frontiers in Environmental Science

ORIGINAL RESEARCH
published: 21 October 2020
doi: 10.3389/fenvs.2020.577181

Relationship of Freshwater Fish Recruitment With Distinct Reproductive Strategies and Flood Attributes: A Long-Term View in the Upper Paraná River Floodplain

Anielly Galego de Oliveira[1], Taise Miranda Lopes[1], Mirtha Amanda Angulo-Valencia[1], Rosa Maria Dias[1], Harumi Irene Suzuki[2], Isadora Cristina Bianchi Costa[2] and Angelo Antonio Agostinho[1,2]*

[1] Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos (PEA), Universidade Estadual de Maringá (UEM), Maringá, Brazil, [2] Núcleo de Pesquisa em Ictiologia, Limnologia e Aquicultura (Nupélia), Maringá, Brazil

OPEN ACCESS

Edited by:
Pierre Girard,
Federal University of Mato Grosso, Brazil

Reviewed by:
Jean Remy Davee Guimaraes,
Federal University of Rio de Janeiro, Brazil
Yongjiu Cai,
Nanjing Institute of Geography and Limnology (CAS), China

***Correspondence:**
Anielly Galego de Oliveira
anielly_oliveira@hotmail.com

Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: 28 June 2020
Accepted: 16 September 2020
Published: 21 October 2020

Citation:
Oliveira AGd, Lopes TM, Angulo-Valencia MA, Dias RM, Suzuki HI, Costa ICB and Agostinho AA (2020) Relationship of Freshwater Fish Recruitment With Distinct Reproductive Strategies and Flood Attributes: A Long-Term View in the Upper Paraná River Floodplain. Front. Environ. Sci. 8:577181. doi: 10.3389/fenvs.2020.577181

The flood pulse is the main driving force for communities' structure and functioning in river-floodplain systems. High synchrony exists between the hydrological cycle and reproductive cycle events for several fish species. However, species with different reproductive strategies can respond in different ways to the flood regime. Thus, this study intends to evaluate the relationship between the recruitment of different reproductive guilds of freshwater fish and flood attributes (flood duration, maximum annual water level, and delay of flood) from a time series of 20 years in the Upper Paraná River floodplain, Brazil. The abundance of four guilds was evaluated: (i) long-distance migratory with external fertilization and without parental care (LMEF); (ii) non-migratory or short-distance migratory with external fertilization and without parental care (NEFW); (iii) non-migratory or short-distance migratory with external fertilization and parental care (NEFP); and (iv) non-migratory or short-distance migratory with internal fertilization and without parental care (NIF). Multiple regression analyses were applied between flood attributes and abundance of young-of-the-year or juveniles for each reproductive guild. This study observed a consistent pattern of long-lasting flooding positively influencing the recruitment of all reproductive guilds, while water level intensity and the time of the onset of flooding also influenced some non-migratory strategies. We can conclude that the conservation of fish populations and the maintenance of ecosystem functions and services associated with them need to be considered in the operating protocols of upstream hydroelectric plants, since they are dependent on the flooding controlled by them.

Keywords: ichthyofauna, migratory fish, parental care, internal fertilization, flow control, dams

INTRODUCTION

Dams for hydropower generation have been considered among the most impactful anthropogenic activities for freshwater ecosystems, due to flow modification, invasive species facilitation, and habitat fragmentation (Agostinho et al., 2007; Abell et al., 2008; Timpe and Kaplan, 2017). In the Southern Hemisphere, where the most biodiverse river basins are located (e.g., Amazon, Congo, Mekong), there are an unprecedented number of dam projects (Winemiller et al., 2016). Downstream, the impacts mainly include the alteration of seasonal flood cycles. These effects are exacerbated in stretches of floodplain where dams are cascaded (Agostinho et al., 2008). For fish, these impacts can be on the structure and functions of the assemblages, with changes in the availability of shelter and food, reproductive processes, and rates of growth, mortality, competition, predation, and parasitism (Agostinho et al., 2004). Dams can also alter ecosystem processes and services in which fish are involved, such as feeding supply for aquatic and terrestrial consumers, fisheries, nutrient cycling and transportation, food web regulation, and their roles as environmental engineers (Mormul et al., 2012; Humphries and Walker, 2013).

The hydrologic regime is the selective force behind the diverse livelihood strategies of species, including life-history traits (Wootton, 1990; Zeug and Winemiller, 2007; Abrial et al., 2019; Humphries et al., 2020). The reproductive dynamics and flood regime are closely related (Gomes and Agostinho, 1997; Humphries et al., 1999; Bailly et al., 2008). The occurrence of the natural and periodic flood pulses in tropical floodplains led the biota, especially fish, to develop strategies that maximize reproductive success (Welcomme, 1979; Vazzoler, 1996) and diminish the predation risk on their offspring (Suzuki et al., 2009). A gradient of morphological, physiological, and ecological attributes characterizes the diversity of methods by which fish of freshwater systems reproduce (Winemiller, 1989). Consequently, the flood regime differentially affects the reproduction and recruitment of species [i.e., the addition of new individuals to populations; Gaillard et al. (2008)] with different life histories (Agostinho et al., 2004; Winemiller, 2005; Bailly et al., 2008).

Inundations tend to favor the reproduction of long-distance migratory species because there is a high degree of synchronization between the hydrological regime variation and essential events in the reproductive cycle (Junk et al., 1989; Agostinho et al., 2004). Increases in photoperiod and temperature lead to gonadal development and maturation. The first rains act as a cue for the formation of schools and migrations upstream to search for the best environmental conditions for spawning (Vazzoler and Menezes, 1992; Cowx et al., 1998; Suzuki et al., 2004). The migratory fish usually spawn in the uppermost regions of the basin and use flooded area, dozens of kilometers downstream, as nurseries for their early stages of development (Nakatani et al., 2001; Wantzen and Junk, 2006; Silva et al., 2017; Rosa et al., 2018). For these species, long-lasting floods in the warmer season can maximize recruitment (Gomes and Agostinho, 1997; Oliveira et al., 2015), providing shelter and food for more extended periods.

The influence of the hydrological regime on fish recruitment becomes relevant when we consider the threats imposed by the rapid expansion of impoundments in most basins in Brazil. The results obtained from studies on fish recruitment responses to the flood regime have been divergent, especially if considered fish that do not perform long reproductive migrations for spawning. In the upper Paraná River basin, the reproduction of sedentary species with parental care, internal fertilization, and short-distance migration seems to be less dependent on flooding. Still, the abundance of young-of-the-year (for example migratory species), can be low in years with no or incipient flooding (Agostinho et al., 2004). In the opposite, for the Cuiabá River, floods also appear to have a relevant role in reproduction and recruitment for species with parental care and internal fertilization. In contrast, reproduction of short-distance migrants (SM) appears to be less dependent on flooding (Bailly et al., 2008). Other studies considering adult species members besides the juveniles, report that short-distance migrants (SM) show moderated flood dependence (Fernandes et al., 2009; Vasconcelos et al., 2013).

Migratory fish are even more vulnerable to hydropower plants. In addition to controlling seasonal flooding, dam operation intercepts migratory routes (Agostinho et al., 2005; Pelicice et al., 2015; Lima et al., 2017). The impacts resulting from changes in the hydrological regime and barrier interposed by barrages to fish movements are quite conspicuous in the upper Paraná River basin (Agostinho et al., 2008). The stretch concentrates the largest number of large reservoirs in South America, and the impacts from these reservoirs can be cumulative (Agostinho et al., 2007; dos Santos et al., 2017; Pelicice et al., 2018).

