

Fish structure in channel networks of a large anabranching floodplain: effect of isolation/connection processes.

E. Abrial¹, L.A. Espínola¹, M.L. Amsler¹, A.P. Rabuffetti¹, F.G. Latosinski², R.N. Szupiany², M.F. Eurich¹, M.C.M. Blettler¹

¹ National Institute of Limnology (INALI, UNL-CONICET), Santa Fe, Argentina.

² Faculty of Engineering and Water Sciences, Littoral National University, Santa Fe, Argentina.

Key points

Weak relationship between local hydro-morphological features of floodplain channels and fish assemblages when surrounding lakes are available;

Scour holes in floodplain channels as refuges for fish when isolation stages approach;

Ecological relevance of the interaction of geomorphology and hydrology in a large anabranching floodplain.

Abstract

Channel networks of floodplain rivers are the main routes for water, sediment, organic matter and aquatic organisms between main channels and lakes, playing a substantial role in floodplain dynamics. Despite their importance most investigations in large floodplain rivers focus on main channels and lentic water bodies. This research deals with fish assemblage variations in different lotic sites (scour holes and straight reaches) of one of the many channels which shape the wide anabranching floodplain of the middle reach of the Paraná River. We considered the influence of environmental factors, such as hydro-geomorphological features and water quality of the channel, connections with surrounding lentic water bodies, seasonality, and interannual flow variations. The results showed two main ecological patterns closely related to floodplain connectivity. In-channel habitat heterogeneity has low influence on fish assemblages when minor channels are connected to significant flooded areas (sampling period 2013-2016). Spatial or temporal predictions of fish structure during these stages is not easy due to the interaction of several environmental

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factors. However, during very low water levels (winter of 2018) most lentic areas become isolated from the nearby channel network, and floodplain fish are forced to move into the numerous scour holes of the floodplain channels where water conditions resemble those in lentic habitats. Our work highlights the importance of in-channel characteristics of floodplain river networks and their crucial role for fish conservation, particularly during very low water stages.

Keywords: fish assemblages; lotic environments; geomorphic and hydraulic features; connectivity changes; Paraná River.

Introduction

As highly productive ecosystems, large floodplains account for a great portion of the global diversity of aquatic life (Ramsar Convention Secretariat, 2016). Successive expansion/contraction hydrological events are typical in such ecosystems and have been described as strong drivers of life cycles for a wide range of aquatic and terrestrial organisms (Junk et al., 1989; Ward & Tockner, 2001). Regarding fish, many species are well adapted to temporarily inundated floodplains where they breed, feed and grow rapidly during highly productive periods (hot moments; Wantzen & Junk, 2006). However, though heat is generally a favorable condition for fish, floods coinciding with increasing temperatures are critical for the preservation of fish communities in many floodplain-river systems worldwide (e.g. King et al., 2003; Górski et al., 2011; Rabuffetti et al., 2016).

Channel networks are crucial for the ecological integrity of floodplain rivers because they maintain the connectivity of a diversity of water bodies not only with the main channel, but also with floodplain channels of a different hierarchy (Ward & Stanford, 1995; Drago et al., 2003). They have been described as fish refuges when surrounding flooded areas dry up, and as migratory routes to accomplish reproductive, thermal or trophic migrations (Junk & Wantzen, 2004).

Surprisingly, while fish assemblages have been thoroughly studied in a wide range of floodplain lentic water bodies, few investigations have been done within the channel network of large floodplains. This knowledge gap may be explained in part by the fishing difficulties associated with deep and fast-flowing waters (Persat & Copp, 1990). But as most natural floodplains worldwide do not exist anymore, anthropogenic impacts seem to be the principal

factor explaining such a situation (more than 90% of European and North American floodplains are functionally extinct; Tockner & Stanford, 2002).

Fish assemblage structure in floodplain channels (e.g. composition and relative abundance) is expected to vary since such environments are usually highly dynamic due to erosion and sedimentation processes that continuously change their morphology (Herrero et al., 2011; Blettler et al., 2016). The irregular flow configuration interacting with morphology results in a diversity of patchy differentiated sections (Drago et al., 2003), which probably leads to different fish assemblage structures. Thus, habitat selection by fish species is most likely to be affected by substrate texture and hydraulic variables such as water depth and flow velocity, as it has been commonly observed in streams and rivers (Gorman & Karr, 1978; Grossman et al., 1998; Blanck et al., 2007).

However, the expected spatial difference of fish assemblages due to in-channel patchy functional habitats should also be modified by the lateral exchanges between lentic and lotic environments of the floodplain (i.e. between lakes and channels). Hence, hydrological connectivity becomes another key variable to consider in this topic, since fish leave or enter the system through lateral migrations within floodplains during expansion or contraction events (e.g. Bonetto et al., 1969; Fernandes, 1997; Winemiller & Jepsen, 1998; Wantzen et al., 2002).

As fish behavior is expected to be affected by several in-channel environmental variations, we carried out a study designed to address the interplay between main environmental drivers (water quality, hydraulics, geomorphology and hydrology) and fish assemblage structure in a floodplain channel network taken to be representative of large floodplain-river systems. We selected a sector of the large anabranching floodplain of the middle reach of the Paraná River. In this zone, many connections exist between lentic and lotic environments, conferring a high degree of connectivity to the system (Drago, 1980; Abrial et al., 2019). The permanent or temporary character of those connections depends on the frequency, magnitude and duration of the flood and drought pulses (Drago et al., 2003).

In line with the concept of floodplain system dynamics (Thomaz et al., 2007), we hypothesized that during high water levels, similarity between in-channel fish structures increases because of major connections between floodplain habitats (homogenization effect). In contrast, during low water stages fish dispersion within the floodplain is reduced (isolation effect), the influence of in-channel habitat heterogeneity increases, and spatial differences of

fish assemblages becomes important as a result of processes related to local hydraulic conditions.

Methods

Study area

With a huge drainage area of 2,400,000 km², the Paraná River drains a variety of landscapes and climatic regions in Brazil, Bolivia, Paraguay, and Argentina. It is ranked ninth among the largest rivers in the world according to its mean annual discharge to the ocean (18,000 m³/s; Latrubesse, 2008). From the Paraná-Paraguay rivers' confluence to the south of Rosario City (27°25' S to 33° S), the middle reach of the Paraná River presents a large floodplain crossing over more than 600 km and covering around 20,000 km².

We studied an area of one of the five main geomorphic units of the middle reach, the *tributary deltas* (see classification in Iriondo, 2007). The floodplain presents an anabranching pattern, i.e. a system of numerous channels characterized by vegetated or otherwise stable alluvial islands that divide flows at discharges up to bankfull (Nanson & Knighton, 1996).

The channels are relatively small (around 50 m in width) but deep and fast flowing, maintaining permanent connections with the parent river and its floodplain. They present a longitudinal profile typical for its alternation of straight reaches and scour holes. Scour holes are deep (reaching from 15 to 20 m in depth), formed by hydraulic processes generated in anabranch confluences, meanders or levee toes, whereas straight reaches present low and homogeneous depths (Ramonell et al., 2007; Herrero et al., 2011; Blettler et al., 2016).

Because of the ubiquity of straight reaches and scour holes in this geomorphic unit, we focused the study design on these environments (Fig. 1).

