every group were found in August 2010 and December 2010 after that pulse. The increase of diversity is visible for all the groups in August 2011, after the second flood pulse. The number of SM species was then the largest, with a figure similar to that of August 2010 (SM: 11). Despite of its increment in April 2011 (LM: 8; PC: 5), the diversity of PC and LM remained lower than the corresponding figures after the first pulse. Numbers of LM and SM species decreased in the sampling of March 2012 whereas PC were more abundant compared with August 2011.

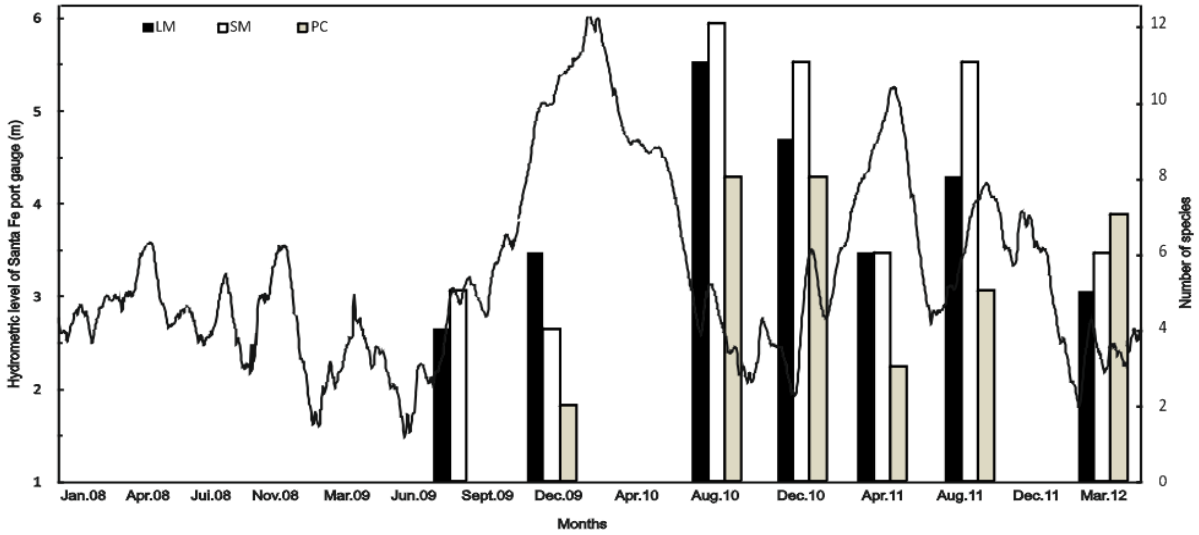

Figure 9: Hydrologic regime and number of species grouped according to their reproductive and migrating strategies within a circular meander pool and a confluence scour hole of the Middle Paraná floodplain. LM: Long-distance migratory fish with external fecundation and no parental care; SM: Short-distance migratory fish with external fecundation and no parental care; PC: Sedentary fish with external fecundation and parental care.

ANOVA revealed significant differences of abundance of LM species between each sampling period (F= 6.9759; p= 0.000075). Distribution of mean log (CPUE) per species seems to be fairly good correlated with the hydrologic regime (Figure 10). Few individuals per species (mean= 1.3±0.17) were sampled in July 2009 at the end of a large period without floods. The mean individual number per species increased in December 2009 during the rising levels of the first flood pulse but with larger SE and SD (mean= 1.65±0.39). The highest mean of LM was found in August 2010 after the flood pulse with a relatively small SE (mean= 2.25±0.15). The maximum abundance (extreme= 3.3) during that sampling corresponded to *Prochilodus lineatus*. A progressive decrement of LM abundance was then recorded in Dec.10 (mean= 1.47±0.12) and Apr.11 (mean= 0.94±0.12). Abundance increased again in August 2011 after

the second flood pulse (mean= 1.45±0.11). Finally poor LM abundances were recorded in Mar.12 with low water levels (mean= 1.3+-0.1).

ANOVA cannot be used for SM fish (F= 6.783733; p= 0.000078). Analyses for that group are based on the mean and standard error values of Figure 10. Samples of 2009 had few species but the highest mean abundances of all samplings (Jul.09: mean= 1.77±0.32; Dec.09: mean= 2.35±0.15). The effects of the two flood pulses are visible on this kind of fish. Mean abundances are higher after both flood events (Aug.10: mean= 1.57±0.13; Aug.11: mean= 1.36±0.1). A decrement was recorded during the subsequent falling water periods (Dec.10: mean= 1.08±0.03; Mar.12: mean= 0.74±0.0).

No sedentary (PC) fish were caught in July 2009 and only one individual of two species were found in December 2009. The largest abundances per species were observed after the first pulse (Aug.10: mean= 1.46±0.14; Dec.10: mean= 1.55±0.12). Similar abundances were recorded in the following samplings (Apr.11: mean= 1.13±0.2; Aug.11: mean= 1.11±0.18; Mar.12: mean= 1.13±0.13). The differences between samples of 2010 and samples of August 2011 and March 2012 were significant (F= 8.8855; p= 0.006684).

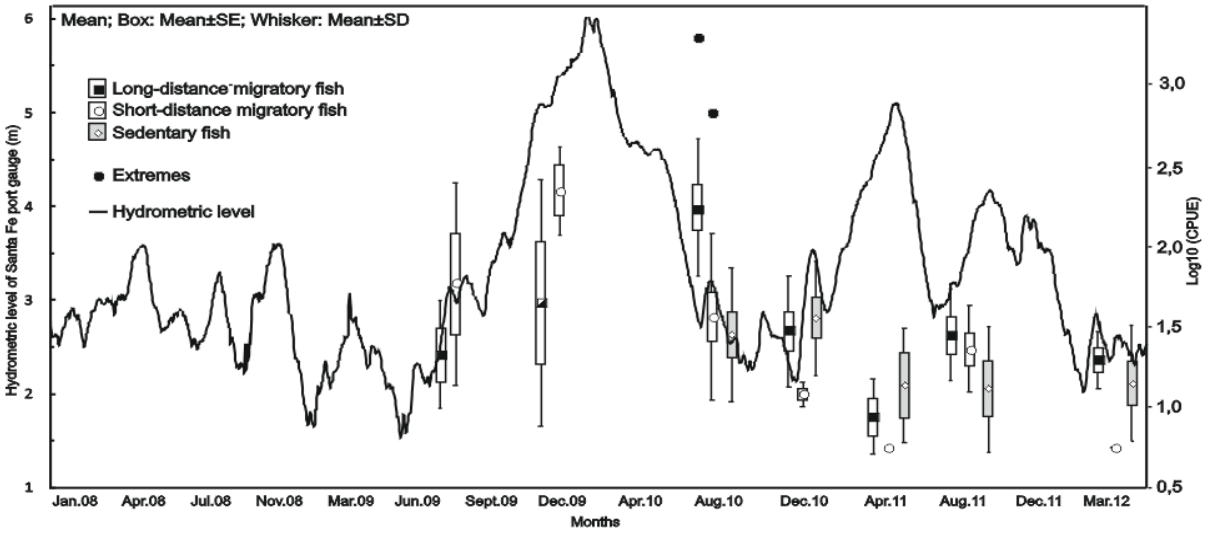

Figure 10: Hydrological regime and fish abundance of sedentary, long-distance and short-distance migratory species within a circular meander pool and a confluence scour hole of the Middle Paraná floodplain (species with only one individual were not included in the analysis).

