

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

E. Abrial, L.A. Espínola, A.P. Rabuffetti, M.L. Amsler, and K.M. Wantzen

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, and 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 of spring–summer floods whatever the intensity and duration, and (iv) equilibrium strategists have low flood dependence and 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 tri-factorielle (traits reproductifs des poissons, conditions hydro-climatiques et 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 avantagées 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 out in the past decades (e.g., Lamouroux et al. 2002; Blanck et al. 2007; Olden and Kennard 2010; Mims and Olden 2012).

Periodic strategists have a long generation time, moderate reproductive effort, large body size, high batch fecundity, and 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, and 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, and 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 occurrence 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

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E. Abrial, L.A. Espínola, A.P. Rabuffetti, and M.L. Amsler. National Institute of Limnology (INALI, CONICET/UNL), Santa Fe, CP 3000, Argentina. K.M. Wantzen. UNESCO Chair “River Culture – Fleuves et Patrimoine”, Interdisciplinary Research Center for Cities, Territories, Environment and Society (CNRS–UMR–CITERES), Université François Rabelais, Tours, CP 37200, France.

Corresponding author: Elie Abrial (email: elieab@live.fr).

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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 are 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 highest inland fish production of Argentina (Baigún et al. 2003), and the diet of many people in this region depends on fish protein (FAO 2014). Over approximately 1000 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 little is actually 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. Furthermore, 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 have 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 to 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 and 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 by different adaptations of fish life histories influenced by the singularity of each of the annual hydroclimatic conditions. The main goal is to present 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

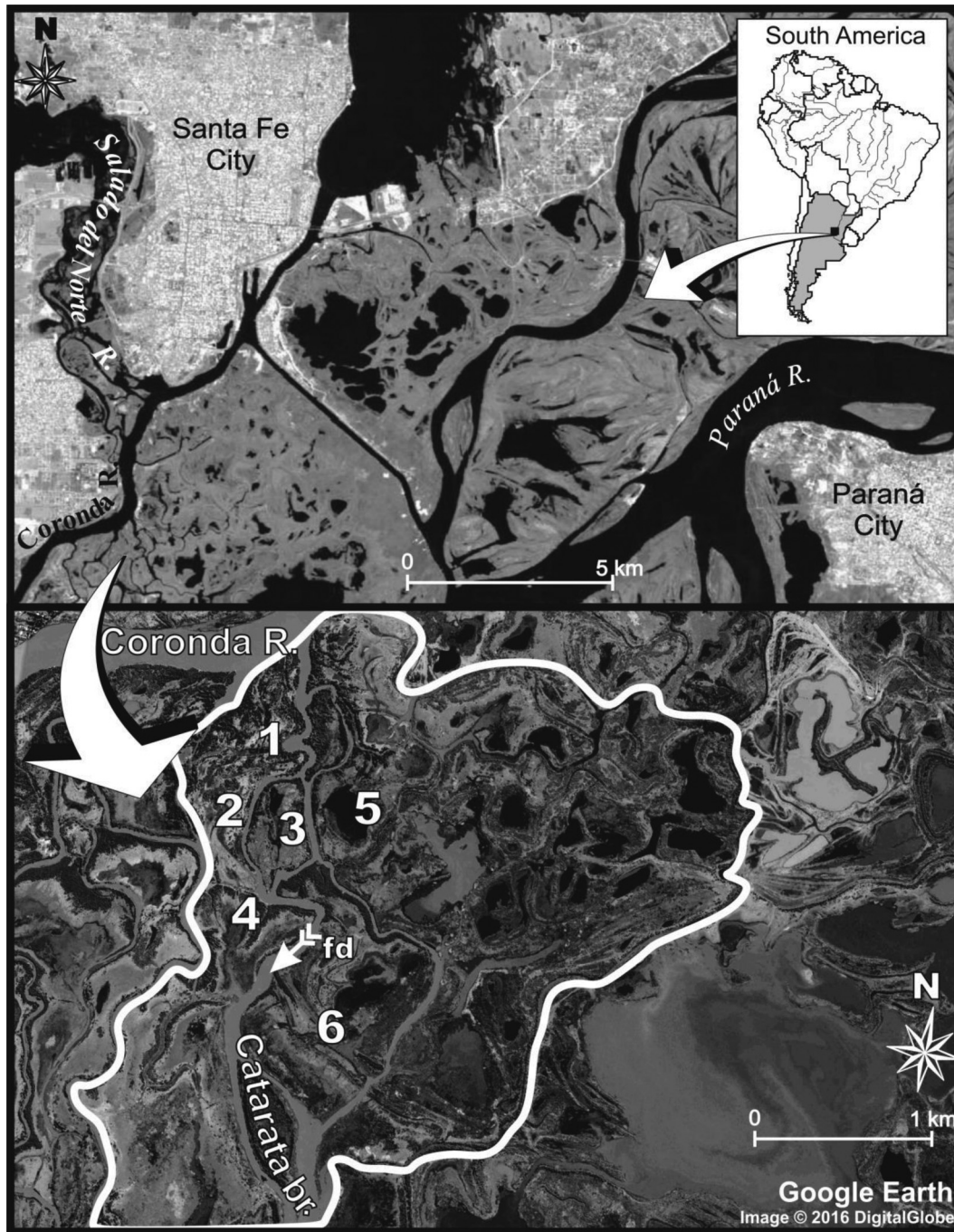
The MPR floodplain south of Santa Fe city presents an anastomosed pattern, an intricate drainage network of high connectivity, comprising a complex mosaic of minor channels and fluvial lakes that covers a large part of the plain (Fig. 1). Fish samplings were located in six sites: four sites of the Catarata 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 that 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 *Eichhornia azurea*).