Environmental factors

Analysis of floodplain connectivity

First of all, we needed to clearly identify under which water levels lotic and lentic floodplain environments are connected or isolated. Daily water levels were supplied by the National Directorate of Waterways of Argentina (Santa Fe gauging station situated a few kilometers upstream from the study area, which provided with representative values of the water level fluctuations). Surfaces of flooded areas were calculated from nine satellite images (around 2 m spatial resolution) obtained from the historical data set of Google Earth Pro (methodology

from Abrial et al., 2018). Each of these covers the study area (15 km²; Fig. 1) at a specific date, and consequently at a specific hydrometric level (HL = 2.05; 2.3; 2.7; 3.2; 3.4; 3.6; 4.0; 4.5 and 6.4 m). From the QGIS software, we georeferenced each image and digitized the contour of the permanent channels (lotic environments) and the flooded areas (lentic environments). Then, for each image we calculated the number and the area of lentic environments connected to the permanent channels. In this way, we obtained a characterization of the increase of the floodplain connectivity along the gradient of water levels.

Sampling and analysis of water quality

As spatial or temporal variations in water quality were expected to trigger some structural changes in fish assemblages, we made routine measurements at sites 1, 2, 3 and 4 (Fig. 1) in each sampling period. We recorded water conductivity (K, $\mu\text{S}/\text{cm}$), superficial dissolved oxygen (SDO, mg/L), pH, water temperature (T, °C), and water transparency from Secchi depth (Tr, m). As the assumption of homoscedasticity was not verified, we used a non-parametric analysis of variance (Kruskal-Wallis' test) to analyze the spatial and temporal variations of each parameter. In the following, when applying non-parametric analysis of variance, we refer to Kruskal-Wallis' test.

Measurements and analysis of hydro-morphological characteristics

Hydro-morphological surveys were performed with a Teledyne RDI Acoustic Doppler Current Profiler (ADCP) working at a frequency of 1200 kHz. Because the ADCP was deployed from a moving vessel, it was linked to a Leica real-time kinematic differential global positioning system (RTK DGPS) to provide horizontal positions with an accuracy of about ± 0.02 m at approximately 1 Hz. More details regarding equipment operation are available in Gordon (1989), Szupiany et al. (2007) and Mueller & Wagner (2009).

In order to obtain a general overview of the hydro-morphological characteristics of the Catarata stream, the bathymetry and the intensity of flow velocity measurements were sampled for the whole channel from upstream site 1 to downstream site 2, realizing series of cross-section measurements spaced 30 m apart. Then, we made detailed measurements of streamwise flow magnitude (primary velocities) at each sampling site (1, 2, 3 and 4; Fig. 1) during distinct hydrological conditions (12 periods of measurement covering water levels from 2.3 to 5.35 m). To obtain representative values of the time-averaged velocities, four

repeated transects were recorded at each cross-section, subsequently averaged (according to Szupiany et al., 2007), and processed by using the Velocity Mapping Toolbox (Parsons et al., 2013).

To compare velocity patterns between the cross-sections of the four sampling sites, we undertook linear regressions of primary velocities in relation with discharge increase. We used Kruskal-Wallis' test and performed Pairwise Wilcoxon Rank Sum Tests to check the significance of differences observed between flow velocities at the sampling sites.

In-channel fish assemblages

To realize samplings during connection and isolation periods of the floodplain, we planned a study design along several years (from 2013 to 2016) covering in detail fish assemblages at four sites of a permanent channel. Isolation periods occurred only twice but lasted a few days and consequently, fish samplings during such conditions were not possible. In the winter of 2018, a significant isolation period occurred. The ephemeral character of the hydrological event prompted us to reorganize sample design in order to quickly respond to it (since the previous sampling period had ended, it was not possible to undertake the same design in such a short period of time). The methodology used to analyze the two fish sampling periods is presented below.

Floodplain connection conditions (2013-2016)

Fish assemblages were analyzed in two scour holes (1, 2) and two straight reaches (3, 4) of a permanent floodplain channel (the Catarata stream; Fig. 1), repeating the same methodology ten times from 2013 to 2016. Sampling was undertaken each year at the same period (end of March/beginning of April, end of July/beginning of August and December). Only the 2016 March/April sample was undertaken a month later. Fish were collected with gill nets of stretched mesh size (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm between opposite knots), covering an area of 180.9 m², exposed over 24 hours and checked every 8 hours. On two occasions, collection of fish at site 3 was not feasible, consequently site 4 was sampled twice, in two different locations. All specimens were anaesthetized with 5% benzocaine and sacrificed. Easy-to-identify specimens were processed in the field. Other fish were preserved in 10% formalin, identified in laboratory with the available keys of the Paraná River basin and deposited at the fish collection of the National Institute of Limnology (INALI, UNL-CONICET), Santa Fe, Argentina. Note that we assigned in the text *summer* for samples

undertaken in December, *autumn* for those undertaken in March/April and *winter* for those undertaken in July/August.

We used a non-parametric multivariate analysis technique (PERMANOVA: Anderson, 2001) to analyze differences between fish assemblage structures of scour holes and straight reaches. For this purpose, we applied a permutational analysis ($n = 999$) to the dissimilarity matrix of Bray-Curtis, which is defined from the abundance of each species caught per site and sampling date. Because some environmental factors were expected to affect fish assemblage structures too, we analyzed whether differences between fish assemblage structures exist according to the influence of the following factors: seasonality (summer, autumn, winter), year (2013, 2014, 2015, 2016) and floodplain connectivity (low connectivity, high connectivity, overflow; classification based on the result part *Connectivity patterns*).

Because no spatial differences were found between fish assemblages, we considered analysis at species level, i.e. some species may prefer scour holes or straight reaches but without a significant modification of the fish assemblage structure. For that, we used the analysis of the species indicator value (Dufrière & Legendre, 1997), which combines the mean abundance of a species and its frequency of occurrence within a group of sites considered (scour hole or straight reach). A high indicator value combines a high mean abundance of a species within a group compared with the others (specificity) and the presence of this species in most sites of the group (fidelity). The data matrix was created from CPUE values per species at each site and sampling date from 2013 to 2016.

Floodplain isolation conditions (winter of 2018)

In order to respond rapidly to the momentary character of the hydrological event, we first made measurements with a single-beam echo sounder (Raytheon model DE-719C; 208 kHz) to detect fish echoes in scour holes and straight reaches. We sampled seven scour holes and five straight reaches of the Catarata channel (Fig. 1) at a water level of 2.1 m (2 August 2018), repeating three transects at each cross-section.

Fish densities at each sampling site were computed by applying the echo trace method, i.e. the fish echoes that appear in an echogram as echo traces were counted and divided by the sampled volume of water (e.g. Forbes & Nakken, 1972; Tablado et al., 1988; Espínola et al., 2014). By knowing the distance travelled by the boat, the angle of the transducer beam, and

the depths as given by the echograms, the sample water volume of each transect can be calculated from the following formula (Mathisen, 1980; Burczynski, 1982):

$$V_i = \left(\frac{1}{3}\right) * D_i * \operatorname{tg}\left(\frac{A}{2}\right) * (H_1 * H_1 + H_2 * H_2 + H_1 * H_2)$$

where: V_i : volume of transect i ; D_i : distance travelled by the boat at the given transect; tg : symbol of tangent; A : angle of the transducer beam; H_1 : initial depth; H_2 : final depth.

Differences of fish density and fish number between scour holes and straight reaches were analyzed from the Kruskal-Wallis' test.

Then, we repeated echo sounding measurements in sites 1, 2, 3 and 4 (Fig. 1) on 17 August (hydrometric level of 2.3 m), and simultaneously, we fished for a short time at each site in order to estimate the abundance and the kind of species detected with echo sounding. We used two 10 m long gill nets (50 and 60 mm between opposite knots) at each site, exposed during three hours at the place where echo sounding measurements recorded higher fish concentrations. On the boat, fish were identified at species level, measured (total and standard length) and returned back to their environment. This kind of methodology (i.e. four sampling sites close together, few gill nets and fish immediately returned to their environment) was preferred because it allows rapid samplings at each site comparable between them (same daily period of fishing, same sampling effort).

