

# Temporal and spatial distributions of the fish larval assemblages of the Ivinheima River sub-basin (Brazil)

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**Abstract** Fish, like other animals, choose environments for reproduction that are favorable for their offspring's initial development. For example, these environments may be chosen to provide shelter and food. This study examined the fish larvae inhabiting the Ivinheima River sub-basin. The study aimed to (i) characterize the taxonomic composition of the larval fish fauna, (ii) analyze the structure of the larval assemblage, and (iii) verify the relationship between the larval assemblages and environmental variables. The sampling areas included three environments: the Ivinheima River, the Finado Raimundo Lagoon and the Patos Lagoon. Sampling was performed between October 2002 and March 2006 during four reproductive periods (RPs). The data were analyzed with correspondence analysis (CA) and canonical correlation analysis (CCA). A total of 120 619 larvae were collected. These larvae belonged to several species

characterized by different reproductive strategies. Our results showed differences between the composition of the Ivinheima River's assemblages, where there were more larvae of migratory fish, and the lagoons, where larvae of sedentary species were predominant. In addition, differences were found among the RPs evaluated in the Ivinheima River: the first and second RPs were characterized by milder floods and by a greater abundance of migratory piscivore larvae, whereas the third and fourth RPs had more outflow and a greater abundance of larvae of detritivore and omnivore species. We conclude that the Ivinheima River plays a significant role in the maintenance of native migratory fish stocks in the upper Paraná River basin and that the environment shows a segregation of the spatial and temporal composition and abundance of larvae related to running and flooding/standing water.

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## Introduction

Regular reproduction is a key element in the maintenance of viable populations because the success of a species depends on recruitment. The absence of reproduction during consecutive years or the absence of reproductive stimuli due to habitat modification may cause the depletion and extinction of natural stocks

(Welcomme 1979; Humphries et al. 1999; Agostinho et al. 2004). One of the key elements of successful reproduction is to select the right moment for reproduction so that the offspring always have sufficient food and shelter from predators, that varies in space and time (Nikolski 1978). Accordingly, optimum environmental conditions for the development and survival of fish eggs and larvae appear to be the factor responsible for the choice of a spawning period and locality (Humphries et al. 2002; Agostinho et al. 2004).

Studies of the relationship between fish communities and their environment have shown that hydrodynamic factors (at many spatial and temporal scales) represent the primary direct influences on the reproductive strategies of different populations of rheophilic fish and on the beginning and end of the reproductive period (Winemiller 1989; Humphries et al. 1999; Humphries et al. 2002). For these populations, specific water-level thresholds can act as a trigger that elicits reproduction (Bone et al. 1995; Paugy 2002). On the upper Paraná River in Brazil, where the Ivinheima sub-basin is located, fish spawning is related to the flood regime, particularly for migratory species (Oldani 1990; Agostinho et al. 2004). However, despite many previous studies, the true roles of flooding and other environmental variables for fish species in the upper Paraná River plain with different life strategies still require additional study.

The lower Ivinheima River and its floodplain in the Ivinheima State Park are fundamental for the preservation of local biodiversity due to the high level of environmental and habitat heterogeneity. Past and present hydrological conditions, in addition to the co-occurrence of ecosystems of similar and different successional status, have a strong influence on habitat diversity and fish reproductive potential in this type of ecosystem (Copp 1989). The fish fauna in this floodplain (which represents only 0.4 % of the Atlantic Forest) encompasses 50 % of the fish species catalogued for the entire biome (176 species; Agostinho et al. 2004; Agostinho et al. 2005). Among these fish species are several of the larger migratory species of the basin, including *Pseudoplatystoma corruscans*, *Salminus brasiliensis*, *Prochilodus lineatus*, *Rhaphiodon vulpinus*, *Brycon orbignyanus*, and *Sorubim lima*, whose populations have been reduced or have disappeared from several sections of the upper Paraná basin due to anthropogenic impact (Carolsfeld et al. 2003; Agostinho et al. 2004; Reynalte-Tataje et al. 2011).

Despite several previous studies on the distribution of eggs and larvae in the upper Paraná River basin (Nakatani et al. 1997; Baumgartner et al. 2004; Bialezki et al. 2005), studies that evaluate the temporal variation in fish larval assemblages during several reproductive periods (information that is crucial in evaluating the relationship of these assemblages with environmental variables) are scarce. Based on the variation in the spatiotemporal composition of the ichthyoplankton over a 4-year period, we test the hypothesis that this variation is related to environmental factors. To address this hypothesis, the objectives of this study were (i) to characterize the taxonomic composition of larvae of freshwater fishes present at the Ivinheima River, (ii) to determine the spatial and temporal distribution of the fish larval assemblage, and (iii) to analyze the influence of environmental variables on the fish larval assemblage.

