Environ Biol Fish (2012) 94:403–419
DOI 10.1007/s10641-011-9955-3

Spatial and temporal variation of the ichthyoplankton in a subtropical river in Brazil

David Augusto Reynalte-Tataje · Angelo Antônio Agostinho · Andrea Bialetzki · Samara Hermes-Silva · Rodrigo Fernandes · Evoy Zaniboni-Filho

Received: 16 February 2011 / Accepted: 27 October 2011 / Published online: 25 November 2011

Abstract Studies that assess reproduction dynamics and ichthyoplankton distributions are scarce for the upper Uruguay River, especially in environments such as tributary mouths. Therefore, this study aimed to evaluate: (i) ichthyoplankton composition; (ii) spatial and temporal variation in ichthyoplankton abundance; and (iii) relationships between environmental variables and the abundance of ichthyoplankton during one annual cycle in this region. Monthly samples were collected from September 2001 to August 2002 in 48 h cycles at 6 h intervals between each sampling. Samples of eggs and larvae were collected from three of the main tributaries of the region (Ligeiro, Palomas and Chapecó rivers) and from three stretches of the Uruguay River near the confluence of these tributaries. Surface samples were collected with a 0.5 mm mesh cylindro-conical net. In general, reproductive seasonality was well-defined between October and February. It was most intense from November to January, when the photoperiod reached its highest values, flow was decreased, and the water temperature was increased. Based on egg and larval distributions, we found that spawning occurred mainly in the Ligeiro and Chapecó tributaries and in the Uruguay/Chapecó section. In contrast, fish spawning in the sites downstream of dams was more restricted. Finally, a difference was observed between the egg and larval distributions of the main river and its tributaries: the greatest reproductive activity in the tributaries occurred during periods of high flow and increased water temperature, while in the main river, more eggs and larvae were observed when the flow decreased and the water temperature increased.

Keywords Eggs and larvae · Spawning season · Uruguay river · Temperature · Freshwater fish

Electronic supplementary material The online version of this article (doi:10.1007/s10641-011-9955-3) contains supplementary material, which is available to authorized users.

D. A. Reynalte-Tataje (✉) · S. Hermes-Silva · E. Zaniboni-Filho
Laboratório de Biologia e Cultivo de Peixes de Água Doce (LAPAD), Universidade Federal de Santa Catarina, Rodovia SC 406, 3532, Armação, Florianópolis, Santa Catarina, Brazil CEP 88066-000
e-mail: reynalted@hotmail.com

A. A. Agostinho · A. Bialetzki
Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupelia), Universidade Estadual de Maringa, Av. Colombo 5760, Bloco G-90, CEP 87020-900 Maringa, PR, Brazil

A. Bialetzki
e-mail: bialetzki@nupelia.uem.br

R. Fernandes
Laboratório de Ecologia Quantitativa, Universidade Federal Rural do Semi-Arido, Av. Francisco Mota 572, CEP 59625-900 Mossoro, RN, Brazil

R. Fernandes
e-mail: rfernandes@ufersa.edu.br

Introduction

Most freshwater fish species exhibit seasonal reproductive cycles related to favorable environmental conditions that maximize egg fertilization and offspring development (Baumgartner et al. 2008; Suzuki et al. 2009). However, reproductive behavior varies between different environments, and is totally dependent on local and regional environmental factors (Humphries et al. 1999), such as geographic latitude (Barletta et al. 2010).

Studies on freshwater ecosystems of temperate regions have demonstrated that the seasonality of reproductive cycles of fish species is closely related to variations in photoperiod, water temperature and increasing food availability (Vlaming 1972; Lowe-McConnell 1987; Munro 1990). In tropical regions, fish exhibit longer reproductive periods compared to temperate regions. However, even tropical species may exhibit seasonal changes in their reproductive activity. At these latitudes, increases in water level, precipitation and electrical conductivity are considered determinants of the reproductive periodicity of fishes (Baumgartner et al. 2008; Fernandes et al. 2009; Suzuki et al. 2009). In contrast, in subtropical environments, especially in the southern hemisphere, knowledge of the variables determining reproductive periodicity and the way they affect reproductive processes is still incipient (Humphries et al. 1999; Barletta et al. 2010).

Brazil is characterized by many hydrographic basins, all of which are located in tropical and subtropical latitudes. Despite the existence of many basins, most studies of fish reproduction have been conducted in the tropical regions of the two major basins of the country: the Amazon and Paraná basins (Barletta et al. 2010).

In tropical rivers, fish reproduction is seasonal and, for most fish species, spawning occurs during flood events (Welcomme 1979; Vazzoler 1996), when the precipitation regime and the increasing water volume act as synchronizing agents, and the flood indicates the end of the reproductive period (Vazzoler et al. 1997; Agostinho et al. 2004). Studies in the upper Parana River show that the highest larval densities are observed between September and February (Nakatani et al. 1997); in the Amazon river, they are observed between January and April (Araujo-Lima 1994); and in the Paraná river, they are highest between November and February (Nascimento and Nakatani 2005; Tondato et al. 2010); which are all periods that coincide with increases in precipitation and, consequently, an increase in water volume (Suzuki et al. 2009). In Brazilian subtropical rivers, however, studies on fish reproduction are scarce, and little information is available related to reproductive periods and about which abiotic variables influence the reproduction of the existing fish communities at these latitudes (Hermes-Silva et al. 2009).

The Uruguay River, together with the Paraná and Paraguay rivers, forms the La Plata basin, which has an area of approximately 3.1 million square km and is considered the second largest of the world (OEA 1969). This river is divided into three portions (the upper, middle and lower Uruguay), and most of its basin is located in subtropical latitudes, with the exception of the lower Uruguay River, which is located in temperate latitudes.

Currently, due to the lack of knowledge on fish reproduction in the upper Uruguay River (Hermes-Silva et al. 2009), studies in this region use as reference studies from the Paraná River, which is a basin located in the tropical region that presents many floodplains (Daga et al. 2009; Reynalte-Tataje et al. 2011) and is much different from the upper Uruguay River, which runs through a steep valley with no floodplain (Reynalte-Tataje et al. 2008).

In this region, due to the absence of floodplains, it is believed that fish reproduction occurs in the lower stretches of tributaries, and larval rearing occurs at river mouths. These areas of confluence are normally dammed by the main river, creating special conditions that would allow planktonic development, providing favorable environments for fish larval and juvenile rearing (Zaniboni-Filho and Schulz 2003). Studies carried out with ichthyoplankton seem to indicate the importance of these environments for fish reproduction (Reynalte-Tataje et al. 2008; Hermes-Silva et al. 2009). However, there are still some doubts about the relevance of the main river and the tributaries in this region and the influence of abiotic factors on fish reproduction activity (Reynalte-Tataje et al. 2008). Knowledge on the influence of the dams recently installed at this basin (Itá Dam in 1999 and Machadinho Dam in 2001) on fish reproduction and how they may influence the spatiotemporal distribution of ichthyoplankton at this region is equally scarce.

