Environ Biol Fish (2015) 98:1327–1337
DOI 10.1007/s10641-014-0361-5

Interspecific variation in migratory fish recruitment in the Upper Paraná River: effects of the duration and timing of floods

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Received: 10 March 2014 / Accepted: 21 October 2014 / Published online: 11 November 2014

Abstract This study evaluated the relationship between the young of year (YOY) abundance of migratory fish species and the interannual variations in the duration and delay of floods in the Upper Paraná River floodplain. YOY of the most abundant migratory species *Brycon orbignyanus*, *Hemisorubim platyrhynchos*, *Leporinus elongatus*, *Leporinus macrocephalus*, *Leporinus obtusidens*, *Pseudoplatystoma corruscans*, *Pterodoras granulosus*, *Prochilodus lineatus*, *Salminus brasiliensis* and *Sorubim lima* were studied in a stretch of the Paraná river influenced by dams. Multiple regression analyses were performed with flood duration and delay as predictors for YOY abundances. There were differences among the species in the responses to flood duration and delay. The species *B. orbignyanus*, *L. elongatus*, *L. macrocephalus*, *L. obtusidens*, and *P. lineatus* exhibited an exponential increase in YOY abundance with flood duration. An exponential decrease in YOY abundance with flood delay was found for most of the studied species. Nevertheless, flood delay and flood duration were significant predictors of YOY abundance for *L. elongatus*, *L. obtusidens*, *P. corruscans* and *P. lineatus*. For these species, flood delays may result in failure of recruitment because these species migrate early in the season to adjust their energy reserves and their swimming patterns. Therefore, any efforts to preserve migratory fish should consider discharge manipulation from reservoirs upstream of the study areas. It is crucial that reservoirs are operated in such a way that the quantity, duration and timing of water release are compatible with the viability of spawning and the survival of early life stages of migratory fish.

Keywords Paraná River · Fishes · Migration · Recruitment · Impact mitigation · Flooding attributes

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Introduction

In river-floodplain systems, the hydrologic regime displays seasonal variations in hydrometric levels, and the alternating periods of drought and flood have important effects on the processes and functioning of the biota (Welcomme 1979; Junk et al. 1989; Neiff 1990). The hydrologic regime is also the selective force behind the diverse livelihood strategies of species related to food, maintenance and reproduction (Wootton 1990).

For Neotropical fishes, there is a high degree of synchronisation between the hydrologic cycle and the major events in the reproductive cycle (Godoy 1975; Vazzoler 1996; Agostinho et al. 2004a; Bailly et al. 2008). This synchronisation is even more pronounced in long-distance migratory species, (sensu Agostinho et al. 2007), that have high commercial value and are usually large, produce many small eggs and do not display parental care (Winemiller 1989; Agostinho and Júlio Jr 1999; Agostinho et al. 2004a). In these species, increases in photoperiod and temperature act as indicators of development and gonadal maturation (Vazzoler and Menezes 1992; Suzuki et al. 2004), and the first rains in the basin mark the formation of schools and migrations in search of the highest stretches of rivers and tributaries for spawning (Cowx and Welcomme 1998). The beginning of flooding then acts as a synchronising trigger for spawning, and the peak flood level marks the end of the reproductive period (Vazzoler 1996).

This synchronisation with the hydrologic cycle allows the eggs of these species to develop in well-oxygenated waters with lower predation risk (due to higher turbity during floods), and the larvae that reach the flooded area have greater access to food and shelter, which favours survival in the early life stages (Welcomme 1979; Agostinho et al. 1993, 2004a; Vazzoler et al. 1997).

In the Upper Paraná River floodplain, high water levels during the summer and autumn favour the survival of juveniles by providing shelter and food for longer periods such that the individuals leaving the plain are already larger in size and are consequently less susceptible to predation (Agostinho et al. 2004a). Intense floods (above 610 cm) that last more than 50 days result in improved recruitment of the young-of-year (YOY) of migratory species in this environment (Suzuki et al. 2009).

In addition to the threats that are common to all species of fish, such as pollution, habitat destruction, deforestation and the introduction of non-native species, migratory species also suffer from overfishing and, mostly, the construction and operation of dams for hydroelectric purposes. The high dependency of recruitment success on attributes of the hydrologic regime make migratory fish highly vulnerable to flow control and the interruption of upward migration routes by dams (Agostinho et al. 2005). This problem is further compounded by the arrangement of reservoirs in cascades, as in the Upper Paraná River basin, which results in the sporadic trapping of migratory species in the Grande, Tietê, Paranaíba and Paranapanema Rivers (Agostinho et al. 2003).