Data obtained from long-term ecological studies (LTES) of the last remaining stretch of a natural river-floodplain system in the upper Paraná River, downstream from a cascade of reservoirs, can facilitate a better understanding of the relationship between the flood and reproductive aspects of fish that are mediated by dam regulation. These studies provide data on a wider variety of hydrological cycles and environmental conditions, allowing a more detailed analysis of how fish assemblages respond to these conditions. Therefore, the data allows researchers to identify a more consistent pattern of recruitment responses over time, including crucial information about how different reproductive guilds can be affected by hydrological variations. In addition, LTES may support the operational management of hydro plants, providing information about the quantity of the water that needs to pass through the dams while maintaining adequate hydrological regimes to ensure acceptable levels of fish reproduction and recruitment.

Thus, this study aims to evaluate the relationship between recruitment of different reproductive guilds and flood attributes (flood duration, maximum annual water level, and flood delay) based on a time series of 20 years in the upper Paraná River floodplain, Brazil. We expect a stronger correlation between the flood regimes and the annual recruitment of long-distance migratory fish than of sedentary fish (i.e., non-migratory). Specifically, this research expects a positive relationship between the recruitment of large migratory fish and the maximum annual water level and duration of flood, and a negative relationship between the recruitment of large migratory fish and the delay in the onset of flooding.

MATERIALS AND METHODS

Study Area

The upper Paraná River floodplain is located on the west bank of the Paraná River (23°43′ – 25°33′S; 54°35′ −53°10′ W) between

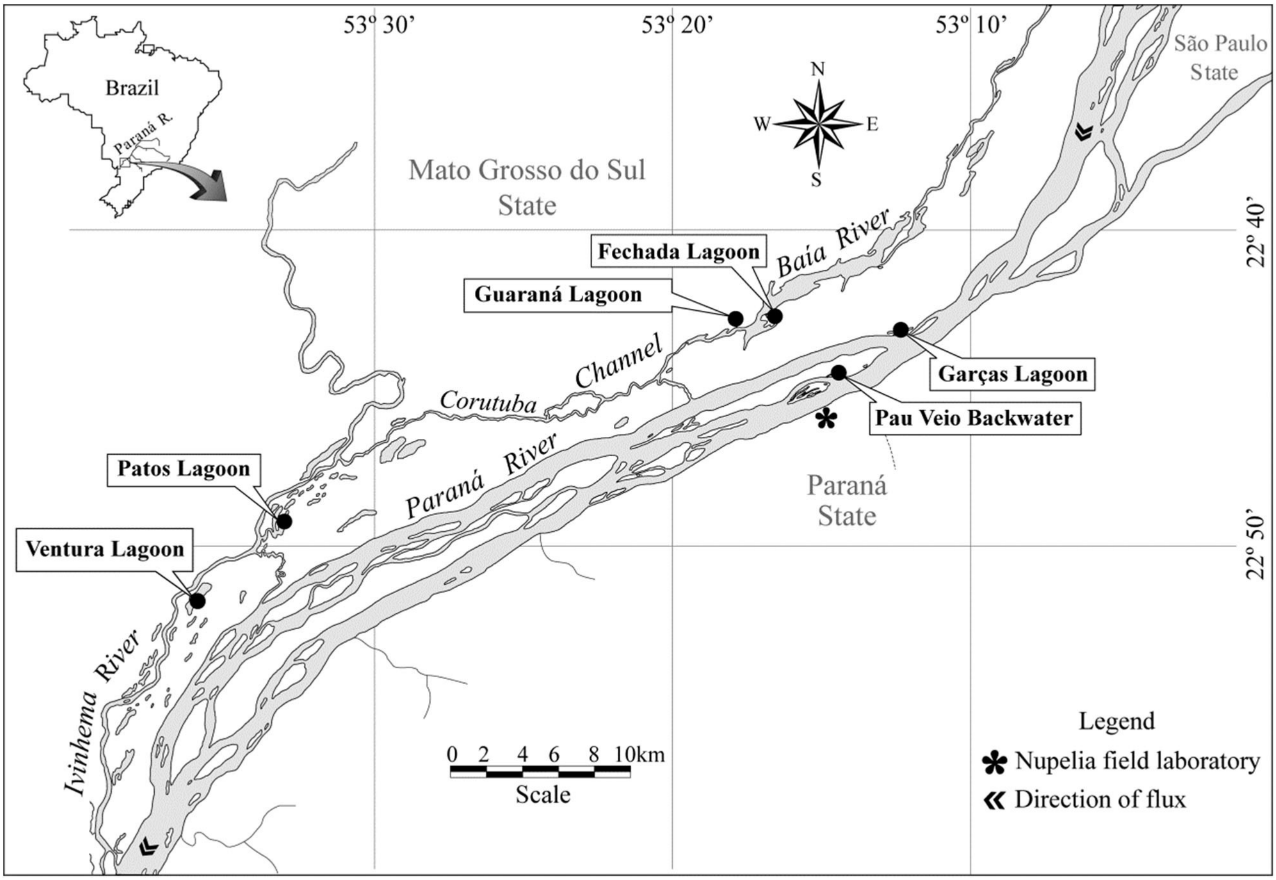

FIGURE 1 | Upper Paraná River floodplain, and location of sampling sites.

the states of Mato Grosso do Sul and Paraná. This region is subjected to variations in the level of the Paraná River and the two tributaries of the west bank, the Baía, and Ivinhema Rivers (Thomaz et al., 2007). The stretch of 230 km with lotic characteristics is the remaining of a 480 km long floodplain, before the Engenheiro Sérgio Motta "Porto Primavera" dam, upstream. Downstream, currently, the floodplain extends on to the Itaipu Reservoir (Souza-Filho and Stevaux, 2004). Porto Primavera is the first of dozens of upstream hydroelectric dams, composing reservoir cascades in the main channel of the Paraná River, as well in the tributaries like Paranapanema River, Tietê River, Grande River, and Paranaíba River, besides the dams are widespread all over the upper Paraná basin (Agostinho et al., 2008).

Sampling

Sampling was conducted quarterly from March 2000 until December 2019 in three rivers and six lakes within the floodplain (**Figure 1**). Fishes were collected using gillnets of different mesh sizes (2.4, 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots) that were exposed for 24 h and checked every 8 h (at 8, 16, and 24 h). Captured fish were anesthetized with 5% benzocaine and euthanized. All captured fish were identified according to Graça and Pavanelli (2007) and Ota et al. (2018). The abundance of fish caught in gillnets was indexed by the catch per unit effort (CPUE; individuals/1,000 m^2 of gillnets exposed during 24 h) for each year. The data for Paraná and Baía rivers were used together, as the latter follows the same hydrological cycle as Paraná River.

The reproductive guilds of fish were divided according to the classification proposed by Suzuki et al. (2004) based on their migratory behaviors for spawning, type of fertilization, and parental care: (i) long-distance migratory with external fertilization and without parental care (LMEF); (ii) non-migratory or short-distance migratory with external fertilization and without parental care (NEFW); (iii) non-migratory or short-distance migratory with external fertilization and parental care (NEFP); and (iv) non-migratory or short-distance migratory with internal fertilization and without parental care (NIF). Species that were not previously classified into the four referenced guilds were categorized based on the existing literature by considering their life histories or following the pattern of their genus according to Oliveira et al. (2018).