Fish were collected with gill nets of stretched mesh size (3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots) covering an area of 180.9 m² and exposed over 24 h and checked every 8 h. 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 Agostinho and Zalewski 1995; Saint-Paul et al. 2000; Scarabotti et al. 2017). Stretched mesh size range (3–16 cm between opposite knots) was efficient in catching specimens between 5 and 60 cm 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.

To reduce the possible effect of habitat complexity on the variation of fish assemblage structure, gill nets 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 gillnet 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 (centimetres), body mass (grams), and state of gonad maturation). Other fishes were preserved in 10% formalin and identified in the 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, CONICET/UNL), Santa Fe, Argentina. Additionally,

Fig. 1. Study area in the alluvial plain of the Middle Paraná River. 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 (white perimeter, flow direction (fd)).



water temperature (degrees Celcius) was recorded at each sampling site.

Data analysis

Variation of connectivity

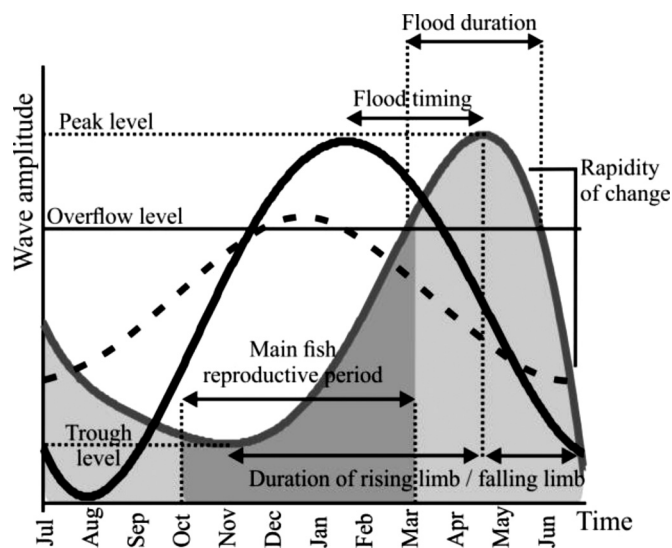
To provide a representative overview of fish habitat availability in the floodplain from low to high water levels, we analyzed the hydrological connectivity based on six satellite images obtained from the historical data set of Google Earth Pro (see Fig. 2). Each of these represents the area studied (15 km²) at a specific date and consequently at a specific hydrometric level (2.26, 3.19, 3.4, 3.63, 4.04, and 4.5 m). 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 were connected or isolated from the lotic ones. In 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