Therefore, effective mitigation measures must be imposed on dam operating to ensure that the quantity, duration and timing of flood waters meet the demands of these species for spawning and initial development (Agostinho et al. 2004b, 2005). Using dam operation as a possible mitigation strategy has been already endorsed to conserve migratory fish populations in the Upper Paraná River between the Engenheiro Sérgio Motta (Porto Primavera) and Itaipu reservoirs (Agostinho et al. 2004b, 2009).

Although the role of the hydrological regime in the recruitment of Neotropical migratory fish is well recognized, the influence of flood duration and time when the flood begin on the reproductive success of different long-distance migratory species remains unknown. This study analyzes the hypothesis that variations in the attributes of flooding regime differentially affect distinct groups of migratory fish. In this context, the present study examined the relationship between the recruitment success of the ten most abundant migratory fish species and some flooding attributes in twelve different annual cycles in the upper Paraná River floodplain, located immediately below a cascade of dams. The results of this study will be used to determine the appropriate conservation measures to promote the hydrologic conditions necessary for the preservation of populations of all migratory species without risking loss of biodiversity.

Materials and methods

Study area

The studied stretch of the Upper Paraná River is the last remaining free floodplain of this river in the Brazilian territory, and it is located between the Porto Primavera dam and the Itaipu Reservoir. Situated on the right (West) margin of the Paraná River, the floodplain is characterised by a high diversity of biotopes, with broad floodplains, islands and lagoons that have different degrees of connectivity to the main river and channels. These regions are subjected to variations in the levels of the Paraná River and the two tributaries of the right bank, the Baía and Ivinhema Rivers (Thomaz et al. 2007) (Fig. 1).

The ichthyofauna of Upper Paraná River is composed of 182 catalogued species (Graça and Pavanelli 2007). In the floodplain there are large migratory species (Agostinho et al. 2003), which are virtually absent from the upper tributaries, which plays a key role in maintaining aquatic biodiversity and fisheries in the region (Agostinho and Zalewski 1996).