In accordance with observations made in other rivers of the La Plata basin (Sanches et al. 2006; Fernandes et al. 2009; Hermes-Silva et al. 2009; Agostinho et al. 2008), we hypothesize that there is a variation in the spatiotemporal distribution of ichthyoplankton in the Uruguay River and that this variation is related to environmental and anthropogenic factors, such as the presence of dams. Thus, to address this hypothesis, the objectives of this study were the following: (i) to determine the influence of environmental variables and reservoirs on the distribution of eggs and larval abundance during an annual cycle; (ii) to determine the spatiotemporal variation of fish eggs and larval abundance during an annual cycle; (iii) to verify the relevance of the main river and tributaries to the distribution of ichthyoplankton organisms. In general, the objective of this study is to complement and to further elaborate on the first comments on the spatial and temporal distribution of ichthyoplankton carried through the region (Hermes-Silva et al. 2009), as well as to provide a tool for the definition of the "defeso" period (prohibition of the fishing period) in the upper Uruguay River.

Materials and methods

Study area

The upper Uruguay River is located in an extremely steep subtropical valley in southern Brazil. Its hydrographic basin rests upon the sedimentary and volcanic rocks. The geotechtonic characteristics are associated with the two predominant lithological blocks of sedimentary rocks and basalt. The rainy period in this region is less conspicuous than for most Brazilian drainage basins and may yield rapid flood pulses at different times of the year. Despite this fact, the end of winter and the beginning of spring have historically had the highest rates of precipitation, while the summer months and the beginning of autumn are the driest period (Sartori 2003). In the last decade, the landscape and the hydrodynamics of this basin have been modified by the construction of many hydroelectric power plants (HEP).

This study was carried out in an area under the influence of the Itá and Machadinho HEPs (states of Santa Catarina and Rio Grande do Sul), covering an area of approximately 290 km of the upper Uruguay River (Fig. 1).

Samples of eggs and larvae were collected from three of the main tributaries of the region and from three stretches of the Uruguay River near the confluence with these tributaries, referred to here as sampling sections: (a) Ligeiro (27°31′S; 51°50′W): located 5 km downstream from the Machadinho HEP and approximately 130 km upstream of the Itá Dam. The Ligeiro River (tributary) flows into the only lotic stretch of the Uruguay River (approximately 6 km) between the Machadinho and Itá HEPs. This sampling section comprises site ULIG (8 to 11 m depth), which is located in the Uruguay River (the main river) upstream of the confluence with the Ligeiro River, and site LIG, which is located in the Ligeiro River. The soil of the LIG site normally has a block of sedimentary rocks and basalt, in general, has a 1 to 3 m depth. (b) Palomas (27°17′S; 52°19′W): located less than 1 km downstream from the Itá dam. This sampling section is directly influenced by the water discharged and/or pumped by the power plant. The Palomas River is the first tributary downstream of the Itá dam. Two sites were selected in this section: site UPAL (12 to 15 m depth) located in the Uruguay River upstream of the confluence with the Palomas River and site PAL located in the Palomas River. The soil of the PAL site normally has a block of sedimentary rocks and basalt, in general, has a 1 to 3 m depth. (c) Chapecó (27°05′S; 53°01′W): located approximately 110 km downstream from the Itá HEP and far from the influence of the dams. The Chapecó River is considered one of the main tributaries of the upper Uruguay River. Two sites were selected in this section: site UCH (9 to 11 m depth) located in the Uruguay River upstream of the confluence with the Chapecó River and site CH located in the Chapecó River. The soil of the CH site normally has a high clay content and, in general, has a depth of 2 to 4 m.

Sampling

Egg and larval samplings were carried out monthly between September 2001 and August 2002 during a typical hydrologic year of the region, with no influence of the El Niño and La Niña phenomena. For each section, two samplings were conducted simultaneously at both sites in 48 h cycles at 6 h intervals (four samplings per day). The ichthyoplankton

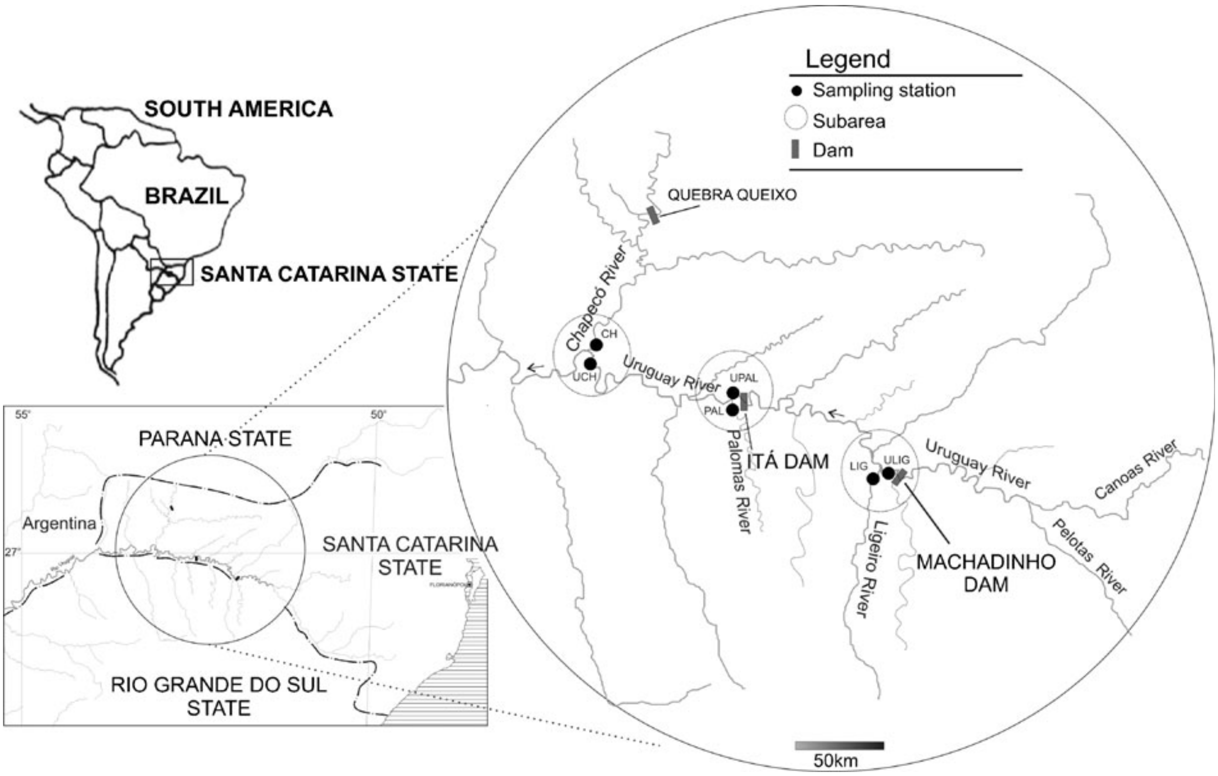


Fig. 1 Location of the sampling stations

abundance of each sample was represented by the sum of the four samplings of the day, which thus totaled four replicates per month for each sampling site (two samples x two days). Conical-cylindrical plankton nets with 0.5-mm mesh and a mouth area of 0.11 m^2 (the net designs have a length-to-mouth ratio of 5:1) were used for these samplings, and a mechanical flow meter (General Oceanic) was attached to the mouth of each net to measure the volume of water filtered (Nakatani et al. 2001; Bialetzki et al. 2005). The equipment was placed in the subsurface (approximately 20 cm below of the surface) for 1 h at both sampling sites in each section tied to a cable stretched between the margins of the river (Hermes-Silva et al. 2009). In addition, in situations in which a tributary was dammed by the main river (stream speed <0.01 m/s), surface trawls were carried out for 20 min with the boat operating at low speed. Samples were fixed in a buffered 4% formalin solution.

