**Interannual flow variability in a large subtropical-temperate
floodplain: a challenge for fish reproduction**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0579.R1
Manuscript Type:	Article
Date Submitted by the Author:	24-Apr-2018
Complete List of Authors:	Abrial, Elie; Instituto Nacional de Limnologia Espinola, Luis; Instituto Nacional de Limnologia Rabuffetti, Ana; Instituto Nacional de Limnologia Amsler, Mario; Instituto Nacional de Limnologia Wantzen, Karl; Cites Territoires Environnement et Societes
Keyword:	Hydroclimatic conditions, fish life history, recruitment patterns, natural floodplain
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
- 10
- 11
- 12
- 13
- 14
- 15
- 16
- 17
- 18
- 19

Abstract

Fluctuations of temperature and water levels are the two main drivers of aquatic life in river floodplain ecosystems. The large Middle Paraná River floodplain exhibits marked seasons and important interannual hydrological changes. Using a three-factor-based approach (fish reproductive traits, hydroclimatic conditions, floodplain recruitment patterns), we analyzed how fish life history evolves within this fluctuating environment. We observed that hydroclimatic conditions can be considered through three main interannual variations that prompt the most abundant Paraná species to adopt four different main reproductive strategies: (i) typical periodic strategists are dependent on large spring-summer floods and juveniles strongly predominate in the floodplain when such a condition occurs; (ii) periodic-opportunistic strategists are associated with floods, regardless of their timing; (iii) periodic-equilibrium strategists take advantage from spring-summer floods whatever the intensity and duration; and (iv) equilibrium strategists have low flood dependence and the higher stability in temporal fish recruitment. This work brings forth a first synthesis of fish life history in the Middle Paraná River and evidences how important both hydrological and temperature fluctuations are to interpret its complexity.

20 **Résumé**

21 Les fluctuations de la température et des niveaux d'eau sont deux facteurs décisifs pour le
22 développement de la vie aquatique dans les plaines d'inondation. En utilisant une approche tri-
23 factorielle (traits reproductifs des poissons, conditions hydro-climatiques, patrons de
24 recrutement), nous avons analysé l'histoire de vie des poissons du cours moyen du Paraná. Les
25 conditions hydro-climatiques peuvent être considérées à partir de trois scénarios qui poussent
26 les espèces les plus abondantes à adopter différentes stratégies reproductives: (i) certaines
27 espèces typiquement périodiques dépendent des grandes inondations de printemps-été et, en
28 de telles conditions, leurs juvéniles prédominent dans la plaine; (ii) les espèces périodique-
29 opportunistes s'associent aux inondations, indépendamment de leur occurrence annuelle; (iii)
30 les espèces périodique-équilibrées sont avantagées par les inondations de printemps-été
31 quelques soient leur intensité et durée; et (iv) les espèces équilibrées semblent peu
32 dépendantes des inondations et le recrutement de juvéniles est plus stable dans le temps. Cette
33 étude apporte une première synthèse de l'histoire de vie des poissons du cours moyen du
34 Paraná et souligne l'importance des fluctuations hydrologiques et thermiques pour en
35 interpréter sa complexité.

36 **Introduction**

37 Fish life history theories seek to explain the evolution of organism traits as adaptive responses
38 to environmental variations (Winemiller 2005). This trait-based approach is particularly
39 useful to understand how fish assemblage structure is shaped by adaptation to variability,
40 predictability, and seasonality of flow regimens over broad biogeographic scales (Mims and
41 Olden 2012). The most comprehensive model, firstly built from tropical freshwater fishes of
42 Venezuela (Winemiller 1989) and marine and freshwater fishes of North America
43 (Winemiller and Rose 1992), involves three primary fish life history strategies as endpoints
44 on a triangular surface (periodic, equilibrium and opportunistic). This model represents the
45 essential trade-offs among the basic demographic parameters of survival, fecundity, and onset
46 and duration of reproduction (Winemiller 2005), and has been solidly supported for a large
47 range of fish species through many studies carried along the past decades (e.g. Mims and
48 Olden 2012; Olden and Kennard 2010; Blank et al. 2007; Lamouroux et al. 2002).

49 Periodic strategists have a long generation time, moderate reproductive effort, large body size,
50 high batch fecundity, low investment per offspring and are likely to be favored in highly
51 seasonal environments. Equilibrium strategists have a moderate to long generation time,
52 variable body size, low batch fecundity, high juvenile survivorship largely due to high
53 parental care and are predicted to be favored in more stable habitats with low environmental
54 variations. Opportunistic strategists are small-bodied species with early maturation, low batch
55 fecundity, low investment per offspring and are predicted to be associated with habitats
56 defined by frequent and intense disturbance.

57 In river floodplain systems where fluvial dynamics and temperatures appear to be the major
58 physical drivers (Poff and Ward 1989), fish life history is expected to be largely dependent on
59 the occurring of floods in phase with the warm period. Because temperatures vary relatively

60 little in tropical or subtropical floodplains, the hydrological regime is the major factor that
61 drives reproduction and fish recruitment (Junk et al. 1989; Junk and Wantzen 2004). Fish are
62 mostly seasonal strategists combining reproductive periods with rising waters or rainy
63 seasons. A recently flooded floodplain is a biochemical turntable for nutrients, providing
64 important food sources for fish (Wantzen et al. 2002) and better protection from predators
65 (Suzuki et al. 2009). Many fish species have adapted their reproductive behavior to this, either
66 by spawning directly in the floodplain during the flood, or by spawning earlier upstream, so
67 that juveniles can migrate to the floodplain (Wantzen and Junk 2006). The shape of the flood
68 pulse (and its interannual variations) and its match or mismatch with the current ecological
69 requirements of the species is decisive for the survival and successful establishment (windows
70 of opportunity) or failure (windows of susceptibility) of the offspring (Junk and Wantzen
71 2004).

72 That 'tropical-seasonal model' usually dominates in the research into the ecology of river-
73 floodplain systems (Winemiller 2004), but the balance of driving forces in temperate
74 floodplains can be disrupted. The biota also reacts to the combination of day length and
75 temperature (light/temperature pulse) –a cycle that is superimposed on the flood pulse (Junk
76 2001). The magnitude of flooding in most temperate rivers is highly variable between years
77 (Junk and Wantzen 2004), i.e. stochastic between-year variation may seriously challenge
78 adaptive responses to seasonal environmental periodicity (Winemiller 2004). Moreover, most
79 temperate floodplains have been modified (Tockner and Stanford 2002), their ecological
80 functionality and interaction with fish recruitment dynamics have been declining and river
81 channels have become more important (Thorp and Delong 1994; Thorp et al. 1998).

82 Fisheries in the Middle Paraná River (MPR) bring the higher production of continental fishing
83 in Argentina (Baigún et al. 2003) and diet of many people in this region depends on fish
84 protein (FAO 2014). Over approximately 1,000 km long and 30 km wide, this quasi-pristine

85 undammed subtropical-temperate reach is one of the few of this magnitude among floodplain
86 rivers in the world (Iriondo et al. 2007). General knowledge on fish ecology is mainly based
87 on migratory species of commercial value and states that the role of flooding is crucial for the
88 life cycle of most MPR species (Bonetto et al. 1965, 1970; Oldani and Oliveros 1984), but
89 actually little is known about fish life history and its relation to environmental variables.

90 Fish reproduction tends to be more seasonal in zones with stronger fluctuations of rain
91 intensity or temperature (Munro 1990). Because annual variations of temperature and day
92 length are high in the MPR, fish reproductive strategies are then supposed to be strongly
93 related to springtime warming. What's more, besides the high discharges coming normally
94 during summer from Brazil (Paoli and Cacik 2000), the interannual flow variability increases
95 in the middle reach due to the inputs of the Iguazú and Paraguay rivers during autumn-winter.
96 Recent investigations have dealt with this hydrological variability and shown an important
97 decline in fish abundance for main species when floods do not coincide with warm
98 temperatures (Abrial et al. 2014; Espínola et al. 2016; Rabuffetti et al. 2017).

