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Temporal variability of fish larvae assemblages: influence of natural and anthropogenic disturbances

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Natural and induced disturbances greatly influence the temporal distribution of ichthyoplankton abundance. This study assesses and compares the temporal variability of fish larvae assemblages in controlled and free environments to determine the influence of environment variables on the main taxa in these systems. The study was conducted at the Chapecó (without dam impact) and Ligeiro (with dam impact) river mouths, which are located in the upper Uruguay River. Samples were made between October 2001 and March 2004 during three reproductive periods. The larvae assemblages were composed of small and medium-sized Characiformes and Siluriformes. The variation in the distribution of larvae was mainly temporal (>85%). When the three reproductive periods were compared, it was observed in the second period, characterized by a larger water flow and a lower temperature, that there was a reduction in abundance, a lower number of taxa, an absence of stages in post-flexion and a high dissimilarity in larvae assemblage structure. In general, the environmental variables of water flow and temperature most influenced the distribution of egg and larvae abundance. In the studied area, a smaller temporal variability was observed in the structure of larvae assemblages at the sampling sites in the Chapecó River mouth than in in the Ligeiro River mouth under the influence of dams.

Os distúrbios naturais e induzidos têm notável influência na distribuição temporal da abundância do ictioplâncton. Este estudo visa avaliar e comparar a variabilidade temporal das assembleias de larvas de peixes, entre ambientes regulados e ambientes livres, bem como, determinar a influência das variáveis ambientais sobre os principais táxons presentes nestes ambientes. O trabalho foi conduzido na foz dos rios Chapecó (sem impacto de barramento) e Ligeiro (impactado por barragens), ambos localizados no alto rio Uruguai. As coletas foram realizadas entre outubro de 2001 e março de 2004 durante três períodos reprodutivos. As assembléias de larvas estiveram compostas principalmente por Characiformes e Siluriformes de pequeno e médio porte. A variação na distribuição de larvas foi principalmente temporal (>85%). Quando comparados os três períodos reprodutivos, foi observado que no segundo período, caracterizado por uma maior vazão da água e menor temperatura, houve redução na abundância, menor número de táxons, ausência de estágios em pós-flexão e elevada dissimilaridade na estrutura da assembléia de larvas. Em geral, as variáveis ambientais vazão e temperatura da água foram as que mais influenciaram a distribuição da abundância de ovos e larvas. Nos ambientes estudados, foi observado que existe uma menor variabilidade temporal na estrutura das assembléias de larvas das estações presentes na foz do rio Chapecó do que naquelas presentes na foz do rio Ligeiro, o qual esta sob influência dos barramentos.

Key words: Dams, Environmental variables, Ichthyoplankton, Reproduction.

Introduction

A central theme in community ecology is the study of abundance fluctuations commonly observed in biological populations, including range and time intervals of these phenomena (Andrewartha & Birch, 1982). Among the mechanisms controlling population fluctuations, natural (such as seasonal and/or annual cycles) and induced (for example, anthropogenic changes) disturbances are recognized as the most important (Wittings *et al*., 1999; Agostinho *et al*., 2007). In both cases, the disturbances promote changes in spatial and temporal heterogeneity of ecosystems, causing extreme changes in the relative abundance of species (Pickett & White, 1985).

In tropical and subtropical river environments, the seasonal variations in fluviometric levels (natural disturbances) are, for some authors (Welcomme, 1979; Oldani, 1990; Agostinho *et*

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al., 2004a), the main force influencing the population dynamics of several aquatic communities. The increase in river level homogenizes the limnologic conditions of environments (Thomaz *et al*., 2007), increases physical space for colonizers and the availability of resources and shelter (Agostinho *et al*., 2004b), and is responsible for maintaining species diversity (Agostinho & Zalewski, 1995). However, the interruption of the rivers to construct dams negatively influences these characteristics because it changes the physical and chemical conditions of the water and also influences the abundance and quality of specific habitat types (Agostinho *et al*., 2007).

As a consequence of dams, these and other changes create pronounced alterations in the fish fauna, mainly in the composition and structure of fish assemblages, causing a variable period of instability (Petrere Jr., 1996; Agostinho *et al*., 2004b). Several studies have evaluated the changes in the organization of adult fish assemblages (Ponton & Vauchel, 1998; Agostinho *et al*., 2004b), but studies that consider the changes in the structure of ichthyoplankton assemblages are scarce (Humphries & Lake, 2000; Sanches *et al*., 2006).

Information on the ecology of fish eggs and larvae is extremely important for understanding the biology of species, since the early stages represent a critical period in their life cycle (Fuiman, 2002). Some studies have shown that environmental variables are the main determinants of ichthyoplankton abundance, structure and composition variation (Keckeis *et al*., 2000; Reynalte-Tataje *et al*., 2012). However, the effect of dams on the ichthyoplankton community is rarely investigated (Humphries & Lake, 2000; Sanches *et al*., 2006).