Figure 11 shows mean and standard error values of species abundance for each migratory group after the first and second flood pulse (August 2010 and 2011). Results indicate that intensity, duration and timing of flood pulses have a significant influence on long-distance

migratory species (F= 15.6087; p=0.001659) but not on short-distance migratory species (F= 0.8957; p=0.357185) and sedentary species (F= 2.1303; p=0.172369).

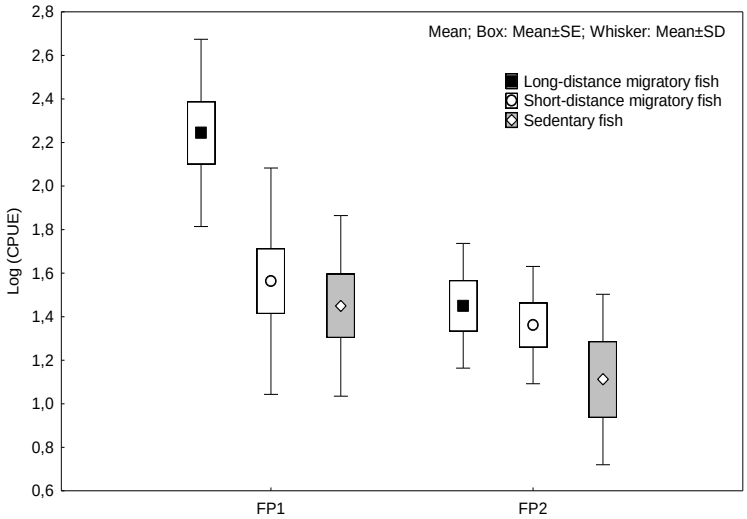

Figure 11: Fish abundance of PC, LM and SM migratory species after the two flood pulses in a circular meander pool and a confluence scour hole of the Middle Paraná floodplain. FP1: Flood pulse with high intensity and long duration occurred during the summer-autumn of 2009/2010; FP2: Flood pulse with lower intensity and duration occurred later in summer-autumn of 2011.

2.5.2. Analysis of sizes of long-distance and short-distance migratory species related to the extent of floods

The Kruskal-Wallis test used for analyses of long-distance migratory fish (Figure 12) indicates that significant differences of size exist after floods of distinct extent (H =44.28800; p =0.0000). At the end of the long-dry period (No FP), LM fish had relatively large sizes (median= 29.4) with standard lengths between 24.95 to 29.05 cm for 50% of individuals. LM were significantly larger in comparison to those of FP2 (p= 0.001101) and still more to those of FP1 (p= 0.0000). After the large flood pulse (FP1), the gross of LM were small with similar standard lengths (median= 15.5; $Q_{1\text{-}3}$= 14.3-17.4). Subsequently to FP2 in the late summer-autumn of 2011, the size distribution pattern was significantly distinct to that of FP1 (p= 0.014229). Individuals were larger (median= 21.1) with heterogeneous sizes: 50% of them had standard lengths from 13.4 to 24.5 cm and an extended size range (min= 8.5; max= 43.6).

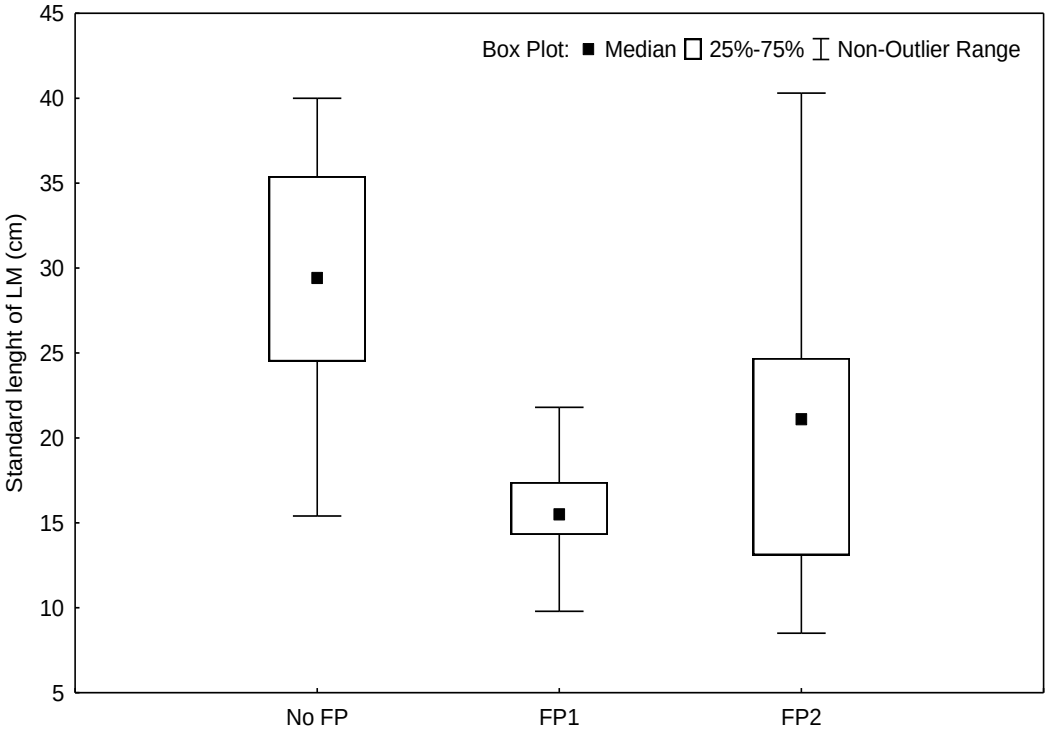

Figure 12: Distribution of sizes of long-distance migratory fish after floods of distinct extent in a circular meander pool and a confluence scour hole of the Middle Paraná floodplain. No FP: No flooding during a large period (sample of July 29th 2009); FP1: Flood pulse with high intensity and long duration occurred during the summer-autumn season (sample of August 11th 2010); FP2: Flood pulse of lower intensity and duration occurred in the late summer-autumn season (sample of August 9th 2011).

The Kruskal-Wallis test used for analyses of short-distance migratory fish (Figure 13) also indicates the existence of significant differences of size distribution after the three periods of distinct flood pulses (H= 139.0456; p= 0,000). The sizes of SM were very heterogeneous at the end of the large period without flood (No FP; Q_{1-3}= 8.1-23.25; min= 6.4; max= 40.4) and the majority of individuals were small (median= 12.05). No significant difference in fish size was found between No FP and FP1 (p= 0.084718) whereas it exists important difference between No FP and FP2 (p= 0.0000). After the major pulse (FP1), SM fish had relatively small standard lengths (median= 17.5; Q_{1-3}= 12.3-20.1) and a size range (min= 6.8: max= 27.5) less extended than that of individuals captured at the end of the period without floods. The size distribution of FP2 was significantly lower than FP1 (p= 0.0000). The gross of SM had very small lengths (median= 8.1; Q_{1-3}= 7.625-9.2) and a homogeneous size range (min= 6.7; max= 9.4).