99 Given the high interannual flow variability of the middle reach coupled with strong seasonal
100 fluctuations in temperature, the correspondence with the "tropical seasonal model" is low.
101 Thus, to cope with this highly fluctuating environment, we expect to find alternative (or
102 adaptive) reproductive strategies in the MPR, principally from species with periodic behavior.
103 Some questions arise, such as; are MPR fishes able to recruit under low flow conditions
104 during spring-summer?; are some species able to delay the spawning period until a future
105 flood?

106 In this study, we compare the abundance of young-of-the-year (YOY) of the 25 most
107 abundant species in the MPR floodplain during six consecutive years, their reproductive traits
108 and the annual hydroclimatic conditions. The objective is to analyze the diversity of

recruitment patterns among those species, and to define if reproduction success can be explained from different adaptations of fish life histories influenced by the singularity of each annual hydroclimatic conditions. The main goal is to bring a first general overview of the complexity of fish reproduction in a large subtropical-temperate natural floodplain subject to different interannual phases of flow and temperature conditions.

Materials and methods

Study area and data collection

The MPR floodplain south of Santa Fe city presents an anastomosed pattern –an intricate drainage network of high connectivity– comprising a complex mosaic of minor channels and fluvial lakes that covers a large part of the plain (Fig. 1). Fish samplings were located in six sites –four sites of the Catarata secondary channel (less than 1 km apart from each other) and two fluvial lakes with permanent connections to the channel. The latter is 50 m wide, with an average depth of 5 m, and bank vegetation cover is homogeneous along the stretch studied, with a strong dominance of the rooted macrophyte *Panicum elephantipes*. Floodplain lakes are shallow and cover an extensive area which fluctuates according to water level. Vegetation cover strongly decreases from summer to winter or when water levels are high, and its composition is generally dominated by rooted macrophytes at medium to high water levels but floating species can rapidly colonize during low water periods (principally *Eichhornia crassipes* and *E. azurea*).

Fish were collected by gillnets 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. Gill nets are selective and do not provide an unbiased estimate of species-relative density. Morphological characteristics, such as spines, may increase a species

susceptibility to collection by gill nets. Highly vagile species and species that prey on fish caught in nets may be overestimated due to high net encounter rates, whereas sedentary species may be underestimated due to low net encounter rates (Hoeinghaus et al. 2003). However, we preferred this method because standardized samples with gill nets can be compared within and between years as the same biases can be assumed to operate at each site (see Scarabotti et al. 2017; Saint-Paul et al. 2000, Agostinho & Zalewski 1995). Stretched mesh size range (3 to 16 cm between opposite knots) was efficient to catch specimens between 5 and 60 cm of standard length. Because of the high growth rate of fishes during spring-summer in the MPR floodplain, we could easily catch YOY of the most abundant species. Some small-bodied fish species only (principally the small characids *Cheirodon spp.*, *Odontostilbe spp.*, *Aphyocharax spp.*, *Hyphessobrycon spp.* and *Bryconamericus spp.*), were not considered using this sampling design.

In order to reduce the possible effect of habitat complexity on the variation of fish assemblage structure, gillnets were put at the same place from year to year, looking for the most representative sector at each sampling site. In the channel, they were located close to the bank in zones of low water velocity and with a representative vegetation cover. In the fluvial lakes, they were located in zones of high density of common macrophytes and floating vegetation. The same sampling method was repeated in August and December 2010, April and August 2011 and three times a year from 2012 to 2015 (April, August and December), but samplings in sites 2 and 3 (Fig. 1) were only done from 2013 because of lower financial resources prior to that date. When comparing gill-net samples, special consideration should be paid to possible effects of seasonality such as variation in mean size of individuals and activity patterns (e.g. migration or nesting). Because we sampled the same sites during the same months of consecutive years, we have no reason to suspect that the biases mentioned above should vary significantly among our sampling periods.

All specimens were anaesthetized with 5% benzocaine and sacrificed. Easy-to-identify specimens were processed in the field (species determination, standard length (Ls, cm), bodyweight (Wt, g) and state of gonad maturation). Other fishes were preserved in 10% formalin and identified in laboratory with the available keys of the Paraná River Basin. All collected material was deposited at the fish collection of the National Institute of Limnology (INALI-UNL/CONICET), Santa Fe, Argentina. Additionally, water temperature (T, °C) was recorded at each sampling site.

Figure 1.

Data analysis

Variation of connectivity

In order to provide a representative overview of fish habitat availability in the floodplain from low to high water levels, we analyzed the hydrological connectivity based on six satellite images obtained from the historical data set of Google Earth Pro (see Fig. 3). Each of them represents the area studied (15 km²) at a specific date, and consequently at a specific hydrometric level (HL = 2.26m; 3.19m; 3.4m; 3.63m; 4.04m; 4.5m). The corresponding hydrometric level of each satellite image was supplied by the National Directorate of Waterways of Argentina (Santa Fe Port gauge). From the QGIS software, we georeferenced each image and digitalized the contour of the different environments under water, discriminating lentic to lotic environments. Then, we determined when the lentic ones are connected or isolated from the lotic ones. By this way, we could quantify at each hydrometric level the floodplain area connected to the lotic environments.

Estimation of daily water temperature

Day length and daily air temperature were obtained from the meteorological station of Sauce Viejo Airport, close to the area studied and with similar climatic and geographic characteristics. As no daily records of water temperature (T_w) are available in the MPR, the method of estimation of T_w proposed by Drago (1984) was adapted to the area in order to obtain a value of daily water temperatures for our period of research.

For each sampling period, we measured T_w at each sampling site; it was very similar between sites (permanent connections between them explain those similarities). From the results of T_w measured, we calculated an average temperature –a better representation of the value of T_w across all the area studied in each sampling period. That mean value will here be called ' T_w measured', as opposed to daily ' T_w ' calculated as follows.

Drago's method consists in estimating daily water temperature (T_w) according to daily air temperature (T_a), considering that T_w is largely dependent on T_a , albeit changing with a slight delay. A linear regression was carried out between T_w measured (fifteen figures) and the corresponding T_a registered at the meteorological station (daily data). The same was repeated replacing each T_a by $(T_a + T_{a \text{ day before}})/2$, then by $(T_a + T_{a \text{ day before}} + T_{a \text{ 2days before}})/3$, until 30 days before each sampling date so as to obtain every time the corresponding coefficient of determination (R^2) - the higher R^2 is expected to give the better time-lag of warming/cooling of T_w measured in the channel. The linear regression between T_w measured and T_a seven days before each sampling date resulted in the best R^2 (0.96) and was used to calculate the daily value of T_w during the whole period considered, from 2009 to 2015:

$$T_w = 1.064 * (T_a + T_{a \text{ day before}} + \dots + T_{a \text{ 7days before}}) / 8 + 2.017$$

Characterization of interannual hydroclimatic conditions

To analyze the interannual hydroclimatic variations during the period studied, we considered the datasets of daily water temperatures, daily water levels and day length. From the three daily datasets, we defined seven hydroclimatic variables that would have some relevance on fish reproductive ecology. To obtain non-dimensional datasets comparable between them, all daily data were divided by the means of each dataset. The resulting variables were considered at annual scale –from July, 1st to June, 30th of the following year–, considering the increase of water temperature and day length as the main predictive trigger of fish reproductive periods (following to Suzuki et al. 2004). An explanatory graph shows the variable metrics and helps to understand how hydroclimatic variables were constructed (Fig. 2). The definition, the potential application and the mathematical formula of every hydroclimatic variables are available in Table S1 (see supplementary material in electronic version). To compare hydroclimatic characteristics between years, we applied a hierarchical clustering analysis (Ward's algorithm; Ward 1963). As no collinearity was found between variables (criteria of collinearity: Pearson's $r > 0.6$), we used the seven variables in the analysis.