In the laboratory, samples were sorted, and fish eggs and larvae were separated from the rest of the plankton and then quantified. The total abundance of fish eggs and larvae was standardized to a volume of 10 m^3 (Tanaka 1973). Due to difficulties in egg identification, only the larvae were classified to the lowest taxonomic level possible, based on Nakatani et al. (2001).

The following measurements were taken at the surface at each sampling site: water temperature (°C) and dissolved oxygen (mg/l) were measured using a YSI 55 Multiparameter probe; pH and electrical conductivity (μS/cm) were measured using a YSI 63 Multiparameter probe; water transparency (cm) was determined using a Secchi disc. Precipitation and tributary flow data were provided by *ANEEL* (*Agência Nacional de Energia Elétrica*); data on the flow rate of the Uruguay River was provided by Tractebel Energia.

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 and Moser (1976) and modified by Nakatani et al. (2001). The sites with larvae in the final stages of development (FL and FP) were considered areas for the growth and feeding of larvae (nurseries) and drifting areas were considered the sites where the larvae were mainly in the initial stages (LY and PF).

A nested ANOVA (Analysis of Variance) was applied to evaluate the spatial and temporal variation (factors: sampling sites and months, respectively) in the total abundance of eggs and larvae (dependent variables). When the ANOVA results were significant, Tukey's post hoc test was applied to detect these differences. Variations in the spatial and temporal scales were also calculated using a total comparison explained by the R^2 model and also by the coefficient of variation (CV) for each scale. The same procedure was adopted for the ten most abundant larval species (frequency of occurrence – FO>10.0%). This analysis was only carried out with samples obtained between October 2001 and February 2002, which comprised approximately 95% of the ichthyoplankton captured during the year.

Principal Components Analysis (PCA) was used to reduce the dimensions of the environmental variables. All of the variables (except for pH) were log-transformed ($\log_{10}$ x +1) to linearize inter-variable relationships (Peters 1986). Only the axes with eigenvalues higher than those generated randomly were interpreted (broken-stick criterion; Jackson 1993). The environmental variables with a structure coefficient >0.40 (Hair et al. 1984) were correlated with egg and larval density (transformed into $\log_{10}$ x +1) using Pearson's correlation. A nested ANOVA was used for the variables that were significantly correlated to the ichthyoplankton organisms.

Based on the results of the Pearson's correlation, the variables that were correlated with the abundance of the ichthyoplankton organisms (a co-factor) were linked to the total abundance of eggs and larvae by considering the difference between localities (a factor) through an analysis of covariance (ANCOVA).

Results

Spatial and temporal distribution of ichthyoplankton

During the study period, 2463 samples were collected, among which 52 485 eggs (94.6% of the ichthyoplankton collected) and 2989 larvae were found. The nested ANOVA showed differences in egg distributions among the sampling sites (F=95.05; df=5; P< 0.05), as well as temporal variations (F=54.44; df= 11; P<0.05). The highest abundance values were observed at the LIG site during the month of November (1.69 eggs/10 m^3; Tukey's P<0.05), followed by the UCH site in January (1.04 eggs/ 10 m^3; Tukey's P<0.05). A general analysis showed that fish eggs were collected mainly between October and January.

Spatial (F=149.68; df=5; P<0.05) and temporal differences (F=11.79; d=11; P<0.05) were also found for larval distributions. The greatest abundances were observed at the CH site in November and December (0.75 larvae/10 m^3 and 0.50 larvae/10 m^3, respectively), followed by the UCH and LIG sites in November (0.54 larvae/10 m^3 and 0.42 larvae/10 m^3, respectively; Tukey's P<0.05). In general, the highest abundance of larvae was detected in November and the lowest was observed during the winter months (Fig. 2a and b).

Taxonomic composition of larval assemblages

Of the 2989 larvae captured, the larvae in the initial stages of development (LY and PF) corresponded to the highest proportion of capture in all the environments (84%). The sites located in the Uruguay River showed 88% of larvae in the initial stages, emphasizing the highest capture of these stages at the sampling sites. No clear temporal trend was observed in the distribution of the larval stages (Fig. 3).

The larvae captured belonged to five orders, 20 families, 39 genera, and 41 species (Table 1): 43.4% Characiformes, 39.2% Siluriformes, and 12.9% Gymnotiformes. Individuals belonging to orders Perciformes and Atheriniformes and the unidentified larvae represented 4.5% of the total larvae captured.

The sampling sections presented different larval assemblage compositions related to the predominant orders. In the Chapecó section, the Characiformes comprised 57.1% of the total larvae captured and the Siluriformes comprised 21.7%. In the Ligeiro section, however, Characiformes represented 44.1%, while Siluriformes totaled 50.7%. Larvae from the order Siluriformes were also predominant in the Palomas section (86.1%).