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



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 to obtain a value of daily T_w values 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 of 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 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 (15 figures) and the corresponding T_a registered at the meteorological station (daily data). The same was repeated replacing each T_a by $(T_a + T_{a \text{ day before}})/2$ and then by $(T_a + T_{a \text{ day before}} + T_{a \text{ 2 days before}})/3$ until 30 days before each sampling date so as to obtain each time the corresponding coefficient of determination (R^2); the higher R^2 is expected to give a better time lag of warming/cooling of T_w measured in the channel. The linear regression between T_w measured and T_a 7 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:

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

Characterization of interannual hydroclimatic conditions

To analyze the interannual hydroclimatic variations during the period studied, we considered the data sets of daily water temperatures, daily water levels, and day length. From the three daily data sets, we defined seven hydroclimatic variables that would have some relevance on fish reproductive ecology. To obtain non-dimensional data sets comparable between them, all daily data were divided by the means of each data set. The resulting variables were considered at an annual scale, from 1 July to 30 June of the

following year, considering the increase of water temperature and day length as the main predictive trigger of fish reproductive periods (following Suzuki et al. 2004). An explanatory graph shows the variable metrics and helps to understand how hydroclimatic variables were constructed (Fig. 3). The definition, potential application, and mathematical formula of each hydroclimatic variable are available in Table S1¹ (see supplementary material). 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.

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 intraspecific variations (e.g., spawning area and spawning support, timing and duration of the reproductive period, and 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 extrapolation to the MPR (see literature references in Table 1): (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, and 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 vicinity close to the area studied, (5) oocyte diameter in fully developed ovaries, and (6) total fecundity: number of oocytes per female with fully developed ovaries.

In Table 1, fecundity and oocyte diameter refer to data stemming 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 the species level and we used the information available at the genus level from the closer vicinity. Moreover, to simplify the results, some species were considered at the genus level, as they had equivalent morphological characteristics and reproductive traits and presented similar temporal recruitment patterns during the period studied (see Table 1 for more details on the life history data set).

We used a multiple factor analysis (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 of the data by the first eigenvalue obtained from its principal components analysis. According to the Kaiser–Guttman criterion (Jackson 1993), the axes with eigenvalues higher than 1 were retained for interpretation. Species reproductive diversity carried out by the multiple factor analysis was compared and discussed within the classic fish life history framework (Winemiller and Rose 1992).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0579>.

Fig. 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.

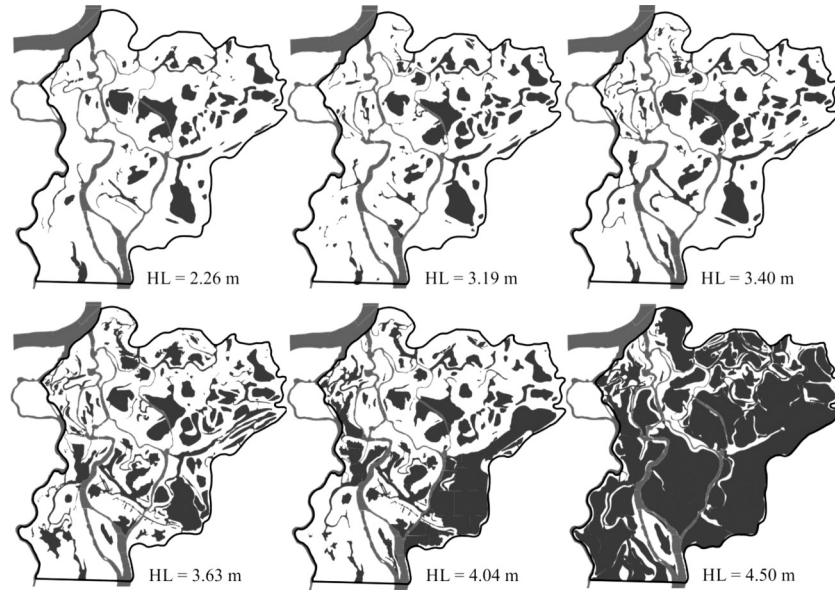


Table 1. Details of variables related to fish reproduction and population structure of the 25 most abundant fish species caught during the study.