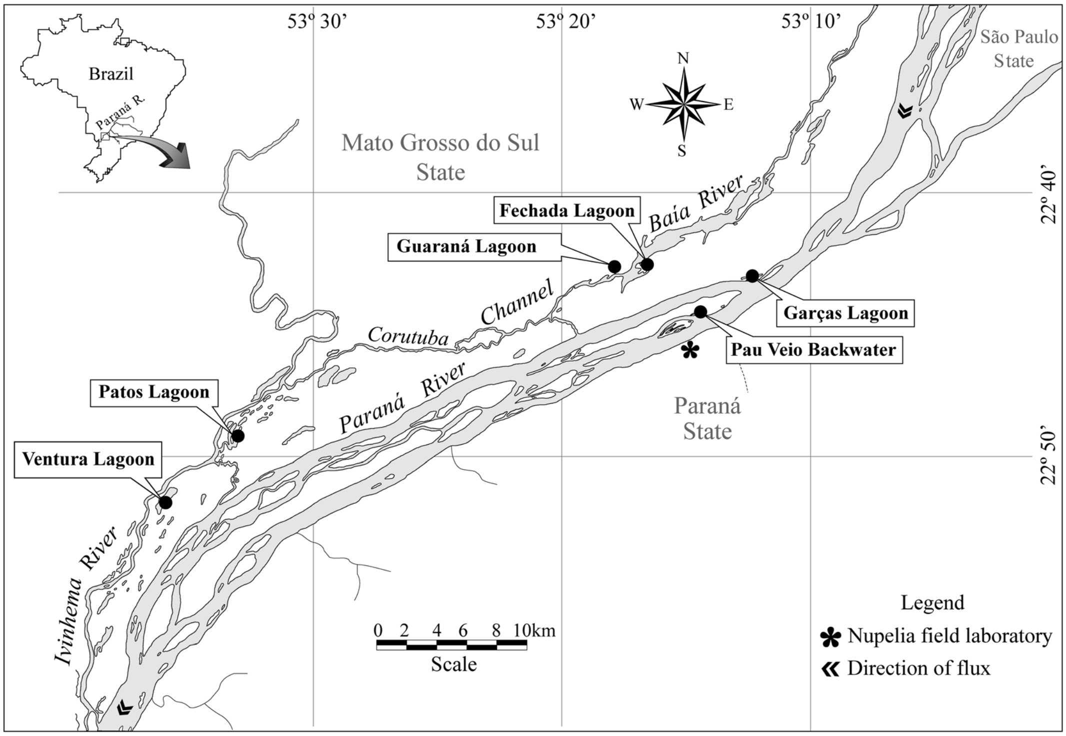

Fig. 1 The study area, including nine sampling stations: the Ventura, Patos, Guaraná, Fechada, Garças and Pau Véio Lagoons; and the Paraná, Baía and Ivinhema rivers

Sampling

Sampling was conducted quarterly from March 2000 until December 2011 in six lagoons (Ventura, Patos, Guaraná, Pau Véio, Garças and Fechada) and three rivers (the Paraná, Baía and Ivinhema rivers) within the floodplain of the upper Paraná River (Fig. 1). Gillnets of different mesh sizes were used to catch fish (2.4, 3, 4, 5, 6, 7, 8, 9, 10, 11 and 12 cm between alternate knots). The nets were set for a total of 24 h at each sampling station and were checked every 8 h. Captured fish were anaesthetised with 5 % benzocaine and sacrificed. After, each fish was identified; its total and standard length and weight were recorded. The quantity of fish caught in gillnets was indexed by the catch per unit effort (CPUE; individuals/1,000 m^2 of gillnets during 24 h).

YOY of the following species were evaluated: *Brycon orbignyianus* (Valenciennes, 1850), *Hemisorubim platyrhynchos* (Valenciennes, 1840), *Leporinus elongatus* Valenciennes 1850, *Leporinus macrocephalus* Garavello & Britski, 1988, *Leporinus obtusidens* (Valenciennes, 1837), *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *Prochilodus lineatus* (Valenciennes, 1836), *Pterodoras granulosus* (Valenciennes, 1821), *Salminus brasiliensis* (Cuvier, 1816) and *Sorubim lima* (Bloch & Schneider, 1801). These species are the most abundant among the long distance migratory fish, representing almost 50.0 % of total number (20 species; Agostinho et al. 2003; Vasconcelos et al. 2014), 5.5 % of the regional fish fauna (182 species; Graça and Pavanelli 2007) and around ¼ of the total biomass. Lengths at age of YOY were determined using published growth curves (Table 1). For species with no published data, parameters of the von Bertalanffy growth curves (Bertalanffy 1938) were estimated based on the variations in the values of the modes obtained from the quarterly length frequency distribution (data of two consecutive years were used) (Santos 1978) (Oliveira AG, unpubl. data).

River levels were provided by the National Water Agency (Agência Nacional das Águas-ANA – Sistema Nacional de Informações sobre Recursos Hídricos – SNIRH) based on data obtained at the Porto São José hydrometric station (64575001/2253018). A threshold level of 450 cm had previously been established as the level at which the Paraná River overflows onto the plain (Comunello et al. 2003). This threshold level (450 cm)

Table 1 Size range of fishes analysed and young-of-year length per species

Species	Size range	YOY length
B. orbignyanus	13.0–43.4 cm	23.0 cm (unpubl. data)
H. platyrhynchos	10.0–60.0 cm	21.1 cm (Penha et al. 2004b)
L. elongatus	9.0–49.0 cm	14.6 cm (unpubl. data)
L. macrocephalus	18.0–60.5 cm	21.9 cm (unpubl. data)
L. obtusidens	8.0–54.0 cm	17.3 cm (F) 16.6 cm (M) (Araya et al. 2005)
P. corruscans	8.9–105.0 cm	54.9 cm (Mateus and Petrere Jr 2004)
P. granulosus	6.2–71.0 cm	18.2 cm (Feitoza et al. 2004)
P. lineatus	4.3–62.0 cm	17.0 cm (Vicentin et al. 2012)
S. brasiliensis	12.5–80.0 cm	28.3 cm (F) 21.4 (M) (Barbieri et al. 2001)
S. lima	14.0–61.5 cm	26.4 cm (Penha et al. 2004a)

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). The examined flood period lasted from October until May, a time when floods and the spawning of long-distance migratory species have historically occurred in the region (Agostinho et al. 2004a). Floods were characterised according to the following attributes: (i) flood duration (number of days when the river level remained above 450 cm); (ii) number of days of uninterrupted flooding (the longest number of continuous days of flooding above 450 cm); (iii) intensity of flooding (the highest recorded annual river level); (iv) delay in the flooding (the number of 15-day periods between October 1 and the start of flooding).