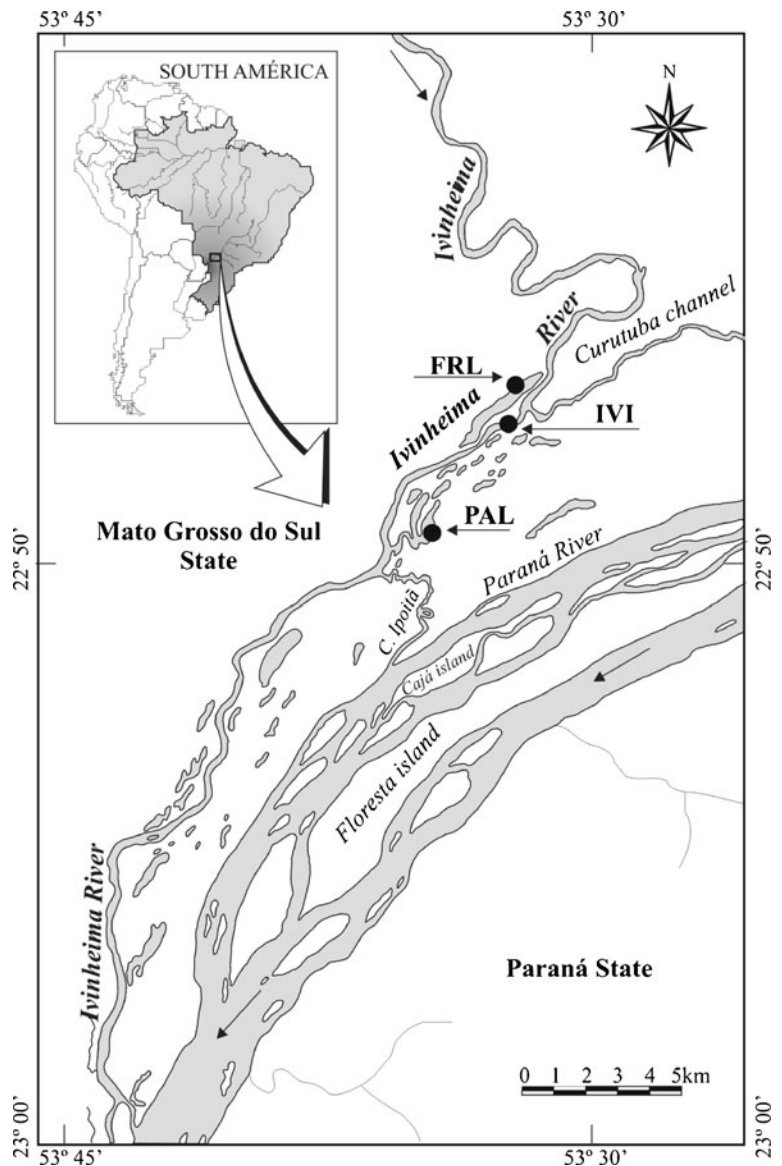
## Materials and methods

### Study area

The Ivinheima River is located on the right margin of the Paraná River (Mato Grosso do Sul State, Brazil) and is approximately 230 km in length. The upper and medium portions flow in a north-south direction, whereas the lower section runs parallel to the Paraná River (in a northeast-southwest direction) until it converges with this river. The Ivinheima River sub-basin is part of the upper Paraná River plain and has none of the damming or outflow control typically found in most of the remaining sub-basins.

The area studied, located on the lower portion of the Ivinheima River (22° 47'59"S; 53° 32'21"W), is presently within the conservation unit known as Parque Estadual do Ivinheima (Ivinheima State Park). In addition to the main channel, many aquatic environments with different hydrodynamic characteristics occur in this region. The Ivinheima River sampling station (IVI) is located approximately 6 km upstream from the Ipoitã channel, 5 km from the Patos Lagoon (PAL) and 1 km from the Finado Raimundo Lagoon (FRL). These two lagoons, selected for this study, are always connected to the river (Fig. 1).

**Fig. 1** Location of the sampling stations



The Patos Lagoon (22°49'33"S; 53° 33'09"W) is the larger of the two lagoons, with ridges that form small bays. The average depth is 3.50 m. The lagoon is approximately 113.8 ha in size, 2065 m long, and has a perimeter of 14783 m. Although it is located only 10 m from the Ivinheima River across a 0.5-m high dike, the lagoon and the river are also connected by an 8-m wide channel.

The Finado Raimundo Lagoon (22° 47'57"S; 53° 29'21"W) is 2918 m long, 3.2 m deep (on average) has a 7151-m perimeter and is 84.9 ha wide. It is connected to the river through a 50-m long and 20-m wide channel (PELD 2000).

### Sampling

Larvae were collected during four reproductive periods (RPs): from October 2002 through March 2003 (RP1), from October 2003 through March 2004 (RP2), from October 2004 through March 2005 (RP3), and from October 2005 through March 2006 (RP4). Sampling was performed using conical-cylindrical plankton nets (500- $\mu$ m mesh) equipped with a mechanical flow meter. All samples were taken from the subsurface and during the night (20:00, 0:00 and 04:00 h). Collecting during the night has been recommended by different authors who have worked in

neotropical environments and who have observed a decrease in the occurrence of larvae in the water column during the day (Nakatani et al. 2001; Hermes-Silva et al. 2009). At the lagoons, horizontal trawling for 10-min periods was used for sample collection, whereas passive 15-min collections were conducted at station IVI using three nets tied to a cable that was stretched between the two river banks. The methodology used in the floodplain lagoons and the river was related to the difference in hydrodynamic environments (Nakatani et al. 2001). The trawls in the lagoon were performed from a boat at a slow speed (<3 km/h) using the boat's 25-hp outboard. The material collected was fixed in 4 % formaldehyde buffered with calcium carbonate. The samples were sorted in the laboratory. The larvae were separated from the rest of the material and were later identified to the lowest taxonomic level possible according to Nakatani et al. (2001) and Reynalte-Tataje and Zaniboni-Filho (2008). The abundance was expressed as the number of larvae per 10 m<sup>3</sup> of water based on the filtered volume.

Simultaneously with the ichthyoplankton sampling, the following environmental variables were measured: temperature (°C), dissolved oxygen (mg/L), pH and electrical conductivity (µS/cm). The values of rainfall and outflow were provided by Itaipu Binacional based on data obtained from the Ivinheima hydrometeorological station.

#### Data analysis

A correspondence analysis (CA) was applied to examine the relationship between the fish larval assemblages and the three sampling sites (IVI, PAL, FRL). This ordering method was selected because most species showed a unimodal distribution throughout the reproductive periods (Legendre and Legendre 1998). To minimize the effect of rare species on this classification, only those species with occurrence frequencies (OF) higher than 10 % throughout the study period were selected for analysis. Three different CAs were conducted. In the first, we investigated the relationship between the species abundance data and the sampling site and reproductive period. In the second, we explored the relationship between the data on different reproductive strategies (sedentary, short and long migratory; Agostinho et al. 2004; Reynalte-Tataje and Zaniboni-Filho 2008) and the sampling site and reproductive period. In all cases, we reorganized the

abundance data by pooling species belonging to similar categories or strategies. In the third, we investigated the relationship between different trophic categories (detritivores, invertivores, insectivores, omnivores, piscivores and planktivores; Hahn et al. 2004) and the sampling site and reproductive period. The normality of the abundance data was tested with a Shapiro-Wilks test. The abundance data for all the species followed a normal distribution ( $P>0.05$ ). A chi-square test was applied to investigate possible associations between different species abundances, reproductive strategies and trophic categories and the sampling site and reproductive period. To evaluate the differences in these groups and to highlight the patterns observed with the CA, the same set of data used in each of the three CAs was analyzed with a Multiple Response Permutation Procedure (MRPP). To determine the consistency of the groupings in this test, the T value was used to evaluate statistical significance, whereas the A value was used to verify homogeneity among the groups (McCune and Mefford 1999).