Species	Name abbreviation	Spawning type	Parental care	Migration type	Maximum standard length (cm)	Oocyte size (µm)	Fecundity (no. of oocytes)	Consulted literature [‡]
<i>Prochilodus lineatus</i>	<i>P lin</i>	Total	None	Long	52.1	1450.1	1 600 000	1, 11, 13, 17, 21, 23, 24
<i>Leporinus obtusidens</i>	<i>L obt</i>	Total	None	Long	44.5	1005.1	538 000	1, 3, 5, 13, 24
<i>Salminus brasiliensis</i>	<i>S bra</i>	Total	None	Long	54.5	1350.6	2 600 000	1, 11, 13, 18, 21, 23, 24
<i>Pimelodus maculatus</i>	<i>P mac</i>	Repeated	None	Long	29	770.3	200 000	1, 3, 6, 9, 13, 17, 21, 24
<i>Pterodoras granulosus</i>	<i>P gra</i>	Repeated	None	Long	38	1056.1	296 000	19, 21, 24
<i>Rhaphiodon vulpinus</i>	<i>R vul</i>	Total	None	Long	60.5	980	98 185	1, 13, 14, 24
<i>Schizodon</i> spp. [†]	<i>Sch.</i>	Total	None	Short	38.4	896.2	80 000*	13, 16, 19, 21, 24
<i>Cyphocharax platanus</i>	<i>C pla</i>	Total*	None	Short	16.5	806.1*	36 600*	7, 20, 24
<i>Cyphocharax voga</i>	<i>C vog</i>	Total*	None	Short	25.5	806.1*	36 600	7, 20, 24
<i>Astyanax asuncionensis</i>	<i>A asu</i>	Repeated*	None	Short*	17.5	775.5*	9 560*	11, 13, 17, 21, 23, 24, 25
<i>Astyanax abramis</i>	<i>A abr</i>	Repeated*	None	Short*	13.5	775.5*	9 560*	11, 13, 17, 21, 23, 24, 25
<i>Astyanax rutilus</i>	<i>A rut</i>	Repeated*	None	Short*	12	775.5*	9 560*	11, 13, 17, 21, 23, 24, 25
<i>Acestrorhynchus pantaneiro</i>	<i>A pan</i>	Repeated	None	None	30	897.5	33 470	8, 12, 17, 19, 21, 23, 24
<i>Ageneiosus militaris</i>	<i>A mil</i>	Total*	Mating	Short*	34.5	1849.5*	18 500*	13, 19, 21, 24
<i>Ageneiosus inermis</i>	<i>A ine</i>	Total	Mating	Short	40.5	1849.5*	18 500	13, 19, 21, 24
<i>Trachelyopterus</i> spp. [†]	<i>Tra.</i>	Repeated	Mating and parental care	None	17.5	2300	1 536	10, 13, 18, 19, 21, 24
<i>Serrasalmus</i> spp. [†]	<i>Ser.</i>	Repeated	Mating and parental care	None	22.5	1816.3	2 800*	9, 13, 19, 21, 24
<i>Pygocentrus nattereri</i>	<i>P nat</i>	Repeated	Mating	None	31	1635	19 000	2, 4, 16, 19
<i>Hoplias</i> aff. <i>Malabaricus</i>	<i>H mal</i>	Repeated	Mating and parental care	None	49	2445.2	61 000	11, 13, 15, 19, 21, 24
<i>Hypostomus commersoni</i>	<i>H com</i>	Total*	Mating and parental care*	None*	48.5	4360*	2 802*	15, 21, 22
<i>Loricariichthys</i> spp. [†]	<i>Lor.</i>	Repeated	Mating and parental care	None	39.5	3197.1	1 450	13, 21, 22, 24

*Information on the reproductive trait based at the genus level.