Figure 2.

Life history diversity

Little is known about fish reproductive biology in the MPR. For the 25 most abundant species caught during the period studied, we propose an estimation of life history traits based on a large review of the available information on fish reproductive biology over a wide geographic scale including south America. We acknowledge that fish biology may differ according to the geographic zone –in this sense we observed that life history traits related to climatic conditions or river geomorphic characteristics present intra-specific variations (e.g. spawning area and spawning support, timing and duration of the reproductive period, reproductive periodicity). If that makes it difficult for us to extrapolate the information to the MPR, some

traits are however more homogeneous across this large geographic scale and were selected for the extrapolation to the MPR (see references of literature in table 2):

(1) total or repeated spawning: repeated spawning can occur twice or three times along the reproductive period;

(2) investment per offspring: species developing or not mating and rituals related to reproduction, and care of the offspring;

(3) reproductive displacements: species with long upstream migrations within the main channels; species with short migrations principally from the floodplain to the secondary channels; floodplain dwellers without reproductive migrations;

(4) maximum standard length: based on the specimens studied during the field surveys. In some cases, i.e. when the abundance of adult specimens was low for a species, this information was replaced by literature data from a close vicinity of the area studied;

(5) oocyte diameter in fully developed ovaries;

(6) total fecundity - number of oocytes per female with fully developed ovaries.

In table 2, fecundity and oocyte diameter refer to data stem from the closer vicinity of our site of study. However, several factors make (5) and (6) extremely variable within a species, e.g. the fat storage of the female prior to egg production, the female size or the climatic conditions. Thus, those two parameters should be considered as tendencies rather than exact values for each species.

In some cases, the information was not available at species level and we used the information available at genus level from the closer vicinity. Moreover, in order to simplify the result part, some species were considered at genus level as they have equivalent morphological

characteristics and reproductive traits and presented similar temporal recruitment patterns during the period studied (see table 2 for more details on the life history dataset).

We used a Multiple Factor Analysis (MFA, Escofier and Pagès 1994) to represent the major life history traits of the 25 species along a reduced number of axes, combining categorical and continuous variables. Continuous variables were firstly ln-transformed and centered, and then weighed by dividing all the data by the first eigenvalue obtained from its PCA. According to the Kaiser–Guttman criterion (Jackson 1993), the axes with eigenvalues higher than one were retained for interpretation. Species reproductive diversity carried out by the MFA was compared and discussed within the classic fish life history framework (Winemiller & Rose 1992).

Abundance of YOY

Published data on age determination of species present high intra-specific variations, making its use difficult. According to geographical areas, climate or food supply prior to a sampling period the relation age/length can be considerably different within juveniles of a species. In this study, though, by analyzing the histograms of standard length frequency of each sampling period, it was relatively easy to separate YOY from the other specimens, and to define the fish cohorts of the 25 species considered above. For each year, it was totaled the abundance of YOY, i.e. all young fishes from a new cohort whose size corresponds to an individual born during the previous reproductive period. This methodology was supported with existing literature on age determination when the information was available from a close vicinity (e.g. Araya et al. 2005; Balboni et al. 2011; Domanico et al. 1993; Carroza and Cordiviola de Yuan 1991). YOY abundance was standardized according to the catch per unit effort (CPUE; number of individuals per 1000 m² of gill-nets per 24 h).

Based on results of MFA and interannual YOY abundances, it was defined four groups of species with similar recruitment pattern and life history strategy. Because assumption of homoscedasticity was not verified, nonparametric one way ANOVA using the Kruskal-Wallis rank sum test was applied to analyze temporal differences in the abundance of YOY of the groups defined, and pairwise comparisons using the Wilcoxon rank sum test were done between years for each group. Finally, two histograms were used to synthesize the abundance of YOY in the plain from 2010 to 2015 –the total CPUE was represented first and the percentage of CPUE by life history strategy, i.e. the probability to find a young specimen from a strategy during a given year, afterwards.

All statistical analyses were implemented with the R statistical software (R Development Core Team 2011). A significance level of $p < 0.05$ was accepted to indicate significance for every computation.

Results

Variations of connectivity, water levels and temperature

From 2010 to 2015, the higher and lower hydrometric levels recorded at the Santa Fe Port gauge were 6.02 and 1.8, respectively. Figure 3 shows a representative view of the increase of connectivity in the area studied, and in what extent availability to flooded habitats depends on water level fluctuations. Within a range of 2.26 and 3.4 m of water levels, the increase of connections between lotic and lentic environments is low (inundation of floodplain area varies only from 7.5 to 11.5%). When levels rise up to 3.4 m, connectivity expands abruptly up to 85% of inundated area when levels reach 4.5 m (the overflow level in the study area of alluvial plain; all water bodies are connected).

Figure 3.

From year to year, water temperatures had similar fluctuations, varying from 10-15°C in winter to 30°C during summer (Figure 4). On the other hand, the annual fluctuations of water level changed considerably. Flood/flow pulses occurred at each season and the floodplain was totally flooded several times during the period studied but the duration was extremely different (flood duration varied between 19 to 194 days, see Table 1).

Figure 4.

The hierarchical clustering classified the 6 years in three groups according to their hydroclimatic characteristics (Fig. 5). The 2009/10 year was unique: a flood pulse of very high intensity and duration with low slopes of the rising/falling limbs occurred in phase with the high temperatures –all hydroclimatic characteristics that match with the current ecological requirements for a successful reproduction of most floodplain fish species (see quantitative values in Table 1). Then, two years were similar (2010/11 and 2013/14) showing ordinary floods out of phase with the warm period, and the slopes of the rising/falling limbs were higher. The third group was marked by low intensity and duration of the hydrological events; a small flood pulse with low rapidity of change of the rising/falling limbs occurred in phase with the warm period (2014/15), whereas no floods occurred during the two other years (2011/12 and 2012/13).

Figure 5.

Table 1.

Paraná fish life history

Overall, 90 species were obtained from the surveys. The 25 most abundant species considered in this study reached a total of 5,380 individuals and 87% of total abundance. Those species exhibited a wide range of life history traits (Table 2). Spawning frequency ranges from single

(total) to repeated spawning. Parental care may be completely absent, or highly developed, e.g. in the wolf fish *Hoplias* aff. *malabaricus* which builds nests aggressively defended by the parents and some loricariids protecting the eggs bearing them on the ventral part of the body (e.g. *Loricariichthys* spp.). Some species make very long migrations during the spawning period (e.g. *Prochilodus lineatus* and *Salminus brasiliensis*) but many species make short migrations or develop the whole life cycle within the floodplain. Fish sizes ranged from small (e.g. *Astyanax rutilus*. Ls = 12 cm) to large specimens (e.g. *Rhaphiodon vulpinus*. Ls = 60.5 cm). Diameter of mature oocytes ranged from less than 0.8 mm to more than 4 mm; some species spawn a small amount of eggs while other species can spawn more than a million eggs.

Table 2.

Considering reproductive strategies of MPR fishes from the classical life history framework (Winemiller & Rose 1992), species reproductive traits show a clear distribution between periodic and equilibrium strategies (Fig. 6). Left of the vertical axe, all species make short or long migrations, have higher fecundity, small oocytes and no parental care (representative of a periodic behavior). The right side refers to species with reproductive traits mostly related to the equilibrium strategy, e.g. larger oocytes, lower fecundity, repeated spawning and the presence of mating, rituals and/or parental care.