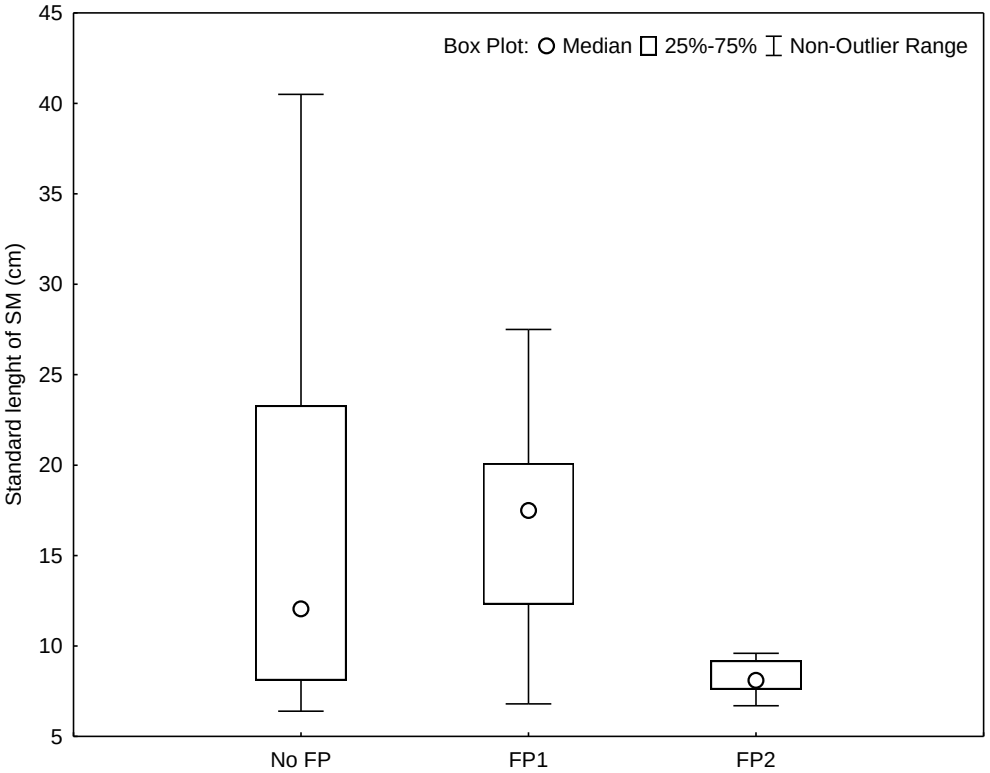

Figure 13: Distribution of sizes of short-distance migratory fish after floods of distinct extent in a circular meander pool and a confluence scour hole of the Middle Paraná floodplain. No FP: At the end of the long-dry period without flooding (sample of July 29th 2009); FP1: After the flood pulse with high intensity and long duration occurred during the summer-autumn season (sample of August 11th 2010,); FP2: After a flood pulse of lower intensity and duration occurred in the late summer-autumn season (sample of August 9th 2011).

3. Discussion

3.1. Influence of the flood regime on abundance and diversity of fish assemblages within the circular meander pool and the confluence scour hole

Many authors, by cueing various biological attributes of fish such as gonad maturation, migration, spawning and larval development, growth and feeding, have well explained the significant role played by the hydrological cycle as driving variable (Welcomme, 1979; Lowe-McConnel, 1987; Junk et al., 1989; Winemiller, 1989; Machado-Allison, 1990; Vazzoler, 1996). Indeed, the rising levels at the beginning of floods trigger the migratory movements of several fish species that spawn upstream in the main channels. With rising water, hydrated eggs of those species drift along the river and spill over alluvial plains, where they complete their development (Godoy, 1975; Agostinho et al., 2004). The high connectivity among floodplain habitats as a result of floods is crucial for all kind of species since it

increases the number of natural nurseries for larvae hatched there or carried by currents from upstream reaches and generates a diversity of highly productive environments, rich in food and shelter for young forms of many species (Gubiani et al., 2007).

In the upper part of the Paraná River, the flood regime has been recognized as the primary factor influencing life histories of fish (Agostinho & Zalewski, 1996; Gomes & Agostinho, 1997; Agostinho et al., 2001). Accordingly the highest abundances and diversities of fish in the circular meander pool and the confluence scour hole were recorded both after the flood pulses showing the close relation between floods and fish living strategies in the Middle Paraná River (Figure 7).

3.1.1. Distinct response of fish community to the flood attributes

King et al. (2003) document the optimum flood conditions for recruitment success as: (i) coincidence with high temperatures; (ii) predictability; (iii) slow rise and fall of the river level; (iv) duration from several weeks to a few months; (v) extensive floodplain area. For the riverine environments of the Upper Paraná floodplain, higher values of species richness and abundance are associated with years of longer floods and greater connectivity (Agostinho et al., 2001). In our case, two flood pulses were recorded with different duration, magnitude and timing. The flood pulse occurred in 2009/2010 seems to have such attributes as to get a good fish recruitment. Its rising period in summer coinciding with elevated temperatures triggers the reproduction process of many species. Its long-lasting inundation of the alluvial plain throughout more than 6 months and the high intensity of flood enabling the interconnection of large areas of food and shelter (Figures 5, 6 and 7), both optimize the growth of larvae and reduce the predation by piscivorous fish, mammals, reptiles and birds (Agostinho et al., 2003). Thus, the highest abundances and diversities considered during 2010 can be easily associated to the first flood which gave rise to really good conditions for fish reproduction, development of larvae and juvenile growth.

On the contrary, Agostinho et al. (2004) showed that small floods in the Upper Paraná River can limit or even frustrate the reproductive processes of many fish species. The diminution of fish density recorded along 15 years in scour holes of the Middle Paraná floodplain is also closely associated to a marked reduction of normal floods magnitudes and connectivity of

channels with the nearby floodplain lakes (Espínola et al., in revision). Accordingly, in this study, the smaller duration and intensity of the second flood inducing lower connectivity of the floodplain habitats and its occurrence in winter at the beginning of autumn, both have produced conditions of reproduction and growth not as good as those of the first flood (Table 2; Figures 5 and 6). As a result, those poorer conditions have been associated to the lower abundances and diversities of August 2011, compared to the sampling of August 2010 (Figure 7).

The deficiency of significant water levels during the reproduction period is linked to the reduction of reproductive processes of several fish species. Similarly the low connectivity between habitats of the alluvial plain is coupled with the increment of biotic and abiotic stressing environmental conditions, such as fish trapping into the mosaic of fragmented pools or the increase of predation (Junk et al., 1989; Fernandes et al., 2009). These reasons may account for the low values of abundance and diversity at the end of the long-dry period (July 2009) and in March 2012 when the inundation of the alluvial plain did not occur during the preceding summer-autumn season (Figure 7). The negative effects of the flood absence on the ictiofauna were recorded in both studied habitats.

3.1.2. Comparison between the fish assemblages of the circular meander pool and the confluence scour hole

It has been shown that species richness is significantly correlated with morphology (width and depth) in streams of the Upper Paraná Basin (Suarez, 2008). Few studies have been conducted on spatial distribution of fish within scour holes of alluvial plains. Arthington et al (2005) observed in an arid-zone floodplain river of Australia that waterholes close each other were more likely to have similar fish faunas than those far apart. However, Balcombe et al. (2009) found a clear separation of three fish assemblage groups within scour holes of another arid-zone floodplain of Australia that were spatially differentiated at the end of the winter-dry season. Fish assemblage patterns were concordant with differences in water chemistry, but not with the geomorphological attributes of channels and floodplain waterholes. After the summer-flow period, when all in-channel river sites receive flow, fish assemblages were less clearly differentiated.