To infer about recruitment from each flood cycle, we used only individual young-of-the-year (YOY) for the long-distance migratory fish guild. The selection was made by species and individuals based on maximum length at an age

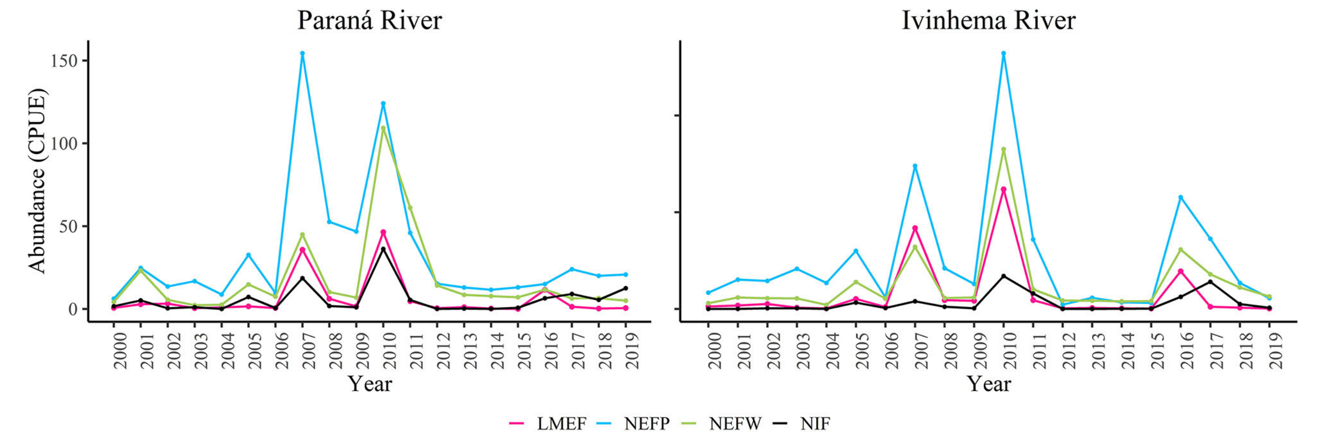

FIGURE 2 | Recruitment of each guild over time (CPUE = catch per unit of effort).

of 1 year, since individuals can remain immature for up to three 3 years. For other guilds that reach lower lengths, the selection of immature individuals was based on the degree of gonadal maturation.

River levels were provided by the National Water Agency (Agência Nacional das Águas—ANA—Sistema Nacional de Informações sobre Recursos Hídricos—SNIRH), which obtains the daily water level (WL; cm in relation to the operation of the Hydrometric Station at 231.8 meters above sea level) from a gauging station in the Paraná River (Porto São José Hydrometric Station; registration number 64575000). A threshold level of 450 cm had previously been established as the level at which the Paraná River overflows onto the floodplain (Comunello et al., 2003). This threshold level (450 cm) corresponds to a discharge of 12,370 m^3/s and a flooded area of 103.5 km^2 out of the 359 km^2 of the floodplain (Rocha et al., 2001). We used only the Paraná River water level, because the nurseries area and recruitment in the Ivinhema floodplain are strongly affected by high levels in the Paraná River.

The examined flood period lasted from October until May of each year, a period when floods and the spawning of long-distance migratory species have historically occurred in the region (Agostinho et al., 2005). Floods were characterized according to the following attributes: (i) flood duration (number of days when the river level remained above 450 cm in Paraná River); (ii) maximum annual water level (intensity; the highest recorded annual river level); and (iii) delay in flooding (the number of 15-day periods between October 1 and the start of flooding) (Suzuki et al., 2009; Oliveira et al., 2015).

Data Analysis

We used the abundance of YOY for LMEF, and juveniles for each other reproductive guild, as an estimate for fish recruitment. The relationships between the annual recruitment and flood attributes for each reproductive guild and river were assessed using a multiple linear regression analysis with model selection (forward-backward), with flood duration, maximum annual water level, and flood delay as predictors of the abundance (dependent variable). We tested the variables for multicollinearity using the variance inflation factor (VIF); we did not use values above 10. The residuals of the models were homoscedastics and the distribution was normal. We chose the best predictor model according to the lowest AIC value and adopted a significance level of 5%. These analyses were performed in the R environment (R Core Team, 2019) using the package car, function "vif;" package MASS, function "stepAIC;" and package stats, function "lm."

RESULTS

Long-term recruitment data for the Upper Paraná River floodplain were available for 103 species of fish (90 in the Paraná-Baía basin with 20 exclusive species and 83 in the Ivinhema basin with 13 exclusive species). The reproductive guild, the occurrence of each species in the basins, the abundance rank by the guild, the length of young-of-the-year of long-distance migratory fish, and the maximum size of juveniles for the other guilds, can be found in the **Table S1**. The recruitment of each guild showed a great difference between the years (**Figure 2**), with the highest values for all guilds in the years 2005, 2007, 2010, 2011, in the Paraná River, and also in 2016 after a local flood in the Ivinhema River, except for NIF, with a later peak in 2017.

Hydrological Cycle

In the Paraná River, during the period between 2000 and 2019, there were two lasting floods (>50 days; longest in 2009–2010 followed by 2006–2007; see **Table 1** and **Figure 3**). The longer-lasting flood was also the largest, with the water levels reaching 717 cm. Moderate floods (between 25 and 50 days) occurred in the cycles 2010–2011, 2004–2005, and 2015–2016, each of which reached high water level (>635 cm). In the other years, the floods were null or incipient. The majority of the floods were onset in January (with seven and eight delays), and just three cycles of flooding began earlier. Two floods (2005–2006 and 2015–2016) were not very long-lasting.

TABLE 1 | Flood attributes for the Paraná River in the studied period.

Flood attributes	Hydrological cycles of Paraná River																			
	99–00	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19
Duration of flood	4	0	12	10	0	33	21	57	10	5	104	40	6	0	0	0	26	0	4	0
Intensity (cm)	507	414	532	504	434	676	516	645	498	506	717	677	498	408	408	341	637	402	473	348
Delay of flood	12	24	10	8	24	7	6	7	12	10	2	8	8	24	24	24	6	24	8	24

Relationship Between Fish Annual Recruitment and Flood Attributes

The reproductive guilds were related to different hydrological attributes, mainly duration and maximum annual river level (**Table 2**). For LMEF (**Figure 4**) the relationship between the annual recruitment and flood duration was positive and significant for both sub-basins (**Figures 4A,B**). Sedentary species with parental care (NEFP; **Figure 5**) also showed a positive and significant relationship between recruitment abundance and flood duration for both sub-basins (**Figures 5A,B**).

Sedentary fish without parental care (NEFW) showed a positive and significant relationship with flood duration in Paraná River (**Figure 6A**) and maximum annual water level and delay of the flood in the Ivinhema River (**Table 2**, **Figures 6B,C**). Those with internal fertilization (NIF) presented a positive and significant relationship with maximum annual water level and negative relationship with the delay of the flood in the Paraná River (**Figures 7A,B**), while for the Ivinhema River, the relationship was positive and significant only for the duration of the flood (**Figure 7C**). All generated models can be found in the **Tables S2**, **S3**.

DISCUSSION

This study evaluated data from a time series of 20 years and found a consistent pattern in which long-lasting floods positively influenced the recruitment of all reproductive guilds, the maximum annual water levels positively influenced some non-migratory guilds, and the delay of flood negatively influenced some non-migratory guilds.

The relationship between flood and migratory fish is well-known. Several studies have described the effects that floods can have on this guild (Agostinho et al., 2004; Bailly et al., 2008; Suzuki et al., 2009; Oliveira et al., 2015). Here, based on a long data series, we confirm this pattern of dependence on fish recruitment in relation to floods, which is null in drought years. However, Mallen-Cooper and Stuart (2003), studying fish in semi-arid and temperate regions in Australia, found two potamodromous species recruiting in years without a flood. The authors, even accepting the flood-pulse concept, discuss a possible plasticity in this reproductive strategy in response to the impacts of hundreds of dams, which regulate water flow.