Nonetheless, some differences within the two groups are considerable, and lead to consider four fish reproductive groups. Species of group A are all highly periodic. They have the higher fecundity and smaller oocytes, migrating behavior, no parental care, and all Characiformes have total spawning (periodic species, Fig. 6). Group D includes small species of the Characidae family, with lower fecundity than the previous group, partial spawning, reduced migrations, and no parental care, all attributes that show a transitional adaptation between periodic and opportunistic behaviors (periodic-opportunistic strategy). In group B,

the species are typical floodplain dwellers with repeated spawning, mating and ritual associated with the reproduction and high parental care (equilibrium species). From another side, species of group C develop mating and rituals but low or no parental care, they are medium to large, make short reproductive displacements or not, with large oocytes but increased fecundity, showing reproductive traits shared mostly by equilibrium and periodic strategists (periodic-equilibrium strategy).

Figure 6.

YOY abundance

Within each reproductive strategy defined in Fig. 6, fish species had similar interannual recruitment patterns (Fig. 7). The ten species of periodic strategy were strongly related to 2010. For all of them, the abundance of YOY was extremely high during this period, and significantly much lower the following years ($p < 0.001$; Fig. 7a). The seven species of periodic-equilibrium strategy showed abundance of YOY significantly higher during the years 2010 and 2015, a bit lower in 2012 and significantly lower the remaining years ($p < 0.001$; Fig. 7b). On the other hand, even if it was higher in 2010 and 2012, no significant difference was observed in the abundance of YOY for the four equilibrium species ($p = 0.072$; Fig. 7c). This group with high investment in parental care showed a relatively constant recruitment from year to year. The last group with periodic-opportunistic reproductive strategy presented irregular recruitment patterns. Peaks of abundance of the small characids *Astyanax spp.* were found in 2010 (*A. asuncionensis*), 2010 and 2011 (*A. abramis*), and 2014 (*A. rutilus*), whereas the abundance of the middle-sized characid *Acestrorhynchus pantaneiro* was stable along the period studied (Fig. 7d).

Figure 7.

It is remarkable to see that the abundance of YOY was extremely high in 2010 (Fig. 8a), and that 70% belonged to the periodic strategy (Fig. 8b). During the following years, the abundance was around ten times lower and periodic strategists represented a small part of YOY abundance. Periodic-equilibrium strategists reached more than 50% of fish recruitment in 2015 and periodic-opportunistic strategists dominated in 2011 and 2014. Percentage of equilibrium strategists' YOY increased when abundance of YOY of the other strategies is low in the plain.

Figure 8.

Discussion

According to the Flood Pulse Concept, as different subsets of the biota may develop in the same place with varying population maxima over the years ("Sequential" biodiversity, Junk & Wantzen 2004), annual and interannual hydrological diversity is the basis for high biological diversity in floodplains. However, an increasing stochasticity of between-year variations poses challenge for species that exploit ephemeral or dynamic ecotonal aquatic habitats, and especially species with periodic behavior (Winemiller 2004).

Such a hydrological variability predominates in the MPR, a subtropical-temperate reach with seasons marked by important periodic variations of water temperatures. From 2009 to 2015, the flow regimen indeed revealed a strong interannual variability. Floods with different characteristics, in phase or out of phase with the warm period, gave rise to significant differences in fish recruitment patterns, between species, and between years. Our results demonstrated that interannual fish recruitment can be explained from the kind of reproductive strategy developed by the species and its relation of dependence with the flood attributes (timing, duration, intensity, slope of the rising and falling limbs).

Annual hydroclimatic conditions can be considered through three main scenario during the period studied that prompt the most abundant species to adopt four reproductive strategies, and consequently, four different recruitment patterns arise (Fig. 9); therefore, this "sequential fish diversity" is most likely to be the result of how fish reproductive behaviors are able to respond to interannual hydroclimatic variability.

Figure 9.

Floods with high intensity and duration in phase with the warm period are commonly accepted as the most favorable condition for fish recruitment success in floodplains (Junk et al. 1989, King et al. 2003, Górski et al. 2011). In the MPR floodplain, while almost all species showed higher YOY abundance when such conditions occurred –around ten times higher than the other years–, typical periodic strategists totally dominated (Fig. 9b). In that category, body size and the distance of migrations may differ but all species make upstream migrations in school synchronized with the rising limb of the flood pulse and spawn in oxygenated zones with high flow velocity (Vazzoler 1996; Agostinho et al. 2003). The flood rising limb must last long enough as to allow the formation of such fish schools and migrations, and the success of incubation and larvae survivorship is mostly dependent on high water levels and temperature since parental care is not a strategic feature of those species. Besides, the coincidence of large floods and temperatures are doubly important in the MPR because the great majority of fish species that sustain commercial fisheries the population's subsistence are typical periodic strategists (e.g. the pimelodid, anostomid and prochilodontid species; Baigún et al. 2008).

Lower floods or flow pulses during springtime warming and summer do not have the same beneficial effect on reproduction, as the plain then remains flooded for a short time (<1 month). In that case, as typical periodic strategists are not favored, YOY abundance in the

plain was mostly represented by strategies related to the equilibrium behavior –e.g. periodic-equilibrium and equilibrium species (Fig. 9a). Serrasalminids and auchenipterids (periodic-equilibrium strategists) develop low or even no parental care and spawn over inundated areas where the adhesiveness allows eggs to remain fastened to the vegetation during incubation time (Sarmiento et al. 2014; Suzuki 1992). That strategy thus depends deeply on the spring-summer flow rise because spawning support is totally subjected to water level fluctuations. On the other hand, as they do not need them directly to reproduce successfully, typical equilibrium strategists characterized by a higher investment in caring offspring, such as nest builders (e.g. *H. aff. malabaricus*) and male bearers (*Loricariichthys spp.*), take advantage from floods indirectly, e.g. higher abundance of prey for juvenile piscivores and major access to shelters and nursery areas.

Floods out of phase with high temperatures and a warm period marked by low water levels lead to the worst conditions for recruitment of most species (Fig. 9c). While waters rise across the plain and open new habitats, temperatures decrease and reach their lower values. Days are shorter, primary production decreases and consequently food supply is harder to find. Temperatures and day length act as an ecological barrier that most Paraná species cannot overcome. Nonetheless, some smaller characids showed significant higher peaks of YOY after the larger floods whatever the water temperature and we observed many adult specimens at final maturation stage during winter floods. Azevedo (2010) hypothesized the origin of small characids as a single event of body size reduction in a common ancestor that could have possibly represented an adaptive advantage in several aspects related to the occupation of new environments. He noted evolutionary responses related to reproductive patterns of many small characids, such as extended reproductive period (reproducing during the colder months), reduced fecundity and multiple spawning. Those findings might explain the recruitment patterns of some periodic-opportunistic strategists in the MPR floodplain.

Concluding remarks

A life history traits-based approach is useful for themes of conservation as species of similar behavior are likely to respond in the same way to environmental fluctuations (Winemiller 2005; Mims & Olden 2012). We have summarized and broadened knowledge of fish reproduction of 25 MPR species representing more than 85% of total abundance in the area studied. We have defined four dominant reproductive strategies, each of them with species of similar reproductive traits and yearly recruitment patterns.

Most of fish species of the Upper Paraná River, upstream to the Itaipú dam, have a seasonal reproductive strategy in relation to floods and increases in temperature (Suzuki et al. 2004). In its middle reach, we observe that the seasonality and success of reproduction of the 25 most abundant species are mostly related to rising waters during the warm period. As it is commonly observed in large river floodplains (e.g. Agostinho et al. 2003; Górski et al. 2011; Rabuffetti et al. 2017), the occurrence of a large spring-summer flood is the condition most suitable for the different reproductive strategies. It should therefore be considered as the key for a successful sustainability of fish diversity, and especially for typical periodic species that sustain most of commercial fisheries in the MPR.