Our results do not show significant differences between the fish assemblages (abundance, diversity) of the circular meander pool and the confluence scour hole. Both sites are 1,600 m apart and permanently connected. These facts seem to be similar to the observations of Arthington et al. (2005). Nonetheless, as clear correlations have been shown to exist between fish assemblages and morphological attributes of streams and waterholes, it might be assumed that similarities between the fish assemblages of the circular meander pool and the confluence scour hole are not always verified. Note that comparisons could not been done when most lakes are disconnected from the floodplain channels during a period sufficiently long. Under these conditions the distinct geomorphologic attributes of both sites might have a major influence on fish assemblage. Thus, more samples are needed – especially at low water levels – to prove that a similar fish distribution can be verified for every hydrological stage in a circular meander pool and a confluence scour hole of the Middle Paraná Floodplain.

3.2. Temporal distribution of three groups of species with distinct strategies of migration and reproduction in the circular meander pool and the confluence scour hole

The influence of the flood regime on the life strategies of long-distance migratory fish is well known and has been studied for many large migrators of the Paraná River (Godoy, 1975; Bonetto, 1971; Oldani, 1990). Though less studied, some authors have also observed the effect of water level variations on species having short lateral migrations between floodplain lakes and channels or spending their whole life in the same area (Cordiviola de Yuan et al., 1984; Agostinho et al., 2003; Bailly et al., 2008). It has been shown in the Upper Paraná River basin that, irrespective of particular life strategies, the hot-moment for most species reproduction precedes the flood peaks, i.e. the association of reproduction with the beginning of the water level increase is a common pattern for the majority of species (Agostinho et al., 2004). Moreover, Suzuki et al. (2004) point out that the flood peak level might signal the cessation of spawning.

In the following analysis, the temporal distribution of three groups of species with distinct strategies of migration and reproduction caught in the two studied environments from 2009 to 2012, has been associated with the irregular flood regime during that period.

3.2.1. Long-distance migrants: a significant influence of the flood regime

- *Association of LM species to a long duration and high intensity flood occurring at summer-autumn season*

Flood duration and availability of a large quantity of lentic/lotic habitats of the floodplain are determinant for the recruitment of long-distance migratory fish in the Paraná River as *Prochilodus lineatus* (Gomes and Agostinho, 1997; Fernandes et al., 2009). In our case, the captures of LM in December 2009, August 2010 and December 2010 ratify the clear relation between that group and the high connectivity of the floodplain induced by the flood pulse. Indeed, the largest abundances and diversities were found in the year 2010, after the period of major connectivity (Figure 6, 9 and 10).

Characiforms spawn generally from October to January whereas siluriforms have a reproduction period that begins in December and extends until March (Agostinho et al., 2003). Thus, the explanation of the heterogeneous values of abundance recorded in December 2009 in the circular meander and the confluence of LM species rely on this lack of simultaneity of spawning. Some species, especially of the Siluriformes' order, had not trigger the reproduction process yet or had just begun to spawn in December 2009 (larvae cannot be caught with gillnets of mesh size ranging from 3 to 16 cm) whereas juveniles had been captured in abundance for other species, such as *Prochilodus lineatus* and *Salminus brasiliensis* – two dominant LM species of this sampling that were mainly composed by individuals of very small size, signifying the previous success of reproduction of those two characiforms.

Many authors have associated the high water levels during summer with the spawning success of migratory species of the Upper Paraná River (Godoy, 1975; Agostinho et al., 1993; Vazzoler, 1996). In the present study, the high abundance and diversity of every LM were recorded in August 2010, revealing the positive effect of the flood pulse on the accomplishment of reproduction. Furthermore, the analysis of sizes shows a dominance of small LM (Figure 12), which supports the conclusion.

The rise of water, coinciding with the high water temperatures, i.e. the period of reproduction of most LM, is a trigger for migration upstream to the main channels in the

upper reach of the Paraná River (Agostinho et al., 2003). Moreover, Bailly et al. (2008) report that smaller catches may be related to an increase in predation by juveniles of large piscivorous during the periods following long-lasting floods. In this study, the decrease of abundances and diversities observed in December 2010 (Figure 9 and 10) and coinciding with a rise of water levels and high temperatures could be correlated with the beginning of migration of some mature LM. A dominance of *Salminus brasiliensis* of about a 30-35 cm standard length was recorded in August 2010. This piscivorous fish is on top of the aquatic food chain in running waters. Thus its presence in the two lotic environments during the sampling preceding December 2010 may explain the reduction of the stock of small LM.

- *Response of LM species to a flood of short duration occurring in the late summer*

A failure of fish reproduction has been reported in the Upper Paraná River as a consequence of the absence of flooding during the spawning season; however, when flooding is delayed most of the migratory species may start spawning in February (Agostinho et al., 2003). Our results ratify the same negative effect due to the lack of a flood in summer since the lowest abundance of the whole studied period was observed in April 2011. Moreover, this extremely low capture of LM could also be associated to the rise of water in February which would have triggered the adult migration upstream to the main channels (Figure 10).

Agostinho et al. (2004) reported that fish migration was favored by annual floods with durations larger than 75 days beginning in the early summer. These ideal conditions comply only for the first flood pulse (Table 2) in this study. Note that the increment of abundance and diversity observed in August 2011 can be associated to the rise of water and the increase of connectivity generated by the second flood pulse occurring during April and May, which permitted the success of the reproduction of some LM. However, the significant difference of abundances compared with those recorded after the first pulse, could be related to the shorter duration and connectivity of the second one (time of overflowing= 47 days) and its timing that did not coincide with the spawning season. Moreover, the analysis of size, do not showing dominance of small individuals, supports this observation.

- *LM species during periods without floods*

Junk et al. (1989) relate the loss of diversity with the lack of connectivity between lentic and lotic habitats of the alluvial plain since the biotic and abiotic stressing environmental conditions increase and the reproductive processes reduce. Moreover, Godoy (1975) reports that large migratory fish do not spawn when the river water level is stable or falling. Additionally, an increased exposure to predation during years without floods may account for the low abundances of juveniles whichever be the reproductive strategy (Agostinho et al., 2003).

In our case, small abundances and the lowest species richness of the whole studied period were observed in July 2009 after a long lasting dry period and in March 2012 following the floodless summer. The lack of significant high water levels during the reproduction period preceding those two samplings would explain the low diversity and abundance of LM. Indeed, the absence of floods before the sampling of July 2009 and in summer 2012 prevented the spawning period of most of LM species from sparking off. The low connectivity in both periods implying reductions of shelter in the alluvial plain would also increment the pressure of predators on pray. The analysis of sizes shows that LM were mainly composed by large individuals in July 2009 at the end of the long-dry period. Thus, the quasi-absence of small individuals supports the possible fail of reproduction and the significant effect of predation on LM juveniles.