A canonical correspondence analysis (CCA) was performed to evaluate the relationship between the structure of fish larval assemblages and the set of environmental variables (ter Braak 1986). The inclusion of environmental variables in the CCA was based on a forward selection procedure. The statistical significance of the species-environment relationship was examined through Monte Carlo tests, starting from 1000 randomizations. The inertia partition method proposed by Borcard et al. (1992) was used to determine the fraction of variation of the larval assemblage structures explained by the environmental variables. All classifications were performed with CANOCO 4.0 software at a significance level of  $P<0.05$ .

## Results

### Spatial and temporal variation of the environmental variables

During the study, the periods with the highest outflow averages were RP3 (381 m<sup>3</sup>/s) and RP4 (431 m<sup>3</sup>/s). During RP4, in December, a brief but notable flood occurred. Conversely, RP1 and RP2 had lower outflow averages (293 m<sup>3</sup>/s and 288 m<sup>3</sup>/s, respectively). The average daily rainfall varied between 4.5 and

5.0 mm for RP1, RP3, and RP4, with the lowest values recorded for RP2 (3.2 mm) (Fig. 2).

The abiotic variables in the areas sampled showed clear variation among the months and years studied. In general, the highest average pH (6.82), electrical conductivity (44.68  $\mu\text{S}/\text{cm}$ ) and dissolved oxygen (5.30 mg/L) were found in the Ivinheima River. Nevertheless, the greatest variations among the abiotic variables were recorded in the lagoons, including critical values of dissolved oxygen (<1.0 mg/L) and pH (<5.5) (Fig. 3).

**Taxonomic composition of the ichthyoplankton**

During the study period, 120 619 larvae were collected. These larvae belonged to five orders, 23 families, 44 genera and 39 species (identified). The most abundant larvae were those of the sedentary species *Hypophthalmus edentatus* and *Plagioscion squamosissimus*, which together represented more than 76 % of the total captured. However, these species were not very abundant at IVI station, which exhibited a great abundance of the larvae of the long-distance migratory species *P. corruscans* and *P. lineatus*. The abundance of the larvae of the most frequent species (OF>10 %) and the different feeding categories and reproductive-strategy categories of these species as adults are presented in Table 1.

**Structure of fish larval assemblages**

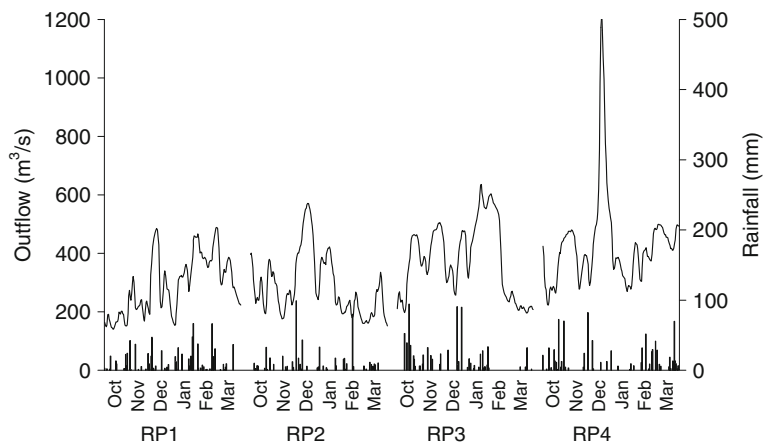
On the first axis of the first CA, the PAL and FRL lagoons showed a clear contrast to the Ivinheima River. Station IVI was characterized by the predominance of

migratory larval species, such as *P. corruscans*, *R. vulpinus*, *Pimelodus* spp., and *Sorubim lima*, whereas larvae of sedentary species were predominant in the lagoons (e.g., *H. edentatus* and *P. squamosissimus*) (Fig. 4a). A chi-square test showed an association between different species abundances and the sampling site and reproductive period (chi-square=4838, d.f.=437,  $p<0.05$ ). The difference between groups within the matrix of data displayed in this CA was confirmed by the MRPP (T=-1.61; A=0.06;  $p<0.05$ ).