However, delays between floods and warm temperatures or lower intensity and duration of floods during spring-summer are frequent in the MPR. That hydroclimatic variability might explain the different behaviors associated with periodic life history (typical periodic, periodic-equilibrium and periodic-opportunistic). Species could have developed different reproductive strategies in response to interannual changes in timing and intensity/duration of floods. As a result, recruitment patterns in the floodplain are different from year to year, reflecting the diversity of MPR life history styles.

This work highlights the multifaceted adaptation of floodplain fishes to successfully reproduce (the "sequential fish diversity") and the need of a detailed analysis of life history strategies to understand differences in yearly recruitment patterns. Altered flow regimes (from natural or human origin) strongly challenge fish reproduction and probably make fishes to diversify their reproductive behaviors in order to subsist in the environment, as we observed for periodic species. Those findings should be deeply considered to get efficient measures of management and conservation of the floodplain and its fishes.

Acknowledgements

The authors thank the National Institute of Limnology (INALI, UNL/CONICET) for logistic support and its technical staff for field assistance. This research was financially supported by the National Scientific and Technical Research Council of Argentina. We thank the two anonymous reviewers for providing valuable comments and Pierre-Luc Abrial for the English revision.

References

- Abrial, E., Rabuffetti, A.P., Espínola, L.A., Amsler, M.L., Blettler, M.C.M., and Paira, A.R. 2014. Influence of hydrological changes on the fish community in two lotic environments of the Middle Paraná floodplain. Argentina. *Aquat. Ecol.* 48(3): 337–349. doi:10.1007/s10452-014-9488-x.
- Agostinho, A.A., Gomes, L.C., Suzuki, H.I., and Júlio, H.F. 2003. Migratory fish from the upper Paraná River basin. Brazil. *In* *Migratory Fishes of South America: Biology. Social Importance and Conservation Status. Edited by Carolsfeld J., Harvey B., Ross C., and Baer A.* World Fisheries Trust, the World Bank and the International Development Research Centre, Victoria. pp. 19–99.

- 482 Agostinho, A.A., Zalewski, M. 1995. The dependence of fish community structure and
483 dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. *Hydrobiologia*.
484 303(1): 141-148. doi: 10.1007/BF00034051
- 485 Almirón, A., Casciotta, J., Ciotek, L., and Giorgis, P. 2015. Guía de los peces del Parque
486 Nacional PreDelta. Editorial APN, Buenos Aires, Argentina.
- 487 Arantes, F.P., Sato, Y., Sampaio, E.V., Rizzo, E., and Bazzoli, N. 2013. Spawning induction
488 and fecundity of commercial native fish species from the São Francisco River basin.
489 Brazil. under hatchery conditions. *Agri. Sci.* 4(8): 382–388. doi:10.4236/as.2013.48055
- 490 Araya, P.R., Agostinho, A.A., and Bechara, J.A. 2005. The influence of dam construction on
491 a population of *Leporinus obtusidens* (Valenciennes, 1847) (Pisces, Anostomidae) in the
492 Yacyreta Reservoir (Argentina). *Fish. Res.* 74: 198–209.
493 doi:10.1016/j.fishres.2005.02.007.
- 494 Azevedo, M.A. 2010. Reproductive characteristics of characid fish species (Teleostei,
495 Characiformes) and their relationship with body size and phylogeny. *Iheringia. Sér. Zool.*,
496 Porto Alegre. 100(4): 469–482. doi:10.1590/S0073-47212010000400020.
- 497 Baigún, C.R.M., Sverlij, S.B., and López, H.L. 2003. Recursos pesqueros y pesquerías del
498 Río de la Plata interior y medio (Margen Argentina). Informes de la División Zoología
499 Vertebrados de la Universidad Nacional de la Plata, Argentina.
- 500 Baigún, C.R.M., Minotti, P.G., Kandus, P., Quintana, R., Vicari, R., Puig, A., Oldani, N.O.,
501 and Nestler, J.Á. 2008. Resource use in the Paraná River delta (Argentina): moving away
502 from an ecohydrological approach? *Ecohydrol. Hydrobiol.* 8(2-4): 245–262.
503 doi:10.2478/v10104-009-0019-7.

- 504 Balboni, L., Colautti, D.C., and Baigún, C.R.M. 2011. Biology of growth of *Hoplias*
505 *malabaricus* (Bloch, 1794) in a shallow Pampean lake (Argentina). *Neotrop. Ichthyol.*
506 9(2): 437–444. doi:10.1590/S1679-62252011000200022
- 507 Blanck, A., Tedesco, P.A., and Lamouroux, N. 2007. Relationships between life-history
508 strategies of European freshwater fish species and their habitat preferences. *Freshwater*
509 *Biol.* 52: 843–859. doi:10.1111/j.1365-2427.2007.01736.x
- 510 Bonetto, A.A., Cordiviola de Yuan, E., Pignalberi, C., and Oliveros, O. 1970. Nuevos aportes
511 al conocimiento de las poblaciones ícticas en cuencas temporarias del valle de inundación
512 del Paraná medio. 2das Jornadas Argentinas de Zoología. Santa Fe (1969). *Acta Zool.*
513 *Lilloana* 27: 135–153.
- 514 Bonetto, A.A., Pignalberi, C., and Cordiviola, E. 1965. Contribución al conocimiento de las
515 poblaciones de peces de las lagunas isleñas en el Paraná medio. II Congreso
516 Latinoamericano de Zoología, Sao Paulo (1962). 2: 131–144.
- 517 Carroza, C., and Cordiviola de Yuan, E. 1991. Estudios ictiológicos en la laguna La
518 Cuarentena
519 (Isla Carabajal), río Paraná, Argentina: Edad y crecimiento del « sábalo » *Prochilodus*
520 *lineatus* (Val.), periodo 1984-1985 (Pisces. Curimatidae). *Rev. Hydrobiol. Trop.* 24(2):
521 119–129.
- 522 Casciotta, J., Almirón, A., and Bechara, J. 2005. Peces del Iberá. Hábitat y Diversidad. La
523 Plata.
- 524 Domanico, A., Delfino, R., and Freyre, L. 1993. Edad y crecimiento de *Hoplias malabaricus*
525 *malabaricus* (Bloch, 1794) (Teleostei, Erytrinae) en la laguna de lobos (Argentina).
526 *Iheringia. Sér. Zool., Porto Alegre* 74: 141–149.

- 527 Drago, E.C. 1984. Estudios limnológicos en una sección transversal del tramo medio del río
528 Paraná. capítulo VI: Temperatura del agua. Rev. Asoc. Cienc. Nat. Litor. 15: 79–92.
- 529 Escofier, B., and Pagès, J. 1994. ‘Multiple factor analysis (afmult package)’. Comput. Stat.
530 Data An. 18(1): 121–140. doi:10.1016/0167-9473(94)90135-X.
- 531 Espínola, L.A., Rabuffetti, A.P., Abrial, E., Amsler, M.L., Blettler, M.C.M., Paira, A.R.,
532 Simões, N.R., and Santos, L.N. 2016. Response of fish assemblage structure to changing
533 flood and flow pulses in a large subtropical river. Mar. Freshwater Res. 68(2): 319–330.
534 doi:10.1071/MF15141.
- 535 FAO. 2014. Perfiles de pesca y acuicultura por países. Argentina. Hojas de datos de perfiles
536 de los países. In Departamento de Pesca y Acuicultura de la FAO [online]. Roma.
537 Actualizado 2014. [21 October 2015]. [http:// www.fao.org/fishery/facp/ARG/es](http://www.fao.org/fishery/facp/ARG/es).
- 538 Felizardo, V.O., Andrade, E.A., Melo, C.C.V., Murgas, L.D.S., Freitas, R.T.F., and Andrade,
539 E.S. 2015. Determination of age and its correlation with biometric variables and seasonal
540 reproductive indices of *Leporinus obtusidens*. Acta Sci. Biol. Sci. 37(3): 265–271. doi:
541 10.4025/actascibiols.v37i3.28003
- 542 Godinho, H.M., Ferri, S., Medeiros, L.O., and Barker, J.M.B. 1974. Morphological changes in
543 the ovary of *Pimelodus maculatus* Lacepède, 1803 (Pisces, Siluroidei) related to the
544 reproductive cycle. Rev. Brasil. Biol. 34: 581–588.
- 545 Godoy, M.P. 1975. Peixes do Brasil. Subordem Characoidei. Bacia do Río Mogí Guassu. Vol.
546 I, II, III & IV. Editora Franciscana.
- 547 Górski, K., De Leeuw, J.J., Winter, H.V., Vekhov, D.A., Minin, A.E., Buijse, A.D.,
548 Nagelkerke, L.A.J. 2011. Fish recruitment in a large, temperate floodplain: the importance
549 of annual flooding, temperature and habitat complexity. Freshwater Biol. 56: 2210–2225.
550 doi:10.1111/j.1365-2427.2011.02647.x