3.2.2. Short-distance migrants: a lower dependence on the flood attributes

- *Effect of two distinct flood pulses on SM species*

At the beginning of rising waters, mature SM start a lateral migration from the floodplain lakes up to the rivers apparently related with spawning (Fernandes, 1997) and show an intense reproductive activity between October and March in the Upper Paraná River (Bailly et al., 2008; Agostinho et al., 2003). According to these observations, the high abundances per species and the highest diversity, recorded in August 2010 and 2011 in this study (Figures 9 and 10), would be related to the increment of water levels as a result of both flood pulses that triggered the reproduction process of SM species. The highest abundance of SM was observed in December 2009, but along with a little diversity. Those high abundances are

due to three species (*Astyanax asuncionensis, Cyphocharax voga, Cyphocharax platanus)* composed by uniform small sizes. Apparently, a previous spawning period occurred with success for those species when the water level begun to rise during the first flood pulse.

No clear correlations have been found between the abundance of young-of-the-year of some SM species and the intensity and duration of floods in the Upper Paraná (Bailly et al., 2008). The same result was obtained in our study since no significant difference in abundance and similar diversity was observed after the two flood pulses (August 2010 and 2011). On the other hand, the analysis of sizes shows a significant difference between both periods (Figure 13). The higher median of sizes after the first flood pulse is due to the dominance of *Schizodon platae* whereas the median after the second one is associated to the high abundance of *Astyanax spp.*, a genus with sizes much smaller than *Schizodon platae*. Thus, the features of floods apparently have a distinct influence according to the SM species. *Schizodon platae* seems to be favored by floods of high intensity and duration whereas *Astyanax spp.* was found in both periods.

- *SM species in periods without floods*

Low diversities were observed in both samplings at the end of periods without floods (July 2009 and March 2012). A low abundance was also recorded in March 2012. Similarly to the LM species, these decreases in SM attributes would be associated with the lack of connectivity of the floodplain and the subsequent reduction of the reproductive processes due to the increment of predation, loss of shelter and increasing trapping of individuals into floodplain depressions.

The high abundances in both studied sites at the end of the long-dry period (July 2009) are associated with the significant number of only two species (*Odontesthes bonariensis, Astyanax asuncionensis).* The distinct sizes of these species (more than 22 cm and 8 cm respectively) account for the highly non uniform sizes recorded in this sampling. An analysis of the maturation stage for individuals of both species and showed a dominance of mature *O. bonariensis* and immature to mature *A. asuncionensis.* Calvo and Dadone (1972) observe that *O. bonariensis* begins its migration in school and spawns from August to November. Rosso & Quiros (2010) report that this species has a preference for lentic environments with

macrophytes when spawning. Regarding *Astyanax spp.,* Ringuelet (1967) remarks that it is one of the most common genera in the Paraná River. Thus, the large quantity of mature *O. bonariensis* caught in July 2009 would be related to the period of migration for reproduction. The various stages of maturation of *A. asuncionensis* do not enable to state any sound explanation. Its presence is associated to the common occurrence of this species in the Paraná River.

- *Heterogeneity of species into the SM group*

Bailly et al. (2008) observe that the SM strategy includes a range of species with very short to moderate reproduction displacements, belonging to different phylogenetic groups. Therefore the heterogeneity of this group could explain why it is difficult to define common patterns related to the flood regime. Species respond differently to the characteristics of floods since may have very distinct periods of reproduction as was observed for *O. bonariensis.* Consequently, particular analyses per species or genus are required to obtain more relevant results about responses of short-distant migratory fish to the influence of hydrological variations.

3.2.3. Sedentary fish: no immediate significant difference between both flood pulses but significant with time

Agostinho et al. (2003) have compared the abundance of adults and juveniles of sedentary species during distinct hydrological conditions (no flooding, moderate flooding, normal flooding) and reported that reproductive activity is greater during drought though abundance of juveniles is the lowest due to factors such as the increased predation. Moreover, the consequences of 291 days of low waters in the Upper Paraná River have influenced the normal reproduction cycle of *Cichla kelbery* since no larvae was observed in the following period of high waters (Espínola, 2005). This species develops a parental care during reproduction as every sedentary species analyzed in our study. As a result, the absence of sedentary fish recorded at the end of the long-dry period could be correlated to the lack of connectivity and the subsequent increment of juveniles predation, i.e. the long-time of very low water levels impacted the normal reproduction of sedentary fish.

Agostinho et al. (2004) observe that sedentary fish developing parental care have lower dependence on floods than for LM species. Still, Bailly et al. (2008) note that in relation to juvenile survival, the occurrence of floods appears to be crucial for those species because such floods increase fish survival in the period of initial development. The major abundance of juveniles of sedentary fish after major floods has also been observed (Agosthino et al., 2003). Our results show a significant increment of abundance and diversity after the first flood pulse – clearly revealing the positive influence of flood on sedentary fish – however, no significant difference in abundance has been found between the two samplings following each of the flood pulses (August 2010 and August 2011) though the highest abundances and species richness were recorded after the major pulse. Apparently better conditions for the survival of juveniles occurred after the larger flood but sedentary fish do not present a dependence on flood as clear as LM species.

According to Agostinho et al. (2001), catch of sedentary species was greater during 2 years of droughts than during wet periods due to the reduction of flooded areas which affect the absolute density and catchability. In the present study, an immediate diminution of abundance and diversity of sedentary fish during the periods following the two floods is not observed (Figures 9 and 10). Hence population structure did not change as rapidly as for the two groups of migratory fish. The persistence after both flood pulses would be associated with the sedentary strategy implying none significant displacements. A lower access to a diversity of habitats inducing a reduction of the dispersion phenomenon, probably influenced also the better catchability for the low water levels after the flood pulses.

4. Influence of floods on fish community in the floodplain of two large rivers – Paraná River (Argentina) and Volga River (Russia)

In this section, we compare the influence of the flood regime on fish communities in the floodplains of the Middle Paraná River and the Lower Volga River. Our results are principally compared with those of Górski et al. (2010, 2011a, 2011b) performed under the project ‘‘Changing flood pulse dynamics and their impact on fish recruitment in large rivers (Volga, Russia)’’ carried out within the Volga-Akhtuba Nature Park of the Lower Volga floodplain. That project is financed by the Netherlands Organization for Scientific Research (NWO) with the participation of the Schure-Beijerinck-Popping Fonds.