Data analysis

To determine possible trends in data distribution, scatterplots comparing the annual YOY abundance of migratory species, with the flooding attributes were created. The data were log-transformed to standardise non-linear trends. The relationships between YOY catch and flooding attributes were then assessed using a multiple linear regression analysis, with flood duration and flood delay as predictors of abundance (dependent variables; the other variables were highly correlate with the duration) to generate the best predictor model.

To identify the partial contribution of each flooding attribute to the explained variance, we verified the squared values of the partial and semi-partial correlation coefficients. These analyses were performed only for the species which more than one predictor was selected. The partial correlation coefficient indicates how much of the variance in a dependent variable (Y) that is not explained by other variables is estimated by a given variable, whereas the semi-partial correlation coefficient indicates how much of the variance in Y is solely due to each variable (Cohen et al. 2003). These analyses were performed using Statistica software 10.0 (Statsoft 2010) with a significance level of 5 %.

Results

Hydrologic cycle

Over the study period, the most intense and long-lasting flooding was documented in the 2009–2010 cycle, followed by the 2006–2007 cycle. Floods with high intensity but a moderate duration (30–50 days above 450 cm) were recorded in the 2004–2005 and 2010–2011 cycles (Table 2). In these four cycles, the maximum river levels exceeded six metres and occurred on more than 30 days. In these, overflow began in the first or second half of January, with the exception of the cycle 2009–2010, when more intense and longer flooding began earlier (during the second half of October). In the other eight periods (1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004, 2005–2006, 2007–2008, 2008–2009), flooding did not occur or was not pronounced (with no more than 9 days of continuous flooding) (Table 2, Fig. 2).

Trends in the relationships between recruitment and flood attributes

The analysis of the relationship between the abundance of YOY and the number of days of flooding during the hydrological cycle indicated that all species showed

Table 2 Flood attributes for the Paraná River in the studied periods

Flood attributes	Hydrological cycles											
	99–00	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11
Duration of flood (days >450 cm)	4	0	12	10	0	33	21	57	10	5	104	40
Maximum of uninterrupted flood (days > 450 cm)	4	0	9	6	0	29	9	57	9	4	75	28
Maximum Intensity (cm)	507	414	532	504	434	676	516	645	498	506	717	677
Delay of flood (fortnight)	12	24	10	8	24	7	6	7	12	10	2	8
Onset of flood (month/day)	Mar 25	–	Feb 16	Jan 30	–	Jan 15	Dec 21	Jan 12	Mar 28	Feb 27	Oct 17	Jan 22

The numbers match a year of the hydrological cycle

significantly higher abundance in years of longer floods. For four species, this relationship was exponential: *B. orbignyanus*, *L. elongatus*, *L. macrocephalus* and *P. lineatus*. The others species (*H. platyrhynchos*, *L. obtusidens*, *P. corruscans*, *P. granulosus*, *S. brasiliensis* and *S. lima*) showed a linear trend, sometimes with high variability among years (Fig. 3). Note that the complete cycle of 2009–2010 was the extreme point of the data (far in the X axis direction). Even this cycle presenting high leverage, we could not pull it off, because it represented one of the longest and highest intensity floods (above >700 cm) along the years studied (these events are usually related to El Nino South Oscillation - ENSO; Fernandes et al. 2009).

Plotting the YOY abundance against the delay in flooding beyond October 1 (measured in fortnights) revealed a negative exponential relationship for almost all the examined species (Fig. 4). Only *Pseudoplatystoma corruscans* and *Salminus brasiliensis* exhibited a linear trend for this relationship.

Partial effects of flood attributes on YOY abundance

The multiple regression analysis using flood duration and delay as predictors of YOY abundance demonstrated that flood duration significantly affected all of the examined migratory species ($p<0.05$ and $F_{[2,10]} >5.55$). Flood delays during the examined flood period (October to May) were significantly related with YOY abundance for *L. elongatus*, *L. obtusidens*, *P. corruscans* and *P. lineatus* (Table 3). However, the partial and semipartial correlation coefficients for the predictor variables showed that, even for the above four species, flood duration explained a higher percentage of variability than flood delay (Table 4).