- 551 Hirt, L.M., and Flores, S.A. 1999. Desarrollo ovocitario y tipo de desove de *Acestrorhynchus*
552 *pantaneiro* (Cypriniformes, Characidae), en un tramo del río Alto Paraná, Argentina.
553 *Revista de Ictiología* 7: 67–74.
- 554 Hoeinghaus, D.J., Layman, C.A., Arrington, D.A., Winemiller, K.O. 2003. Spatiotemporal
555 variation in fish assemblage structure in tropical floodplain creeks. *Environ. Biol. Fish.*
556 67(4):379-387. doi:10.1023/A:1025818721158
- 557 Iriondo, M., Paggi, J.C., Parma, M.J. 2007. The Middle Paraná River. *Limnology of a*
558 *Subtropical Wetland*. Springer-Verlag: Berlin Heidelberg.
- 559 Jackson, D.A. 1993. Stopping rules in principal components analysis: a comparison of
560 heuristical and statistical approaches. *Ecology* 74:(8) 2204–2214. doi:10.2307/1939574
- 561 Junk, W.J. 2001. The flood pulse concept of large rivers: Learning from the tropics. *Verh.*
562 *Internat. Verein. Limnol.* 27: 3950–3953. doi:10.1080/03680770.1998.11901733.
- 563 Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river-floodplain
564 systems. *Can. Spec. Pub. Fish. Aquat. Sci.* 106: 110–127.
- 565 Junk, W.J., and Wantzen, K.M. 2004. The Flood Pulse Concept: New Aspects Approaches
566 and Applications –an Update. *in* *Proceedings of the Second International Symposium on*
567 *the Management of Large Rivers for Fisheries: Vol. 2. Edited by R.L. Welcomme and T.*
568 *Petr. Food and Agriculture Organization & Mekong River Commission, RAP Publication,*
569 *Bangkok pp. 117–140.*
- 570 King, A.J., Humphries, P.. and Lake, P.S. 2003. Fish recruitment on floodplains: the roles of
571 patterns of flooding and life history characteristics. *Can. J. Fish. Aquat. Sci.* 60: 773–786.
572 doi:10.1139/F03-057.

- 573 Lamouroux, N., Poff, N.L., and Angermeier, P.L. 2002. Intercontinental convergence of
574 stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83(7):
575 1792–1807. doi:10.1890/0012-9658(2002)083[1792:ICOSFC]2.0.CO;2.
- 576 Lowe-McConnell, R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge
577 University Press., London.
- 578 Maia, R., Artioli, L.G.S., and Hartz, S.M. 2013. Diet and reproductive dynamics of
579 *Trachelyopterus lucenai* (Siluriformes: Auchenipteridae) in subtropical coastal lagoons in
580 southern Brazil. *Zoologia* 30(3): 255–265. doi:10.1590/S1984-46702013000300002.
- 581 Meschiatti, A.J., and Arcifa, M.S. 2009. A review on the fish fauna of Mogi-Guaçu River
582 basin: a century of studies. *Acta Limnol. Bras.* 21(1): 135–159.
- 583 Meurer, S., and Zaniboni-Filho, E. 2012. Reproductive and feeding biology of
584 *Acestrorhynchus pantaneiro* Menezes, 1992 (Osteichthyes: Acestrorhynchidae) in areas
585 under the influence of dams in the upper Uruguay River, Brazil. *Neotrop. Ichthyol.* 10(1):
586 159–166. doi:10.1590/S1679-62252012000100015.
- 587 Mims, M.C., and Olden, J.D. 2012. Life history theory predicts fish assemblage response to
588 hydrologic regimes. *Ecology* 93(1): 35–45. doi:10.1890/11-0370.1.
- 589 Munro, A.D. 1990. General introduction. *in* *Reproductive seasonality in teleosts:*
590 *environmental influences. Edited by A.D. Munro, A.P. Scott, and T.J. Lam.* CRS Press,
591 Florida pp. 1–11.
- 592 Nakatani, K., Agostinho, A.A., Baumgartner, G., Bialecki, A., Vanderlei, P., Cavicchioli, M.,
593 and Pavanelli, C. 2001. *Ovos e larvas de peixes de água doce. desenvolvimento e manual*
594 *de identificação*. Editora da Universidade Estadual de Maringá, Maringá.

- 595 Neuberger, A.L., Marques, E.E., Agostinho, C.S., and de Oliveira, R.J. 2007. Reproductive
596 biology of *Rhaphiodon vulpinus* (Ostariophysi: Cynodontidae) in the Tocantins River
597 Basin, Brazil. *Neotrop. Ichthyol.* 5(4): 479–484. doi:10.1590/S1679-62252007000400007.
- 598 Oldani, N., and Oliveros, O. 1984. Estudios limnológicos en una sección transversal del tramo
599 medio del río Paraná. XII: Dinámica temporal de peces de importancia económica. *Rev.*
600 *Asoc. Cienc. Nat. del Litoral* 15(2): 175–183.
- 601 Olden, J.D., and Kennard, M.J. 2010. Intercontinental comparison of fish life history
602 strategies along a gradient of hydrologic variability. *In* Community ecology of stream
603 fishes: concepts, approaches, and techniques. *Edited by* K.B. Gido and D.A. Jackson.
604 American Fisheries Society, Bethesda, Maryland, USA, pp. 83–107.
- 605 Paoli, C., and Cacik, P. 2000. Régimen de crecidas y análisis de caudales máximos. *In* El río
606 Paraná en su tramo medio. *Edited by* C. Paoli and M. Schreider. Centro de Publicaciones,
607 Universidad Nacional del Litoral, Santa Fe, Argentina, pp. 27–68.
- 608 Poff, N.L., and Ward, J.V. 1989. Implications of stream flow variability and predictability for
609 lotic community structure: an analysis of stream flow patterns. *Can. J. Fish. Aquat. Sci.*
610 46(10): 1805–1818. doi:10.1139/f89-228.
- 611 Ponton, D., and Tito de Moraes, L. 1994. Les stratégies de reproduction et les premiers stades
612 de vie des poissons du fleuve Sinnamary (Guyane française) : une revue bibliographique.
613 *Rev. Hydrobiol. Trop.* 27(4): 441–465.
- 614 R Development Core Team. 2011. R: a language and environment for statistical computing. R
615 Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- 616 Rabuffetti, A.P., Górski, K., Espínola, L.A., Abrial, E., Amsler, M.L., and Paira, A.R. 2017.
617 Long-term hydrologic variability in a large subtropical floodplain river: effects on
618 commercial fisheries. *River Res. Applic.* 33(3): 353–363. doi:10.1002/rra.3100.