Unlike migratory fish, the recruitment responses to flood attributes by species of other reproductive strategies are less studied, especially in long-term studies (Agostinho et al., 2004, 2007). In the upper Paraná River, previous studies have shown that flooding could have less effect on the recruitment of short-distance migratory assemblages (Fernandes et al., 2009; Vasconcelos et al., 2013, 2014). However, our results revealed that, at least partially, the recruitment of non-migratory fish responds to flood duration and/or maximum annual water level as well as the delay of flooding. These results corroborate with Agostinho et al. (2004), who verified that the abundance of juveniles for species of all reproductive strategies was low in the floodless year, which was attributed

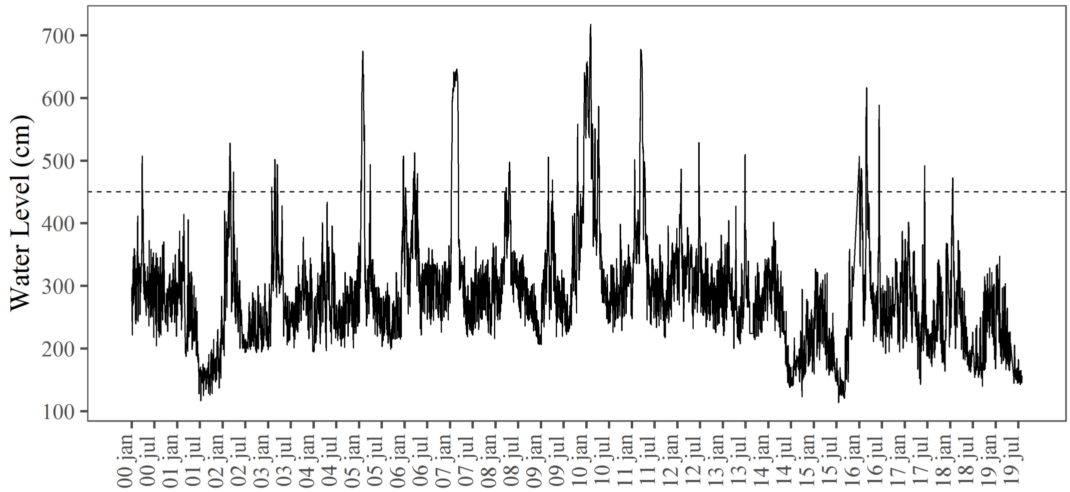

FIGURE 3 | Daily mean river levels in the Paraná River between 2000 and 2019. The dashed line represents the level (450 cm) at which the river overflowed onto the floodplain.

TABLE 2 | Result of the multiple linear regression analysis using the flood attributes as a predictor of the abundance of different reproductive guilds.

	Reproductive guild	X1	X2	X3	Adjusted R^2	F-statistic, (degree of freedom)	Model
Paraná	LMEF	***			0.46	18.06 (1,19)***	Y = 9.008X1
	NEFW	***			0.55	25.96 (1,19)***	Y = 22.55X1
	NEFP	***			0.62	34.14 (1,19)***	Y = 38.62X1
	NIF		**	*	0.43	8.76 (2,18)***	Y = 7.88X2–14.42X3
Ivinhema	LMEF	***			0.47	19.29 (1,19)***	Y = 11.75X1
	NEFW		***	**	0.69	24.22 (2,18)***	Y = 23.88X2–40.85X3
	NEFP	***			0.70	47.78 (1,19)***	Y = 46.13X1
	NIF	***			0.48	20.2 (1,19)***	Y = 3.82X1

*LMEF, Long-distance migratory with external fertilization; NEFW, Non-migratory with external fertilization, without parental care; NEFP, Non-migratory with external fertilization, with parental care; NIF, Non-migratory with internal fertilization; X1, Duration of the flood, X2, Maximum annual water level, X3, Delay of the flood. Significant variables are identified with *(0 '***'0.001, '**'0.01, '*'0.05, ''1).*

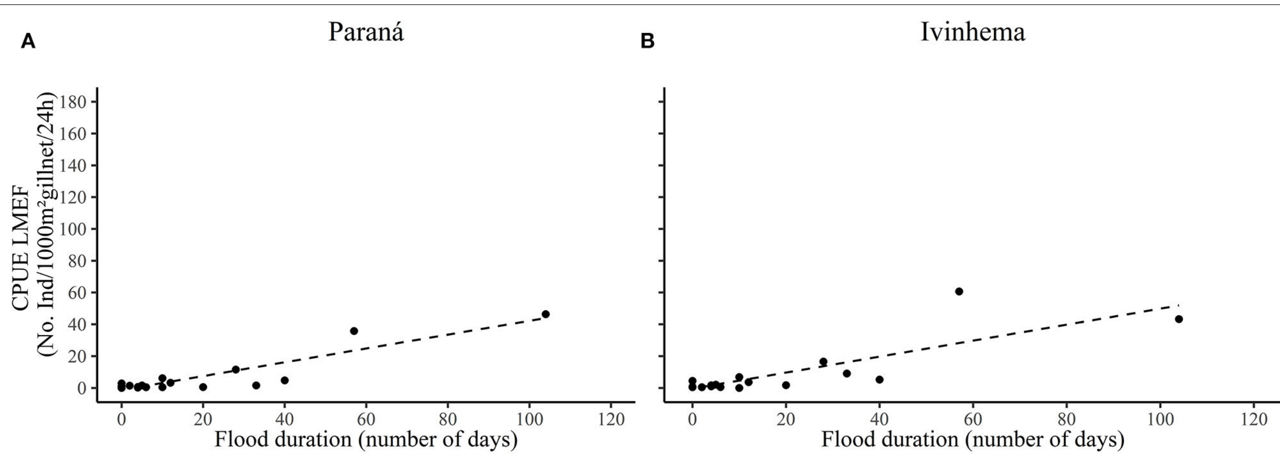

FIGURE 4 | Relationship between the long-distance migratory fish abundance (LMEF; CPUE = catch per unit of effort) and duration of flood in the Paraná River **(A)** and the Ivinhema River **(B)**.

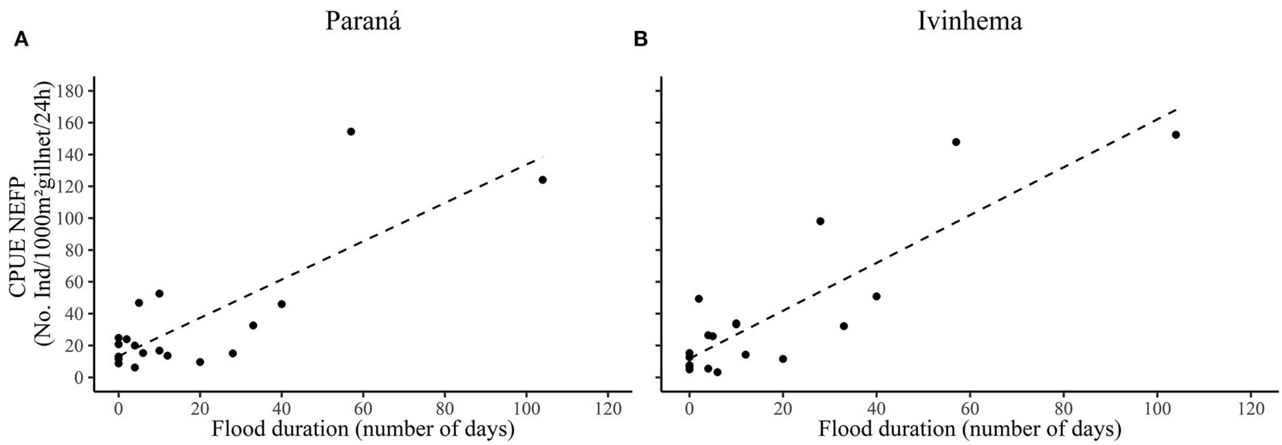

FIGURE 5 | Relationship between non-migratory fish with external fertilization and parental care (NEFP; CPUE = catch per unit effort) and duration of flood in Paraná River **(A)** and Ivinhema River **(B)**.