Studies evaluating the temporal variation of fish larvae assemblages for several reproductive periods are nonexistent for the upper Uruguay River region and rare for the Prata River basin as a whole. Such studies would be extremely useful for understanding the relationship of the ichthyoplankton community to different environments and for evaluating dam impacts on that community. This study evaluates the temporal variability of larval assemblages in the upper Uruguay River mouth environments. Specifically, the objectives are: (i) to characterize the taxonomic composition and ichthyoplankton larval development; (ii) to assess and compare the temporal variability of assemblages and (iii) to determine the influence of environmental variables in the main taxa in a controlled river mouth environment and a free river mouth environment. Our hypotheses are: a) seasonal sequence in the occurrence of species or in the structure of larvae assemblages varies drastically among years and this pattern is associated with inter-annual variation in larval supply; b) sampling sites influenced by dams suffer different variation on larval assemblage structure than those sites situated in the stretches of the river free of dams.

Material and Methods

Study area

The upper Uruguay River region is situated in an enclosed valley, characterized by a steep incline and a flood regime determined largely by rain in the riverbed. The main river is characterized by areas of still water separated by rapids, waterfalls and gorges, while the tributaries, which are not very long, have many waterfalls, making the movement of rheophilic species from the main river and back more difficult (Zaniboni-Filho & Schulz, 2003). Despite the lack of floodplain areas (known as nurseries), previous regional studies have shown that during the rainy season, areas near the tributaries mouths are dammed by the Uruguay River and form backwaters, which are ideal places for the initial stages of fish development (Zaniboni-Filho & Schulz, 2003; Hermes-Silva *et al*., 2009).

Because it shows a steep incline, the upper Uruguay River region has been a focus of interest from entities involved in hydroelectric development, and six dams have been set up, two of which are situated at the Uruguay River itself: the Itá HPP (Hydroelectric Power Plant), which began operations in 2000, is situated approximately 230 km from the confluence of Canoas and Pelotas Rivers (Uruguay River beginning); and the Machadinho HPP, which was dammed in 2001, and is 135 km upstream from Itá. This study was conducted at the mouth of the two tributaries of the Uruguay River (Ligeiro and Chapecó) located between the states of Santa Catarina and Rio Grande do Sul in Brazil (Fig. 1). The selected sections were the following:

a. Ligeiro (27º31'S 51º50'W) located 5 km downstream from Machadinho HPP and approximately 130 km upstream from the Itá dam. This tributary flows into the Uruguay River in the only lotic stretch (approximately 6 km) between those two dams. This section encompasses the Uruguay-Ligeiro (ULIG) sampling site on the Uruguay River (main river) and the Ligeiro (LIG) sampling site on the Ligeiro River. The Itá and Machadinho HPPs directly influence the fish fauna of this section.

b. Chapecó (27º05'S 53º01'W), located downstream from Itá HPP, is approximately 110 km from the dam. The Chapecó River is a main tributary of the upper portion of the Uruguay River basin. In this section, the Uruguay-Chapecó (UCH) sampling site on the Uruguay River (main river) and the Chapecó (CH) sampling site on the Chapecó River were selected. Due to the distance from the Itá HPP and based on monitoring studies conducted in the region (Zaniboni-Filho *et al*., 2008), it is believed that the dams upstream do not impact the environment.

Sampling

The sampling procedures to obtain the eggs and larvae were conducted during three consecutive reproductive periods (RP): October 2001 to March 2002 (RP1), October 2002 to March 2003 (RP2) and October 2003 to March 2004 (RP3). Within each sampling site, the collections were conducted at 2 points for 2 days in 6-hour intervals (0300h, 0900h, 1500h and 2100h). The abundance of each site was represented by the sum of the abundance of the