- Renno, J.F., García, C., Duponchelle, F., and Nuñez, J. 2005. Biología de las Poblaciones de Peces de la Amazonía y Piscicultura. Comunicaciones del Primer coloquio de la Red de Investigación sobre la Ictiofauna Amazónica, Iquitos, Perú. IIAP-IQUITOS/IRD-PARIS.
- Rizzo, E., Sato, Y., Barreto, B.P., and Godinho, H.P. 2002. Adhesiveness and surface patterns of eggs in neotropical freshwater teleosts. J. Fish Biol. 61(3): 615–632. doi:10.1111/j.1095-8649.2002.tb00900.x.
- Saint-Paul, U., Zuanon, J., Correa, M.A.V., Garcia, M., Fabre, N.N., Berger, U., Junk, W.J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. Environ. Biol. Fish., 57(3): 235-250. doi:10.1023/A:1007699130333.
- Scarabotti, P.A., Demontes, L.D., Pouilly, M. 2017. Climatic seasonality, hydrological variability, and geomorphology shape fish assemblage structure in a subtropical floodplain. Freshwater. Sci. doi:10.1086/693441.
- Santos, H.B., Arantes, F.P., Sampaio, E.V., and Sato, Y. 2013. Artificial reproduction and reproductive parameters of the internally inseminated driftwood catfish *Trachelyopterus galeatus* (Siluriformes: Auchenipteridae). Ichthyol. Res. 60(2): 142–148. doi:10.1007/s10228-012-0324-9.
- Sarmiento, J., Bigorne, R., Carvajal-Vallejos, F., Maldonado, M., and Oberdorff, T. 2014. Peces de Bolivia/Bolivian Fishes. Book IRD, BioFresh (EU), Plural Editores, La Paz.
- Schifino, L.C., Fialho, C.B., and Verani, J.R. 1998. Reproductive aspects of *Cyphocharax voga* (Hensel) from Custódias lagoon, rio Grande do Sul, Brazil (Characiformes, Curimatidae). Rev. Bras. Zool. 15(3): 767–773. doi:10.1590/S0101-81751998000300019.
- Suzuki, H.I. 1992. Variações na morfologia ovariana e no desenvolvimento do folículo de peixes teleósteos da bacia do rio Paraná. M.Sc. thesis, Universidade Federal do Paraná, Curitiba.

- 643 Suzuki, H.I., Agostinho, A.A., Bailly, D., Gimenes, M.F., Júlio-Junior, H.F., and Gomes,
644 L.C. 2009. Inter-annual variations in the abundance of young-of-the-year of migratory
645 fishes in the Upper Paraná River floodplain: relations with hydrographic attributes. *Braz.*
646 *J. Biol.* 69(2): 649–660. doi:10.1590/S1519-69842009000300019.
- 647 Suzuki, H.I., Vazzoler, A.E.A.M., Marques, E.E., Perez-Lizama, M.A., and Inada, P. 2004.
648 Reproductive ecology of the fish assemblages. *In* The Upper Paraná River and its
649 Floodplain: Physical Aspects. Ecology and Conservation. *Edited by* S.M. Thomaz, A.A.
650 Agostinho and N.S. Hahn. Backhuys Publishers, Leiden, pp. 271–292.
- 651 Suzuki, H.I., Agostinho, A.A., and Winemiller, K.O. 2000. Relationship between oocyte
652 morphology and reproductive strategy in loricariid catfishes of the Paraná River. *Braz. J.*
653 *Fish Biol.* 57(3): 791–807. doi:10.1111/j.1095-8649.2000.tb00275.x.
- 654 Thorp, J.H., and DeLong, M.D. 1994. The riverine productivity model: An heuristic view of
655 carbon sources and organic processing in large river ecosystems. *Oikos* 70(2): 305–308.
656 doi:10.2307/3545642
- 657 Thorp, J.H., DeLong, M.D., Greenwood, K.S., and Casper, A.F. 1998. Isotopic analysis of
658 three food web theories in constricted and floodplain regions of a large river. *Oecologia*
659 117(4): 551–563. doi:10.1007/s004420050692.
- 660 Tockner, K., and Stanford, J.A. 2002. Riverine flood plains: present state and future trends.
661 *Environ. Conserv.* 29(3): 308–330. doi:10.1017/S037689290200022X.
- 662 Vazzoler, A.E.A.M. 1996. *Biologia da reprodução de peixes teleósteos: teoria e prática.*
663 Editora da Universidade, Maringá, Brazil.
- 664 Vazzoler, A.E.A.M., and Menezes, N.A. 1992. Síntese de conhecimentos sobre o
665 comportamento reprodutivo dos Characiformes da América do Sul (Teleostei.
666 Ostariophysi). *Rev. Bras. Biol.* 52: 627–640.

- 667 Wantzen, K.M., and Junk, W.J. 2006. Aquatic-terrestrial linkages from streams to rivers:
668 biotic hot spots and hot moments. *Large Rivers* 16(4): 595–611.
669 doi:10.1127/lr/16/2006/595.
- 670 Wantzen, K.M., Machado, F.D., Voss, M., Boriss, H., and Junk, W.J. 2002. Seasonal isotopic
671 shifts in fish of the Pantanal wetland, Brazil. *Aquat. Sci.* 64(3): 239–251.
672 doi:10.1007/PL00013196.
- 673 Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.*
674 58(301): 236–244. doi:10.1080/01621459.1963.10500845.
- 675 Winemiller, K.O. 2004. Floodplain river food webs: generalizations and implications for
676 fisheries management. Pages 285–312. *In* Proceedings of the Second International
677 Symposium on the Management of Large Rivers for Fisheries: Vol. 2. *Edited by* R.L.
- 678 Welcomme and T. Petr. Food and Agriculture Organization & Mekong River Commission.
679 RAP Publication, Bangkok.
- 680 Winemiller, K.O. 2005. Life history strategies. population regulation. and implications for
681 fisheries management. *Can. J. Fish. Aquat. Sci.* 62(4): 872–885. doi:10.1139/f05-040.
- 682 Winemiller, K.O. 1989. Patterns of variation in life-history among South American fishes in
683 seasonal environments. *Oecologia* 81(2): 225–241. doi:10.1007/BF00379810.
- 684 Winemiller, K.O., and Rose, K.A. 1992. Patterns of life history diversification in North
685 American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* 49(10):
686 2196–2218. doi:10.1139/f92-242.

Table 1. Values of each hydroclimatic variable used to analyze the interannual variations of hydrology and temperature in the MPR (years are considered from July, 1st to June, 30th of the following year). Rep.Con: floodplain connectivity during the main fish reproductive period; Fld.Tim: flood timing, coincidence between flood and temperature peak; Hyd.Var: hydrological variability; Ris.Limb: Rate of change of rising limb; Fal.Limb: Rate of change of falling limb; Fld.Int: flood intensity; Fld.Dur: flood duration. (see Table S1 for more details on each variable).

Years	Rep.Con (integral)	Fld.Tim (%)	Hyd.Var (ad.)	Ris.Limb (m/day)	Fal.Limb (m/day)	Fld.Int (m)	Fld.Dur (days)
2009/10	255	95	1.02	0.017	0.017	6.02	194
2010/11	160	49	0.81	0.020	0.042	5.10	47
2011/12	153	33	0.57	0.017	0.016	4.17	0
2012/13	139	42	0.58	0.031	0.025	3.97	0
2013/14	151	15	0.71	0.038	0.043	5.21	29
2014/15	200	95	0.66	0.022	0.021	4.68	19

Table 2. Details of variables related to fish reproduction and population structure of the 25 most abundant fish species caught during the study. SL = Standard length.