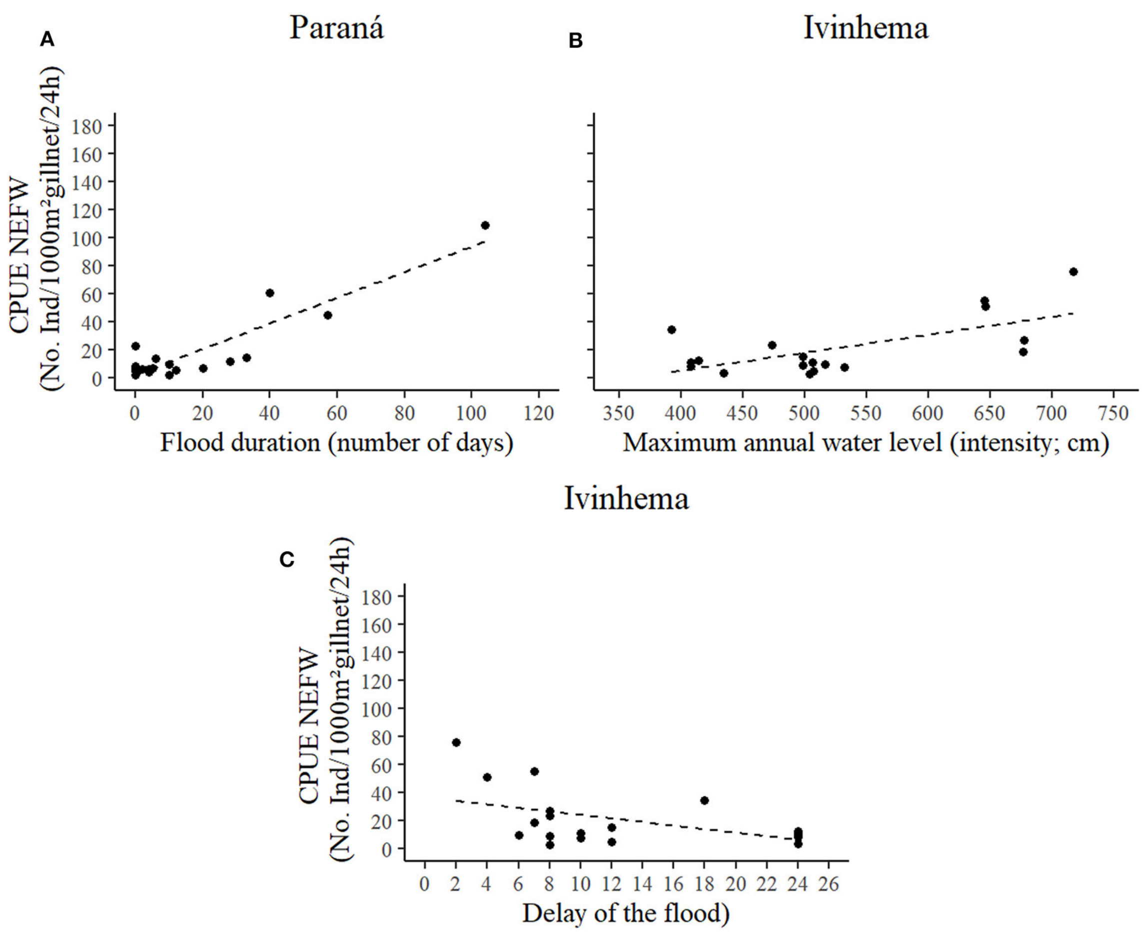

FIGURE 6 | Relationship between non-migratory fish with external fertilization and without parental care (NEFW; CPUE = catch per unit effort) and flood duration in the Paraná River **(A)**, and maximum annual water level **(B)**, and delay of flood **(C)** in the Ivinhema River.

to the pressure of predation, higher in more restricted aquatic environments, like those of the floodplain while the water recedes.

Long-lasting floods, those longer than 50 days, favor the survival of juveniles by providing higher availability of shelter and food for more extended periods before the waterline recedes

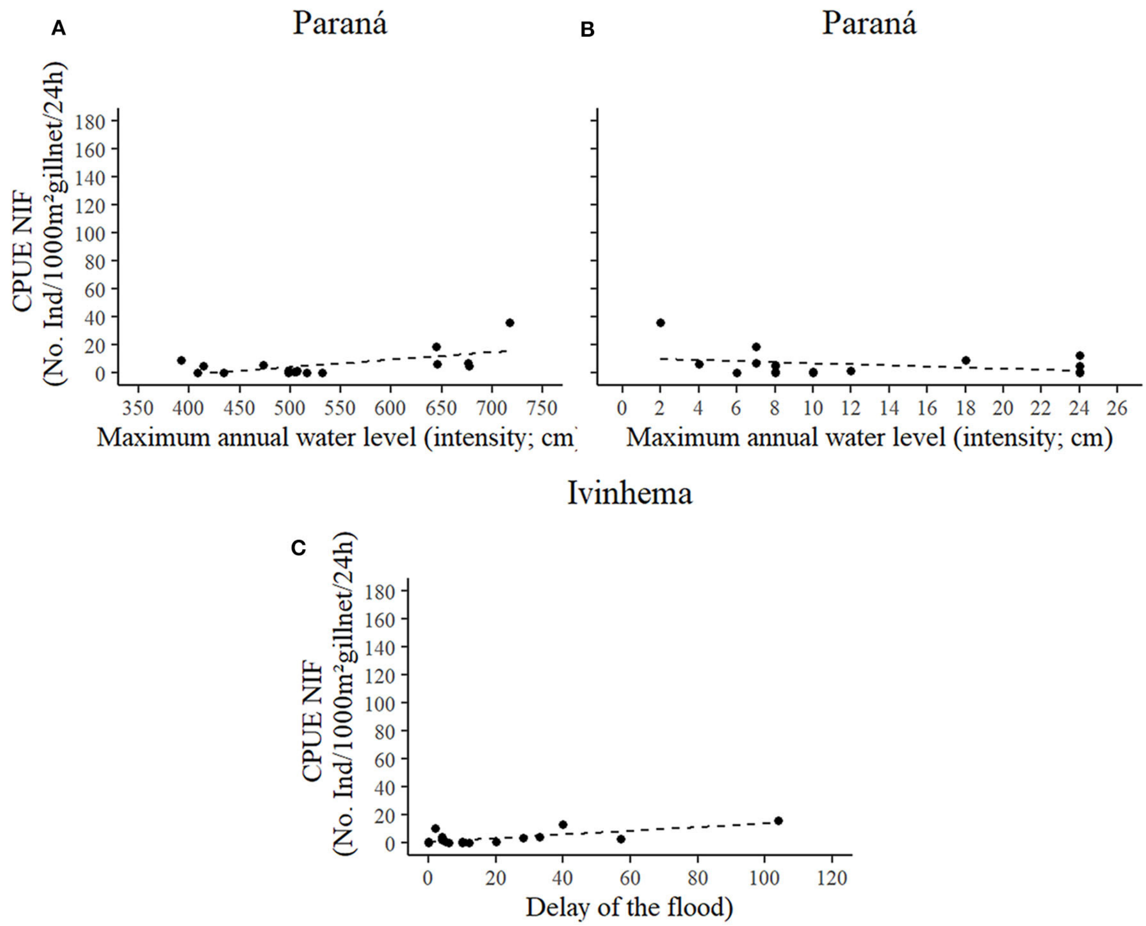

FIGURE 7 | Relationship between non-migratory fish with internal fertilization (NIF; CPUE = catch per unit effort) and maximum annual water level **(A)** and delay of the flood **(B)** in the Paraná River and duration of flood in the Ivinhema River **(C)**.