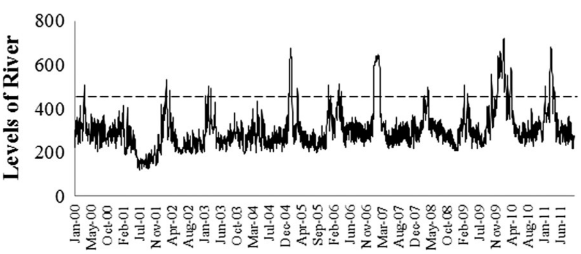

Fig. 2 Daily mean river levels in the Paraná River between 2000 and 2011. *Dashed line* represents the level (450 cm) at which the river overflowed onto the floodplain

Discussion

There is a well-known positive relationship between the recruitment of long-distance migratory fish and flooding duration, which ensures the proper conditions for the development of early life stages (Agostinho et al. 2004a; Suzuki et al. 2009). However, this study, which analysed a time series of 12 years, demonstrated variability in the responses of different species to flood duration and, in some species, delays in the onset of flooding.

Recruitment of migratory species has been reported to not occur or to be hindered in years when flooding is absent, short or delayed (Agostinho et al. 2009; Fernandes et al. 2009). However, in this study, some of the species responded successfully to moderate flooding (>30 and <50 days), although somewhat delayed, as was the case for *H. platyrhynchos*, *L. macrocephalus*, *P. corruscans*, *P. granulosus*, *P. lineatus*, *S. brasiliensis* and *S. lima*. For the other species, floods of moderate duration, even those continuing for more than 30 days,