[†]Species considered at the genus level: *Schizodon* spp. (*Schizodon borellii* and *Schizodon platae*), *Trachelyopterus* spp. (*Trachelyopterus* aff. *galeatus* and *Trachelyopterus lucenai*), *Serrasalmus* spp. (*Serrasalmus maculatus* and *Serrasalmus marginatus*, and *Loricariichthys* spp. (*Loricariichthys platymetopon* and *Loricariichthys melanocheilus*).

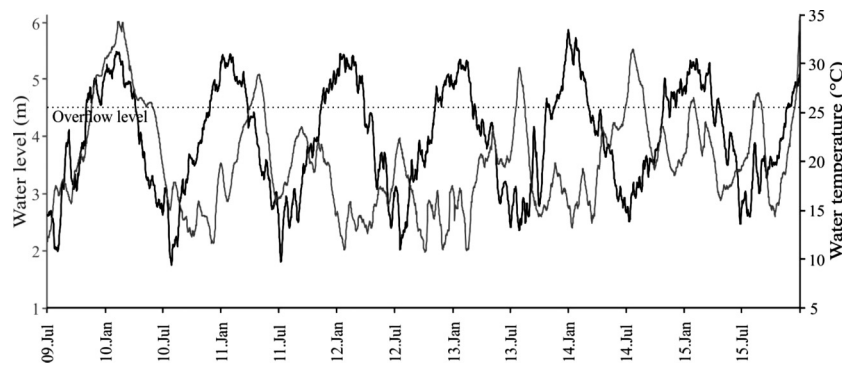
[‡]Consulted literature: 1, Agostinho et al. 2003; 2, Almirón et al. 2015; 3, Arantes et al. 2013; 4, Casciotta et al. 2005; 5, Felizardo et al. 2015; 6, Godinho et al. 1974; 7, Godoy 1975; 8, Hirt and Flores 1999; 9, Lowe-McConnell 1987; 10, Maia et al. 2013; 11, Meschiatti and Arcifa 2009; 12, Meurer and Zaniboni-Filho 2012; 13, Nakatani et al. 2001; 14, Neuberger et al. 2007; 15, Ponton and Tito de Moraes 1994; 16, Renno et al. 2005; 17, Rizzo et al. 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 and Menezes 1992; 24, Vazzoler 1996; 25, Winemiller 1989.

Abundance of YOY

Published data on age determination of species present high intraspecific variations, making their use difficult. According to geographical areas, climate, or food supply prior to a sampling period, the age-length relation can be considerably different

within juveniles of a species. In this study, however, 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, the abundance of YOY was totaled, i.e., all

Fig. 4. Yearly variation of water temperature and water levels in the Middle Paraná River from July 2009 to December 2015. Black line, water temperature; grey line, water level.



young fishes from a new cohort whose size corresponds to an individual born during the previous reproductive period. This methodology was supported by the existing literature on age determination when the information was available from a close vicinity (e.g., Carroza and Cordiviola de Yuan 1991; Domanico et al. 1993; Araya et al. 2005; Balboni et al. 2011). YOY abundance was standardized according to catch per unit effort (number of individuals per 1000 m² of gill nets per 24 h).

Based on the results of multiple factor analysis and interannual YOY abundances, four groups of species were defined with similar recruitment pattern and life history strategy. Because the 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 catch per unit effort was represented first and the percentage of catch per unit effort 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 to what extent availability to flooded habitats depends on water level fluctuations. Within a range of 2.26–3.4 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, and when they reach 4.5 m, 85% of the total area is inundated (the overflow level in the study area of alluvial plain; all water bodies are connected).

From year to year, water temperatures had similar fluctuations, varying from 10–15 °C in winter to 30 °C during summer (Fig. 4). On the other hand, the annual fluctuations of water level changed considerably. Flood/flow pulses occurred in 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 and 194 days; see Table 2).

