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

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

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

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

In river floodplain systems where fluvial dynamics and temperatures appear to be the major physical drivers (Poff and Ward 1989), fish life history is expected to be largely dependent on the occurring of floods in phase with the warm period. Because temperatures vary relatively
little in tropical or subtropical floodplains, the hydrological regime is the major factor that
drives reproduction and fish recruitment (Junk et al. 1989; Junk and Wantzen 2004). Fish are
mostly seasonal strategists combining reproductive periods with rising waters or rainy
seasons. A recently flooded floodplain is a biochemical turntable for nutrients, providing
important food sources for fish (Wantzen et al. 2002) and better protection from predators
(Suzuki et al. 2009). Many fish species have adapted their reproductive behavior to this, either
by spawning directly in the floodplain during the flood, or by spawning earlier upstream, so
that juveniles can migrate to the floodplain (Wantzen and Junk 2006). The shape of the flood
pulse (and its interannual variations) and its match or mismatch with the current ecological
requirements of the species is decisive for the survival and successful establishment (windows
of opportunity) or failure (windows of susceptibility) of the offspring (Junk and Wantzen
2004).

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

Fisheries in the Middle Paraná River (MPR) bring the higher production of continental fishing
in Argentina (Baigún et al. 2003) and diet of many people in this region depends on fish
protein (FAO 2014). Over approximately 1,000 km long and 30 km wide, this quasi-pristine
undammed subtropical-temperate reach is one of the few of this magnitude among floodplain rivers in the world (Iriondo et al. 2007). General knowledge on fish ecology is mainly based on migratory species of commercial value and states that the role of flooding is crucial for the life cycle of most MPR species (Bonetto et al. 1965, 1970; Oldani and Oliveros 1984), but actually little is known about fish life history and its relation to environmental variables.

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

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

In this study, we compare the abundance of young-of-the-year (YOY) of the 25 most abundant species in the MPR floodplain during six consecutive years, their reproductive traits 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 $(T_a + T_a$ day before)/2, then by $(T_a + T_a$ day before + $T_a$ 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:

$$T_w = 1.064 \times (T_a + T_a \text{ day before} + \ldots + T_a \text{ 7days before}) / 8 + 2.017$$
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 scenarios 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 larval 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). Serrasalmids 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

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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, 1\textsuperscript{st} to June, 30\textsuperscript{th} 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).