Fish abundances between isolation conditions (winters of 2013, 2014, 2015 and 2016) and connection conditions (winter of 2018) were analyzed. To compare the abundances during the connection period with the isolation one, we only used data recorded with gill nets of the same mesh sizes (50 and 60 mm between opposite knots). As fishing time was longer during the first period (diurnal fishing period from 8 a.m. to 4 p.m.), fish abundances were adjusted to 37.5% of the 8h-diurnal abundance to obtained equivalence with the 3h-diurnal abundance of the winter of 2018. By this way, we compared fish abundances from the same sites, the same gill nets, the same season and the same fishing duration. Nonetheless, it should be note that a sampling bias persists since fish activity changes during the day, and thus, the capture efficiency with nets will depend on the hour of fishing.

Finally, we provided fish abundance data in scour holes from echo sounding records undertaken for the same floodplain area during the isolation periods of the winters of 2005 and 2009 (data from Espínola *et al.*, 2014), and we compared them with echo sounding

measurements undertaken in the winter of 2018 (as the same methodology was used to analyze fish abundance).

All statistical analyses were implemented with the R statistical software (R Development Core Team, 2011), from the packages *vegan* (Oksanen et al., 2017) and *indicspecies* (De Caceres & Legendre, 2009). A significance level of $p < 0.05$ was adopted for every test.

Results

Connectivity patterns

For a water level of 2.3 m at the Santa Fe port gauge, the areas of floodplain lakes and lotic environments are comparable (116 Ha vs 98 Ha, respectively; Figs. 2 and 3). The flooded area reduces abruptly below that level (from 116 to 41 Ha between 2.3-2.05 m), leading to the isolation of most lentic habitats available for fish within the plain. On the other hand, from 2.3 m up, floodplain lentic areas progressively increase until 3.5 m approximately. At higher water levels, a marked increment is observed until 4.5 m, and flooded areas connected to the channels increase from 10 to 85% of the total area (Fig. 3). On the basis of these analyses, four main connectivity patterns are highlighted: isolation conditions (water levels < 2.3 m), low connectivity conditions (2.3 m $<$ water levels < 3.5 m), high connectivity conditions (3.5 m $<$ water levels < 4.5 m) and overflowing conditions (> 4.5 m).

Spatiotemporal changes in water quality

Water quality values measured at each sampling showed small spatial variations but changed significantly through time for every physicochemical parameter (Kruskal Wallis' test; $p < 0.001$; Fig. 4). However, concentrations for every parameter match typical values reported for the Paraná River (Depetris & Pasquini, 2007). Within this context, some tendencies can be observed: a decrease of conductivity and pH and an increase of transparency at higher water levels; a reduction of water temperature and larger dissolved oxygen contents from summer to winter. Note also that water remained turbid during all the sampling period with a maximum transparency of 45 cm.

Hydraulic and geomorphologic characteristics

The Catarata stream has an irregular channel with straight zones of relatively uniform width and depth and with deeper and wider zones in meanders and confluences. At mean water levels, channel widths range between 50 and 150 m, depths vary from 2-3 m in straight

reaches to 12-17 m in scour holes (Fig. 5a). Figure 5b shows low velocity areas (less than 0.3 m/s) in scour holes and near the channel banks where macrophyte expansion increases the flow resistance. Higher velocities were recorded for shallow depths along the straight reaches.

The discharge rating curve at the entrance of the study area is shown in Figure 6a. Note that the discharge varied with water levels from 50 m³/s (around 2 m at Santa Fe gauging station) up to nearly 300 m³/s (5 m at SF gauging station). Scour holes (1 and 2) and straight channel reaches (3 and 4) are hydro-morphologically different environments. Larger primary velocities were recorded for every discharge in the straight reaches, compared with the scour holes (Fig. 6b). Detailed streamwise flow magnitude recorded in the four sampling sites for different water stages are presented in Figure S1. Note that the majority of discharge and higher primary velocities at sections 1 and 2 flows through the deeper regions. Close to the banks, primary velocities decrease and backwater zones develop. Flow velocity fields are more homogeneous in straight reaches. As mentioned above, the lowest primary velocities are found close to the banks in a region with a higher flow resistance due to the vegetation cover. Small backwater areas with a substrate rich in organic matter may be found along the banks.

In-channel fish assemblages when floodplain environments are connected

We caught 1527 specimens from 2013 to 2016 in the Catarata stream belonging to 75 fish species (Table S1). The difference in fish assemblage structures between sampling sites was not significant (PERMANOVA; F. model = 1.41; p = 0.067). On the other hand, we detected significant variations of fish structure between summer, autumn and winter (PERMANOVA; F. Model = 2.36; p < 0.001), low, high and overflow degrees of connectivity (PERMANOVA; F. Model = 1.93; p = 0.002) and years (PERMANOVA; F. Model = 2.65; p < 0.001) and significant interactions were also observed between the three factors (PERMANOVA; p < 0.01 for each interaction). Summarizing, the scour holes and straight reaches appear to be two distinct environments with peculiar hydro-morphologic features but with rather similar fish assemblages.

At species level, the analysis of the species indicator value showed that 43 out of 75 species caught in the Catarata stream did not present specificity or fidelity values with any type of lotic environment. These were among the most abundant species representing 76% of the total catches. For the 32 remaining species, 14 were only caught once during the whole

period of study (rare species). Most of the other 18 species did not show significant values of indicator species (because of their low values of fidelity). However, 9 species showed a high relation of specificity with the two scour holes and 9 species with the two straight reaches (Table S2). In these latter sites, 5 species were small-sized Characiformes from the Curimatidae and Characidae families, 3 Siluriformes and 1 Atheriniformes whereas in scour holes, 8 species were Siluriformes from the Auchenipteridae, Loricariidae, Pimelodidae and Doradidae families.

Scour holes relevance during isolation conditions

By echo-sounding at isolation stages (very low hydrometric levels between 2.1 and 2.3 m during the winter of 2018), we observed fish echoes in the scour holes significantly higher than in the straight reaches of the Catarata stream (Kruskal Wallis' test; fish density: $p < 0.001$; fish number: $p < 0.001$). An example of echograms supporting these results is shown in Figure 7.

Numerous fish echoes were recorded in all the scour holes during the two field surveys. The average number of fish echoes recorded in the 27 cross-sections was 49 (lowest and highest values: 19 and 121, respectively; Fig. 8). On the contrary, we observed only one echo trace in two cross-sections of the straight reaches. Short-duration fishing in the four sample sites showed similar results. Higher fish abundances were recorded in scour holes than in straight reaches (22 fish in sites 1 and 2 against 3 fish in sites 3 and 4; Table S3). All were common species with sizes corresponding to young individuals, most of them from 1 to 2 years old. The most abundant species belonged to the Anostomidae family (*Megaleporinus obtusidens* and *Schizodon platae*).

Comparing the previous fish abundances with the abundances of the winter samples made at higher hydrometric levels (2013, 2014, 2015 and 2016), we observed that they were much higher in scour holes during isolation conditions, while they were similar in straight reaches. Indeed, considering a 3h-fishing effort with two 10 m long gill nets, the mean values of the winter catches from 2013 to 2016 were 0.8 specimens in scour holes and 2.8 in straight reaches, whereas the catches during the winter of 2018 showed 22 specimens in scour holes and 3 in straight reaches.