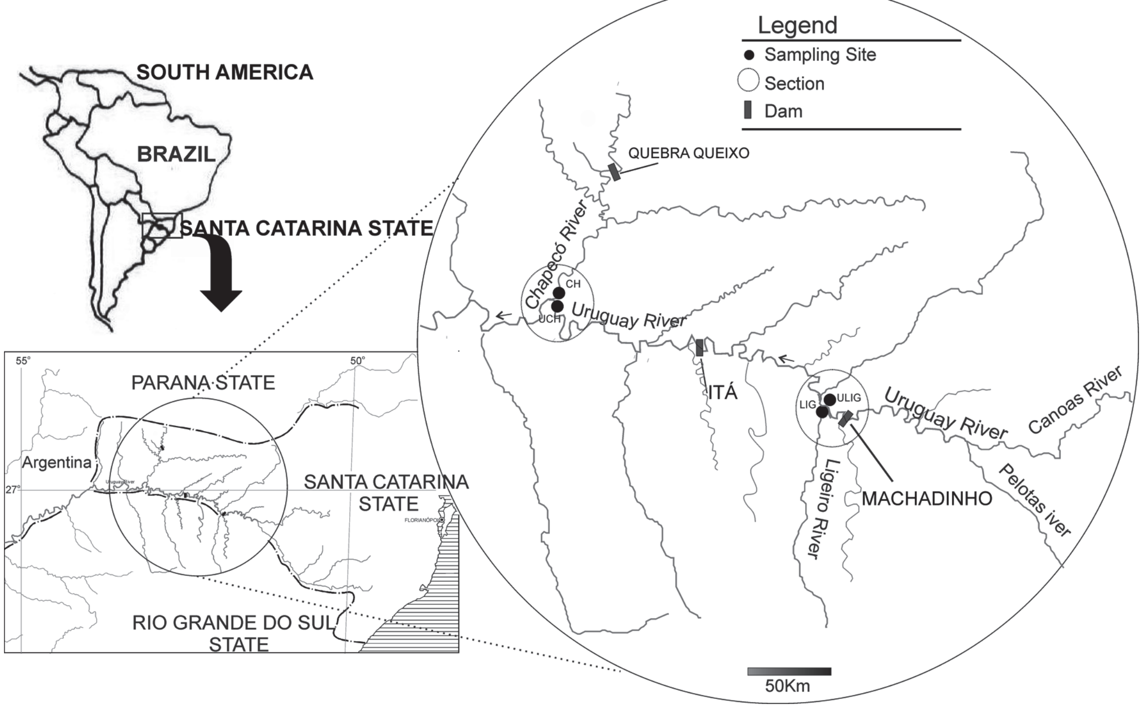

Fig. 1. Location of the sampling sites in the upper Uruguay River in southern Brazil. Samplings sites: LIG: Ligeiro, ULIG: Uruguay-Ligeiro, CH: Chapecó, UCH: Uruguay-Chapecó.

4 collections, which summed up 4 estimates of larvae abundance each month for each sampling site (2 points x 2 days). For this study, 0.5 mm mesh cylindroconical plankton nets with a mouth area of 0.109 m^2 were used, and a flow meter was attached to each net to record the volume of filtered water. The nets remained in the water, at the same time of day for 1 hour, at all the sampling sites and were tied to a cable stretched from one bank of the river to the other at each sampling site (Hermes-Silva *et al.*, 2009). In situations where the tributary river was dammed by the main river (stream speed <0.01 $m.s^{-1}$), surface trawls were done for 20 minutes by a boat at low speed. All the material collected was fixed in 4% formalin buffered with $CaCO_3$.

At each sampling site, water temperature (°C), dissolved oxygen ($mg.L^{-1}$), pH and water transparency (cm) were measured. Water precipitation and stream flow data were obtained through records supplied by ANEEL (National Electric Energy Agency) and by the Itá and Machadinho HPP control' house.

The samples content were checked in laboratory, and the larvae were separated from the rest of the plankton. Based on Tanaka (1973), the abundance of larvae was standardized for a 10 m^3 volume. The larvae were removed from the collected material and classified into the lowest possible taxonomic level, according to Nakatani *et al.* (2001) and Reynalte-Tataje & Zaniboni-Filho (2008).

Data analysis

The separated larvae were classified, in stages, according to their degree of development: larval yolk (LY), pre-flexion (PF), flexion (FL) and post-flexion (FP), according to Ahlstrom & Moser (1976) and modified by Nakatani *et al.* (2001). The stations with larvae in the final stages of development (FL and FP) were considered growing and feeding areas for larvae (nurseries) and drifting areas for those stations where the larvae were mainly in the initial stages (LY and PF).

To evaluate the space-time variation (factors: sampling sites, reproductive period and months) of the most abundant species in the assemblages (frequency of occurrence [F.O]. > 5.0%), a nested analysis of variance (nested ANOVA) was applied (Hicks, 1993). To reduce the variability of abundance data and achieve the assumptions of ANOVA the densities were log-transformed ($\log_{10} x + 1$). The variation fraction explained by the spatial and temporal scales (monthly and annual) for each species and compared to the model (R^2) was also calculated (Hicks 1993; Witting *et al.*, 1999). These calculations were done in the SYSTAT v10 software (Wilkinson, 1998).

To test the temporal persistence in the structure of fish larvae assemblages from different sampling sites, Spearman correlations among the abundance of different reproductive periods were used, and the abundances of species were ranked for each reproductive period (Sokal & Rohlf, 1981).

To evaluate the influence of environmental variables in the abundance of larvae, Pearson correlations were performed. Previously, to reduce the dimensionality of environmental variables, a Principal Components Analysis (PCA) was applied. All the variables, with the exception of pH, were transformed ($\log_{10}$ x) to linearize the intervariable correlations (Peters, 1986). Environmental variables that showed higher than 0.4 structural coefficients were considered biologically important (Hair *et al*., 1984). Only the axes, which showed auto-values higher than those randomly generated, were retained for interpretation (*Broken-Stick* criteria; Jackson, 1993).

Results

Taxonomic composition and larval development of the ichthyoplankton

During the study period, 264 samples were collected, among which 118,415 eggs and 6,321 larvae were found (5.3% of the ichthyoplankton collected). These larvae belonged to five orders, 20 families, 39 genera and 41 species. Out of the total number of larvae caught, the Characiformes contributed 45.5%, the Siluriformes 40.1% and the Gymnotiformes 6.3%. The Perciformes and Atheriniformes orders and the larvae that were not identified represented approximately 8% of the captured larvae. In general, the larval assemblages were composed mostly of small and medium-sized Characiformes and Siluriformes, and they show short migrations. Larvae of species that make long reproductive migrations, such as the *Prochilodus lineatus* and *Leporinus obtusidens*, were not very frequent (1.9% and 0.8% respectively), and they were restricted to the Chapecó section. Larvae of *P. lineatus* were observed between November and January in RP1 and RP2, whereas the *L. obtusidens* larvae were recorded only in RP1. Table 1 shows the most frequent taxa (F.O. > 5%) during the period of study.