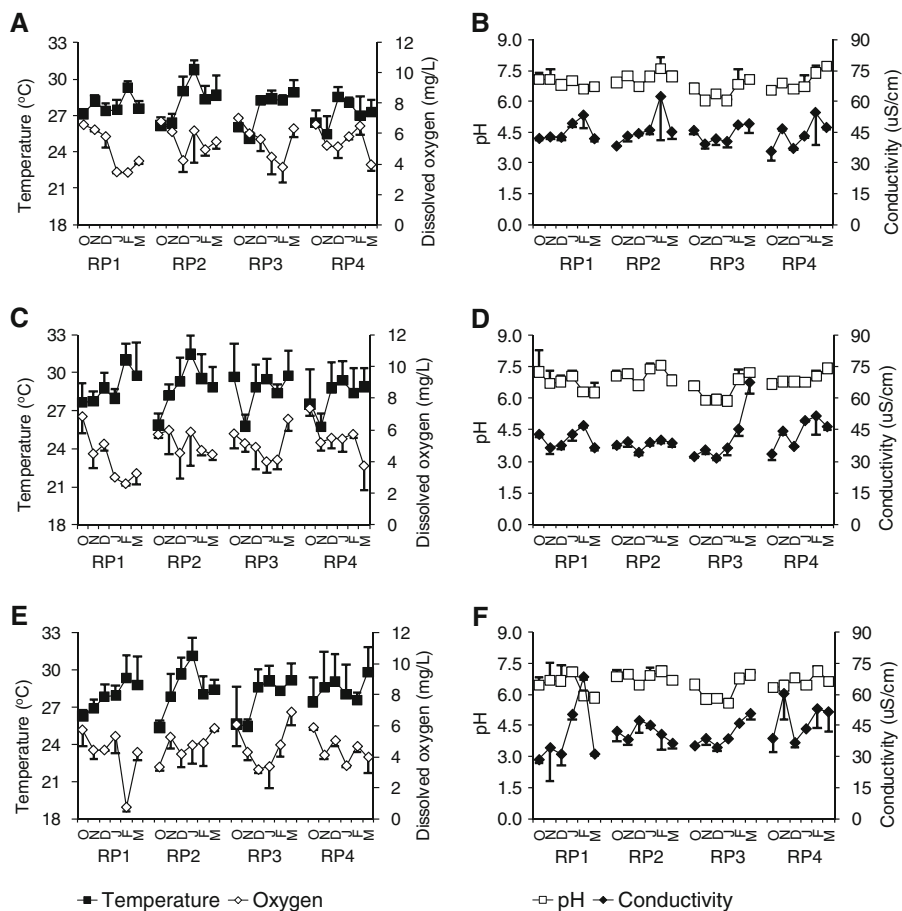
The pooled data on reproductive strategies in the second CA also showed a marked segregation of the lagoons on the first axis. Larvae of sedentary species were more abundant in the lagoons, whereas we observed more larvae of migratory species in the river (Fig. 4b). A chi-square test showed an association between different reproductive strategies and the sampling site and reproductive period (chi-square=120, d.f.=46,  $p<0.05$ ). The separation of the groups in this CA was also significant in the MRPP (T=-4.61; A=0.16;  $p<0.05$ ).

The data on the abundance of larvae grouped by trophic category of adults in the third CA showed a spatial separation between the planktivore *H. edentatus* and other trophic categories on the first axis. However, the second axis showed a temporal separation in the Ivinheima River. Periods RP1 and RP2 were characterized by greater abundances of the larvae of detritivores and insectivores, whereas RP3 and RP4 were characterized by the presence of the larvae of piscivores (Fig. 4c). A chi-square test showed an association between different reproductive strategies and the sampling site and trophic categories (chi-square=1685, d.f.=115,  $p<0.05$ ). The MRPP applied to the

**Fig. 2** Daily outflow (lines) and rainfall (bars) values recorded at the Ivinheima River sub-basin in the reproductive periods (RPs) between October 2002 and March 2006



**Fig. 3** Average monthly values ( $\pm$ standard error) of the environmental variables obtained from the Ivinheima River sub-basin during four consecutive reproductive periods (RPs) between October 2002 and March 2006. **a** and **b** = Ivinheima River; **c** and **d** = Finado Raimundo Lagoon; and **e** and **f** = Patos Lagoon



data matrix used in this third CA showed no difference among the groups ( $T=-0.71$ ;  $A=0.02$ ;  $p>0.05$ ).

#### Influence of environmental variables on the principal taxa

The structure of the fish larval assemblages was related to the set of environmental variables ( $P<0.01$ ), explaining 22.6 % of the total variation in the abundance of the taxa. The only variables selected by the CCA (forward selection) were electrical conductivity, outflow, temperature and pH (Table 2). The first CCA axis revealed a gradient among the biotypes explained by the environmental variables most representative of the first axis (Fig. 5). During all of the periods, the lagoons had lower pH ( $6.55\pm 0.51$ ), electrical conductivity ( $41.76\pm 10.83$  µS/cm) and temperature ( $27.40\pm 1.82$  °C) values, on average. In general, the association of larval abundance with these environmental variables was shown by the pattern observed in Fig. 4a. In this context, the species most strongly correlated with

the environmental conditions of the lagoons were *H. edentatus* ( $r=-0.73$ ) and *P. squamosissimus* ( $r=-0.68$ ). The larvae of *P. corruscans* ( $r=0.57$ ) and *P. lineatus* ( $r=0.54$ ) were the most strongly correlated with the conditions of the Ivinheima River.

The second CCA axis showed a gradient in the variation of water outflow and a clear separation between the reproductive periods at the IVI station (Fig. 5). In this sense, the species that were correlated with the positive portion of axis 2, where the outflow was higher in the Ivinheima River, were *P. lineatus* ( $r=0.42$ ) and *B. orbignyanus* ( $r=0.35$ ). The piscivores *P. squamosissimus* ( $r=-0.77$ ), *R. vulpinus* ( $r=-0.44$ ) and *S. brasiliensis* ( $r=-0.32$ ) were more strongly correlated with the negative portion of axis 2.

#### Discussion

Our results indicate differences between the roles of the floodplain lagoons and the river channel in the

**Table 1** Feeding category, reproductive strategy and average abundance (individuals/10 m<sup>3</sup>) of the most abundant fish taxa as verified during the four reproductive periods (RPs) studied

between October 2002 and March 2006 at the Ivinheima River sub-basin (IVI = Ivinheima River; FRL = Finado Raimundo Lagoon; PAL = Patos Lagoon)