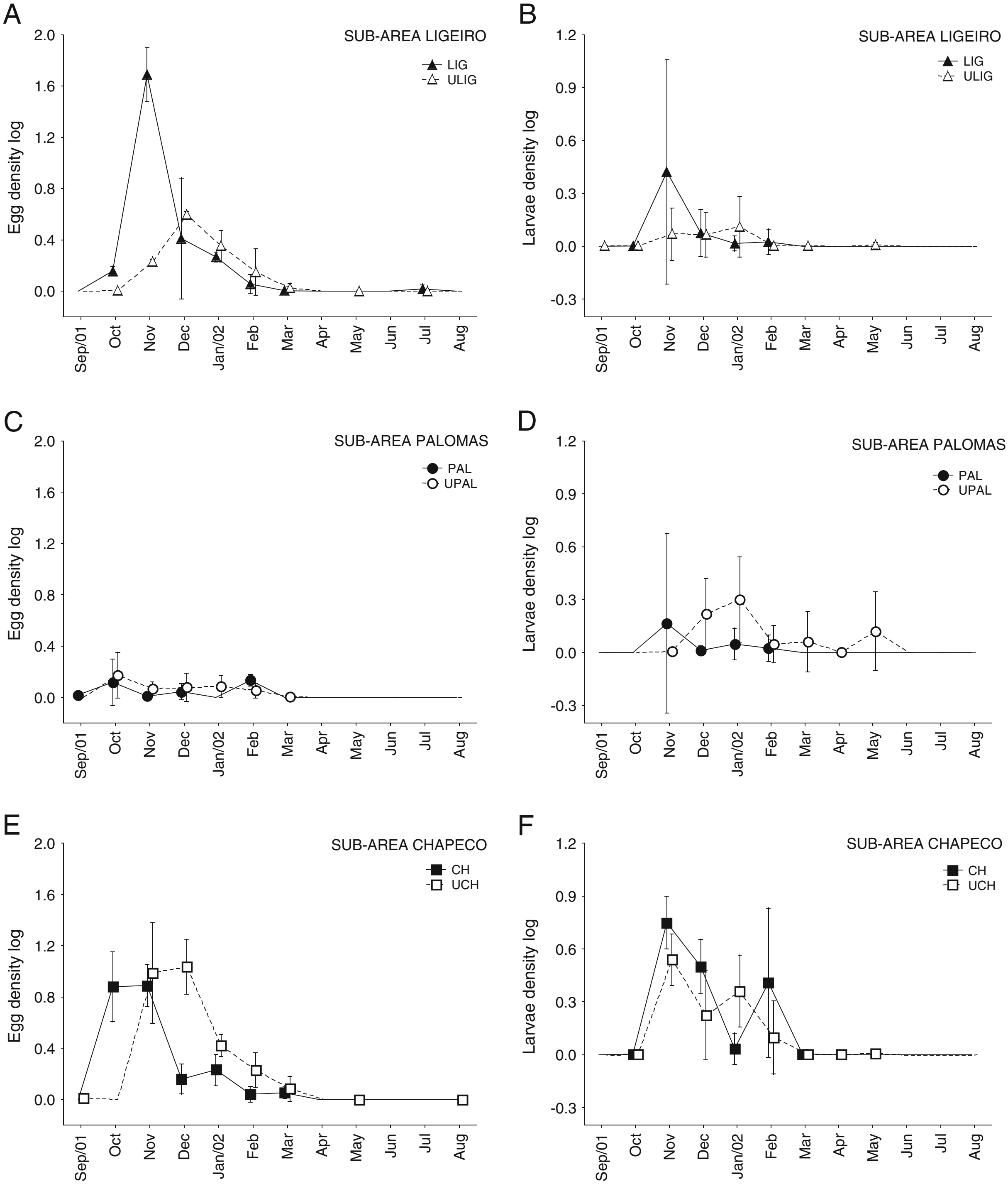


Fig. 2 Mean values and standard error of fish egg (**a**, **c** and **e**) and larvae (**b**, **d** and **f**) densities in the different sites sampled in the upper Uruguay River between September 2001 and August 2002

Nested ANOVA showed that the nature of the variation of egg and larval abundances during the reproductive period was temporal rather than spatial, which was true for most of the abundant species in the study (Table 2). In general, the dominant species had high densities in only a few months of the

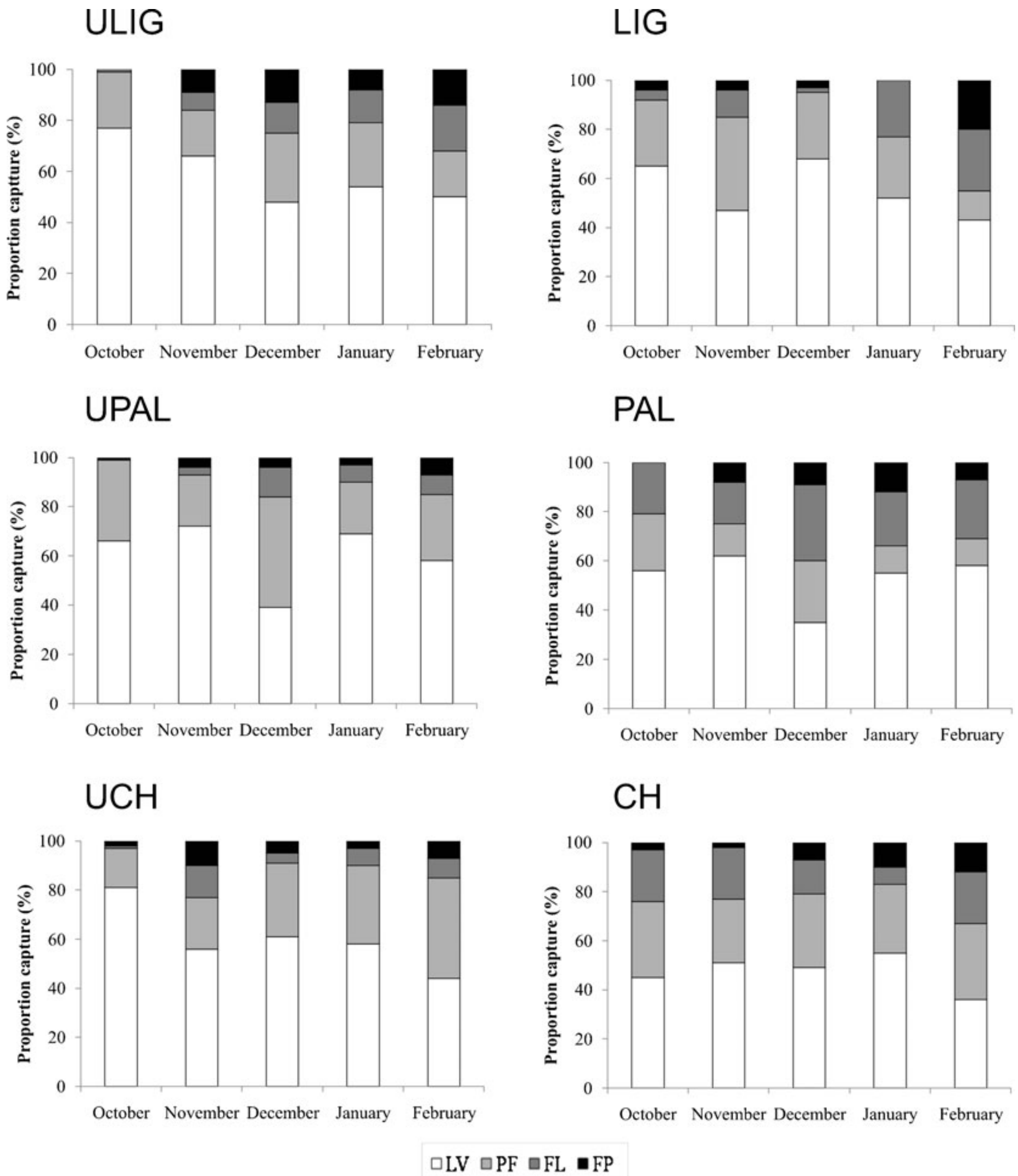


Fig. 3 Proportion capture (%) of fish larvae in different stages of development recorded in the sampling sites of the upper Uruguay river, between October 2001 and February 2002. Larval development stages: LY = Larval Yolk; PF = Pre-flexion; FL = Flexion and FP = Post-flexion

reproductive period (Table 1). The species with the highest temporal variations at the different stations during the reproductive period were *Astyanax* gr. *scabripinnis* (81.2%), *Schizodon nasutus* (79.8%), and *Pimelodus maculatus* (78.5%), though their densities were only very high in a single month (November) and low in the other months (Tables 1 and 2). Among the dominant species, only the spatial variation in *Parapimelodus valenciennis* was higher than its temporal variation. This different distribution pattern was confirmed by the high CV (182.2%) between the two areas and the lower temporal variation of its abundance when compared to other dominant species (CV=99.5%) (Table 2).