(Suzuki et al., 2009; Oliveira et al., 2015; Humphries et al., 2020). With lasting floods, the individuals leaving the flooded areas in the ebb period are larger in body size and consequently less susceptible to predation (Agostinho et al., 2004). Thus, this direct relationship between flood duration and resource availability influences a large number of species classified into the four reproductive guilds (LMEF, NEFW, NEFP, and NFI). For long-distance migratory fishes, recruitment can be null or incipient in years when flood is absent, short in duration, or delayed (Agostinho et al., 2004; Suzuki et al., 2009; Oliveira et al., 2015). In this study, migratory fish recruitment was significantly related to flood duration in both dammed (Paraná River) and undammed (Ivinhema River) sub-basins. In fact, recruitment success among these fish is the result of previous processes linked to migration, spawning, egg drift, and initial development, all of them in some way affected by one or more attributes of the flood regime (Vazzoler, 1996; Agostinho et al., 2003, 2007).

Previous studies state that the abundance of non-migratory species, whatever the internal fertilization strategy or attention to offspring, is more independent of the flood regime than the abundance of large, migratory fish. Non-migratory species can take advantage of the environment in other ways when flood is not relevant (Agostinho et al., 2004). Increasing density due to drought shrinks the wet surface, which affects the catchability and can influence the results (Agostinho et al., 2004). When evaluating the recruitment of these groups in a long time-series, the flood response pattern is consistent. Bailly et al. (2008), also using the young-of-the-year as an indicator of the reproductive success of each guild in the Cuiabá River floodplain, found no relationship of non-migratory guild NEFW with any hydrological attribute, despite the abundance of LMEF, NEFP, and NIF related to the flood duration and river levels. As mentioned previously, floods increase the resource inflow in the river-plain system and sustain individuals in the early stages of life for all reproductive guilds (King et al., 2003; Górski et al., 2011). The dilutive effects of the flooding increase the inundated area, relaxing predators' pressure on juveniles. Also, the flood duration protects eggs from exposure to air and desiccation, especially for species that adhere their eggs to substrates or plants in shallow areas or deposit them in nests built close or into the bank, reducing mortality and increasing reproductive success (Agostinho et al., 2007).

Although the absence of floods does not affect the reproduction process of fishes without parental care (NEFW) and with internal fertilization (NIF; Agostinho et al., 2004; Bailly et al., 2008), our results indicate that these species could also be favored by lasting flood conditions and moderate values of maximum annual water level. This trend is especially evident in the Paraná River, where the water is transparent, due to the sediment retention in dozens of upstream dams. Thus, long-lasting floods can benefit NEFW since the recruitment of these species are more dependent of shelter availability (e.g., flooded vegetation and higher turbidity) for a longer time. Even though internal fertilization reduces the time of exposure of gametes and eggs to predation, the higher availability of shelter and food provided by seasonal and high water level floods benefits the survival of larvae and juveniles because of protection for the parent fish. High water levels represent overflow of a larger area, with intermediate elevations also flooded (Souza Filho, 2009) and a large input of different autochthonous resources, benefiting the nutritional condition of the species (Gomes and Agostinho, 1997; Abujanra et al., 2009). On the other hand, the Ivinhema River has more pristine conditions and high turbidity (Roberto et al., 2009), which provide shelter against predation and increased survival, independent from the floods. As the relationship with high levels was positive and significant for NEFW, the flooding of new environments can benefit this guild. Lower water levels are associated with high transparency and less availability of shelter, which increases the predation rate for distinct guilds and reduces juvenile survival (Agostinho et al., 2007). In the same way, NIF can take advantage of the better conditions provided for the long-lasting floods, because of the extended higher shelter availability, food, and the weakening of the interspecific relationships, like predation over the offspring.

The guilds NEFW and NIF showed a negative and significant relationship with delayed flooding. Despite no significant relationship with the annual abundance of juveniles for LMEF and NEFP guilds in this regard, the delay in onset of floods may be important for all reproductive guilds. The species can be affected by delayed flooding because they lose the time of synchronization between the gonadal development and the climatic and pluviometric conditions of the hydrological cycle. The more delayed the flood, the more likely it is to be shorter; therefore, the individuals leaving the shelters will be smaller in size, and the predation risk increases. Among the hydrological cycles evaluated, the flood delay was inversely proportional to the flood duration, since longer floods corresponded to flooding periods with shorter delays. The absence of flood delay associated with lasting floods allows fish get an advantage under suitable conditions of temperature and photoperiod to ensure recruitment success (Górski et al., 2011). When evaluated individually, flood delay can relate significantly to the recruitment of some migratory fish species [*Megaleporinus* spp., *Pseudopimelodus corruscans* and *Prochilodus lineatus*—Oliveira et al. (2015)]. Earlier migrations are a strategy for the fish to avoid expending a higher amount of energy due to a lower swimming capacity to reach the upper stretches of the basin where spawning occurs (Lucas and Baras, 2008). If these species do not migrate earlier, the eggs and larvae fail to reach the nurseries while the floodplain is flooded (Agostinho et al., 2008).

We emphasize that grouping several fish species in the same reproductive guilds is a useful procedure for ecosystems management. Although grouping solves the difficulty of examining several species simultaneously (Winemiller, 1989), each group can hold species with marked differences in life-history strategies and tactics, which can present a wide gradient within the guild. Indeed, this must be considered when proposing management actions since species can exhibit different responses to the same environmental conditions (Oliveira et al., 2015). While species respond in different ways to the floods, other assemblage components such as functional diversity, can exhibit immediate and short responses (e.g., functional richness) or delayed and long-lasting responses for those indices which include abundance and are dependent on the recruitment success (Baumgartner et al., 2018).

As these results demonstrate, long-term ecological studies are necessary and useful for identifying consistent patterns in fundamental aspects of species biology and thus could be applied in conservation measures. Data from this long-term study allowed us to identify the importance of water level, flood duration, and the time of the onset of flooding for the recruitment of species with different reproductive strategies, as well as the different responses of these species to a wide variety of environmental conditions in hydrological cycles with different attributes. Since the flood regime is affected by the operation of hydropower dams, the maintenance of the ecosystem functions and services provided by fish fauna implies that managers and policy-makers understand these relationships. It is necessary to balance the human demands of hydroelectricity with the long-term conservation of biodiversity and stock. An important step and scientific challenge for the future is to calculate the trade-offs between different demands for water, including environmental ones, which could lead to a reservoir operation optimization model.

DATA AVAILABILITY STATEMENT

Requests to access the datasets should be directed to harumi@nupelia.uem.br.