Available echo-sounder measurements in three scour holes of the study area during the last occurrence of floodplain isolation conditions (winters of 2005 and 2009) showed high

abundances of fish in all cases. Fish densities were lower than those observed in 2018, but the higher water volumes sampled may explain the lower densities, e.g. the highest number of fish observed in scour holes (52 in average) recorded in 2009 but with a much lower density than in 2018 (Table 1).

Discussion

Floodplain environments in large rivers are dynamic systems continuously modified by changes in hydrologic connectivity (Amoros & Roux, 1988; Junk et al., 1989). In this study, we identified the 2.3 m of water level (at Santa Fe gauging station) as an inflection point: below this level, isolation of most floodplain lakes occurs, above it a greater flooded area is available for fish (Figs. 2 and 3). This environmental distinction between connection and isolation conditions has been the basis for explaining fish assemblage distribution within the minor channels of the study area (Fig. 9). We discuss below the main ecological phenomena intimately related to the environmental factors associated with both floodplain conditions.

Low in-channel spatial heterogeneity of fish assemblages during connection stages (HL > 2.3 m)

The anabranching pattern of the geomorphological unit *tributary deltas* displays a myriad of minor channels that present two main types of environments: deep scour holes with low velocity flows and shallow fast-flowing straight reaches (Fig. 5). The clear distinction of substrate and hydro-morphological conditions between them (Figs. 6 and S1) was expected to cause different fish assemblages, since spatial variations of lotic fish communities are known to be influenced by substrate, flow velocity and water depth over a broad range of rivers worldwide (e.g. Lamouroux et al., 2002; Paxton, 2008; Leal et al., 2011).

However, during the connection phases of lentic and lotic environments (i.e. available flooded areas up to 100 Ha; Figs. 2 and 3), fish assemblage structure did not change significantly between the different channel sites. Environmental factors such as seasonality, floods and connection/isolation processes had a greater influence on the fish structure of the floodplain channels. Indeed, interannual variability of flood characteristics and the associated connectivity patterns of the floodplain result in significant temporal changes in fish recruitment (Abrial et al., 2018), fish body condition (Rabuffetti et al., 2017) and fish abundance and species richness (Espínola et al., 2016; Abrial et al., 2019) in the study area.

In addition, it is well-known that seasonality modifies fish assemblage structure as fish activity mostly depends on the temperature gradient (Helfman et al., 2009).

Summarizing, the combined effects of hydrology and temperature account for the high temporal variability of lotic fish assemblages and largely hide a possible in-channel fish habitat selectivity. More than half of all species were uniformly distributed in scour holes and straight reaches. Most are abundant and vagile species that, besides inhabiting lotic habitats, typically use flooded areas for feeding activities (Almirón et al., 2015). This weak spatial distinction of fish assemblages is likely to be related to the homogenization processes that occur when the connectivity increases in floodplains (Thomaz et al., 2007). In-channel spatial heterogeneity is consequently hardly evident at the assemblage scale during these conditions.

However, when considering the species functional traits, some discernible relationships to the hydro-morphological features of the channels surface. Most species with high values of specificity caught in scour holes belonged to Siluriformes (Table S2). Individuals of this order have primarily tactile and chemical orientation and feeding habits in connection with the river-bottom conditions (Arratia et al., 2003). Hence, the larger abundance of Siluriformes would be explained by the typical high water turbidity of lotic habitats in the Paraná River (Fig. 4) together with low flow velocities and backwater sectors allowing particulate organic matter to deposit. Moreover, bank erosion in scour holes (Blettler et al., 2016) prevents the settlement of rooted macrophytes and, thus, the existence of refuges for preys. To this is associated the presence of large predators, e.g. catfishes (*A. inermis*, *A. militaris* and *L. pati*), and piranhas (*P. nattereri*).

Bank erosion in straight channel reaches with an approximate uniform flow (Fig. S1) is rather limited, which allows colonization processes of rooted macrophytes such as *Panicum elephantipes* and *Polygonum punctatum*. Filtration effects of vegetation roots retain significant amounts of sediment (Marchetti & Ramonell, 2014), increasing water transparency in small and densely-vegetated areas close to the river banks (Poi de Neiff et al., 1994). Species with large-sized eyes –typical of visually oriented fish–, are commonly found in vegetated and clear waters (e.g. families of Curimatidae, Characidae and Cichlidae; Scarabotti et al., 2011). Small preys also seek refuge against predators in densely-vegetated areas and find excellent reproductive sites to spawn on vegetation (Winemiller & Jepsen, 1998). The larger abundance of small-sized characid and curimatid species (Table S2) with a visually oriented strategy has a close relation to the features of these functional zones.

Fish refuges during isolation conditions (HL < 2.3 m)

Few floodplain lakes remain connected to the minor channels when water levels are lower than 2.3 m in the study area (Figs. 2 and 3). Most fish are forced to leave the reduced lentic areas and to look for better conditions in permanent waters, as it is common in floodplain ecosystems (Junk & Wantzen, 2004). Straight channel reaches maintain rather high primary flow velocities under such conditions (mean: 0.6 m/s, approximately; Figs. 6 and S1) and barely favor species that usually colonize lentic habitats. On the contrary, scour holes offer more suitable conditions with nearby stagnant water, especially at their boundaries (Figs. 6 and S1).

Consequently, the scour holes of the study area harbor significant fish concentrations during such floodplain isolation periods (Figs. 7 and 8), i.e. these lotic habitats resemble the frequently observed stream pools where fish refuge (Beesley & Prince, 2010; Espírito Santo & Zuanon, 2017). There, most fish were young individuals belonging to vagile species that typically utilize floodplain habitats (Table S3). For example, the herbivorous *S. platae*, whose body condition significantly increases with the occurrence of floods (Rabuffetti et al., 2017), was the most abundant. The other species, such as *M. obtusidens*, *P. lineatus*, *P. curviventris*, *S. brasiliensis* and *P. maculatus* are also typical migrants that use the flooded areas to grow during their early life stages (Bonetto, Pignalberi & Cordiviola, 1965; Sverlij et al., 2013).

It is therefore very likely that most fish concentrating in scour holes during isolation conditions came from the surrounding floodplain lakes. This is supported by the significant higher fish abundances observed in scour holes during the winter of 2018 (isolation conditions) than in all the other sites sampled during the winters from 2013 to 2016 (connection conditions). It must be noted, nonetheless, that the difference in the fish sampling methods utilized in the study may mitigate the strength of the conclusions on the opposition between connection and isolation periods. In this sense, future researches comparing the two periods based on standardized sampling efforts would be relevant to confirm the ecological implication of scour holes observed in this study.

Implication of the historical increase of low water levels in the middle reach of the Paraná River

When the last three more prominent isolation periods occurred in the middle reach of the Paraná River (2005, 2009, 2018; Table 1), the high concentration of fish in scour holes

supports the previous statement about the role of those habitats for floodplain fish during low water stages (Fig. 9). As the floodplain is located in a subtropical-temperate region in Argentina, its channel network does not totally dry during very low water stages unlike floodplain rivers in arid-zones where more extreme drought conditions cause the waterholes to become the ultimate refuge for fish (Arthington et al., 2010; Arthington & Balcombe, 2011). However, even though fish always have lotic environments to colonize during isolation conditions, the observation that they concentrated in deeper waterholes regardless confirms the ecological importance during isolation.

In addition, longer, more prominent and frequent low water stages occurred in this reach of the Paraná River before the 1970's. Indeed, whilst floodplain isolation periods longer than 30 days had a yearly recurrence from 1930 to 1973 (42 isolation periods; Fig. 10b), they only occurred every four years from 1974 to 2018 (11 isolation periods; Fig. 10c). Moreover, long-time isolation of the floodplain, which was something common before the 1970's (e.g. 28 isolation periods lasted more than 60 days from 1930 to 1973, 19 of which lasted more than 100 days; Fig. 10b), is something atypical nowadays (only 2 isolation periods have lasted more than 60 days since 1974; Fig. 10c).