The hierarchical clustering classified the 6 years in the three groups according to their hydroclimatic characteristics (Fig. 5). The 2009–2010 year was unique: a flood pulse of very high intensity and duration with low slopes of the rising/falling limbs oc-

curred 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 2). Then, two years were similar (2010–2011 and 2013–2014) 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 (2014–2015), whereas no floods occurred during the two other years (2011–2012 and 2012–2013).

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 5380 individuals and 87% of total abundance. Those species exhibited a wide range of life history traits (Table 1). 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 loriciids 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 rubrilus*, standard length = 12 cm) to large specimens (e.g., *Rhaphiodon vulpinus*, standard length = 60.5 cm). The 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.

Considering the reproductive strategies of MPR fishes from the classical life history framework (Winemiller and Rose 1992), species reproductive traits show a clear distribution between periodic and equilibrium strategies (Fig. 6). Left of the vertical axis, all species make short or long migrations and 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.

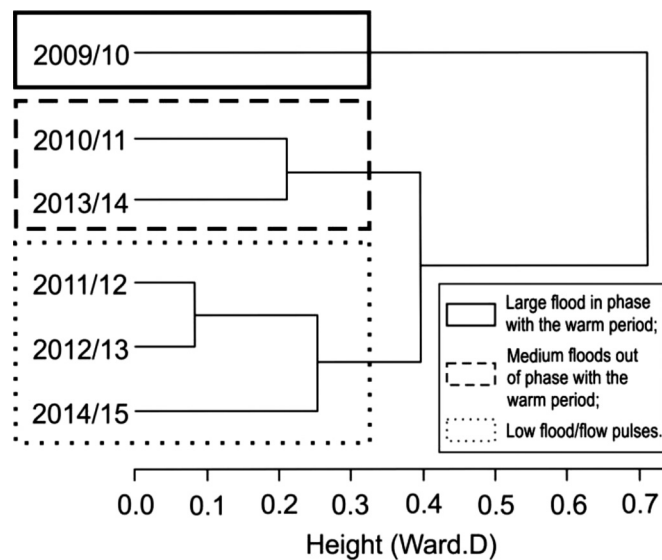
Nonetheless, some differences within the two groups are considerable and lead to considering four fish reproductive groups. Species of group A are all highly periodic. They have higher fecundity and smaller oocytes, migrating behavior, and no parental care and all Characiformes have total spawning (periodic 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 be-

Table 2. Values of each hydroclimatic variable used to analyze the interannual variations of hydrology and temperature in the Middle Paraná River (years are considered from 1 July to 30 June of the following year).

Years	Rep.Con (integral)	Fld.Tim (%)	Hyd.Var (ad.)	Ris.Limb (m/day)	Fal.Limb (m/day)	Fld.Int (m)	Fld.Dur (days)
2009–2010	255	95	1.02	0.017	0.017	6.02	194
2010–2011	160	49	0.81	0.020	0.042	5.10	47
2011–2012	153	33	0.57	0.017	0.016	4.17	0
2012–2013	139	42	0.58	0.031	0.025	3.97	0
2013–2014	151	15	0.71	0.038	0.043	5.21	29
2014–2015	200	95	0.66	0.022	0.021	4.68	19

Note: 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).

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



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

YOY abundance

Within each reproductive strategy defined in Fig. 6, fish species had similar interannual recruitment patterns (Fig. 7). The 10 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 the periodic–equilibrium strategy showed abundance of YOY significantly higher during the years 2010 and 2015, a little lower in 2012, and significantly lower during 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 a periodic–opportunistic reproductive strategy presented irregular recruitment patterns. Peaks of abundance of the small characids *Astyanax* spp. were found in 2010 (*Astyanax asuncionensis*), 2010 and 2011 (*Astyanax abramis*), and 2014 (*A. rutilus*), whereas the abundance of the middle-sized characid *Acestrorhynchus pantaneiro* was stable along the period studied (Fig. 7d).