Larval development analysis showed clear differences in the composition of initial stages during reproductive periods. RP1 and RP3 showed similar abundances for initial stages (LY and PF). However, RP1 showed a higher flexion and post-flexion larvae density. In RP2, the densities for all the stages were lower, and there was a steady reduction of larvae density in late stages, and no individual was observed in post-flexion during this studied period in any of the sampling sites (Fig. 2).

Space-time variation of main taxa

During the study, approximately 85% of the variation in the distribution of larvae during the reproductive period was temporal (53.0% monthly and 33.9% from the reproductive period), and the spatial influenced only 13.1%. *Parapimelodus valenciennis* was the species with higher spatial variation at 35.1%. *Oligosarcus jenynsii* and *Acestrorhynchus pantaneiro* showed the highest variation between the years, and *Leporinus amae* with 66.7%, had the highest monthly variation (Table 2).

Temporal variability of larvae assemblages

Differences in the temporal variability of the assemblage structures were observed among the sampling sites. The larvae assemblage from the LIG section showed that RP2 was

Table 1. Composition, average density (larvae.10 m^{-3}), frequency of occurrence (F.O. %) and the occurrence of fish larvae collected in different months and sampling sites in the upper Uruguay River from October 2001 to March 2004. * 1= RP1; 2= RP2 and 3= RP3. ** X= Indicates the presence in the sampling sites: LIG: Ligeiro, ULIG: Uruguay-Ligeiro, CH: Chapecó, UCH: Uruguay-Chapecó. [1] S= Sedentary, SM= Short migration. U= Unknown reproductive strategy.

Taxa	[1]Reproductive Strategy	Dens.	F.O.%	Month*						Sampling Sites**			
				Oct	Nov	Dec	Jan	Feb	Mar	LIG	ULIG	CH	UCH
Acestrorhynchus pantaneiro	U	8.8	6.18	3	1,3	1	3			x	x	x	x
Apareiodon affinis	SM	8.9	7.08		1,3	1	1,2,3	1		x		x	x
Astyanax jacuhiensis	S	65.5	8.39	1,2,3	1,2,3	1,2,3	1,3	2	3	x	x	x	x
Astyanax fasciatus	SM	29.2	25.29	1,3	1,2,3	1,2,3	1,3	2	3	x	x	x	x
Astyanax gr. *scabripinnis*	SM	14.8	20.58	3	1,2,3	1,2	1,2,3	1,3	2,3	x	x	x	x
Bryconamericus iheringii	SM	22.5	13.17	1,3	1,2,3	1,3	1,2,3	1,3	1,2,3	x	x	x	x
Bryconamericus stramineus	SM	30.8	16.29	3	1,3	1,3	1,2,3	1,3	2,3	x	x	x	x
Eigenmannia virescens	S	8.1	17.26		1,3	1,2,3	1,2,3	1,2,3	3	x	x	x	x
Gymnotus carapo	S	3.6	6.94		1,2	1	1,2,3	1,2		x	x	x	x
Hoplias spp.	S	3.7	8.95		1,3	1,2,3	1,2,3	1,2,3	1,3	x	x	x	x
Hypostomus spp.	S	15.1	7.56	1	1,2,3	1,3	1,2,3	1,2	2,1	x	x	x	x
Leporinus amae	SM	5.2	9.02		1,2,3	1,3	1,2,3	3		x	x	x	x
Oligosarcus jenynsii	U	1.1	7.63		1,3	3	1,2,3	1,3	3	x	x	x	x
Parapimelodus valenciennis	SM	52.7	13.93	1,3	1,3	1,2,3	1,2,3	1,3	1,3	x	x	x	x
Pimelodella sp.	SM	1.2	6.52		1,3	1	1,3	1	1	x	x	x	x
Pimelodus absconditus	SM	29.4	6.18		1,3	1,2	1			x		x	x
Pimelodus atrobrunneus	SM	27.7	8.53		1,2,3	1,2	3	1	3	x	x	x	x
Pimelodus maculatus	SM	4.4	32.77	3	1,2,3	1,2,3	2,3	1,2,3	3	x	x	x	x
Rhamdia quelen	SM	1.7	33.81	1,3	1,2,3	1,3	1,2,3	1,3	2,3	x	x	x	x
Schizodon nasutus	SM	10.1	16.43	3	1,2,3	1,3	1,2,3	3	3	x	x	x	x
Steindachnerina spp.	SM	12.1	6.94		1,2,3	1		3		x	x	x	x