Species	Name abbrev.	Spawning type	Parental care	Migration type	SL max (cm)	Oocyte Size (µm)	Fecundity (nb of oocytes)	Consulted Lit.***
<i>Prochilodus lineatus</i> (Valenciennes 1837)	<i>P lin</i>	Total	No care	Long mig.	52.1	1450.1	1600000	1. 11. 13. 17. 21. 23. 24
<i>Leporinus obtusidens</i> (Valenciennes 1837)	<i>L obt</i>	Total	No care	Long mig.	44.5	1005.1	538000	1. 3. 5. 13. 24
<i>Salminus brasiliensis</i> (Cuvier 1816)	<i>S bra</i>	Total	No care	Long mig.	54.5	1350.6	2600000	1. 11. 13. 18. 21. 23. 24
<i>Pimelodus maculatus</i> (Lacepède 1803)	<i>P mac</i>	Repeated	No care	Long mig.	29	770.3	200000	1. 3. 6. 9. 13. 17. 21. 24
<i>Pterodoras granulosus</i> (Valenciennes 1821)	<i>P gra</i>	Repeated	No care	Long mig.	38	1056.1	296000	19. 21. 24
<i>Rhaphiodon vulpinus</i> (Spix & Agassiz 1829)	<i>R vul</i>	Total	No care	Long mig.	60.5	980	98185	1. 13. 14. 24
<i>Schizodon</i> spp.**	<i>Sch.</i>	Total	No care	Short mig.	38.4	896.2	80000*	13. 16. 19. 21. 24
<i>Cyphocharax platanus</i> (Günther 1880)	<i>C pla</i>	Total*	No care	Short mig.	16.5	806.1*	36600*	7. 20. 24
<i>Cyphocharax voga</i> (Hensel 1870)	<i>C vog</i>	Total*	No care	Short mig.	25.5	806.1*	36600	7. 20. 24
<i>Astyanax asuncionensis</i> (Géry 1972)	<i>A asu</i>	Repeated*	No care	Short mig.*	17.5	775.5*	9560*	11. 13. 17. 21. 23. 25. 26
<i>Astyanax abramis</i> (Jenyns 1842)	<i>A abr</i>	Repeated*	No care	Short mig.*	13.5	775.5*	9560*	11. 13. 17. 21. 23. 24. 25
<i>Astyanax rutilus</i> (Jenyns 1842)	<i>A rut</i>	Repeated*	No care	Short mig.*	12	775.5*	9560*	11. 13. 17. 21. 23. 24. 25
<i>Acestrorhynchus pantaneiro</i> (Menezes 1992)	<i>A pan</i>	Repeated	No care	No mig.	30	897.5	33470	8. 12. 17. 19. 21. 23. 24
<i>Ageneiosus militaris</i> (Valenciennes 1835)	<i>A mil</i>	Total*	Mating	Short mig.*	34.5	1849.5*	18500*	13. 19. 21. 24
<i>Ageneiosus inermis</i> (Linnaeus 1766)	<i>A ine</i>	Total	Mating	Short mig.	40.5	1849.5*	18500	13. 19. 21. 24
<i>Trachelyopterus</i> spp.**	<i>Tra.</i>	Repeated	Mating & CP	No mig.	17.5	2300	1536	10. 13. 18. 19. 21. 24

<i>Serrasalmus</i> spp.**	<i>Ser.</i>	Repeated	Mating & CP	No mig.	22.5	1816.3	2800*	9. 13. 19. 21. 24
<i>Pygocentrus nattereri</i> (Kner 1858)	<i>P nat</i>	Repeated	Mating	No mig.	31	1635	19000	2. 4. 16. 19
<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch 1794)	<i>H mal</i>	Repeated	Mating & CP	No mig.	49	2445.2	61000	11. 13. 15. 19. 21. 24
<i>Hypostomus commersoni</i> (Valenciennes 1836)	<i>H com</i>	Total*	Mating & CP*	No mig.*	48.5	4360*	2802*	15. 21. 22
<i>Loricariichthys</i> spp. **	<i>Lor.</i>	Repeated	Mating & CP	No mig.	39.5	3197.1	1450	13. 21. 22. 24

*Information on the reproductive trait based at genus level.

**Species considered at genus level: *Schizodon* spp. (*S. borellii* Boulenger 1900; *S. platae* Garman 1890); *Trachelyopterus* spp. (*T. aff. galeatus*. Linné 1766; *T. lucenai*. Bertolotti. Pezzi da Silva & Pereira 1995); *Serrasalmus* spp. (*S. maculatus*. Kner 1858; *S. marginatus*. Valenciennes 1837); *Loricariichthys* spp. (*L. platymetopon*. Isbrücker & Nijssen 1979; *L. melanocheilus*. Reis & Pereira 2000).

***Consulted literature: (1) Agostinho et al. 2003; (2) Almiron et al. 2015; (3) Arantes et al. 2013; (4) Casciotta et al. 2005; (5) Felizardo et al. 2015; (6) Godinho et al. 1974; (7) Godoy 1975; (8) Hirt & Flores 1999; (9) Lowe-McConnell 1987; (10) Maia et al. 2013; (11) Meschiatti & Arcifa 2009; (12) Meurer & Zaniboni-Filho 2012; (13) Nakatani et al. 2001; (14) Neuberger et al. 2007; (15) Ponton & Tito de Morais 1994; (16) Renno et al. 2005; (17) Rizzo 2002; (18) Santos et al. 2013; (19) Sarmiento et al. 2014; (20) Schifino et al. 1998; (21) Suzuki 1992; (22) Suzuki et al. 2000; (23) Vazzoler & Menezes 1992; (24) Vazzoler 1996; (25) Winemiller 1989.

Figure 1. Study area in the alluvial plain of the MPR; sampling sites in the Catarata secondary channel (1, 2, 3 and 4), and fluvial lakes (5 and 6); area considered for analysis of variations of connectivity, see Fig. 3 (white curve); flow direction (fd).

Figure 2. Schematic graph showing the metrics used to construct the variables related to the yearly fluctuations of water temperature (black curve), day length (dotted curve) and water levels (grey curve) in the MPR floodplain (this figure is based on the polynomial tendency of the three variables from July 2010 to June 2011).

Figure 3. Increase of hydrological connectivity in the area studied from six hydrometric levels registered from the Santa Fe port gauge. Grey = lotic environments; black = lentic environments.

Figure 4. Yearly variation of water temperature and water levels in the MPR from July 2009 to December 2015. Black line: water temperature; grey line: water level.

Draft

Figure 5. Cluster analysis (Ward method; Ward 1963) of the hydroclimatic data recorded in the MPR from July 2009 to the end of June 2015. We used 7 variables mainly based on the daily variations of water levels and water temperature (see table S1 for more details on hydroclimatic variables).

Figure 6. Results of the multiple factor analysis of life history of the 25 most abundant fish species caught in the MPR floodplain. (a) species scores; (b) reproductive traits scores (see table 2 for abbreviations). Black circles gather species together in groups of similar reproductive behavior; (A) periodic strategists; (B) periodic-equilibrium strategists; (C) equilibrium strategists; (D) periodic-opportunistic strategists.

Figure 7. Abundance of YOY according to the reproductive strategy: (a) periodic strategists; (b) periodic-equilibrium strategists; (c) equilibrium strategists; (d) periodic-opportunistic strategists. When significant between-year differences of the YOY abundance exist, p-values are included in the figure.

Figure 8. (a) total CPUE of YOY caught in the MPR floodplain from 2010 to 2015; (b) percentage of CPUE of YOY of the four reproductive strategies from 2010 to 2015: black bar: periodic strategists; white bar: periodic-equilibrium strategists; dark grey bar: equilibrium strategists; light grey bar: periodic-opportunistic strategists.

Figure 9. Synthetic scheme of annual flow variability in the MPR and its influence on recruitment patterns of floodplain fishes adopting different life history strategies. Black line: water temperature; Grey line: water level; dotted line: overflow level.