Table 1 Composition and mean density (individuals/10 m^3) of fish larvae in different months at sampling stations in the upper Uruguay River drainage basin between September 2001 and August 2002

Taxa	Month												Sites					
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	LIG	ULIG	PAL	UPAL	CH	UCH
Atheriniformes																		
Atherinopsidae																		
Odonthestes aff. *perugiae*				<0.01													x	
[a]Characiformes			0.02	0.01	<0.01								x	x			x	x
[b]Anostomidae																		
Leporinus amae			0.03	0.02	<0. 01								x				x	x
Leporinus obtusidens			<0.01		<0. 01												x	x
Leporinus striatus				<0.01										x				
Schizodon nasutus			0.22	0.01	0.02								x	x			xx	xx
[b]Characidae			0.03	<0.01	0.01								x	x			x	x
Acestrorhynchus pantaneiro			<0.01	<0.01												x	x	x
Astyanax bimaculatus		<0.01	0.33	0.03	<0.01								x	x			x	xx
Astyanax eigenmaniorum			<0.01	<0.01									x					x
Astyanax fasciatus		0.01	0.12	0.10	0.01	0.21	<0.01						x	x			xx	xx
Astyanax gr. *scabripinnis*			0.12	0.01	0.02	<0.01							xx	x			x	x
Astyanax spp.			<0. 01															x
Bryconamericus iheringii		<0.01	0.25	0.22	0.02	0.01	<0.01		<0.01				xx	x		x	xx	xx
Bryconamericus stramineus			0.17	0.03	0.08	<0.01							xx	x	x	x	x	xx
Bryconamericus spp.			0.14	<0. 01									x		xx			
Galeocharax humeralis			<0.01			<0.01			0.05					x		x		x
Oligosarcus jenynsii	<0.01		<0.01		0.01	0.01		<0.01	0.02			<0.01	x	x	x	x	x	x
Salminus brasiliensis				<0.01												x		
Serrasalmus spp.			0.06														x	
Curimatidae																		
Steindachnerina spp.			0.01	0.04										x			x	x
Erythrinidae																		
Hoplias spp.			0.02	0.01	0.09	<0.01	<0.01						x			x	xx	x
Paradontidae																		
Apareiodon affinis			0.01	0.01	0.01	0.01							x				x	x
Prochilodontidae																		
Prochilodus lineatus				0.01													x	x
Gymnotiformes																		

Table 1 (continued)

Taxa	Month												Sites					
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	LIG	ULIG	PAL	UPAL	CH	UCH
Apterodontidae																		
Porotergus ellisi			<0.01	<0.01														x
Gymnotidae																		
Gymnotus carapo				<0.01	<0.01	<0.01							x	x		x	x	x
Sternopygidae																		
Eigenmannia virescens			0.10	0.17	0.03	<0.01							x	xx		x	xx	x
Perciformes																		
[b]Cichlidae			<0.01				<0.01						x	x				x
Sciaenidae																		
Pachyurus bonariensis							<0.01										x	
[a]Siluriformes		<0.01	<0.01	<0.01	<0.01								x	x		x		x
Aspredinidae																		
Bunocephalus doriae			<0.01															x
Auchenipteridae																		
Auchenipterus sp.			<0.01	<0.01		<0.01							x	x			x	x
Tatia spp.			0.01	<0.01									x	x			x	
Cetopsidae																		
Cetopsis gobioides			<0.01	<0.01									x				x	x
Heptapteridae																		
Imparfinis sp.			<0.01															
Pimelodella sp.			<0.01	<0.01	<0.01	<0.01	<0.01						x	x				x
Rhamdia quelen		<0.01	0.26	0.16	0.02	<0.01							xx	xx		x	xx	x
Rhamdella longiuscula				<0. 01										x				
Loricariidae																		
Ancistrus taunayi				<0.01														
Cf. *Rhinelepis*			<0.01															x
Hypostomus spp.		<0.01	<0.01	<0.01	<0.01	0.01	<0.01						x	x		x	x	x
Loricariichthys spp.		<0.01	<0.01	<0. 01									x					x
Paraloricaria vetula				<0. 01										x				
Rineloricaria sp.		<0.01	0.01	<0.01		<0.01								x			x	x
[b]Pimelodidae			<0.01	<0.01		<0.01									x			x
Iheringichthys labrosus			<0.01	0.02			<0.01						x			x	x	x
Parapimelodus valenciennis		<0. 01	0.06	0.11	0.17	0.02	0.30	<0.01					xx		x	xx	x	x

Table 1 (continued)

Taxa	Month												Sites					
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	LIG	ULIG	PAL	UPAL	CH	UCH
Pimelodus absconditus			0.01	<0.01	<0.01											x	x	x
Pimelodus atrobrunneus			0.03	<0.01		0.04							x				x	x
Pimelodus maculatus			0.41	0.01		0.01							x			x	xx	xx
Pimelodus spp.			0.12	<0.01									x			x	xx	x
Steindachneridion scriptum		0.03	0.03											x				
[b]Pseudopimelodidae					0.03	0.11											xx	x
Microglanis eurystoma			0.01	<0.02	<0.01		<0.01						x	x			x	x
Trichomycteridae																		
Paravandellia bertoni		<0.01																x
Trichomycterus sp.			<0.01	<0.01									x	x				

[a] Identified to the order level; [b] Identified to the family level; x = density ≤ 0.1 larvae/10m^3; xx = density >0.1 larvae/10m^3

Environmental variables

The two first axes of the PCA were selected based on the *broken-stick* criterion. The first axis of the PCA (PC 1) showed a flow (r=−0.69; P<0.001) and water temperature (r=0.50; P<0.001) gradient for the year. In this gradient, the hottest and driest months had the highest positive values, and the months with the highest flow had the most negative values. This axis also showed a gradient among the sampling sections, such that the Ligeiro section generally had the most negative values, and the Chapecó section had the most positive. The second axis (PC 2) spatially separated the sampling sites located in the tributaries from those in the main river, such that they were mostly influenced negatively by water transparency (r=−0.60; P<0.001) and flow (r=−0.52; P<0.001) and positively by water temperature (r=0.68; P<0.001) (Fig. 4).

The PCA showed that there are great spatiotemporal differences related to abiotic variables, in particular, temporal differences are seen in PC1 (P<0.05) and spatial differences (between tributaries and the main river) in PC2 (P<0.05). The month of October was significantly different (P<0.05) from the summer months (December, January and February) in PC1 (Tukey's P<0.05). October presented higher flow than the summer months, which had lower flows and higher temperatures. On the other hand, PC2 showed that the sites of the main river (ULIG, UPAL, and UCH) had higher transparency and flow values and lower values of water temperature compared to the sites located in the tributaries (Tukey, P<0.05) (Fig. 4).

The ANOVA revealed significant differences for flow (F=336.8; df=20; P<0.05) and water temperature (F=438.2; df=20; P<0.05) between the distinct sampling sites and months for each environment (Fig. 5a, b).