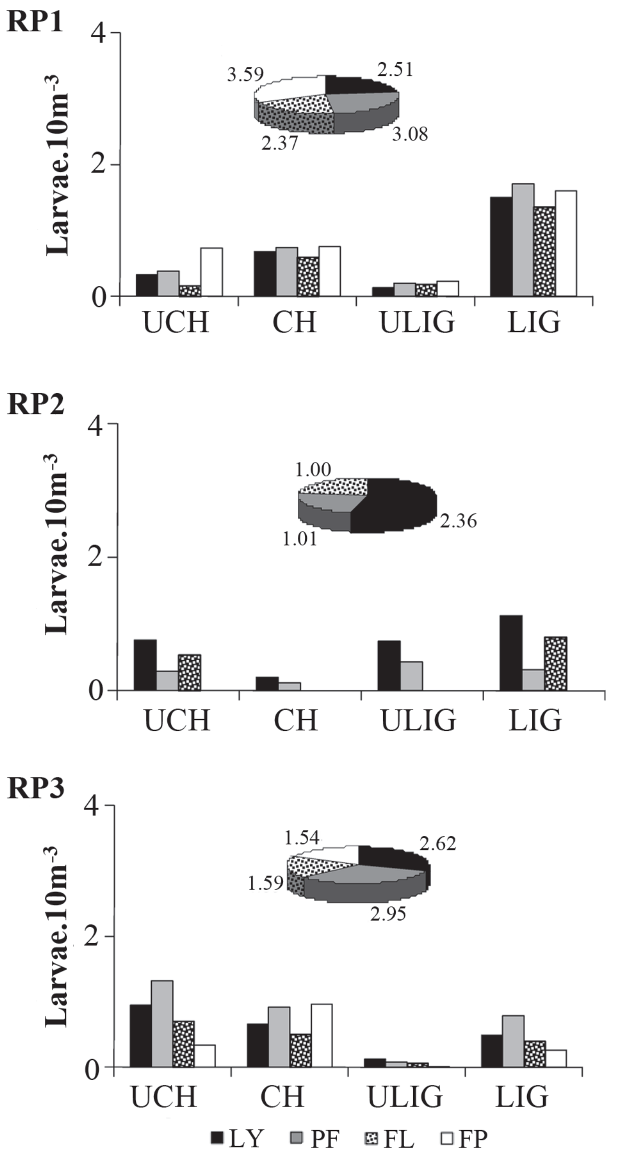

Fig. 2. Abundance of fish larvae in different stages of development recorded in the sampling sites of the upper Uruguay River from October 2001 to March 2004. Larval development stages: LY = Larval Yolk; PF = Pre-flexion; FL = Flexion and FP = Post-flexion. Sampling sites: LIG: Ligeiro, ULIG: Uruguay-Ligeiro, CH: Chapecó and UCH: Uruguay-Chapecó. Reproductive Periods: RP1: First Reproductive Period, RP2: Second Reproductive Period and RP3: Third Reproductive Period.

consistent with RP1 (r=0.40; p<0.05), whereas RP3 showed a different composition from that found in RP1 (r=0.24; p>0.05) and RP2 (r=0.00; p>0.05) (Table 3).

Larval assemblages showed similarities between RP1 and RP3 at ULIG (r=0.40; p<0.05) and CH sites (r=0.57; p<0.05). However, the RP2 assemblage was different in both sites (Table 3). The larval assemblage structure at the UCH site showed differences between RP2 and RP3.

In general, the larval assemblage structure at the Ligeiro (LIG=0.38; ULIG=0.30) section showed a higher temporal variability than the larval assemblage of the Chapecó section (CH=0.48; UCH=0.51) (Table 3).

Environmental variables and their influence on the main taxa

When combined, the two axes selected by the *broken-stick* criteria explained 59.5% of the data variability. The first axis (PC1) showed an auto-value of 2.31 and explained 39.4% of the variability. The environmental variable that contributed most negatively to its formation was the stream flow (r= -0.62; p<0.01), and the variables that contributed most positively were temperature (r= 0.57; p<0.01) and water transparency (r= 0.49; p<0.05). In the second axis (PC2, with an auto-value of 1.44), pH contributed negatively (r= -0.58; p<0.01) and dissolved oxygen contributed positively (r= 0.51; p<0.01), which explained 20.1% of the variability (Fig. 3).

The PCA showed differences among the three reproductive periods. RP2 showed higher stream flow values when compared to RP1 and RP3, which showed lower water flow values and higher water temperature and transparency, with the exception of the month of October at RP1, which showed inverse values. In general, this period showed higher water disturbances than the other two (Fig. 3).

The highest egg densities were recorded when low water flow values were predominant (r=-0.473; P<0.05), whereas the larvae density showed a positive correlation with temperature (r=0.563; P<0.05) and an inverse correlation with water flow (r=-0.331; P<0.05). The most abundant taxa density correlation with environmental variables is shown on Table 4.

Discussion

Larval assemblages were mainly composed of small and medium-sized Characiformes and Siluriformes. From the 41 species identified, 32 are opportunists, *i.e.*, species that show alternate spawning, long reproductive periods, small eggs, lack of parental care and small reproductive migrations (Suzuki *et al*., 2005). The larvae of large migratory Characiformes (*Leporinus obtusidens* and *Prochilodus lineatus*) were recorded only in the Chapecó section despite the fact that adult individual fish have been recorded in all the studied environments (Zaniboni-Filho *et al*., 2008). In the three studied years, the absence of those migratory species upstream from the Itá dam indicates that they present low reproductive activity in the stretch between the Machadinho and Itá HPPs or those species are unable to reproduce.