ETHICS STATEMENT

The animal study was reviewed and approved by Ethical conduct in the use of experimental animals of Universidade Estadual de Maringá (CEUA; Technical Advice n° 1420221018 (ID001974) 06/11/18).

AUTHOR CONTRIBUTIONS

AO have conceived the idea and performed the formal analysis. AO, TL, RD, and AA discussed the idea. AO, TL, and HS curated the data. AO, TL, MA-V, RD, HS, and IC organized the data. AO and AA did the project administration. AA supervised the manuscript. AO and TL wrote the original draft. All authors reviewed and edited the writing.

ACKNOWLEDGMENTS

The authors aknowledge all NUPÉLIA staff for the several years of work collecting these data. The collections were supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) in the Long-Term Ecological Research (Programa de Pesquisas Ecológicas de longa duração—PELD—Sítio 6 A planície de inundação do alto Rio Paraná). CNPq was also responsible to support AO and TL post-doctoral scholarship and AA productivity grant. RD, MA-V, ICBC thank the Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES—PROEX) for post-doctoral research, Ph.D., and undergraduation scholarship, respectively.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.577181/full#supplementary-material

REFERENCES

Abell, R., Thieme, M. L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., et al. (2008). Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *Bioscience* 58, 403–414. doi: 10.1641/B580507

Abrial, E., Espínola, L. A., Rabuffetti, A. P., Amsler, M. L., and Wantzen, K. M. (2019). Interannual flow variability in a large subtropical–temperate floodplain: a challenge for fish reproduction. *Can. J. Fish. Aquat. Sci.* 76, 390–400. doi: 10.1139/cjfas-2017-0579

Abujanra, F., Agostinho, A., and Hahn, N. (2009). Effects of the flood regime on the body condition of fish of different trophic guilds in the Upper Paraná River floodplain, Brazil. *Brazilian J. Biol.* 69, 469–479. doi: 10.1590/S1519-69842009000300003

Agostinho, A., Pelicice, F., and Gomes, L. (2008). Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian J. Biol.* 68, 1119–1132. doi: 10.1590/S1519-69842008000500019

Agostinho, A. A., Gomes, L. C., and Pelicice, F. M. (2007). *Ecologia e manejo dos recursos pesqueiros em reservatórios do Brasil*. Maringá: EDUEM.

Agostinho, A. A., Gomes, L. C., Suzuki, H. I., and Julio Jr, H. F. (2003). "Migratory fish from the upper Paraná River basin, Brazil," in *Migratory Fishes of South America: Biology, Social Importance and Conservation Status*, eds J. Carosfeld, B. Harvey, C. Ross, A. Baer, and C. *Ross (Victoria: World Fisheries Trust, the World Bank and the International Development Centre)*, 19–99.

Agostinho, A. A., Gomes, L. C., Veríssimo, S., and Okada, E. K. (2004). Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Rev. Fish Biol. Fish.* 14, 11–19. doi: 10.1007/s11160-004-3551-y

Agostinho, A. A., Thomaz, S. M., and Gomes, L. C. (2005). Conservation of the biodiversity of Brazil's Inland Waters. *Conserv. Biol.* 19, 646–652. doi: 10.1111/j.1523-1739.2005.00701.x

Bailly, D., Agostinho, A. A., and Suzuki, H. I. (2008). Species with different reproductive strategies in the cuiaba river, upper Pantanal Brazil. *River Res. Appl.* 1229, 1218–1229. doi: 10.1002/rra.1147

Baumgartner, M. T., de Oliveira, A. G., Agostinho, A. A., and Gomes, L. C. (2018). Fish functional diversity responses following flood pulses in the upper Paraná River floodplain. *Ecol. Freshw. Fish* 27, 910–919. doi: 10.1111/eff.12402

Comunello, E., Souza-Filho, E. E., Rocha, P. C., and Nanni, M. (2003). "Dinâmica de inundação de áreas sazonalmente alagáveis na planície aluvial do Alto Rio Paraná: estudo preliminar,". *in Anais do XI Congresso Brasileiro de Sensoriamento Remoto* (Belo Horizonte: INPE), 2459–2466.

Cowx, I. G., Ian, G., Welcomme, R. L., and European Inland Fisheries Advisory Commission. (1998). *Rehabilitation of rivers for fish : a study undertaken by the European Inland Fisheries Advisory Commission of FAO*. Published by arrangement with the Food and Agriculture Organization of the United Nations by Fishing News Books Available online at: http://agris.fao.org/agris-search/search.do?recordID=GB1997048203 (accessed August 13, 2019).

dos Santos, N. C. L., de Santana, H. S., Ortega, J. C. G., Dias, R. M., Stegmann, L. F., da Silva Araújo, I. M., et al. (2017). Environmental filters predict the trait composition of fish communities in reservoir cascades. *Hydrobiologia* 802, 245–253. doi: 10.1007/s10750-017-3274-4

Fernandes, R., Gomes, L. C., Pelicice, F. M., and Agostinho, A. A. (2009). Temporal organization of fish assemblages in floodplain lagoons: the role of hydrological connectivity. *Environ. Biol. Fishes* 85, 99–108. doi: 10.1007/s10641-009-9466-7

Gaillard, J. M., Coulson, T., and Festa-Bianchet, M. (2008). "Recruitment," in *Encyclopedia of Ecology, Five-Volume Set*, eds S. E. Jørgensen and B. D. Fath (Amsterdam: Elsevier Inc.), 2982–2986. doi: 10.1016/B978-008045405-4.00655-8

Gomes, L. C., and Agostinho, A. A. (1997). Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in Upper Paraná River, Brazil. *Fish. Manag. Ecol.* 4, 263–274. doi: 10.1046/j.1365-2400.1997.00119.x

Górski, K., De Leeuw, J. J., Winter, H. V., Vekhov, D. A., Minin, A. E., Buijse, A. D., et al. (2011). Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshw. Biol.* 56, 2210–2225. doi: 10.1111/j.1365-2427.2011.02647.x

Graça, W. J., and Pavanelli, C. S. (2007). *Peixes da Planície de Inundação do alto Rio Paraná e áreas adjacentes*. Maringá: EDUEM. Available online at: https://www.scienceopen.com/document?vid=950b394a-c7b6-4cb2-80b7-ba59c7db724c (accessed August 14, 2019).

Humphries, P., King, A., McCasker, N., Kopf, R. K., Stoffels, R., Zampatti, B., et al. (2020). Riverscape recruitment: a conceptual synthesis of drivers of fish recruitment in rivers. *Can. J. Fish. Aquat. Sci.* 77, 213–225. doi: 10.1139/cjfas-2018-0138

Humphries, P., King, A. J., and Koehn, J. D. (1999). Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray–Darling River system, Australia. *Environ. Biol. Fishes* 56, 129–151. doi: 10.1023/A:1007536009916

Humphries, P., and Walker, K. (2013). *Ecology of Australian Freshwater Fishes. Collingwood: CSIRO Publishing*. doi: 10.1071/9780643097445

Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). "The flood pulse concept in river - floodplain systems," in *Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science* 106, 110–127.

King, A. J., Humphries, P., and Lake, P. S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Can. J. Fish. Aquat. Sci.* 60, 773–786. doi: 10.1139/f03-057

Lima, M. A. L., Kaplan, D. A., Doria, C. R., and da C. (2017). Hydrological controls of fisheries production in a major Amazonian tributary. *Ecohydrology* 10:e1899. doi: 10.1002/eco.1899

Lucas, M., and Baras, E. (2008). *Migration of Freshwater Fishes*. London: John Wiley & Sons, Ltd.