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 10 times lower and periodic strategists represented a small part of the YOY abundance. Periodic–equilibrium strategists reached more than 50% of fish recruitment in 2015 and periodic–opportunistic strategists dominated in 2011 and 2014. The percentage of equilibrium strategists’ YOY increased when abundance of YOY of the other strategies was low in the plain.

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 and 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 a 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 by the kind of reproductive strategy developed by the species and its relation of dependence with the flood attributes (timing, duration, intensity, and 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.

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

Fig. 6. Results of the multiple factor analysis of life history of the 25 most abundant fish species caught in the Middle Paraná River floodplain. (a) Species scores; (b) reproductive traits scores (see Table 1 for abbreviations). The circles gather species together in groups of similar reproductive behavior. A, periodic strategists; B, periodic–equilibrium strategists; C, equilibrium strategists; D, periodic–opportunistic strategists.

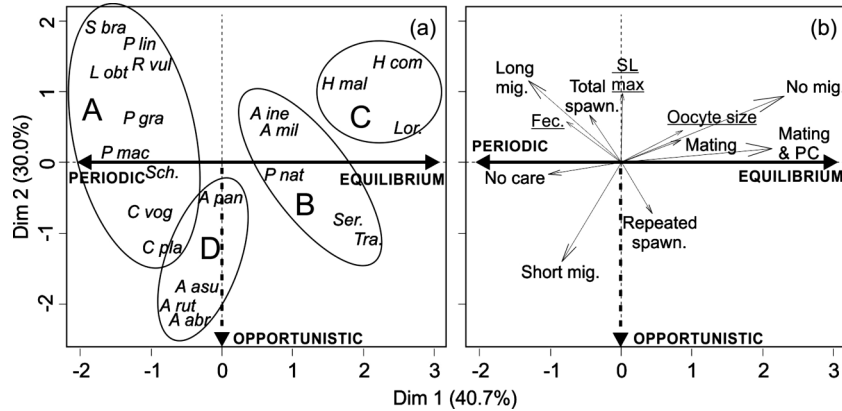


Fig. 7. Abundance (catch per unit effort (CPUE)) of young-of-the-year according to reproductive strategy: (a) periodic strategists, (b) periodic–equilibrium strategists, (c) equilibrium strategists, and (d) periodic–opportunistic strategists. When significant between-year differences of the young-of-the-year abundance exist, *p* values are included in the figure.

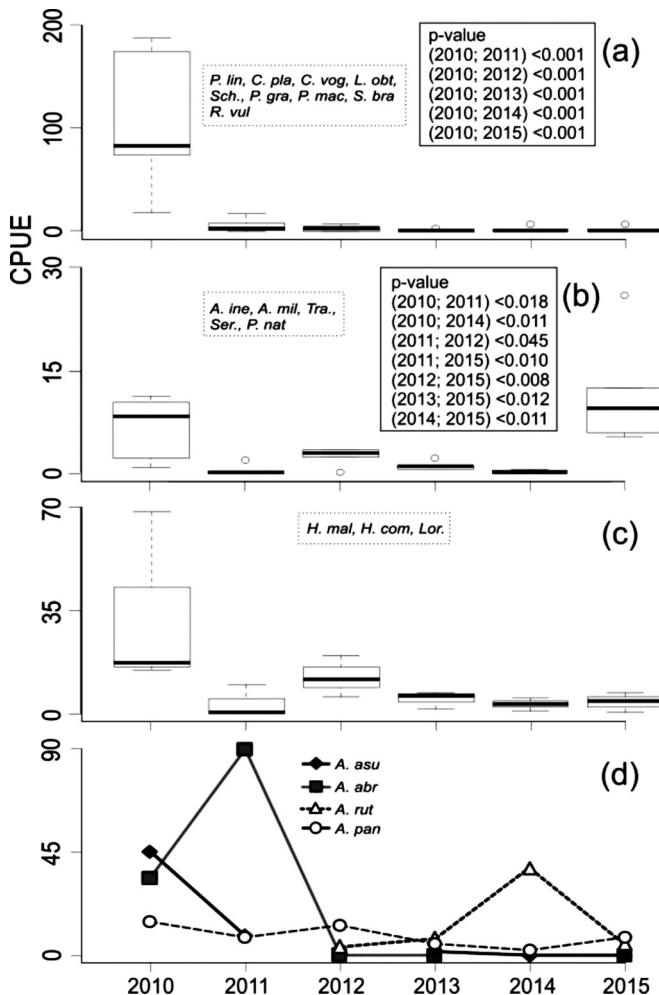
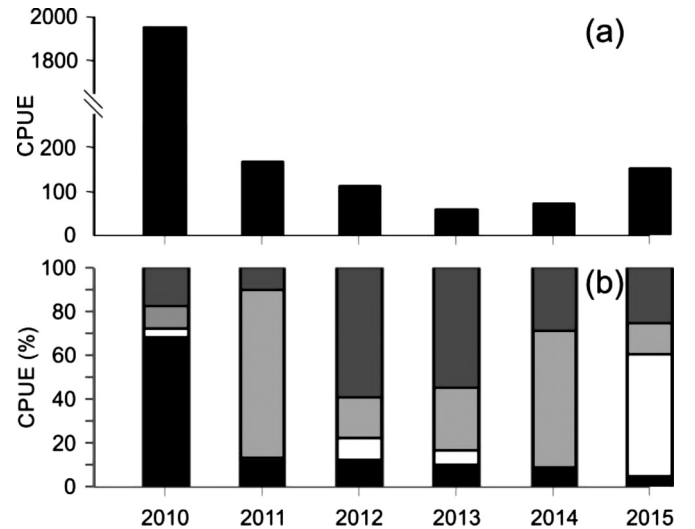