In the four sampling sites, larvae in all stages were recorded, but we observed differences among the three reproductive periods. The greater abundance of larvae in advanced stages (flexion and post-flexion) in RP1 and RP3 seems to indicate the prevalence of environmental conditions, such as the presence of backwater areas and areas of food availability. The low abundance of larvae in flexion and the

Table 2. ANOVA *nested* results in the most abundant taxa density variation in studied environments in the three reproductive periods, between October 2001 and March 2004. Numbers in bold represent p<0.05.

Taxa	R^2	Site		RP (Site)		Month (Site*RP)	
		%	F	%	F	%	F
Acestrorhynchus pantaneiro	**0.45**	7.2	0.99	56.7	**2.80**	36.1	**2.00**
Apareiodon affinis	0.25	6.9	0.79	34.8	0.99	58.3	1.01
Astyanax jacuhiensis	0.26	23.2	**2.72**	16.1	0.46	60.8	1.08
Astyanax fasciatus	**0.44**	17.8	**5.23**	31.7	**2.35**	50.5	**2.27**
Astyanax gr. *scabripinnis*	**0.40**	10.6	2.36	28.9	1.61	60.4	**2.08**
Bryconamericus iheringii	**0.31**	17.0	**3.02**	36.4	1.62	46.7	1.27
Bryconamericus stramineus	**0.32**	18.8	**3.53**	33.9	1.59	47.3	1.31
Eigenmannia virescens	**0.43**	8.8	**3.00**	50.9	**4.28**	40.3	**2.06**
Gymnotus carapo	0.28	15.6	1.98	30.8	0.97	53.6	1.21
Hoplias spp.	0.29	5.8	0.78	31.5	1.05	62.7	1.28
Hypostomus spp.	0.25	5.8	0.63	31.5	0.69	62.7	1.05
Leporinus amae	0.27	2.5	0.29	30.8	0.91	66.7	1.21
Oligosarcus jenynsii	**0.37**	9.0	**2.49**	57.0	**3.19**	34.0	**1.68**
Parapimelodus valenciennis	**0.54**	35.1	**3.36**	35.0	**3.42**	29.9	**3.16**
Pimelodella sp.	0.25	7.0	0.80	44.5	1.23	48.5	0.97
Pimelodus absconditus	0.26	25.1	**2.74**	23.2	0.63	51.7	1.03
Pimelodus atrobrunneus	**0.43**	7.7	1.95	31.9	**2.01**	60.4	**2.33**
Pimelodus maculatus	**0.55**	11.7	**4.77**	26.8	**2.75**	61.5	**3.84**
Rhamdia quelen	**0.52**	10.5	**3.80**	28.7	**2.60**	60.8	**3.36**
Schizodon nasutus	**0.44**	13.1	**3.42**	26.2	1.70	60.6	**2.41**
Steindachnerina spp.	**0.39**	16.7	**3.03**	24.3	1.10	59.0	**1.96**

absence of post-flexion in the RP2 in all the study area could be a result of the hydrodynamics presented during that period (a high water flow and speed and low transparency and water temperature) not allowing the establishment of larvae and/or their food (other planktonic and benthic preys).

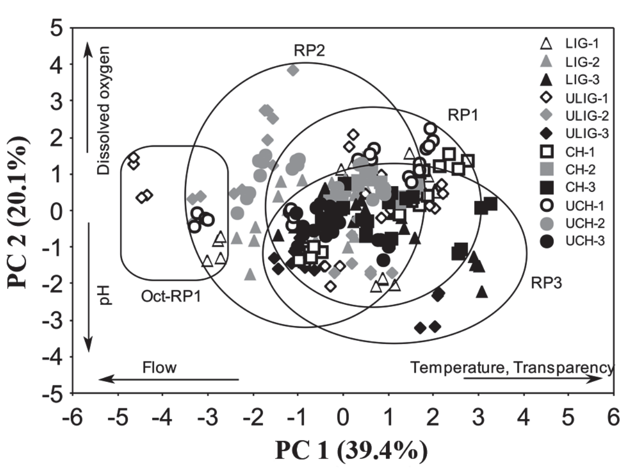

Fig. 3. Principal Components Analysis of the environmental variables' matrixes recorded in the upper Uruguay River between October 2001 and March 2004. Sampling sites: LIG: Ligeiro, ULIG: Uruguay-Ligeiro, CH: Chapecó and UCH: Uruguay-Chapecó. Reproductive Periods: RP1: First Reproductive Period, RP2: Second Reproductive Period and RP3: Third Reproductive Period.

During the studied period, we observed a greater variation in the temporal scale than in the spatial scale among the main taxa presented in the ichthyoplanktonic assemblage, suggesting a high degree of temporal, mainly seasonal, unpredictability. The highest temporal variation could be explained by four factors: first, the fact that the largest part of these species showed pronounced peaks in a few months and, subsequently, showed a decrease or absence in the following months, which would explain the high monthly variation; second, the influence of several environmental variations among the three reproductive periods; third, the fact that the most abundant species were present in most of the studied sites, reducing the spatial variation; and, fourth, mainly in the case of the Ligeiro section, the influence of the dams on the establishment of the community after the filling of these reservoirs.