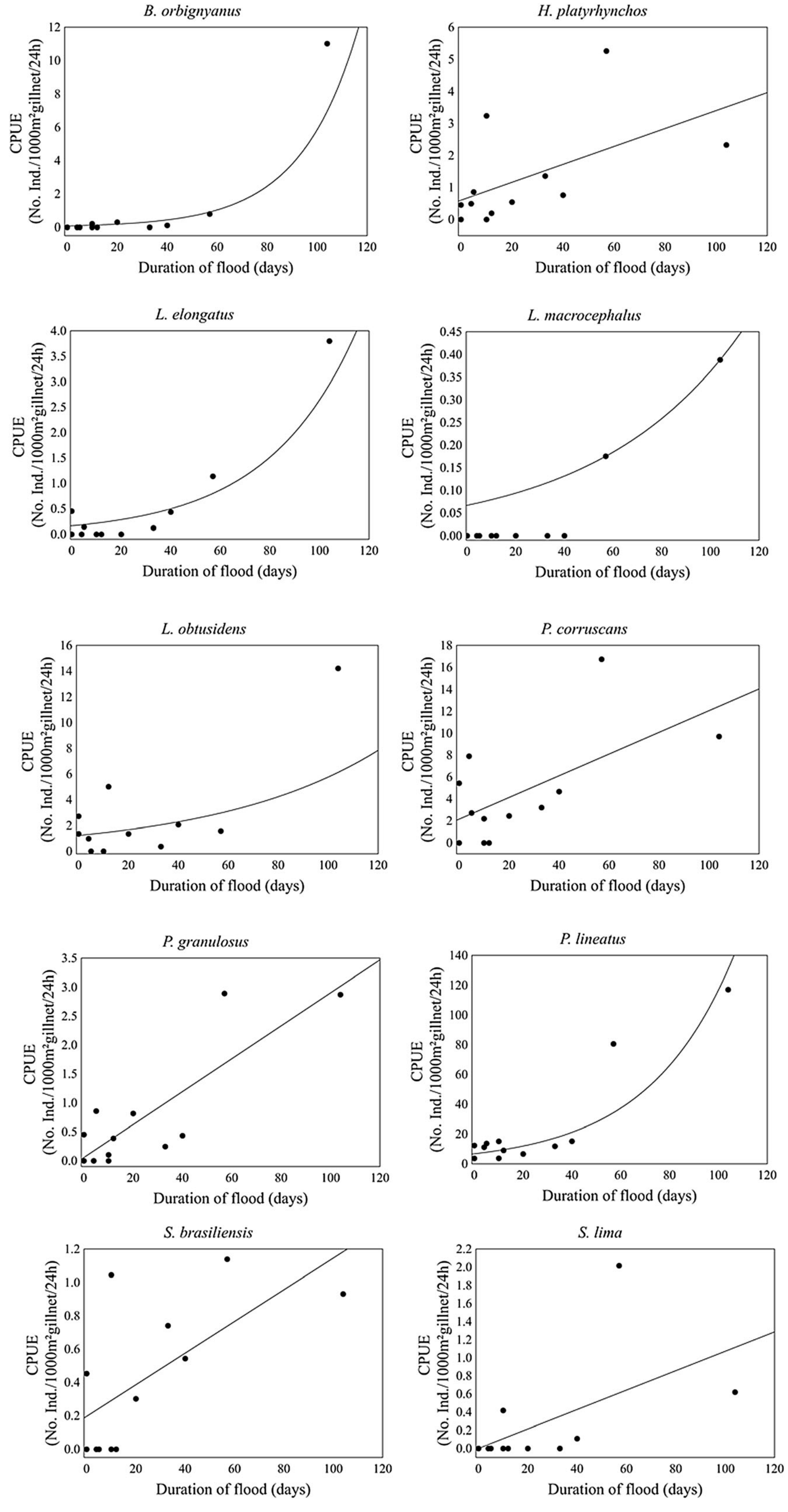

Fig. 3 Relationship between the YOY abundance of each migratory species (CPUE = catch per unit effort) and flood duration (in days)

Fig. 4 Relationship between the YOY abundance of each migratory species (CPUE = catch per unit effort) and delays in the beginning of flooding (number of fortnights after October 1)