Taxa	<sup>a</sup> Feeding categories	<sup>b</sup> Reproductive strategies	Larvae densities (reproductive period)				<sup>c</sup> Larvae densities (sampling stations)		
			RP1	RP2	RP3	RP4	IVI	FRL	PAL
<i>Auchenipterus osteomystax</i>	Insectivore	SM	0.11	0.05	0.09	0.04	0.17	0.01	0.01
<i>Brycon orbignyanus</i>	Omnivore	LM	0.65	0.01	0.71	0.02	0.16	0.04	0
<i>Bryconamericus stramineus</i>	Omnivore	SM	0.09	1.45	0.03	0.05	0.03	0.09	0.02
<i>Catathyridium jenynsii</i>	Piscivore	S	0.01	0.06	0.01	0.01	0.01	0	0
<i>Cetopsis gobioides</i>	Piscivore	SM	>0.01	0.03	>0.01	0.01	0.01	0	0
<i>Gymnotus</i> spp.	Insectivore	S	0.01		0.02	0.01	0.01	0	0
<i>Hoplias</i> aff. <i>malabaricus</i>	Piscivore	S	0.05	0.01	0.07	0.10	0.01	0.01	0.01
<i>Hypophthalmus edentatus</i>	Planktivore	S	12.18	17.55	22.36	15.48	0.55	25.64	29.30
<i>Hoplosternum littorale</i>	Invertivore	S	0.01	0.01	0.07	0.01	0.01	0.01	0
<i>Iheringiichthys labrosus</i>	Invertivore	SM	0.03	0.07	>0.01	0.01	0.01	0.01	0.01
<i>Leporinus</i> spp.	Insectivore	SM	0.09	0.02		0.01	0	0.01	0
<i>Loricariichthys platymetopon</i>	Detritivore	S	0.01	0.02	>0.01	0.01	0.01	0.01	0.01
<i>Megalonema platanum</i>	Piscivore	SM	0.01	0.76	>0.01	0.01	0.52	0.04	0
<i>Moenkhausia sanctaefilomenae</i>	Insectivore	S		0.03	0.06	0.01	0	0	0.01
<i>Parauchenipterus galeatus</i>	Omnivore	S	0.01	0.01	0.03	0.02	0	0	0.01
<i>Pimelodus</i> spp.	Omnivore	LM	0.89	0.71	>0.01	0.02	2.19	0.06	0.01
<i>Plagioscion squamosissimus</i>	Piscivore	S	14.02	14.26	5.98	5.79	3.12	10.94	13.72
<i>Prochilodus lineatus</i>	Detritivore	LM	0.40	0.01	0.04	1.85	1.22	0.55	0.01
<i>Pseudoplatystoma corruscans</i>	Piscivore	LM	1.34	0.70	0.02	0.09	3.71	0.07	0.01
<i>Rhamdia quelen</i>	Omnivore	SM	0.01	0.01	0.02	>0.01	0.01	0.01	0.01
<i>Rhaphiodon vulpinus</i>	Piscivore	LM	0.36	0.04	0.01	0.03	2.24	0.01	0.01
<i>Roeboides paranensis</i>	Insectivore	S	0.01	0.02	0.05		0	0.01	0.01
<i>Salminus brasiliensis</i>	Piscivore	LM	0.41	0.03	0.01	0.01	0.16	0.06	0.01
<i>Serrasalmus</i> spp.	Piscivore	S	0	0.01	0.01	0.03	0	0	0.01
<i>Sorubim lima</i>	Piscivore	LM	0.10	0.01	>0.01	0.01	0.08	0.01	0

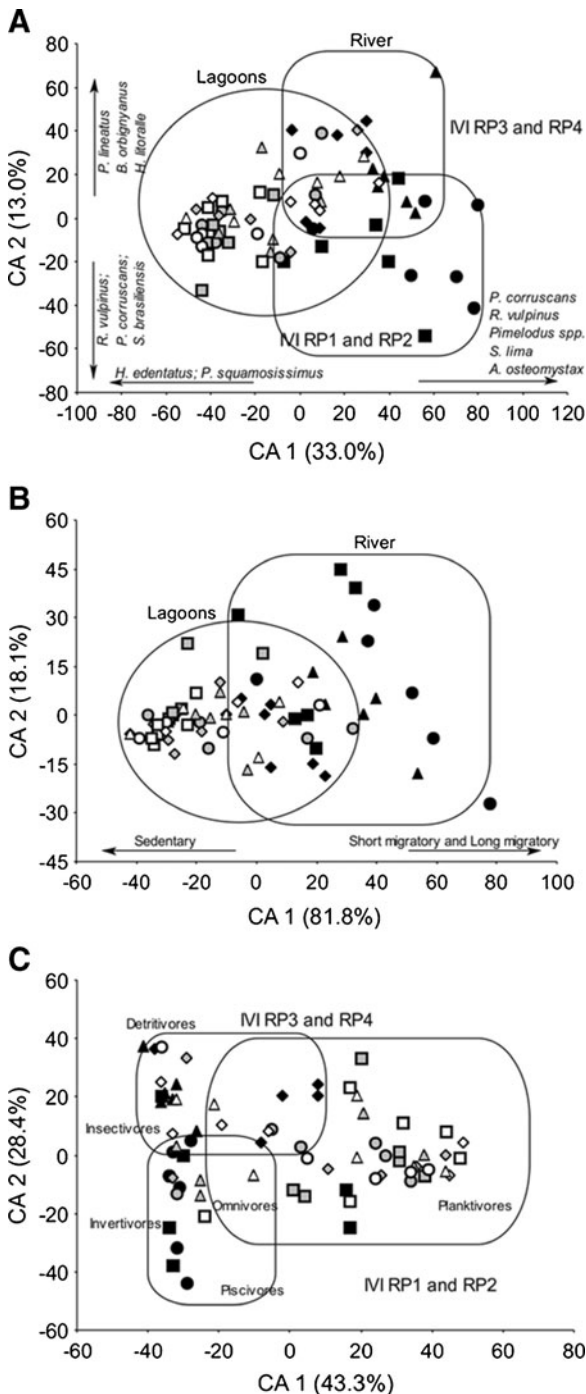
<sup>a</sup> Source: Hahn et al. (2004)

<sup>b</sup> Reproductive strategies: *S* sedentary, *SM* short migration, *LM* long migration (Source: Agostinho et al. 2004).