The correlation analysis among the reproductive periods indicated that the assemblage composition changed substantially over time in the LIG, ULIG and CH sites. For these environments, the correlation values usually remained below 0.5, indicating a low similarity in the total composition and abundance of larvae among years. When comparing the three reproductive periods (with exception of the LIG site), we noticed that there is a major similarity in the structure of larval assemblage between RP1 and RP3. These periods showed higher temperature and water transparency than RP2, which, in turn, showed a higher average water flow when compared to the others, indirectly reducing water temperature and transparency values.

Table 3. Abundance ranking for each reproductive period, by sampling site and average ± standard error (SE) of larvae density from the 21 most frequent species. Correlation matrix between reproductive periods among most abundant species. Numbers in bold represent $p<0.05$.

Taxa	LIG			ULIG			CH			UCH		
	RP1	RP2	RP3	RP1	RP2	RP3	RP1	RP2	RP3	RP1	RP2	RP3
Acestrorhynchus pantaneiro	21	21	6	21	21	16	17	21	21	16	21	14
Apareiodon affinis	16	21	2	21	21	21	12	21	21	12	9	15
Astyanax jacuhiensis	13	21	21	4	10	21	9	21	21	5	3	13
Astyanax fasciatus	6	3	11	6	3	1	1	1	2	1	2	1
Astyanax gr. *scabripinnis*	2	1	21	3	21	5	13	21	4	8	4	3
Bryconamericus iheringii	5	21	12	5	1	6	7	21	5	6	8	4
Bryconamericus stramineus	15	21	21	21	21	21	21	21	21	21	21	21
Eigenmannia virescens	7	21	7	2	7	13	3	3	21	13	10	5
Gymnotus carapo	18	21	10	8	9	21	18	21	21	19	13	21
Hoplias spp.	14	7	8	14	6	15	6	5	8	3	15	7
Hypostomus spp.	8	21	9	10	4	9	15	4	21	18	14	12
Leporinus amae	10	5	21	21	2	8	11	21	7	10	21	9
Oligosarcus jenynsii	17	21	21	7	21	2	14	6	6	20	11	10
Parapimelodus valenciennis	3	6	21	9	21	3	8	21	21	15	5	18
Pimelodella sp.	9	21	21	12	21	12	16	21	21	17	21	17
Pimelodus absconditus	19	21	21	21	21	21	21	21	21	14	7	19
Pimelodus atrobrunneus	12	21	1	21	21	7	10	21	10	4	6	11
Pimelodus maculatus	11	21	4	21	5	14	2	2	1	2	1	2
Rhamdia quelen	1	4	5	1	7	4	5	21	9	9	21	6
Schizodon nasutus	4	2	3	13	21	11	4	21	3	11	16	8
Steindachnerina spp.	21	21	21	11	21	10	21	21	21	7	12	16
		LIG			ULIG			CH			UCH	
RP1*RP2		**0.65**			0.30			**0.47**			**0.52**	
RP1*RP3		0.11			**0.45**			**0.62**			**0.67**	
RP2*RP3		0.00			0.16			0.34			0.33	
Correlation average (site)		0.38			0.30			0.48			0.51	

The reduction in larval abundance, the lower number of taxa, the absence of individuals in post-flexion stage and the high dissimilarity in larval assemblage structure found in RP2, seem to indicate that the environmental conditions in that period acted negatively on the reproductive activity of most fish species of the region. Similar results were also found for other sampling sites in the upper Uruguay River region for the same period (Reynalte-Tataje *et al*., 2008).

Most of the prior studies conducted in the Plata River basin consider that the majority of the reproductive activity happens at the peak of the hydrometric level (Bayley, 1973; Agostinho *et al*., 2004b). However, some studies in the Plata, lower Uruguay and lower Paraná rivers show that variations in hydrometric level are not particularly important and that temperature is the main stimulus for reproduction (Oldani, 1990). Based on our current findings (a higher reproductive success in RP1 and RP3), there are evidences showing the influence of flow and water temperature on the reproductive activity of fish in the upper Uruguay River region, suggesting a hypothesis that water temperature, more than flow, could act as a critical factor influencing the reproduction of the majority fish species at this latitude.

Water temperature may also influence reproduction and, consequently, monthly distribution of ichthyoplankton organisms. During the study, larvae were found between October and March for all the reproductive periods. Nevertheless, some differences were observed. In October of RP2, the presence of only one taxon (*A. jacuhiensis*) was recorded, which contrasted with RP1 and RP3, where 11 taxa were recorded. It is believed that the low temperatures in October of RP2 may have delayed the reproductive activity of species and that the low temperature values in the spring may have negatively influenced reproduction during this reproductive period.

In contrast to RP2, RP1 showed the highest values of abundance and number of taxa and a higher presence of larvae in the final stages of development. In this period, the presence of larvae from migratory species *L. obtusidens* and *P. lineatus* was also recorded in the Chapecó section. This period was characterized by substantial disturbances in hydrological behavior, occurring floods during October and a very pronounced drought in the following months. This variation in hydrodynamics seems to have favored the reproductive success of the fish assemblage.