Relationship between ichthyoplankton and environmental variables

When the environmental variables were correlated to egg and larval abundance, only the flow (eggs: r=−0.31; P<0.05 and larvae: r=−0.42; P<0.05) and the water temperature (eggs: r=0.58; P<0.05 and larvae: r=0.72; P<0.05) yielded significant results.

The ANCOVA showed that the abundance of both eggs and larvae were related to the flow

Table 2 Results of the coefficient of variation (CV) and the nested ANOVA for fish egg and larval densities for the ten most abundant *taxa* in the sampling sites studied from September 2001 to August 2002

Taxa	R^2	Site		Site CV	Month (Site)		Month CV
		%	F		%	F	
Eggs	**0.95**	32.9	**96.05**	148.2	67.1	**54.43**	154.2
Larvae	**0.77**	44.9	**149.68**	133.2	55.1	**11.79**	160.1
Astyanax fasciatus	**0.65**	30.1	**3.17**	146.2	69.9	**2.07**	117.9
Astyanax gr. *scabripinnis*	**0.48**	18.8	**2.55**	151.7	81.2	**3.02**	193.1
Bryconamericus iheringii	0.33	23.5	1.82	85.5	76.5	1.46	126.3
Bryconamericus stramineus	0.34	27.4	2.03	111.9	72.6	1.48	119.5
Eigenmannia virescens	**0.49**	40.9	**5.71**	177.1	59.1	**2.30**	139.3
Hoplias spp.	0.29	24.1	1.30	137.8	75.9	1.27	140.4
Parapimelodus valenciennis	**0.68**	70.7	**24.09**	182.2	29.3	**5.06**	99.5
Pimelodus maculates	**0.69**	21.5	**6.93**	172.3	78.5	**7.00**	231.3
Rhamdia quelen	**0.51**	24.6	**2.90**	94.2	75.4	**3.29**	157.6
Schizodon nasutus	**0.50**	20.2	**2.92**	131.3	79.8	**3.12**	185.9

Bold values are significantly different ($p<0.05$)

(eggs: $F=6.739$; df=5, 113; $P<0.001$ and larvae: $F=11.231$; df=5, 113; $P<0.001$) and to the water temperature (eggs: $F=8.562$; df=5, 113; $P<0.001$ and larvae: $F=9.274$; df=5, 113; $P<0.001$) at the sites of the main river. The same trend was found for the tributaries and also for flow (eggs: $F=5.266$; df=5, 113; $P<0.001$ and larvae: $F=3.455$; df=5, 113; $P<0.001$) and water temperature (eggs: $F=5.459$; df=5, 113; $P<0.001$ and larvae: $F=2.562$; df=5, 113; $P<0.001$).

The results of the ANCOVA showed that there are differences in the reproductive activity between the main river and its tributaries. Among the tributaries (except for site PAL), the abundance of eggs was directly correlated with the flow (LIG: slope=

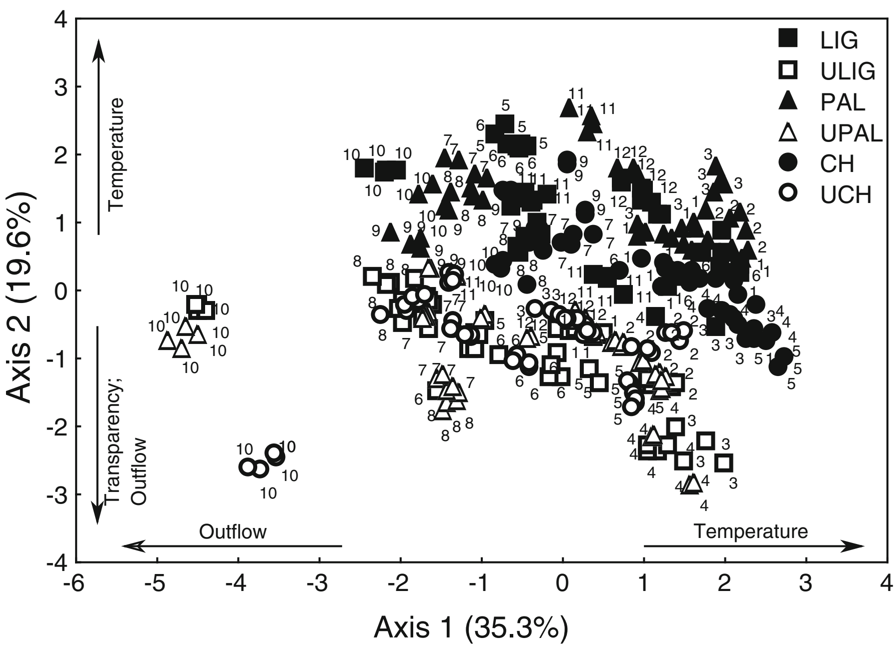


Fig. 4 Principal components analysis (PCA) of the matrix of environmental variables recorded at the upper Uruguay River from September 2001 to August 2002. Months of the year: 1 = January; 2 = February; 3 = March; 4 = April; 5 = May; 6 = June; 7 = July; 8 = August; 9 = September; 10 = October; 11 = November; 12 = December

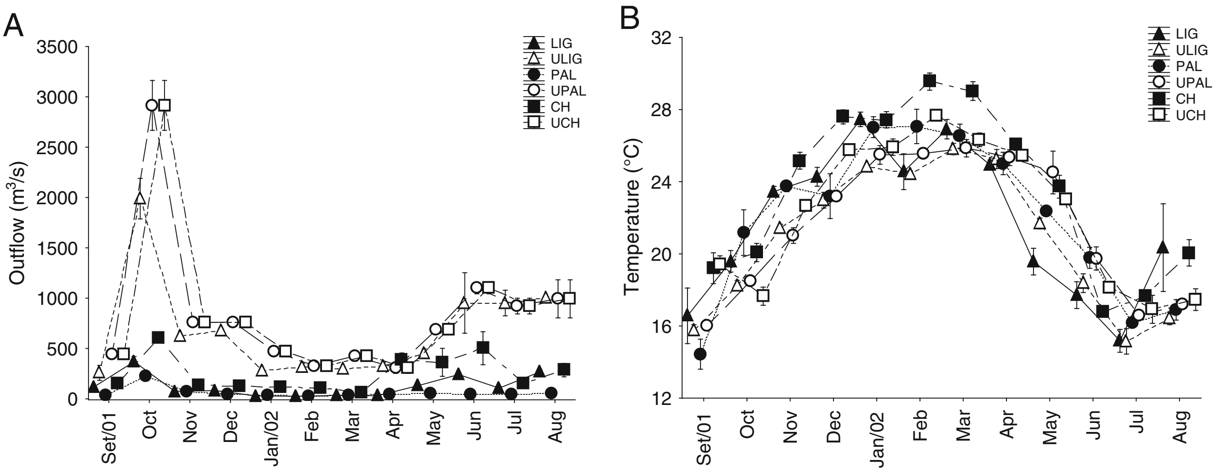


Fig. 5 Mean values and standard error of river flow (**a**) and temperature (**b**) at the different sites sampled in the upper Uruguay River from September 2001 to August 2002

0.126; P=0.026; CH: slope=0.602; P=0.029) and inversely correlated with water temperature (LIG: slope=−1.049; P=0.023; CH: slope=−4.366; P=0.002). However, in the main river (except for site UPAL), the abundance of eggs was inversely correlated with the flow (ULIG: slope=−0.325; P=0.048; UCH: slope=−0.731; P=0.049), and directly correlated with water temperature (ULIG: slope=3.010; P=0.005; UCH: slope=3.889; P=0.034). In general, the egg distribution in the main river was the opposite of that observed in its tributaries.