<sup>c</sup> Larvae densities: *x* < 0.1 larvae/10 m<sup>3</sup>; *xx* = 0.1 to 1.0 larvae/10 m<sup>3</sup>; *xxx* = > 1.0 larvae/10 m<sup>3</sup>.

reproductive cycle of the fishes studied. These results are consistent with suggestions in previous studies about the importance of habitat heterogeneity for maintaining populations of migratory species (Nakatani et al. 1997; Baumgartner et al. 2004, 2008; Sanches et al. 2006). The lagoons studied showed a high abundance of the larvae of sedentary species, particularly *H. edentatus* and *P. squamosissimus*, two non-native species in the upper Paraná River that were dominant in both lagoons. Surveys performed in the same region during the years of 1992

and 1993 showed that these species were rare and were not included in the ten most abundant species (Baumgartner et al. 1997). The current dominance of these species may be related to their opportunistic reproductive strategy, including early gonadal maturation, parceled spawning, high fecundity, and rapid embryonic and larval development (Vazzoler 1996; Araújo-Lima and Oliveira 1998), and/or to the alterations in the fish community produced by the reservoirs in the region of the upper Paraná River. Current studies in different river basins of the world show that



**Fig. 4** Correspondence analysis summarizing the following matrices: **a** Densities of the main larvae; **b** larvae densities grouped by reproductive strategies; and **(c)** larvae densities grouped by feeding category. *IVIRP1* First reproductive period Ivinheima river; *IVIRP2* Second reproductive period Ivinheima river; *IVIRP3* Third reproductive period Ivinheima river; *IVIRP4* Fourth reproductive period Ivinheima river; *FRLRP1* First reproductive period Finado Raimundo Lagoon; *FRLRP2* Second reproductive period Finado Raimundo Lagoon; *FRLRP3* Third reproductive period Finado Raimundo Lagoon; *FRLRP4* Fourth reproductive period Finado Raimundo Lagoon; *PALRP1* First reproductive period do Patos Lagoon; *PALRP2* Second reproductive period do Patos Lagoon; *PALRP3* Third reproductive period do Patos Lagoon; *PALRP4* Fourth reproductive period do Patos Lagoon

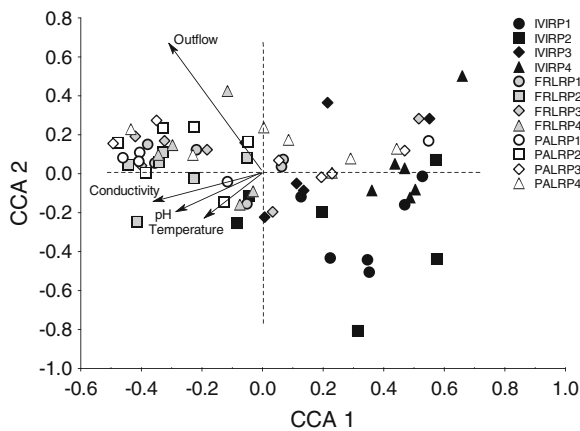
Note that the relative abundance of the larvae of sedentary and migratory species clearly differed in both lakes. This difference was more pronounced in the larger floodplain lagoon (Patos Lagoon), where the larvae of migratory species were less abundant. It is probable that this factor is related to the greater length channel connection to the river, which should have limited the entry of water from the river and the associated transport of the eggs and larvae of the spawning migratory species that occur in the river. The great abundance of the larvae of migratory species in the river observed in this study and the scarcity of these larvae in large lagoons indicate the importance of the river channel and its temporarily flooded

**Table 2** Rests of the canonical correspondence analysis (CCA) as associated with the 25 most abundant taxa and four environmental variables found in the Ivinheima River sub-basin between October 2002 and March 2006. Monte Carlo tests for the significance of the first classification axis  $P < 0.01$  ( $n = 1000$  permutations)

	Axis 1	Axis 2	Axis 3
Autovalues	0.037	0.024	0.010
Cumulative % of the variance explained by the species-environment relationship	8.5	14.1	16.4
Species-environment correlation (r)	0.557	0.670	0.427
Correlations between the environmental variables with the classification axis			
Outflow	-0.222	0.586	0.104
Temperature	-0.237	-0.277	0.319
Conductivity	-0.424	-0.244	0.076
pH	-0.328	-0.298	-0.363

fish communities have low proportional abundances of native species in highly regulated rivers, or, conversely, a greater proportional abundance of alien species (Gehrke and Harris 2001; Agostinho et al. 2007).





**Fig. 5** Canonical correspondence analysis related to the abundance categorization of the 25 most abundant taxa sampled from the Ivinheima River sub-basin (Mato Grosso do Sul State, Brazil) in four reproductive periods between October 2002 and March 2006. *IVIRP1* First reproductive period Ivinheima river; *IVIRP2* Second reproductive period Ivinheima river; *IVIRP3* Third reproductive period Ivinheima river; *IVIRP4* Fourth reproductive period Ivinheima river; *FRLRP1* First reproductive period Finado Raimundo Lagoon; *FRLRP2* Second reproductive period Finado Raimundo Lagoon; *FRLRP3* Third reproductive period Finado Raimundo Lagoon; *FRLRP4* Fourth reproductive period Finado Raimundo Lagoon; *PALRP1* First reproductive period do Patos Lagoon; *PALRP2* Second reproductive period do Patos Lagoon; *PALRP3* Third reproductive period do Patos Lagoon; *PALRP4* Fourth reproductive period do Patos Lagoon

margins as a nursery for these species. The importance of the river channel as a temporary nursery environment in the La Plata River basin has been reviewed recently by Reynalte-Tataje et al. (2008).

The study area showed fluctuating hydrological conditions during the four years of the study, a result of the irregularity of the intensity and magnitude of flooding that has occurred in the region. Large floods increase the area covered by the river and reduce the land area. The forest extends to the riverside, and contact with the marginal lagoons increases. In contrast, the area covered by the river is less during years with less intense floods. The land area increases, and contact with the marginal lagoons is reduced. The sedentary species showed no major changes in abundance during the four years of the study, whereas the populations of the larvae of different migratory species varied with the reproductive period. This variation was related to the hydrology of each year. Generally, the larvae showed temporal clustering according to the adult trophic categories.