The importance of hydrological disturbance in lotic environments has been broadly recognized because it produces a larger number of indicators and induces the reproduction of species with different reproductive strategies (Nesler *et al*., 1988; Poff & Allan, 1995).

Hence, some species, such as *Parapimelodus valenciennis* and *Astyanax fasciatus*, are favored by the increase in water flow, whereas others, such as *Bryconamericus stramineus* and *Rhamdia quelen*, are more abundant in dry periods. In this sense, global hydrological

Table 4. Pearson correlation among the environmental variables and eggs, larvae and the most abundant taxa (density $\log_{10}$ x +1) in the upper Uruguay River from October 2001 to March 2004. Numbers in bold represent $p < 0.05$.

Taxa	Flow ($m^3.s^{-1}$)	Temperature (°C)	Transparency (cm)	Dissolved Oxygen ($mg.L^{-1}$)	pH
Eggs	**-0.473**	0.042	0.043	-0.064	-0.102
Larvae	**-0.331**	**0.563**	0.181	-0.112	0.023
Acestrorhynchus pantaneiro	0.070	0.016	0.055	-0.042	-0.160
Apareiodon affinis	-0.072	0.038	-0.035	0.091	0.082
Astyanax jacuhiensis	**0.230**	-0.054	0.043	0.090	-0.111
Astyanax fasciatus	**0.244**	**0.338**	0.048	-0.000	0.064
Astyanax gr. *scabripinnis*	0.055	-0.001	0.106	-0.041	-0.000
Bryconamericus iheringii	0.100	**0.243**	**0.243**	-0.064	-0.141
Bryconamericus stramineus	**-0.218**	**0.354**	-0.003	-0.092	0.011
Eigenmannia virescens	0.015	**0.353**	0.067	-0.123	0.083
Gymnotus carapo	-0.065	**0.311**	**0.200**	0.000	0.191
Hoplias spp.	0.043	**0.439**	0.072	-0.141	-0.000
Hypostomus spp.	0.007	0.049	0.079	-0.104	-0.094
Leporinus amae	0.018	-0.001	-0.054	-0.051	-0.050
Oligosarcus jenynsii	0.009	**0.385**	**0.284**	-0.162	-0.094
Parapimelodus valenciennis	**0.245**	-0.050	0.039	-0.091	**-0.332**
Pimelodella sp.	0.024	0.007	0.098	0.070	0.102
Pimelodus absconditus	0.072	-0.031	-0.093	0.123	0.142
Pimelodus atrobrunneus	-0.024	-0.003	-0.018	0.081	-0.064
Pimelodus maculatus	0.072	**-0.201**	-0.058	0.052	-0.143
Rhamdia quelen	**-0.195**	-0.075	**0.336**	-0.122	-0.080
Schizodon nasutus	**-0.199**	0.061	-0.026	-0.081	-0.192
Steindachnerina spp.	**0.265**	-0.086	-0.041	-0.030	-0.064

disturbances, such as *El Niño* and *La Niña*, and regional ones, such as the South Atlantic Convergence Zone (SACZ) and the Convective Systems (CS), provide alternating flood and drought periods (Kousky & Cavalcanti, 1984; Mendonça & Boratti, 2008), which could help to increase the richness and the abundance of larvae in the region.

Although the differences in environmental variables influence the abundance and composition of the ichthyoplankton among the reproductive periods, it was also observed some differences in larval assemblage composition among sections. When compared to Chapecó, the higher variability of the Ligeiro section suggests that, besides the influence of environmental variables, there is, for that section, a large contribution from the set-up and operational procedures of the Itá and Machadinho dams. Hence, four years after closing the dam, changes in the fish assemblage still occur inside the Itá reservoir. These results are similar to those found for adult fish captured in the same period in the dam's catchment area (Zaniboni-Filho *et al*., 2008). Similar to adult fish, the impact of dams in the ichthyoplanktonic community includes a reduction in larval abundance (Scheidegger & Bain, 1995), the suppression of growth rates (Weisberg & Burton, 1993), changes in the community structure (Bain *et al*., 1988) and a reduction in species diversity (Gehrke *et al*., 1995), clearly reflecting the impact of the dam in reproduction and recruitment (Agostinho *et al*., 2004a).

Although confined between the Itá and Machadinho dams, the sampling sites of the Ligeiro section show great significance as a reproduction area for most of the fish communities occurring in the Itá reservoir. According to Agostinho *et al*. (2007), most of the species that colonize the dams, including those that present plasticity to reproduction, seek for lateral tributaries, stretches upstream or even more lotic areas for reproduction.

This study showed that the mouths of tributaries are important reproduction and growth environments for fish in the upper Uruguay River region. Larval assemblages in these regions are composed mainly by species that perform short migrations. When comparing the three reproductive periods, a low abundance of larvae and number of taxa, an absence of individuals in post-flexion stages and a high dissimilarity in the larval assemblage structure was observed in the reproductive period with higher flow and lower water temperature. Spatially, there is a lower temporal variability in the larval assemblage structure in the free environment of the reservoir than in the impacted one.

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