Mallen-Cooper, M., and Stuart, I. G. (2003). Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system. *River Res. Appl.* 19, 697–719. doi: 10.1002/rra.714

Mormul, R. P., Thomaz, S. M., Agostinho, A. A., Bonecker, C. C., and Mazzeo, N. (2012). Migratory benthic fishes may induce regime shifts in a tropical floodplain pond. *Freshw. Biol.* 57, 1592–1602. doi: 10.1111/j.1365-2427.2012.02820.x

Nakatani, K., Agostinho, A. A., Baumgartner, G., Bialetzki, A., Sanches, P. V., Makrakis, M. C., et al. (2001). *Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação*. Maringá: EDUEM.

Oliveira, A. G., Baumgartner, M. T., Gomes, L. C., Dias, R. M., and Agostinho, A. A. (2018). Long-term effects of flow regulation by dams simplify fish functional diversity. *Freshw. Biol.* 63, 293–305. doi: 10.1111/fwb.13064

Oliveira, A. G., Suzuki, H. I., Gomes, L. C., and Agostinho, A. A. (2015). Interspecific variation in migratory fish recruitment in the Upper Paraná River: effects of the duration and timing of floods. *Environ. Biol. Fishes* 98, 1327–1337. doi: 10.1007/s10641-014-0361-5

Ota, R. R., Depr,á, G., de, C., Graça, W. J. da, and Pavanelli, C. S. (2018). Peixes da planície de inundação do alto rio Paraná e áreas adjacentes: revised, annotated and updated. *Neotrop. Ichthyol.* 16:94. doi: 10.1590/1982-0224-20170094

Pelicice, F. M., Azevedo-Santos, V. M., Luiz, A., Esguícero, H., Agostinho, A. A., and Arcifa, M. S. (2018). Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. *Neotrop. Ichthyol.* 16:170150. doi: 10.1590/1982-0224-20170150

Pelicice, F. M., Pompeu, P. S., and Agostinho, A. A. (2015). Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish Fish.* 16, 697–715. doi: 10.1111/faf.12089

R Core Team (2019). *R: The R Project for Statistical Computing. R Found*. Available online at: https://www.r-project.org/ (accessed June 4, 2019).

Roberto, M. C., Santana, N. N., and Thomaz, S. M. (2009). Limnology in the Upper Paraná River floodplain: large-scale spatial and temporal patterns, and the influence of reservoirs. *Braz. J. Biol.* 69, 717–725. doi: 10.1590/S1519-69842009000300025

Rocha, P. C., Santos, M., and Souza-Filho, E. E. (2001). "Alterações no regime hidrológico do alto rio Paraná como resposta ao controle de descargas efetuado por grandes barramentos a montante," *in Anais do VIII Encuentro de Geógrafos de América Latina (Santiago)*, 28–39.

Rosa, G. R., Salvador, G. N., Bialetzki, A., and Santos, G. B. (2018). Spatial and temporal distribution of ichthyoplankton during an unusual period of low flow in a tributary of the São Francisco River, Brazil. *River Res. Appl.* 34, 69–82. doi: 10.1002/rra.3225

Silva, J. C., Rosa, R. R., Galdioli, E. M., Soares, C. M., Domingues, W. M., Veríssimo, S., et al. (2017). Importância de trechos livres de represamento para a reprodução dos peixes: O último remanescente do alto rio Paraná. *Acta Limnol. Bras.* 29:e106. doi: 10.1590/s2179-975x10216

Souza Filho, E. (2009). Evaluation of the Upper Paraná River discharge controlled by reservoirs. *Brazilian J. Biol.* 69, 707–716. doi: 10.1590/S1519-69842009000300024

Souza-Filho, E. E., and Stevaux, J. C. (2004). "Geology and geomorphology of the Baia-Curutuba-Ivinheima complex.," in *The Upper Paraná River and its floodplain: physical aspects, ecology and conservation*, eds *S. M. Thomaz, A. A. Agostinho, and N. S. Hahn (Leiden: Backhuys Publishers)*, 1–30.

Suzuki, H. I., Agostinho, A. A., Bailly, D., Gimenes, M. F., Júlio, H. F., and Gomes, L. C. (2009). Inter-annual variations in the abundance of young-of-the-year of migratory fishes in the Upper Paraná River floodplain: relations with hydrographic attributes. *Braz. J. Biol.* 69, 649–60. doi: 10.1590/S1519-69842009000300019

Suzuki, H. I., Vazzoler, A. E. A. M., Marques, E. E., Lizama, De los Angeles Perez Lizama, M., and Inada, P. (2004). "Reproductive ecology of the fish assemblages," in *The Upper Paraná River and Its Floodplain: Physical Aspects, Ecology, Ecology and Conservation*, eds S. M. Thomaz, A. A. Agostinho, and N. S. *Hahn (Leiden: Backhuys Publishers)*, 271–291.

Thomaz, S. M., Bini, L. M., and Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579, 1–13. doi: 10.1007/s10750-006-0285-y

Timpe, K., and Kaplan, D. (2017). The changing hydrology of a dammed Amazon. *Sci. Adv.* 3:e1700611. doi: 10.1126/sciadv.1700611

Vasconcelos, L. P., Alves, D. C., and Gomes, L. C. (2013). Spatial and temporal variations among fish with similar strategies: patterns of reproductive guilds in a floodplain. *Hydrobiologia* 726, 213–228. doi: 10.1007/s10750-013-1767-3

Vasconcelos, L. P., Alves, D. C., and Gomes, L. C. (2014). Fish reproductive guilds downstream of dams. *J. Fish Biol.* 85, 1489–1506. doi: 10.1111/jfb.12501

Vazzoler, A. E. A. M. (1996). Biologia *da reprodução de peixes teleósteos: teoria e prática*. Mar. (Ed. UEM), SBI, São Paulo, 169. Available online at: http://www.academia.edu/3334063/Biologia_da_reproduç~ao_de_peixes_teleósteos_teoria_e_prática (accessed June 4, 2016).

Vazzoler, A. E. A. M., and Menezes, N. A. (1992). Síntese de conhecimentos sobre o comportamento reprodutivo dos Characiformes da América do Su*l* (Teleostei, Ostariophysi). *Rev. Bras. Biol.* 52, 627–640. Available online at: https://www.scienceopen.com/document?vid=eb82f535-fe80-4582-a8b3-7a2d3c172a39 (accessed August 13, 2019).

Wantzen, K. M., and Junk, W. J. (2006). Aquatic-terrestrial linkages fromstreams to rivers: biotic hot spots and hot moments. *Large Rivers*, 16, 595–611. doi: 10.1127/lr/16/2006/595

Welcomme, R. L. (1979). *Fisheries ecology of Floodplain Rivers*. London; New York, NY: Longman.

Winemiller, K. O. (1989). Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81, 225–241. doi: 10.1007/BF00379810

Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* 5, 872–885. doi: 10.1139/f05-040

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., et al. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351, 128–129. doi: 10.1126/science.aac7082

Wootton, R. J. (1990). *Ecology of Teleost Fishes. Chapman and Hall*. Available online at: https://books.google.com.br/books?hl=pt-PT&lr=&id=CFj-CAAAQBAJ&oi=fnd&pg=PP9&dq=Ecology+of+teleost+fishes.&ots=mOhW6jp1Rj&sig=SAA88EtAPHm48EGoNN7NyuwQa0E#v=onepage&q=Ecologyofteleostfishes.&f=false (accessed August 13, 2019).

Zeug, S. C., and Winemiller, K. O. (2007). Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Can. J. Fish. Aquat. Sci.* 64, 1291–1301. doi: 10.1139/f07-094

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.