Such a considerable increase of low water levels (1.4 m higher; Fig. 10a) has been attributed to the sustained increase of damming in the upper Paraná basin (Quirós, 1990). The biological diversity of the upper basin –in particular the fish fauna– has been significantly altered by the construction and exploitation of dams (Agostinho et al. 2008). In the middle reach, the implication for floodplain ecosystem dynamics has tended to be ignored since dam impoundment is located many hundreds kilometers upstream. However, floodplain ecosystems totally depend on the hydrological dynamic (Junk et al., 1989; Ward & Tockner, 2001), and it is surprising that possible ecological consequences triggered by such historical changes have so far rarely been considered in the middle reach of the Paraná River.

Here, we showed the effects on a specific ecological process, i.e. the ecological relevance of scour holes was determinant for fish preservation before the 1970's (typical refuges during the frequent isolation periods) whereas scour hole relevance is reduced nowadays. However, the increase of low water levels (which is the result of the reduction of the frequency and magnitude of the contraction/expansion events) is likely to have altered the natural dynamic of the floodplain, in the middle reach of the Paraná River. It is important to further investigate this kind of ecosystem given the ecological consequences of upstream water exploitation.

Concluding remarks

The structural organization of fish assemblages in minor channels of the anabranching Paraná River floodplain is driven by the interactions of several factors. Depending on the spatial and temporal scale considered, the main factors such as seasonality, in-channel hydro-morphological features and interannual flow variability (which influences floodplain connectivity patterns) affect fish assemblages differently. Predicting fish structure is, thus, a complex task.

Within this context, two main ecological patterns in the lotic habitats surveyed were identified: i) a weak relationship between the local hydro-morphological characteristics of habitats and fish assemblages when connectivity was relatively high (i.e. over $\approx 10\%$ of the floodplain lakes area available); ii) a high structural differentiation when isolation stages approach (i.e. less than $\approx 10\%$ of lakes area available in the nearby floodplain), with significant fish concentrations in scour holes while few fish remain in straight reaches.

These results highlight the complex dynamics of fish assemblages in lotic environments of wide anabranching floodplains. The typical myriad of changing minor channels that drain these types of large fluvial environments are the physical and ecological connections between main channels and lentic areas, i.e. they are crucial ways that enable vast colonization opportunities of a variety of floodplain habitats during rising waters and lotic refuges for numerous species during very low water stages. The functional preservation of such ecosystems is thus critical, implying the conservation of their geomorphic complexities as well as their natural flow regime. The importance increases if due consideration is given to the fact that all the largest rivers of the world are surrounded by anabranching floodplains (Latrubesse, 2008).

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to develop the analyses of the study can be found in the free repository Hydroshare (<http://www.hydroshare.org/resource/497e6663b4d944999a00ce6336e38255>).

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Accepted Article

Table 1. Fish records in scour holes of the study area during three periods of the last two decades in winter and very low water levels. HL: Hydrometric level; N sh: number of scour holes measured with echo sounder; V: mean water volumes of scour holes sampled with echo sounder (standard error included); Fd: fish densities observed in scour holes; N fish: number of fish echoes observed in scour holes.

Date	HL	N sh	V (10^3m^3)	Fd (ind/ 10^3m^3)	N fish
08/2005	2.28	3	2.5±2.0	10.5±6.9	13.3±3.5
06/2009	1.98	3	4.0±2.5	15.7±4.1	52.1±51.4
08/2018	[2.1; 2.3]	10	1.1±0.7	75.5±76.3	49.3±27.9

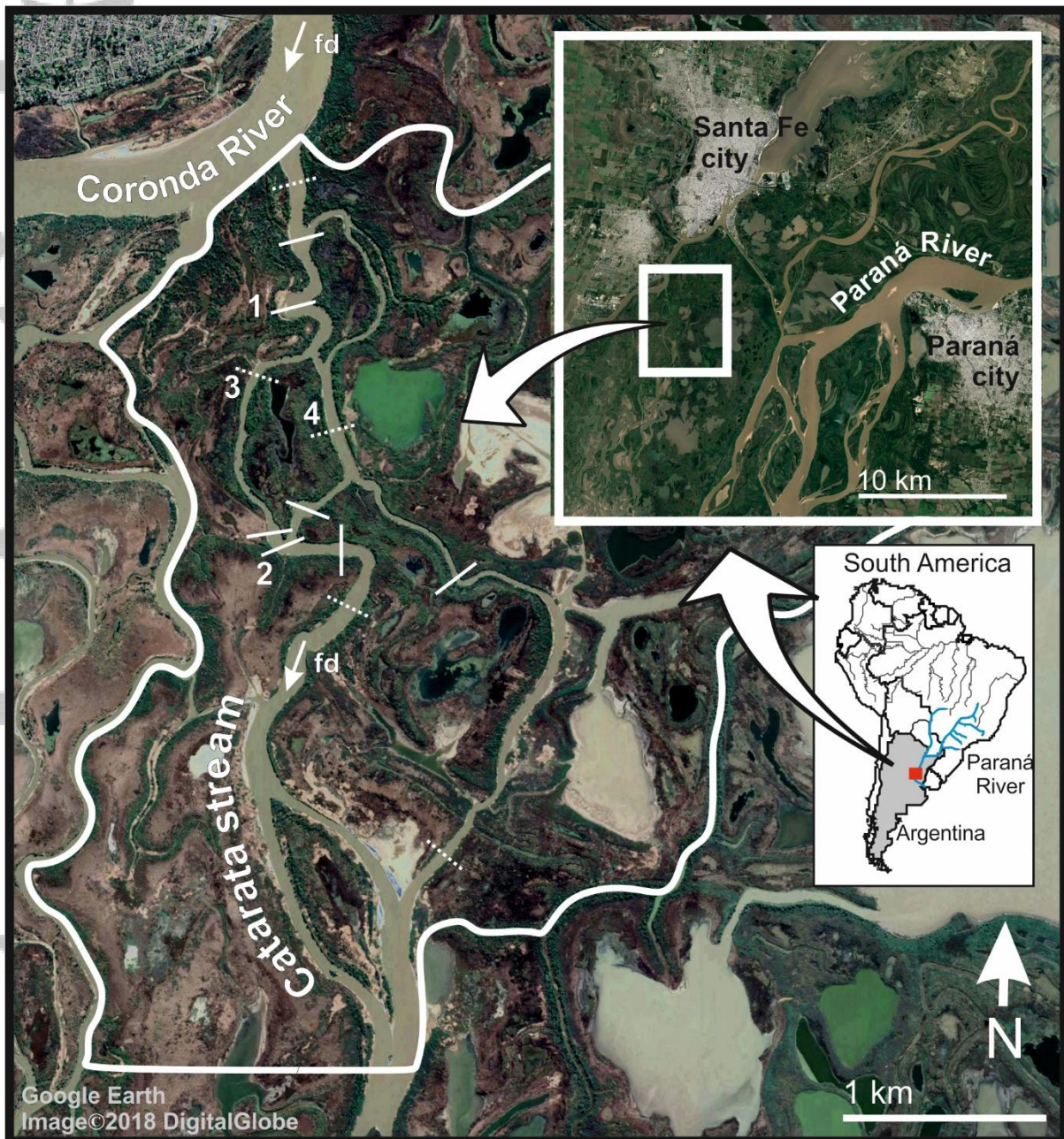


Figure 1. Anabranching configuration of the study area (white perimeter) dissected by the Catarata stream in the middle reach of the Paraná River. Hydrometric level of the satellite image: 2.05 m (Santa Fe Port gauge). Locations of cross-sections for fishing and hydraulic measurements: 1 and 2 (scour holes of a meander and an anabranch confluence, respectively), 3 and 4 (straight reaches). Locations of cross-sections for fish record by echosounding: white lines (scour holes), white dashed lines (straight reaches). fd: flow direction.