The grouping of the larvae of migratory species into food categories for the different reproductive periods appears to suggest the importance of adult feeding for the reproductive strategy of the migratory species. In general, it is accepted that flooding favors the accumulation of nutritional reserves in fish due to the input of biomass and nutrients from runoff (Bennemann et al. 1996) and from the floodable area (Junk et al. 1989; Machado-Allison 1992). Moreover, good feeding conditions increase the probability that individuals will perform a reproductive migration (Engelhard and Heino 2006). Such conditions also increase the fecundity of the breeding individuals and increase the diameter and the viability of the eggs (Thorsen et al. 2006), thus increasing larval abundance. Although the topic of responses to flood and drought years is a controversial subject in the literature (see Abujanra et al. 2009), flooding appears to be positively associated with nutritional reserves for detritivores (Gomes and Agostinho 1997), herbivores (Bennemann et al. 1996; Loubens and Panfili 2001) and omnivores (Bayley 1995). For piscivores, however, the opposite trend can occur, although it is subject to variation depending on the strategy of the species (Luz-Agostinho et al. 2009).

Welcomme and Halls (2005) and Bunn and Arthington (2002) emphasized the significance of changes in the timing, duration, amplitude and other characteristics of flood regimes on various fish species. Most of the literature on the reproductive strategies of migratory species states that flooding stimulates the reproductive activity of this group, as it increases the flooded area and facilitates larval and juvenile development. Okada et al. (2003) reported that the abundance of juveniles was low in a floodless year for all reproductive strategies despite more intense reproductive activity in sedentary species. In contrast to this prediction, our study showed that migratory species use different reproductive strategies under different hydrological conditions and that the density of their larvae could be related to the feeding guild of the adult. Therefore, the relationship between the water outflow and the distribution of the larvae of particular migratory species differs from that observed in juveniles. However, greater densities of larvae of migratory piscivore species during years of reduced outflow may not produce greater recruitment in the future. According to Agostinho et al. (2004), the closure of Porto Primavera Dam (upper Parana River

basin) during the spawning season (flood of 1998-9) elicited a failure of the recruitment of migratory species, even those with high larval densities. These authors attributed this failure to the lack of access to floodplain environments. According to Okada et al. (2003), flooding affects species with different strategies in distinct ways, but all species are affected by an absence of floods during their juvenile phase. However, additional studies should be performed to test the hypothesis that the reproductive success of a species in certain years is related to the adult feeding guild to which the species belongs. An equivalent hypothesis is that the reproduction of several species of the same feeding guild benefits from specific hydrological conditions.

Based on the low densities of the larvae of migratory species observed in the lagoons in this study and the abundance of young-of-the-year reported by other authors (Agostinho et al. 2004; Fernandes et al. 2009; Suzuki et al. 2009), we propose that initial larval development occurs in the river channel and that young fish disperse into the lagoon at a later stage. In contrast, the high larval density of sedentary species, such as *H. edentatus* and *P. squamosissimus*, in lagoons indicates that the spawning and initial development of these species occur in standing water. In general, the environmental variables evaluated in this study appear to influence the abundance of the larvae of migratory species relatively strongly, whereas the larvae of the sedentary species do not show such effects. This generalization is verified by the greater variation shown by different populations of the larvae of the migratory species during the years of the study. In conclusion, the larval assemblages studied show both spatial and temporal stratification, and the taxonomic composition and abundance of the fish larvae studied are related to flooding and running/standing water, as proposed by our initial hypothesis.

The results obtained confirm the importance of the floodplain environments and the flood regime for the maintenance of the stocks of the main migratory species in the Neotropical region. This finding implies that for the conservation of large migratory fishes in the basin, the conservation unit created in the region requires special attention and the control of the river discharge by the upstream reservoir to meet the water demands for fish spawning and larval viability in terms of both quantity and timing.

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## References

- Abujanra F, Agostinho AA, Hahn NS (2009) Effects of the flood regime on the body condition of fish of different trophic guilds in the Upper Paraná River floodplain, Brazil. *Braz J Biol* 69(2):469–479
- Agostinho AA, Gomes LC, Verissimo S, Okada EK (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
- Agostinho AA, Thomaz SM, Gomes LC (2005) Conservation of the biodiversity of Brazil's inland waters. *Conserv Biol* 19(3):646–652
- Agostinho AA, Gomes LC, Pelicice FM (2007) Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. EDUEM, Maringá
- Araújo-Lima CARM, Oliveira EC (1998) Transport of larval fish in the Amazon. *J Fish Biol* 53:297–306
- Baumgartner G, Nakatani K, Cavicchioli M, Baumgartner MST (1997) Some aspects of the ecology of fishes larvae in the floodplain of the high Paraná river, Brazil. *Rev Bras Zool* 14(3):551–563
- Baumgartner G, Nakatani K, Gomes LC, Bialezki A, Sanches PV, Makrakis MC (2004) Identification of spawning sites and natural nurseries of fishes in the upper Parana' River, Brazil. *Environ Biol Fishes* 71:115–125
- Baumgartner G, Nakatani K, Gomes LC, Bialezki A, Sanches PV, Makrakis MC (2008) Fish larvae from the upper Paraná River: do abiotic factors affect larval density? *Neotrop Ichthyol* 6(4):551–558
- Bayley PB (1995) Understanding large river-floodplain ecosystems. *Bioscience* 45:153–158
- Bennemann ST, Orsi ML, Shibatta OA (1996) Atividade alimentar de espécies de peixes do rio Tibagi, relacionada com o desenvolvimento de gordura e das gônadas. *Rev Bras Zool* 13(2):501–512
- Bialezki A, Nakatani K, Sanches PV, Baumgartner G, Gomes LC (2005) Larval fish assemblage in the Baía river (Mato Grosso do Sul State, Brazil): temporal and spatial patterns. *Environ Biol Fishes* 73:37–47
- Bone Q, Marshall NB, Blaxter JHS (1995) Biology of fishes. Blackie Academic and Professional Publishers, Glasgow
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055

- Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ Manage* 30(4):492–507
- Carolsfeld J, Harvey B, Ross C, Baer A (2003) Migratory fishes of South America. Biology, Fisheries and Conservation Status. Ottawa, The World Bank publishers.
- Copp GH (1989) The habitat diversity and fish reproduction function of floodplain ecosystems. *Environ Biol Fishes* 26:1–27
- Engelhard GH, Heino M (2006) Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. *Oecologia* 149:593–603
- Fernandes R, Gomes LC, Pelicice FM, Agostinho AA (2009) Temporal organization of fish assemblages in floodplain lagoons: the role of hydrological connectivity. *Environ Biol Fishes* 85(2):99–108
- Gehrke PC, Harris JH (2001) Regional-Scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regul Rivers: Res Manage* 17:369–391
- Gomes LC, Agostinho AA (1997) The influence of the flooding regime on the nutritional state and recruitment of young *Prochilodus scrofa* Steindachner, 1881, in the high river Paraná, Brazil. *Fish Manag* 4:263–274
- Hahn NS, Fugi R, Adrian IF (2004) Trophic ecology of the fish assemblages. In: Thomaz SM, Agostinho AA, Hahn NS (eds) The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. Backhuys Publishers, Leiden, pp 247–269
- Hermes-Silva S, Reynalte-Tataje DA, Zaniboni-Filho E (2009) Spatial and Temporal distribution of ichthyoplankton in the Upper Uruguay River, Brazil. *Braz Arch Biol Tech* 52(4):933–944
- Humphries P, King AJ, Koehn JD (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
- Humphries P, Serafini LG, King AJ (2002) River regulation and fish larvae: variation through space and time. *Freshw Biol* 47:1307–1331
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of the International Large River Symposium (LARS). Ottawa: Department of Fisheries and Oceans, pp. 110–127. Canadian Special Publication of Fisheries and Aquatic Sciences, 106
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Loubens G, Panfili J (2001) Biologie de *Piaractus brachipomus* Teleostei: serrasalmidae dans basin du Mamoré Amazonie bolivienne. *Ichthyol Explor Freshw* 12:51–64
- Luz-Agostinho KDG, Agostinho AA, Gomes LC, Júlio HF Jr, Fugi R (2009) Effects of flooding regime on the feeding activity and body condition of piscivorous fish in the upper Paraná River floodplain. *Braz J Biol* 69(2):481–490
- Machado-Allison A (1992) Larval ecology of fish of Orinoco Basin. In: Hamlett WC (ed) Reproductive biology of South American vertebrates. Springer, New Cork, pp 45–59
- McCune B, Mefford C (1999) PC-ORD. Multivariate analysis of ecological data, version 4.1. MJM Software Desing, Oregon, pp. 126
- Nakatani K, Baumgartner G, Cavicchioli M (1997) Ecologia de ovos e larvas de peixes. In: de Vazzoler AEA, Agostinho AA, Hahn SH (eds) A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. EDUEM, Maringá, pp 281–306
- Nakatani K, Agostinho AA, Baumgartner G, Bialetzki A, Sanches PV, Makrakis MC, Pavanelli CS (2001) Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação. EDUEM, Maringá
- Nikolski GV (1978) The ecology of fishes. T.F.H. Publications, Neptune City
- Okada EK, Agostinho AA, Petrere M Jr, Penczak T (2003) Factors affecting fish diversity and abundance in drying ponds and lagoons in the upper Paraná River basin, Brazil. *Ecohydrol Hydrobiol* 3(1):97–110
- Oldani NO (1990) Variaciones de la abundancia de peces del valle del río Paraná (Argentina). *Rev Hydrobiol Trop* 23(1):67–76
- Paugy D (2002) Reproductive strategies of fish in a tropical temporary stream of the Upper Senegal basin: Baulé River in Mali. *Aquat Living Resour* 15:424–441
- PELD-CNPq (2000) A planície alagável do alto rio Paraná: Estrutura e Processos ambientais, Sítio 6. Relatório Técnico Pesquisas Ecológicas de Longa Duração-Conselho Nacional de Desenvolvimento Científico e Tecnológico. Maringá: UEM/Nupélia/PELD
- Reynalte-Tataje DA, Zaniboni-Filho E (2008) Biologia e identificação de ovos e larvas de peixes do alto rio Uruguai, Brasil. In: Zaniboni-Filho E, Nuñez APO (eds) Reservatório de. Itá Estudos ambientais, desenvolvimento de tecnologias de cultivo e conservação da ictiofauna. Florianópolis, Editora UFSC, pp 139–154
- Reynalte-Tataje DA, Hermes-Silva S, Zaniboni-Filho E (2008) Locais de crescimento de larvas de peixes na região do alto rio Uruguai, Brasil. In: Zaniboni-Filho E, Nuñez APO (eds) Reservatório de. Itá Estudos ambientais, desenvolvimento de tecnologias de cultivo e conservação da ictiofauna. Florianópolis, Editora UFSC, pp 159–194
- Reynalte-Tataje DA, Nakatani K, Fernandes R, Agostinho AA, Bialetzki A (2011) Temporal distribution of ichthyoplankton in the Ivinheima River (Mato Grosso do Sul State/Brazil): Influence of environmental variables. *Neotrop Ichthyol* 9(2):427–436
- Sanches PV, Nakatani K, Bialetzki A, Baumgartner G, Luiz EA (2006) Flow regulation by dams affecting ichthyoplankton: the case of the Porto Primavera Dam, Paraná River, Brazil. *River Res Appl* 22(5):555–565
- Suzuki HI, Agostinho AA, Bailly D, Gimenes MF, Júlio HF Jr, Gomes LC (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(2):649–660
- Ter Braak CFJ (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179
- Thorsen A, Marshal CT, Kjesbu OS (2006) Comparison of various potential fecundity models for north-east Arctic cod *Gadus morhua*, L. using oocyte diameter as a standardizing factor. *J Fish Biol* 69:1709–1730

- de Vazzoler AEA (1996) *Biologia da reprodução de peixes teleósteos: teoria e prática*. EDUEM, Maringá
- Welcomme RL (1979) *Fisheries ecology of floodplain rivers*. Logman, London
- Welcomme R, Halls A (2005) Dependence of tropical river fisheries on flow. In: Welcomme R, Petr T (eds) *Proceedings of the second international symposium on the management of large rivers for fisheries*. Volume II. FAO Regional Office for Asia and the Pacific, Bangkok, pp 267–283
- Winemiller K (1989) Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81(2):225–241