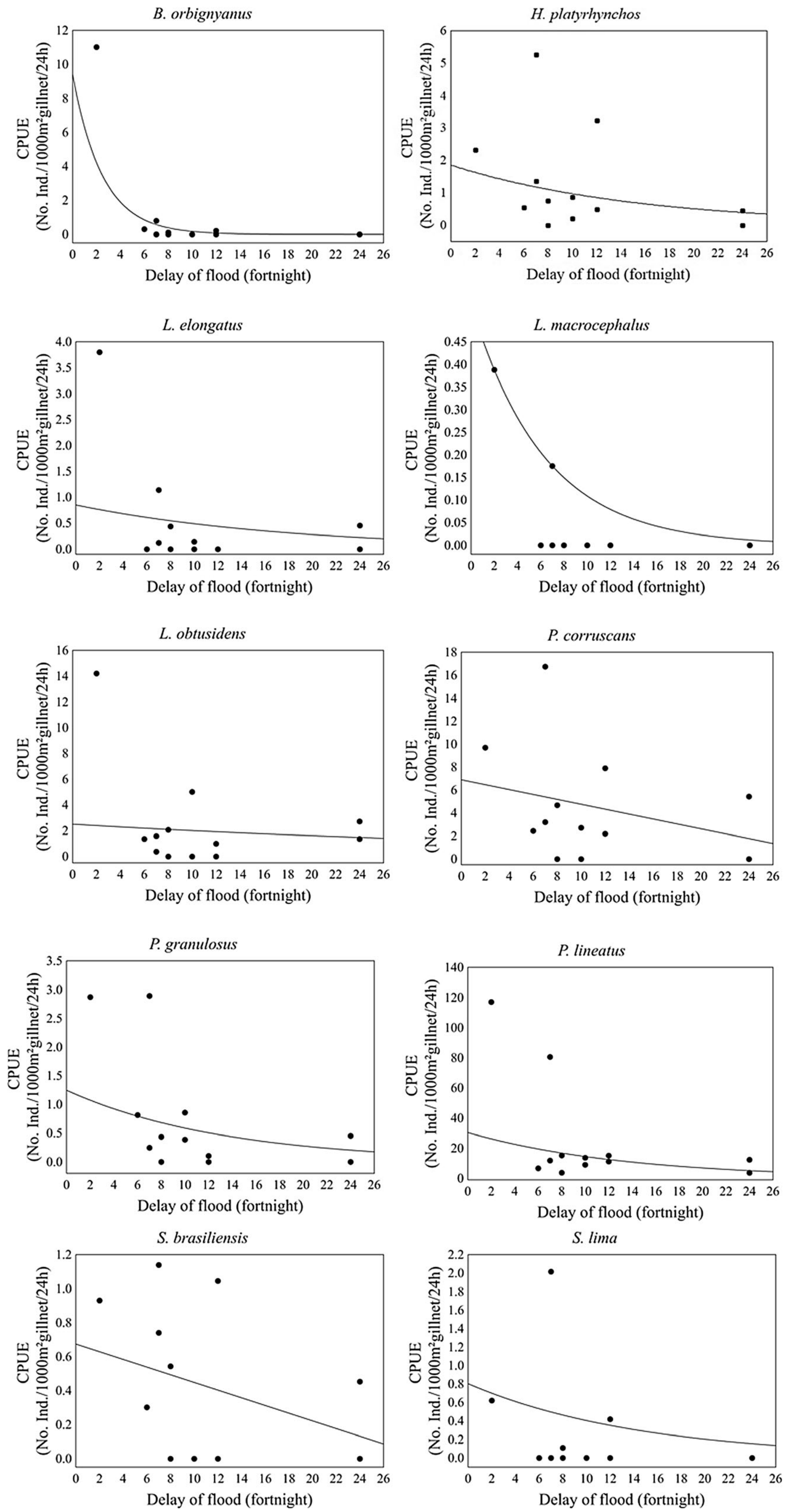

Table 3 Results of the multiple linear regression analysis that used duration (X_1) and delay (X_2) of floods as predictors of the migratory species YOY abundance. Significant variables are identified with * ($p<0.05$)

Species	Duration (X_1)	Delay (X_2)	R^2	Adjusted R^2	Model
B. orbignyanus	<0.001*	0.31	0.80	0.77	$Y=0.007*X_1$
H. platyrhynchos	0.002*	0.106	0.71	0.65	$Y=0.006*X_1$
L. elongatus	<0.001*	0.015*	0.91	0.89	$Y=-0.19+0.007*X_1+0.011X_2$
L. macrocephalus	<0.001*	0.15	0.87	0.84	$Y=-0.038+0.001*X_1$
L. obtusidens	0.001*	0.02*	0.79	0.75	$Y=0.009*X_1+0.016*X_2$
P. corruscans	0.002*	0.019*	0.77	0.72	$Y=0.011*X_1+0.02*X_2$
P. granulosus	<0.001*	0.26	0.81	0.78	$Y=0.006*X_1$
P. lineatus	<0.0013*	<0.001*	0.93	0.92	$Y=0.02*X_1+0.05X_2$
P. mesopotamicus	0.004*	0.42	0.64	0.56	$Y=0.006*X_1$
S. brasiliensis	0.001*	0.11	0.73	0.68	$Y=0.003*X_1$
S. lima	0.01*	0.86	0.52	0.43	$Y=0.002*X_1$

resulted in poor or no recruitment. Although the delayed onset of floods was negatively correlated with YOY abundance in all examined species, flood delay was a significant predictor of recruitment in only four species: *L. elongatus*, *L. obtusidens*, *P. corruscans* and *P. lineatus*.

It should be emphasised that recruitment success, as measured by the YOY abundance of the sample, also depends on the success of previous events, beginning with the gonadal maturation and migration of adult fish and ending in the spawning and survival of the early life stages. With the exception of gonadal maturation, which is associated with climatic seasonality, all of these events are somehow related to the hydrological cycle (Vazzoler 1996). Therefore, different recruitment responses should reflect specific reproductive tactics.

Table 4 Partial and semipartial correlation coefficient predictors for the YOY abundance of migratory species for which both duration and delay were significant in the multiple regression analysis

Species	Predictors	Partial correlation coefficient^2(%)	Semipartial correlation coefficient^2 (%)
L. elongatus	Duration	88.36	75.69
	Delay	49	8.41
L. obtusidens	Duration	67.24	42.25
	Delay	40.96	14.44
P. corruscans	Duration	62.41	37.21
	Delay	43.56	16.81
P. lineatus	Duration	84.64	39.69
	Delay	79.21	26.01

It is known, for example, that there are differences in spawning migration times between species, with some migrating earlier. Lucas and Baras (2001) reported that some species may begin migration earlier as a way to adjust their energy reserves and swimming performance to the higher energy demands required during higher flow rates. For longer migrations, there is a greater advantage to beginning earlier. This phenomenon may provide a parsimonious explanation for the absent or limited recruitment of species with exponential trends, especially species with a significant correlation between recruitment and flooding delays. If spawning occurs in the absence of flooding, the eggs and larvae fail to reach sites conducive to their early development; instead, they are retained in the main channel of the river, where they are exposed to predation, ultimately resulting in the failure of recruitment (Agostinho et al. 2008). There is also the possibility of photoperiod stimulate gonadal maturation, but the absence or delay in floods induce resorption of gonads, resulting in recruitment failure. *Prochilodus lineatus*, for example, begins its migration at the end of the dry season, between September and November, usually after the first rains (Agostinho et al. 1993, 2007). Delays in flooding, depending on their magnitude, can inhibit the migration and spawning of this specie. In addition, if the level of the river rises and subsequently decreases, as is observed in rivers regulated by dams, species that migrate and spawn earlier can become confused and fail to complete their reproductive cycle.