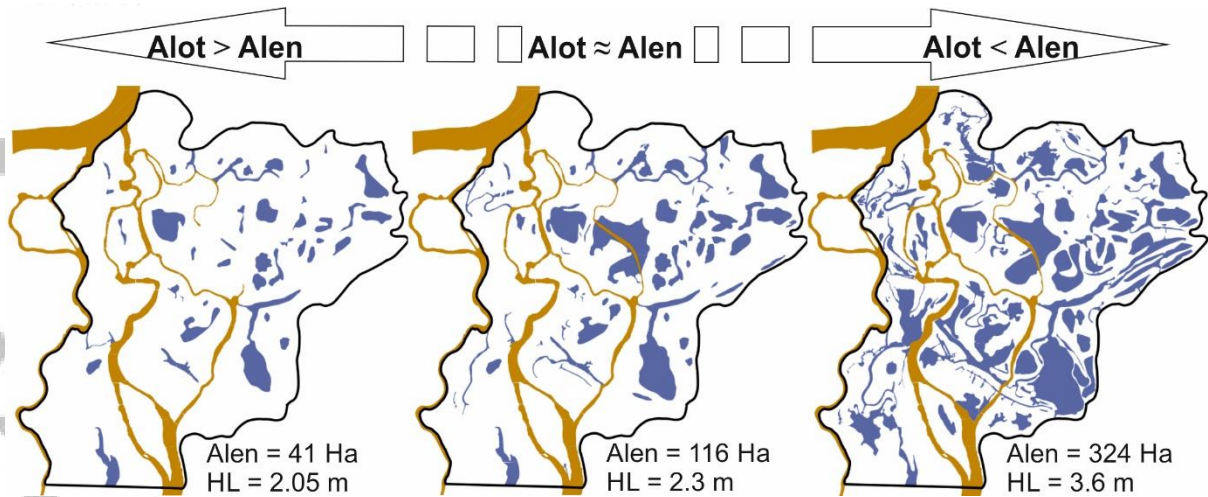


Figure 2. Changes of water surface in the study area highlighting different degrees of connectivity for three water levels (HL) in the Santa Fe port gauge. Alot: area of lotic environments; Alen: area of lentic environments connected to the lotic ones. Brown surface: lotic environments; blue surface: lentic environments. (Modified from Abrial et al., 2018).

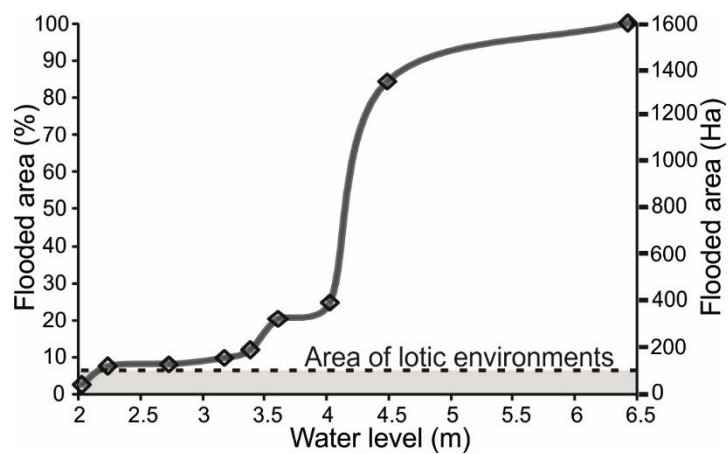


Figure 3. Variations of lentic areas with water levels in the study area of the floodplain. Dashed line: approximate area of permanent lotic environments.

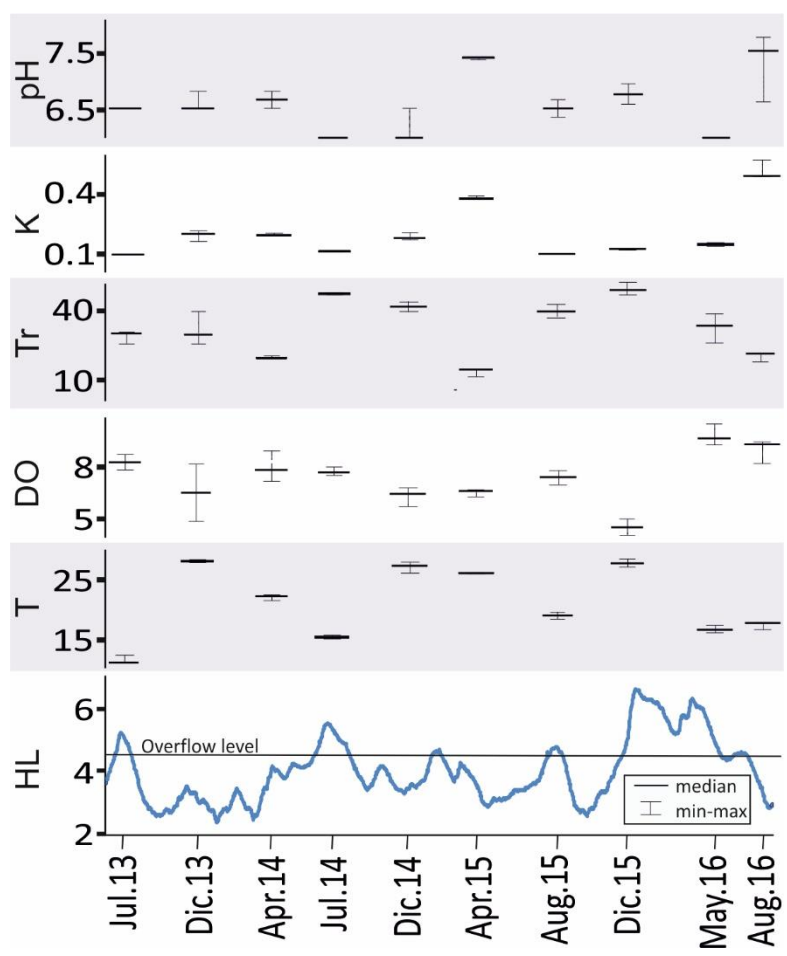


Figure 4. Temporal variations of minimum, maximum and median values of physicochemical parameters measured in the four sampling sites of the Catarata stream. Conductivity (K); transparency (Tr); dissolved oxygen (DO); temperature (T); hydrometric level (HL).