4.1. Consideration of physical, morphological and hydrological characteristics of the two floodplains

4.1.1. Anastomosed pattern of two large floodplains

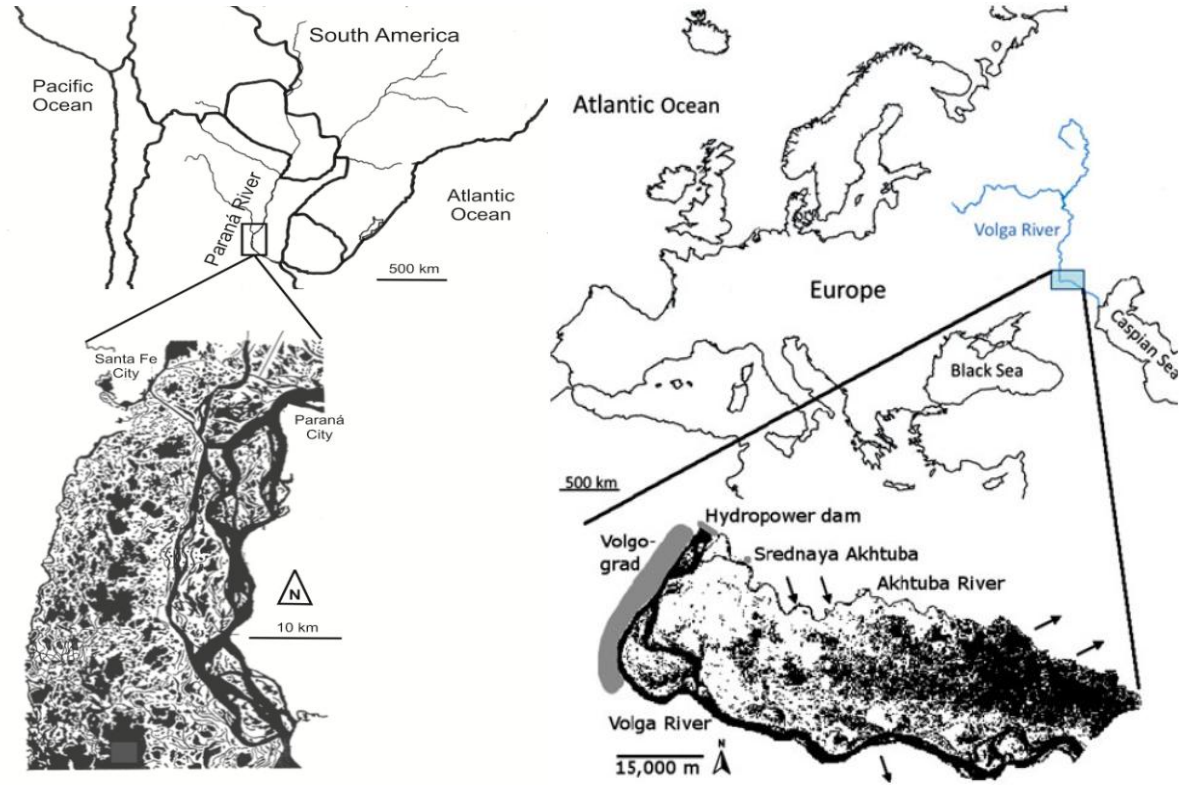

Figure 14: Localisation of the two studied areas; - left: map of the studied reach of the Middle Paraná floodplain in Argentina and its location in South America (modified from Drago et al., 2003); - right: map of the Volga–Akhtuba floodplain in Russia and its location in Europe, the bottom image shows the floodplain area embedded between the Volga River in the south and the Akhtuba River in the north (from van de Wolfshaar et al., 2011). The arrows indicate the areas where the water enters and leaves the floodplain, water is in black.

The Paraná River is the second longest river of South America (4,400 km). The annual average discharge is 16,000 m^3s^{-1}. It is characterized by a subtropical climate with smaller fluctuations of temperature, rarely below 0 °C. Mean daily temperature varies from 10°C in winter to 25°C in summer. As it was previously described, its floodplain of 700 km long and from 6 to 40 km wide located in its middle reach has a high percentage of its surface covered by minor channels, lakes and swamps almost permanently connected, forming an anastomosed network (Figure 14).

The Volga River, with a length of 3,690 km and an average annual discharge of 8,103 m^3s^{-1}, is the longest river in Europe. It is a typical plain-type river characterized by a moderate

continental climate with high differences of temperature, from 20.6 to 25.1 °C in July and -9.6 to -6.9 °C in January. The Volga-Akhtuba floodplain over 300 km long and 10–30 km wide is bordered by the Lower Volga River and Akhtuba River. The Akhtuba River is the main contributory of water to the floodplain, i.e. more than the Lower Volga itself. During floods, water overflows from the upper Akhtuba into part of the Volga–Akhtuba floodplain located just downstream of the dam. The floodplain in the northwestern part of the area is dissected by an anastomosed network of channels and streams with numerous floodplain lakes connected during high water levels (Korotaev et al., 2009) (Figure 14).

4.1.2. Annual changes of flood regime

Our previous results showed year-to-year variations in flood regime. It was observed a flood pulse of high extent in 2010, a minor and lasted pulse in 2011 and two floodless years (2009 and 2012). Figure 15 shows the non similar pattern of water levels for each studied year. In the Middle Paraná River, pulses generally occur in December-January with a peak in February-March (Giacosa et al., 2000).

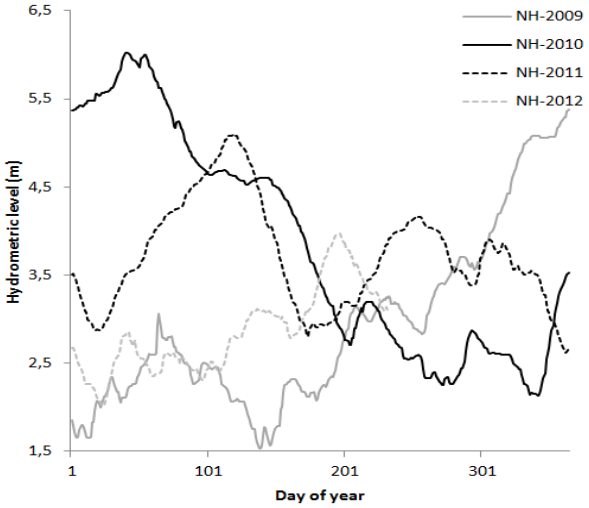

Figure 15: Daily water levels of the Middle Paraná River floodplain measured in the Santa Fe Port gauge during 2009-2012.

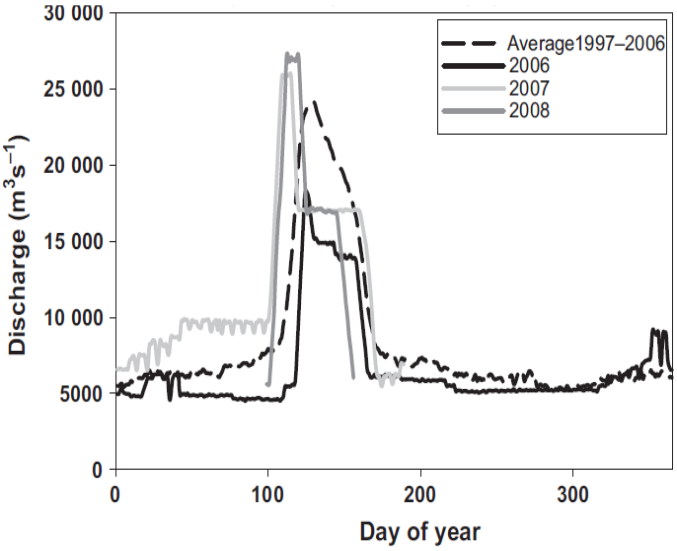

Figure 16: Daily discharge of Volga River during 2006, 2007, 2008 and the average discharge calculated for the years 1997–2006.

The lower Volga valley has a combined rainfall/snowmelt flow regime, with a peak discharge in May–June corresponding with a rise of water temperatures. Fish assemblages were analyzed during three years in distinct areas of the Volga-Akhtuba floodplain (Górski et al., 2011a). Daily discharges are shown for each year in figure 16. Compared with the average flood pulse

during 1997-2006, the peak flow in 2006 was smaller and shorter, whereas peak flows in 2007 and 2008 were both earlier and reached a higher maximum than the average. A conspicuously larger fraction of the floodplain was inundated in 2007 and 2008 than in 2006. Peak flow in 2007 lasted about 3 weeks longer than in 2008. It is also noted that growing season was the warmest in 2007, followed by 2006 and 2008 and the dynamics of flooding differed between different areas in the floodplain.