No correlation was found between larval abundance and the flow or water temperature in the tributaries, with the exception of site CH, where a positive correlation with the flow was observed (slope=0.561; P=0.041). Conversely, the numbers of larvae were negatively correlated with the flow in the main river (sites ULIG: slope=−0.010; P=0.034; UPAL: slope=−0.313; P=0.012; UCH: slope=−0.505; P=0.002) and positively correlated with the water temperature (sites ULIG: slope=0.784; P=0.045; UPAL: slope=2.427; P=0.000; UCH: slope=1.799; P=0.035).

Overall, these results seem to indicate greater reproductive activity in the tributaries during the spring (when the flow is greater and the water temperature is not so high). However, in the main river, the greatest reproductive activity occurred in the summer, when the flow diminishes and the temperature of the water increases (Fig. 5). A simple analysis of the proportion of the eggs and larvae captured in the different sections during the sampled months makes the ANCOVA results even more evident (Fig. 6).

The reproductive pattern observed for these environments at the mouths of tributaries in the upper Uruguay River is visually represented in Fig. 7.

Discussion

The larval assemblages observed in the environments studied in the upper Uruguay River were composed mainly of species from the orders Characiformes and Siluriformes. This study identified 41 of the 98 species that have been recorded in this region (Zaniboni-Filho et al. 2004). In general, the most frequent and abundant species were small- and medium-sized fish characterized by batch spawning, long reproductive periods, small eggs and an absence of parental care that undergo short reproductive migrations, according to the classification suggested by Suzuki et al. (2005).

Overall, the literature indicates that reproduction habitats in neotropical environments are located at the upper portion of large rivers and tributaries. This is related to the high occurrence of reproductively mature (active) adult fish in these areas and to the different distribution of eggs along the stretch of the river, where an increase in egg abundance is observed towards the upper portion of the tributaries (Vazzoler et al. 1997). However, some other studies have