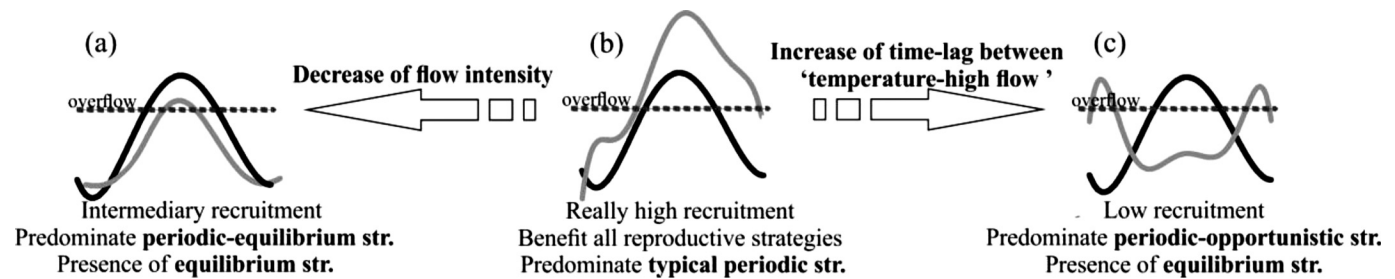
Fig. 8. (a) Total catch per unit effort (CPUE) of young-of-the-year caught in the Middle Paraná River floodplain from 2010 to 2015; (b) percentage of CPUE of young-of-the-year of the four reproductive strategies from 2010 to 2015. Plack bars, periodic strategists; white bars, periodic–equilibrium strategists; dark grey bars, equilibrium strategists; light grey bars, periodic–opportunistic strategists.



all species showed higher YOY abundance when such conditions occurred, around 10 times higher than in 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 schools 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 is doubly important in the MPR because the great majority of fish species that sustain commercial fisheries and 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

Fig. 9. Synthetic scheme of annual flow variability in the Middle Paraná River and its influence on recruitment patterns of floodplain fishes adopting different life history strategies. Black line, water temperature; grey line, water level; broken line, overflow level.



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 the incubation time (Suzuki 1992; Sarmiento et al. 2014). 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 of 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 the 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 and Olden 2012). We have summarized and broadened the knowledge of fish reproduction of 25 MPR species representing more than 85% of the 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 of 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 cause fishes to diversify their reproductive behaviors 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.

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