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Name abbrev.</th>
<th>Spawning type</th>
<th>Parental care</th>
<th>Migration type</th>
<th>SL max (cm)</th>
<th>Oocyte Size (µm)</th>
<th>Fecundity (nb of oocytes)</th>
<th>Consulted Lit.***</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Prochilodus lineatus</em> (Valenciennes 1837)</td>
<td><em>P lin</em></td>
<td>Total</td>
<td>No care</td>
<td>Long mig.</td>
<td>52.1</td>
<td>1450.1</td>
<td>1600000</td>
<td>1. 11. 13. 17. 21. 23. 24</td>
</tr>
<tr>
<td><em>Leporinus obtusidens</em> (Valenciennes 1837)</td>
<td><em>L obt</em></td>
<td>Total</td>
<td>No care</td>
<td>Long mig.</td>
<td>44.5</td>
<td>1005.1</td>
<td>538000</td>
<td>1. 3. 5. 13. 24</td>
</tr>
<tr>
<td><em>Salminus brasiliensis</em> (Cuvier 1816)</td>
<td><em>S bra</em></td>
<td>Total</td>
<td>No care</td>
<td>Long mig.</td>
<td>54.5</td>
<td>1350.6</td>
<td>2600000</td>
<td>1. 11. 13. 18. 21. 23. 24</td>
</tr>
<tr>
<td><em>Pimelodus maculatus</em> (Lacepède 1803)</td>
<td><em>P mac</em></td>
<td>Repeated</td>
<td>No care</td>
<td>Long mig.</td>
<td>29</td>
<td>770.3</td>
<td>200000</td>
<td>1. 3. 6. 9. 13. 17. 21. 24</td>
</tr>
<tr>
<td><em>Rhaphiodon vulpinus</em> (Spix &amp; Agassiz 1829)</td>
<td><em>R vul</em></td>
<td>Total</td>
<td>No care</td>
<td>Long mig.</td>
<td>60.5</td>
<td>980</td>
<td>98185</td>
<td>1. 13. 14. 24</td>
</tr>
<tr>
<td><em>Schizodon spp.</em>***</td>
<td><em>Sch.</em></td>
<td>Total</td>
<td>No care</td>
<td>Short mig.</td>
<td>38.4</td>
<td>896.2</td>
<td>80000*</td>
<td>13. 16. 19. 21. 24</td>
</tr>
<tr>
<td><em>Cyphocharax platanus</em> (Günther 1880)</td>
<td><em>C pla</em></td>
<td>Total*</td>
<td>No care</td>
<td>Short mig.</td>
<td>16.5</td>
<td>806.1*</td>
<td>36600*</td>
<td>7. 20. 24</td>
</tr>
<tr>
<td><em>Cyphocharax voga</em> (Hensel 1870)</td>
<td><em>C vog</em></td>
<td>Total*</td>
<td>No care</td>
<td>Short mig.*</td>
<td>25.5</td>
<td>806.1*</td>
<td>36600</td>
<td>7. 20. 24</td>
</tr>
<tr>
<td><em>Astyanax asuncionensis</em> (Géry 1972)</td>
<td><em>A asu</em></td>
<td>Repeated*</td>
<td>No care</td>
<td>Short mig.*</td>
<td>17.5</td>
<td>775.5*</td>
<td>9560*</td>
<td>11. 13. 17. 21. 23. 25. 26</td>
</tr>
<tr>
<td><em>Astyanax abramis</em> (Jenyns 1842)</td>
<td><em>A abr</em></td>
<td>Repeated*</td>
<td>No care</td>
<td>Short mig.*</td>
<td>13.5</td>
<td>775.5*</td>
<td>9560*</td>
<td>11. 13. 17. 21. 23. 24. 25</td>
</tr>
<tr>
<td><em>Astyanax rutilus</em> (Jenyns 1842)</td>
<td><em>A rut</em></td>
<td>Repeated*</td>
<td>No care</td>
<td>Short mig.*</td>
<td>12</td>
<td>775.5*</td>
<td>9560*</td>
<td>11. 13. 17. 21. 23. 24. 25</td>
</tr>
<tr>
<td><em>Ageneiosus militaris</em> (Valenciennes 1835)</td>
<td><em>A mil</em></td>
<td>Total*</td>
<td>Mating</td>
<td>Short mig.*</td>
<td>34.5</td>
<td>1849.5*</td>
<td>18500*</td>
<td>13. 19. 21. 24</td>
</tr>
<tr>
<td><em>Ageneiosus inermis</em> (Linnaeus 1766)</td>
<td><em>A ine</em></td>
<td>Total</td>
<td>Mating</td>
<td>Short mig.</td>
<td>40.5</td>
<td>1849.5*</td>
<td>18500</td>
<td>13. 19. 21. 24</td>
</tr>
<tr>
<td><em>Trachelyopterus spp.</em>**</td>
<td><em>Tra.</em></td>
<td>Repeated</td>
<td>Mating &amp; CP</td>
<td>No mig.</td>
<td>17.5</td>
<td>2300</td>
<td>1536</td>
<td>10. 13. 18. 19. 21. 24</td>
</tr>
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<tr>
<td>Serrasalmus spp.**</td>
<td>Ser.</td>
<td>Repeated</td>
<td></td>
<td></td>
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<tr>
<td>Pygocentrus nattereri</td>
<td>P nat</td>
<td>Repeated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Hoplias aff. malabaricus</td>
<td>H mal</td>
<td>Repeated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypostomus commersoni</td>
<td>H com</td>
<td>Total*</td>
<td></td>
<td></td>
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<tr>
<td>Loricariichthys spp. **</td>
<td>Lor.</td>
<td>Repeated</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

*Information on the reproductive trait based at genus level.


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.
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.