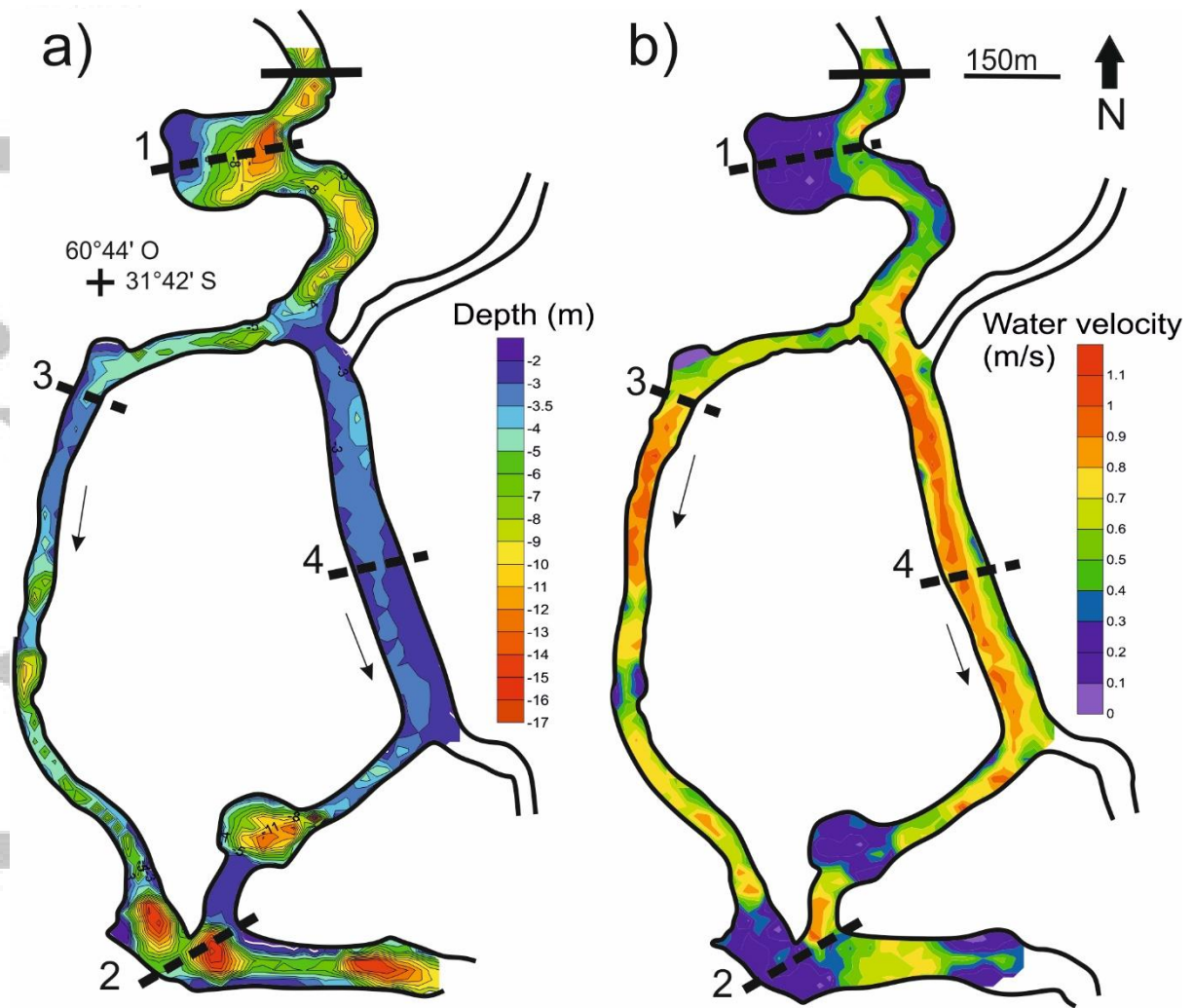


Figure 5. (a) Bathymetry and (b) mean streamwise velocity distribution of the Catarata stream. Black dashed lines: cross-sections where measurements of flow velocity structure were performed (1 and 2: scour holes; 3 and 4: straight reaches). Black line: cross-section where the discharge rating curve was measured. Hydrometric level: 3.5 m (Santa Fe port gauge). (Modified from Blettler et al., 2016).

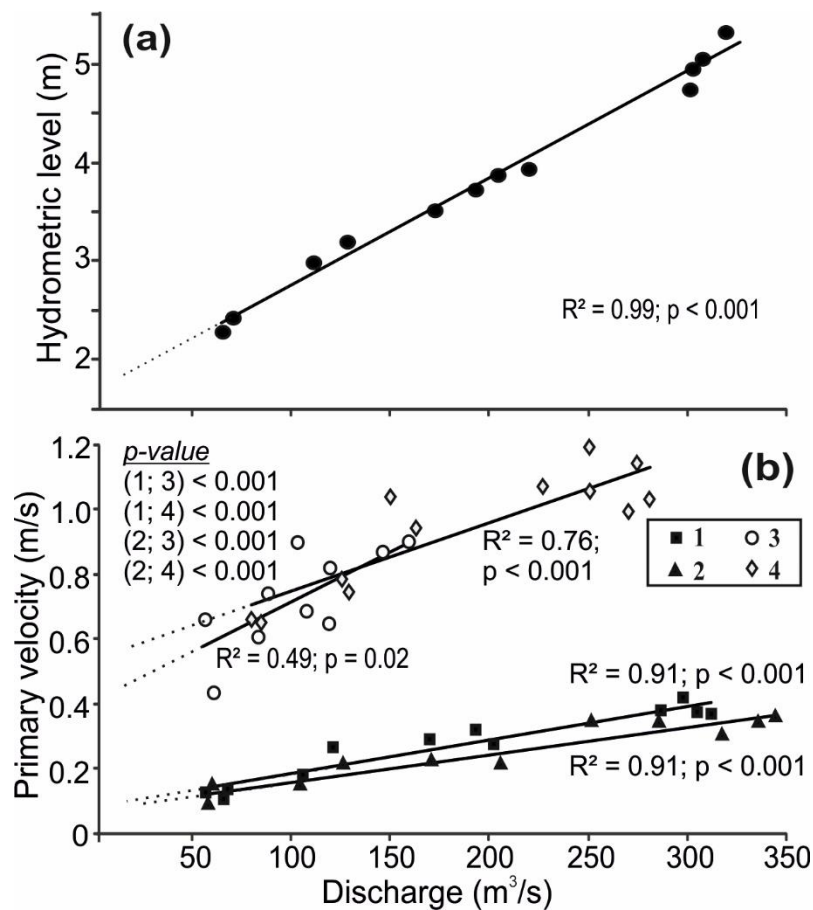


Figure 6. **a)** Discharge rating curve (see the location of the cross-section in Fig. 5); **b)** Variation of primary flow velocities with discharge in scour holes (1, 2) and in straight reaches (3, 4); *p*-value (Pairwise Wilcoxon Rank Sum Tests showing significant differences of flow velocities between scour holes and straight reaches).

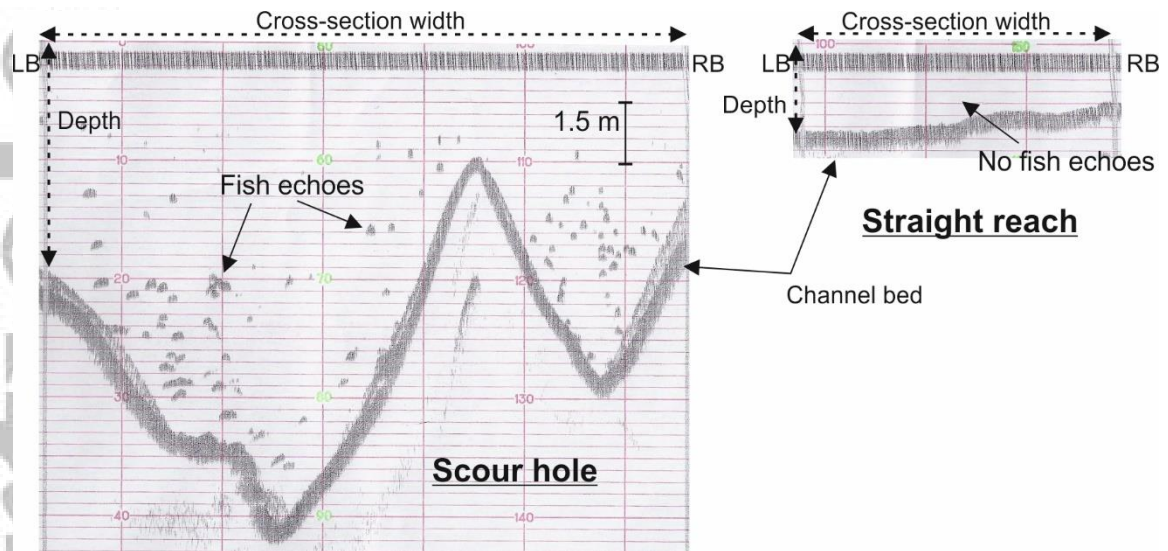


Figure 7. Echo-sounder chart in a scour hole and in a straight reach of the Catarata stream. Note the numerous echo traces in the hole denoting higher fish concentrations than in the straight reach where no echo trace was observed. LB: left bank; RB: right bank.