For species that exhibit no significant relationship with flood delays, migrations may already occur quickly when the river has a higher water flow. Despite having a greater energy cost, this process ensures successful recruitment of the offspring as long as moderate flooding occurs. It is known that *P. granulosus* spawns later than other migratory species (between January and March; Agostinho et al. 2003). However, *H. platyrhynchos* reproduces from November to January and *P. corruscans* reproductive period may extend from November to February (Agostinho et al. 2003). The later reproductive migration seems to be a common pattern among the Siluriformes analysed in this work, explaining the slightly higher recruitment after the 2006–2007 flooding, which was short but began in January. If compared with 2009–2010, which was intense, lasted longer and began earlier as October. An opposite trend was verified among the Characiformes (except *S. brasiliensis*) that started migration earlier.

Studies of reproduction generally group fish species into reproductive guilds to address one of the largest problems in ecosystem management: the difficulty of examining several species simultaneously (Winemiller 1989). Although the formation of guilds is an important tool, there can be significant variation among species grouped into the same guild, which must be considered when proposing management actions. Thus, the results of our study demonstrate that species that comprise the guild of long-distance migratory (seasonal strategy, sensu Winemiller 1989) respond differently to certain attributes of the hydrologic regime; therefore, it is not feasible to group these species into reproductive guilds, when aiming conservation measures.

The hydrologic cycle of the 2009–2010 coincided with a strong El Niño (Southern Oscillation - ENSO) phenomenon, representing a year of exceptional flooding in the Paraná River, which resulted in 104 days of overflow and 75 days of uninterrupted flooding. This flooding resulted in high recruitment of all the studied species; however, some species (those with exponential increases in YOY abundance with flood duration) demonstrated a greater requirement for exceptional flooding events to significantly increase their recruitments.

Flow control by hydroelectric reservoirs has well-known impacts on migratory fish populations, especially on species composition and abundance. Water from the rainy season is retained in storage reservoirs, which prevents flooding in environments downstream of dams, resulting in recruitment failures. Even in tributaries that are free of impoundments, such as the region assessed in this study, an absence of flooding in the channel of the Paraná River can affect the flow rate and flood levels in the lower reaches of these tributaries, which can reduce their role as areas of early development and decrease recruitment.

Brycon orbignyanus is one of the species that has been found to be strictly dependent on the duration of floods. Due to a sharp decline in its natural population, *B. orbignyanus* is on the list of Brazilian species facing a high risk of extinction (Abilhoa and Duboc 2004; Agostinho et al. 2008). About 40 years ago, individuals up to 80 cm were caught, but nowadays the maximum size has been 63 cm, and in this study, the larger individual measured 43.4 cm. Conservation measures for this species generally consist of banning fishing, but this is a controversial measure that is difficult to enforce. Moreover, inadequate enforcement of fishing regulations, flow control in reservoirs and the removal of riparian vegetation appear to be the main threats to this species (Agostinho et al. 2008). There is still a scarcity of studies on species autecology, especially for the other species examined in this work, such as *Salminus brasiliensis*, which is valuable for sport and/or commercial fishing and is classified as vulnerable (Abilhoa and Duboc 2004).

Thus, any efforts to preserve populations of long-distance migratory species in the upper Paraná River should consider flow manipulation in the reservoirs upstream of the study area, which represents the last significant remnant of this river's original floodplain. It is urgent that those reservoirs are operated in such a way that the quantity of water released should provide proper duration and timing of the spawning of migratory species, which will guarantee successful recruitment of large migratory fish.

Acknowledgments The authors are grateful to the Program of Environmental Sciences, of the Maringá State University; to the logistical support by the Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupélia), and financial support was provided by the National Council of Scientific and Technological Development (CNPq) to PELD Site-6 (Process 403686/2012-1) and to AGO (Process 830319/1999-9). CAPES/PROEX also helped funding sampling. AAA and LCG thank CNPq for the "Bolsa Produtividade em Pesquisa".

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