4.1.3. Conclusions of morphological and hydrological characteristics

The Paraná River is larger than the Volga River. Its length of 4,400 km is relatively longer than the Volga River (3,690 km) and its annual mean discharge (16,000 m^3s^{-1}) is two times higher (8,103 m^3s^{-1}). The temperatures infrequently below 0 °C in winter have rarely provoked fish mortality in the Middle Paraná floodplain, however some cases of mortality were reported (El Litoral, 2010). The Volga-Akhtuba floodplain located in the continental climatic zone is exposed to severe winters with long periods of air temperatures below 0 °C (Averina et al., 2000). Subsequently, freezing of water bodies may result in massive fish mortality. Floodplains are dissected both by an anastomosed network of channels and streams connecting numerous floodplain lakes in high water periods. The Middle Paraná floodplain is more than two times longer (700 km to 300 km long) and its width is larger and more variable (6 to 40 km) than the Volga-Akhtuba floodplain (10 to 30 km).

Regarding the flood regime, the period of high water levels corresponds to the rise of water temperatures in both floodplains. Flood peak occurs in summer in the Middle Paraná River (December-January) and in spring (May-June) in the Lower Volga floodplain. In both cases, year-to-year changes in flood regime were observed. However, strong year-to-year changes of flood extents were observed in the case of the Paraná floodplain, whereas lower variations of timing and magnitude of floods is shown for the Lower Volga-Akhtuba floodplain due to controlled spring flooding managed by the gates of the Volgograd Dam (Górski et al., 2011b).

4.2. Biodiversity and biology in fish species of continental and subtropical floodplains

Biodiversity of fish varies between subtropical and continental rivers. As an example, we caught 52 species in the two lotic environments of the middle Paraná floodplain from 2009

to 2012. Górski et al. (2011a) recorded only 23 species captured in years 2006-2008 in four areas of the Volga-Akhtuba floodplain. The harder continental climate poses more stressing conditions for fish life and would account for the differences.

Large upstream migrations along the main rivers or lateral migrations from lakes to secondary channels of the floodplain are common patterns to many fish of the Paraná River. In the Middle Paraná floodplain, we have based some of our previous analyses according to the reproduction strategies of migrating fish. We caught 13 species swimming more than 100 km to spawn, 19 species doing short migrations less than 100 km, with primarily lateral movements and 14 sedentary fish. Those long-distance migrants have generally large size and common reproductive characteristics. They have an external fertilization, no parental care, total spawning, high fecundity, small oocytes, rapid embryonic development and passive egg transport. The short-distance migrants have external fertilization, no parental care, relatively high fecundity and small oocytes. However, size of species varies, spawning may be total or partial, and the reproductive period may extend over several months. The sedentary species also develop parental care, predominantly spawn many times over a long period and have low fecundity and large adhesive eggs with prolonged embryogenesis.

Studies on the Volga-Akhtuba floodplain have not considered migration comportment for the analyses. It is explained that the majority of the spawning stocks originates from the floodplain water bodies (Górski et al., 2010). Thus, the comportment of reproduction of most of the Volga River species is distinct to many species of the Middle Paraná floodplain which leave the floodplain to spawn in the mains channels. Górski et al. (2011a) observed common patterns to fish species according to some characteristics of their reproductive strategy, including the development of parental care (nests, habitat selection), the spawning mode (single or several spawning events), the average fecundity and the maturation age.

4.3. Influence of floods and temperatures on fish community of two large floodplains

4.3.1. Effect of the long duration of floods in fish recruitment

In the Middle Paraná floodplain, significant differences in temporal repartition of fish assemblages exist and are principally correlated with the influence of the flood regime. We have associated the major abundances of fish and diversities of species with the long-lasting

flood pulse (2010) of high magnitude and duration occurred during the period of reproduction of most of the species caught. That pulse gave rise to really good conditions for fish communities as well as for the reproduction of genitors, the development of larvae and the juvenile growth.

In the Volga-Akhtuba floodplain, extensive areas with a long duration of flooding accommodate high densities of young fish. This suggests that the extended inundation improves the recruitment success of river fish. In areas with extensive flooding, the biomass of young-of-the-year of most fish species was about three times higher in 2006 and 2007 than in 2008 (Górski et al., 2011a).

The long duration of flooding shows a positive effect in fish recruitment in temperate as well as subtropical floodplains.

4.3.2. Timing of floods – the importance of temperature

In the Middle Paraná floodplain, we have associated lower abundances and diversities not only with the minor duration and intensity of floods inducing a lower connectivity between habitats but also with its occurrence at the beginning of autumn, out of the period of high water temperatures. Consequently, these facts lead to conditions of reproduction and enlargement not as good as those of spring-summer floods of major extent.

It was hypothesized in the Volga-Akhtuba floodplain that low spring temperatures in 2008 may have caused the reduced recruitment of fish and that a suitably high spring temperature needs to coincide with the flood for successful YOY fish recruitment. The shorter flood duration caused by the regulation of the Volga River increases the probability of a mismatch between flood timing and high temperatures and therefore might reduce fish recruitment success in the long term (Górski et al., 2010).

The short-duration floods that do not coincide with high temperatures have negative effects on fish communities in both floodplains.

4.3.3. Different responses to floods according to fish species

We have observed that long-distance migratory fish show a close dependence on the characteristics of floods. Those temporal differences in abundance and diversity are

associated with the strategy of reproduction of those fish species. They principally need long duration of floods that must coincide with proper temperatures and time of spawning which occurs in summer-autumn. Other groups with distinct strategy of reproduction have a lower dependence on floods.

Górski et al. (2011a) have shown that extensive flooding was particularly favourable for species characterised by large body size, delayed maturation, high fecundity, low parental investment and spawning once a year, such as *Esox lucius*, *Rutilus rutilus* and *Leuciscus idus* but the timing of spawning by eurytopic species was unrelated to flooding. Moreover, it was added that the main river channels act as the main source of water for the floodplain, but not for fish spawning. The majority of the spawning stocks originate in the floodplain water bodies.

Distinct responses of groups of species to flooding were recorded in the Paraná River compared with those in the Volga River. Most of fish species of the Volga River spawn into the floodplain differently from those in the Paraná River which most migrate from the floodplain to the channels to spawn. However, in spite of that different migrating comportment, this comparison shows that fish species which present similar reproductive characteristics such as high fecundity, low parental investment, spawning once a year and even large body show a close dependence to flood duration in subtropical as well as in the continental zone.

4.3.4. Two distinct origins of changing flood regime

Fish communities of the two floodplains are impacted by the reduction of water level after a relatively long-period.

In the Middle Paraná River, the last decade was characterized as a long-dry period compared with the previous years (Figure 17). Moreover, dams built in the upper reach of the Paraná River do not show significant influence on its middle reach. Thus decadal changes in flood regime were associated to climatic fluctuations (Garcia and Vargas, 1998; Espínola et al., unpublished).