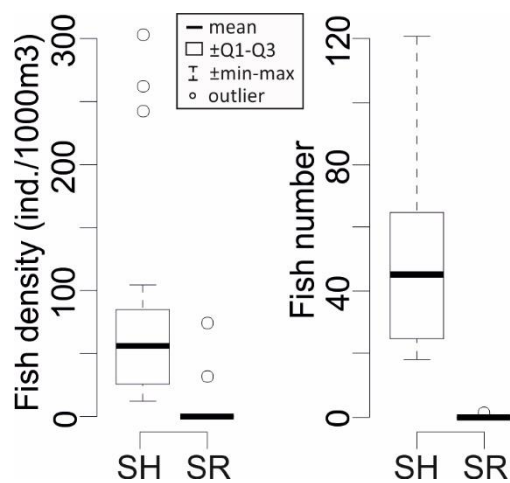


Figure 8. Fish density and fish number in scour holes (SH) and straight reaches (SR) estimated from the number of fish echoes observed in each echo sounder chart. Field surveys of 08/02/2018 and 08/17/2018 (hydrometric levels: 2.1 m and 2.3 m, respectively).

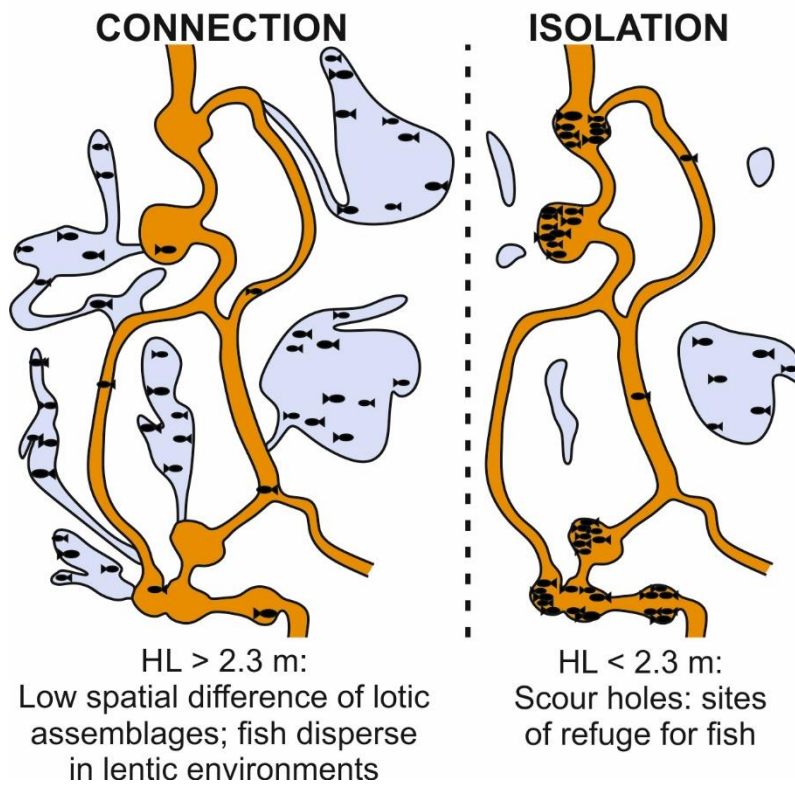


Figure 9. Ecological relevance for fish conservation of the interaction of geomorphology and hydrology in the large anabranching floodplain of the middle reach of the Paraná River. HL: hydrometric level; brown color: lotic environments; blue color: lentic environments.

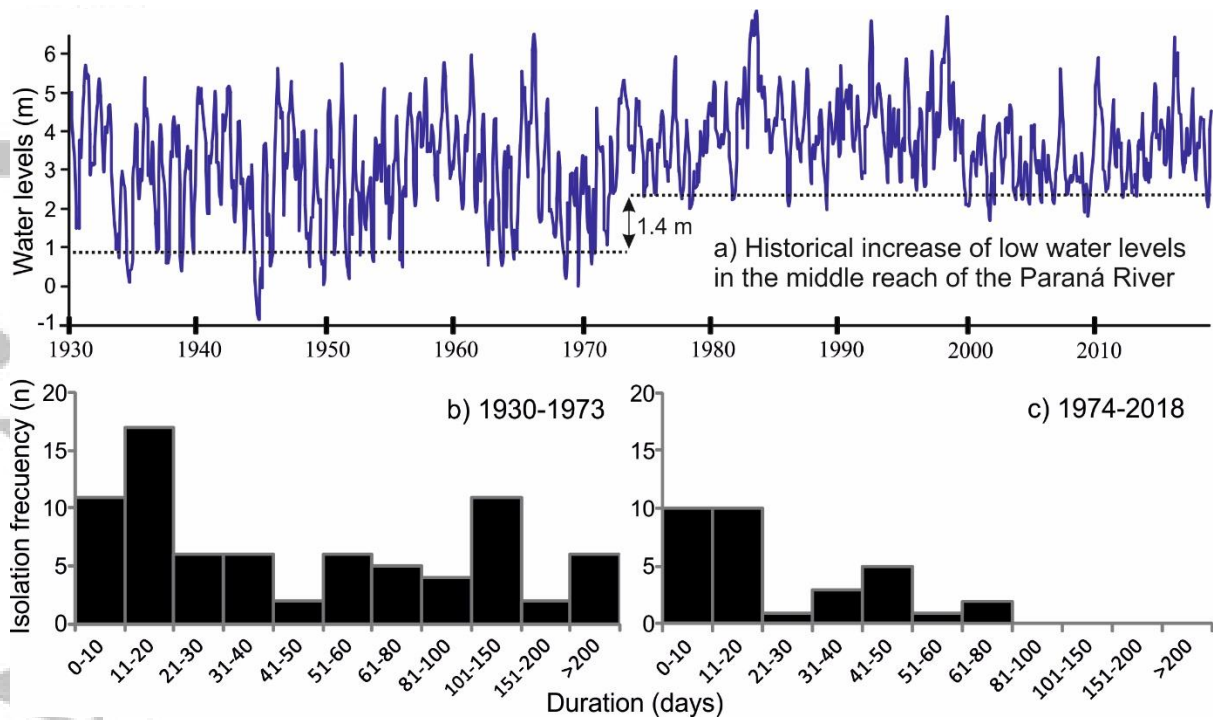


Figure 10. a) Monthly water levels registered in the middle reach of the Paraná River between 1930 and 2018 (from the Santa Fe gauge station). Black dashed lines show the mean value of the lowest water levels registered each year before (1930-1973) and after (1974-2018) the historical increase of low water levels; b) and c) number and duration of the floodplain isolation periods during the two hydrologic periods (floodplain isolation is considered when water levels are under 2.3 m at the Santa Fe gauge station).