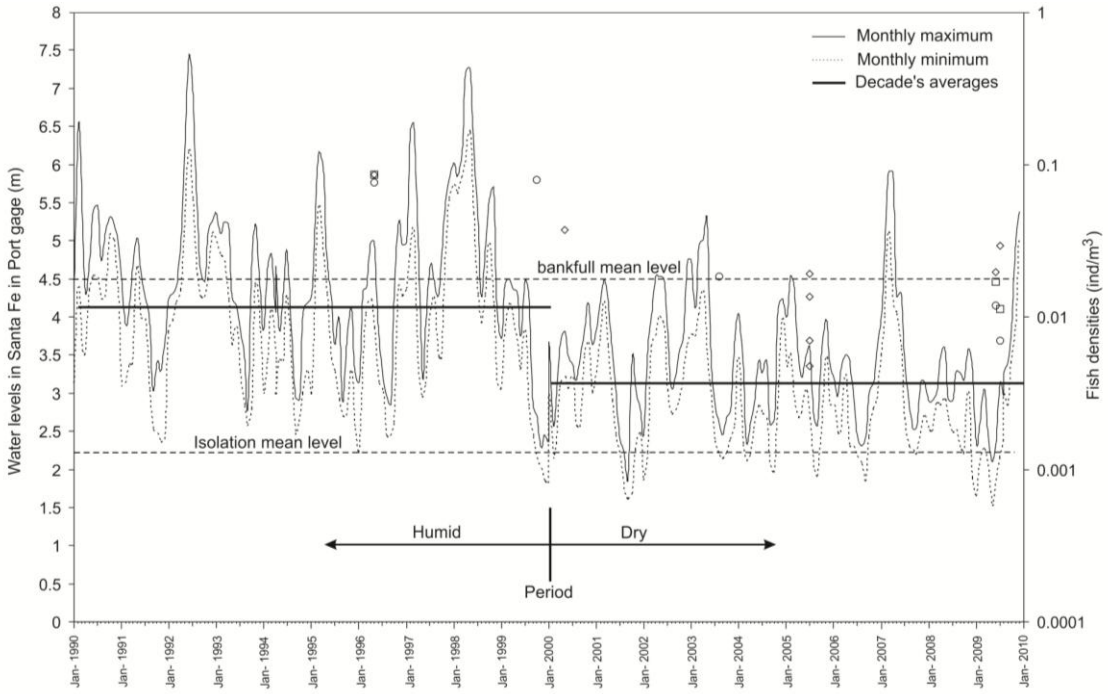

Figure 17: Monthly water levels of the Middle Paraná floodplain (maximum and minimum) during 1990–2009; "bankfull" refers to the level of channels and "isolation" refers to the level of lakes in the studied area Fish densities in meander (◊), confluence (o), and levee toe (□) scour holes are included. (from Espínola et al., unpublished).

Analyses of time series of discharges of the Volga demonstrated that the flood pulse magnitude in the Volga-Akhtuba floodplain has noticeably decreased due to construction in 1960 of the Volgograd Reservoir, at the entrance of the floodplain. Still, in spite of this hydrological control, a certain year-to-year variation in flood magnitude and timing has remained. Flood control is geared to maintain and regulate hydropower production and improve navigation, but fisheries benefits are also considered. Therefore, discharge management still provides significant spring flooding but reservoir regulation resulted in a considerable reduction of the flood magnitudes (Górski et al., 2011b) (Figure 18).

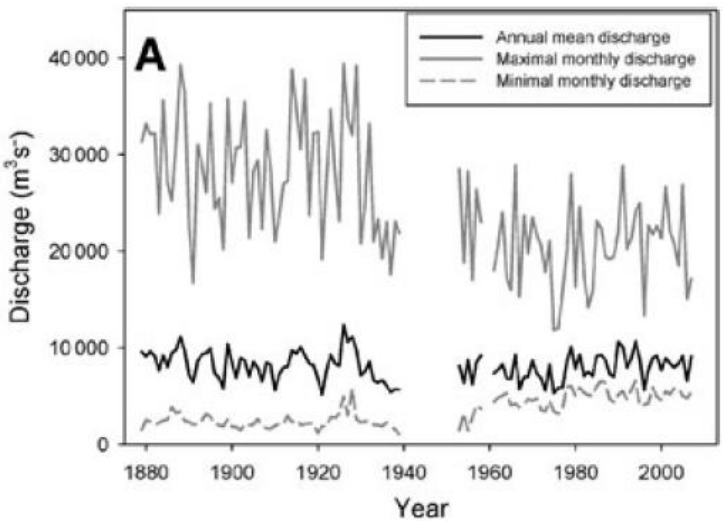

Figure 18: Mean annual discharge, monthly maximum and monthly minimum discharge for the period 1879-2006 (from Górski et al., 2010).

Following the conclusions that characteristics of the flood regime – specifically the flood pulses – determine the recruitment of fish populations in floodplain rivers, it can be inferred that fish community was reduced in both case when water level decreased. In scour holes of the Middle Paraná floodplain, Espínola et al. (unpublished) report larger densities of fish during the previous period to the last decade of very low water levels (Figure 3). In the Volga floodplain, despite of the significantly altered hydrological regime after damming, discharge management still provides significant spring flooding, preserving eco-hydrological functioning of the floodplain (Górski et al., 2011b). However, dam construction resulted in blocking of longitudinal fish migration routes and therefore led to a dramatic decrease in abundance of migratory species such as sturgeons in the Volga River (Khodorevskaya et al., 1997). Thus, the discharge management is effective only for none migrant species or doing primarily lateral migrations. In addition, a dam construction in the middle reach of the Paraná River would be dramatic for its ictiofauna, since many of its species are large migrators and need free migration routes for spawning.

4.4. Concluding remarks and importance of the flood pulses

This comparative study confirms the strong importance of annual flood pulses for fish recruitment in floodplain rivers, in temperate as well as subtropical zones. Species need specific environmental requirements for spawning and growing and they do not react identically to flooding. The long-duration of floods and high temperatures are key factors for fish species which are usually large sized, long lived and spawning once a year. Other species more opportunistic or less dependent on floods seem to adapt their spawning strategy to changes in flood regime, however floods are still determinant to carry the environmental conditions to complete their cycle of life.

As most of fish species reproduce into the Volga-Akhtuba floodplain and do not have a migratory comportment, the discharge management could be a solution to preserve its species diversity. In the Paraná River, a lot of species are long migrators and need free migration routes to spawn. Thus, the dam construction in the middle reach of the Paraná River would be dramatic for its ictiofauna.

Conclusions

The circular meander pool and the confluence scour hole do not present significant difference of fish abundance and richness, but significant temporal differences occurred along the studied period from 2009 to 2012.

The long-lasting pulse of major extent and coinciding with the higher spring-summer temperatures gave rise to the highest abundances and diversities of fish. The delayed pulse of minor magnitude and duration does not present the same positive effect on fish recruitment; fish abundance and richness both are lower. In floodless years, the fish population is considerably reduced.

The influence of floods varies according to the reproductive strategy of fish species. Long-distance migrants are closely dependent to the extent and timing of the flood pulse; short-distance migratory fish show a lower dependence on the characteristics of floods and seem to have distinct responses according to the kind of species; sedentary fish have also a lower dependence on floods and demonstrate a better persistence in abundance and diversity during the low water levels following the inundation of the alluvial plain.

The comparative study with the Volga-Akhtuba floodplain supports various conclusions advanced in this investigation and confirms that the integrity of the annual flood pulse, considering its timing, duration and magnitude, is crucial for fish recruitment in floodplain rivers, either in temperate or subtropical zones.

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