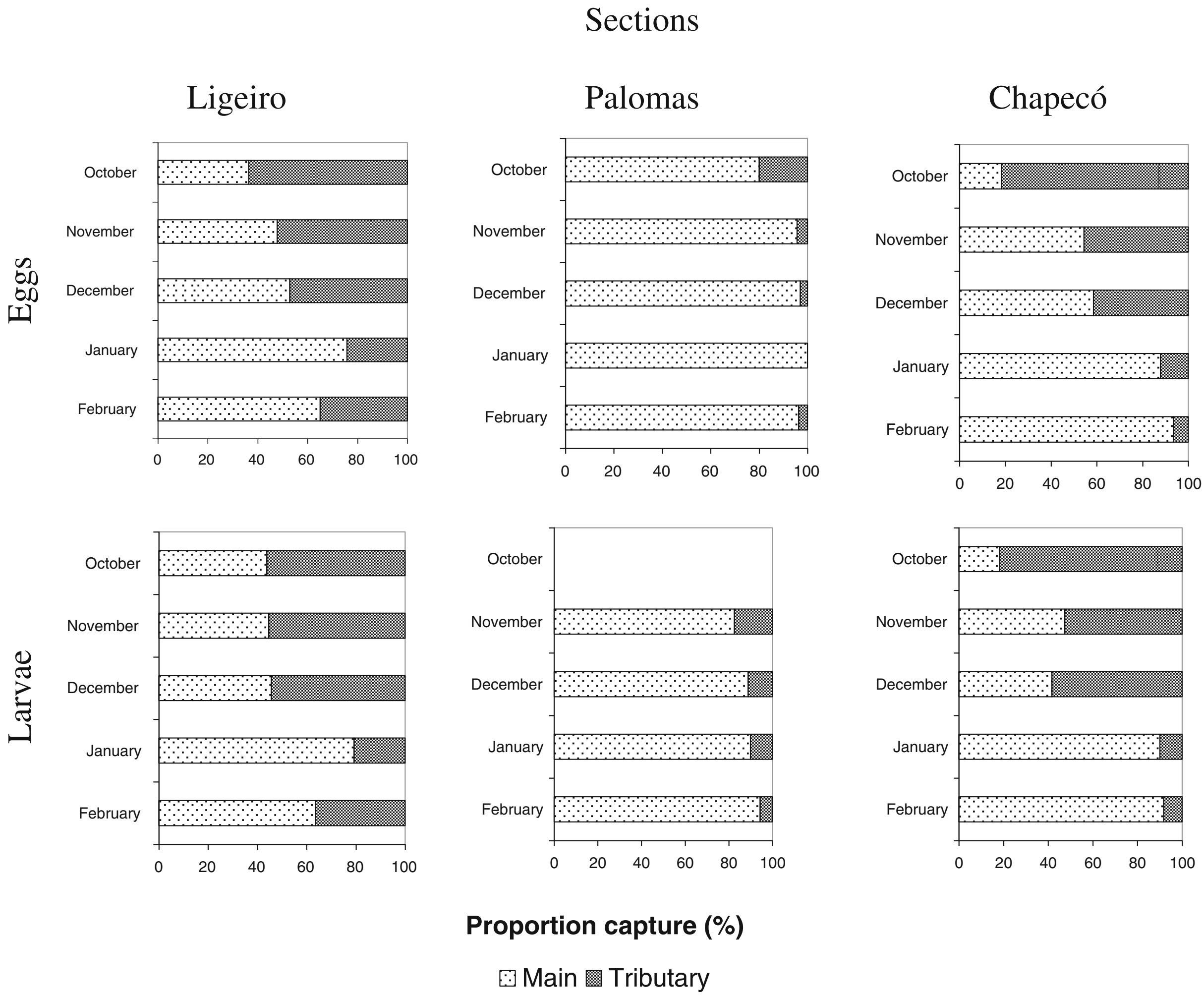


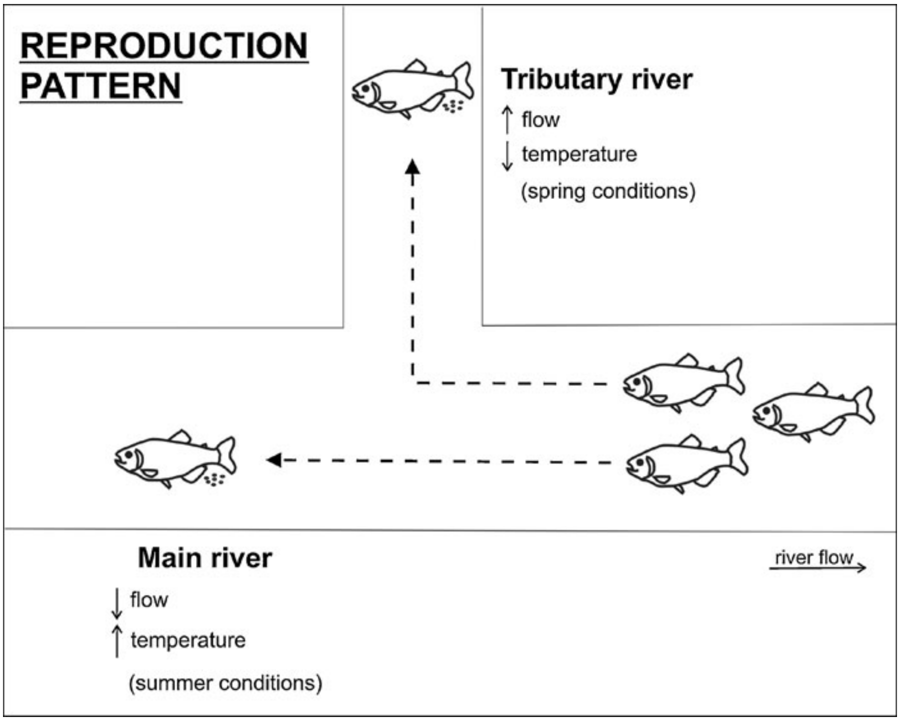
Fig. 6 Proportion of fish eggs and larvae captured in the Chapecó, Ligeiro, and Palomas sections from October 2001 to February 2002

recently shown the occurrence of reproduction of rheophilic fishes in areas of the confluence of rivers (Hermes-Silva et al. 2009).

In the present study, the river mouth areas were shown to be of great importance to fish spawning and larval drift, mainly for small- and medium-sized species. Differences in some abiotic variables between the two rives, such as water temperature, pH and electric conductivity, have been mentioned as the main factors influencing rheophilic fish spawning. However, there is a suspicion, at least for the fishes of La Plata basin, that only positive gradients of these variables (variation from low to high values) may promote spawning (Reynalte-Tataje et al. 2008).

This study detected the occurrence of eggs and larvae at all of the sites sampled, although their distribution was quite heterogeneous. The highest densities were found in tributary rivers, suggesting that reproductive activity may be greater in these environments. The low densities verified in the main river sites closer to the dams indicate low reproductive activity in these areas, possibly influenced by the water quality and quantity discharged from the dam. There is considerable evidence that controlling the water from the turbines of reservoirs may affect the reproductive activity of fish populations located downstream (Agostinho et al. 1993; Sato et al. 2003; Hermes-Silva et al. 2009). Conversely, high densities of eggs and larvae were captured in the downstream main river site which is located more than 130 km downstream of the closest dam and is far from the direct influence of this power plant.

Fig. 7 Reproduction pattern observed in the mouth of tributaries in the upper Uruguay River (Brazil)



Among the three tributaries, the Palomas River had the lowest density and number of species, which may be related to its morphometric and hydrologic characteristics. This river is narrower than the others and has the lowest discharge among them (43 $m^3.s^{-1}$). This characteristic seems to have favored the frequent changes observed in the quantity and quality of this river's water compared to the data recorded for the others, which may, in turn, have inhibited the reproductive activity of local fish populations.

The highest abundance of eggs and larvae was observed between October and February, showing a remarkable seasonality (spring and summer), and the greatest densities were detected between November and January. Agostinho et al. (2007) reported that most fish species of the upper Paraná River have higher reproductive activities between November and February. This period may be extended until April, depending on the type of reproductive strategy adopted by the species. For the larvae of the most abundant species, there was greater temporal than spatial variation during the reproductive period. This pattern can be explained by two main observations: first, the most abundant species are found at most of the sites studied, which reduces their spatial variation, and second, most species have striking peaks of occurrence during a few months (or in a single month), with a reduction, or even overall absence, in the following months.

Parapimelodus valenciennis was the only species that exhibited a different pattern than the other nine predominant species, which was probably due to the high occurrence of this species in the Palomas section and its reduced occurrence in the other environments. During the reproductive period, thousands millions of adults of *P. valenciennis* have been observed in a concentrated area downstream from the Itá HEP. In addition, a considerable increase in the larval density of this species was observed, indicating that *P. valenciennis* actively reproduces immediately downstream from the dam (Reynalte-Tataje et al. 2008). This species is zooplanktivore during its entire life cycle and eats mainly cladocerans (Reynalte-Tataje and Zaniboni-Filho 2008). High concentrations of zooplanktonic organisms coming from the reservoir and downstream from the Itá HEP appear to be one of the factors that support the high densities of this species in this environment. During the last few years, a progressive increase in larval and adult densities of this species has been detected downstream from the Machadinho dam (D.A. Reynalte-Tataje, pers. obs.).

The upper Uruguay River presents distinct kinds of aquatic microhabitats along its course, which may present variations in its biotic and abiotic components (Reynalte-Tataje et al. 2008). In addition, the same kind of microhabitat may present hydrological differences along the river's longitudinal gradient. Environments characterized by the mouths of rivers, which are structured by the convergence of two rivers, provide a good example of the limnological differences that may occur within a single water basin. These differences are the result of unique traits in the drainage area, morphometry, and hydrodynamics of each river. In this study, physico-chemical differences in the water were observed in its lateral (tributary and main river) and longitudinal (section) dimensions. The differences between the main river and its tributaries are mainly related to the size of the drainage basin and to the unique geomorphology of each river.

This study detected clear seasonal variations among the environmental variables tested; the river flow and water temperature were the parameters that correlated with the abundance of eggs and larvae. In general, ichthyoplankton were most abundant in the months of rising water (November through December) and drought (January), when the temperature was above 22.5°C. These results are different from those found in most studies carried out in the La Plata River basin, where it has been reported that the highest reproductive activity occurs at the beginning of the flood cycle (Bailly et al. 2008; Suzuki et al. 2009) or at its peak (Oldani 1990; Reynalte-Tataje et al. 2011). For the lower portions of the La Plata basin (such as La Plata River, lower Uruguay River, and lower Paraná River), several studies have shown that variations in hydrodynamic levels are not as important as temperature, which is the main stimulus for fish reproduction (Oldani 1990). In the upper Uruguay River, some studies of the reproductive biology of rheophilic species have demonstrated that floods proceed the reproductive period (Reynalte-Tataje et al. 2008; Hermes-Silva et al. 2009).

There is a particular water temperature range in which individuals can carry out their final maturation and spawning, and outside of this range, reproduction will not occur. In this study, we observed the presence of larvae of 45 *taxa* in November, when the average temperature was 22.9°C. However, in October, when the water temperature was 19.2°C, larvae from only 11 *taxa* were identified. Godoy (1954) studied the favorable conditions for spawning during the reproductive period in the Mogi-Guaçu River, and showed that these periods coincided with an increase in water turbidity and water temperatures above 23°C. Similar results have been found for the São Francisco River (Sato et al. 2003).

In this study, we observed that the reproductive activity in the tributaries may begin and end sooner than in the main river. The greater temperature of the tributaries compared to the main river may be responsible for the highest number of ichthyoplanktonic organisms being observed in the tributaries at the beginning of the reproductive period. Conversely, during the summer months, a drastic reduction in river flow and an increase in water temperature in the tributaries (which mostly flow over rock slabs) stimulate the fish to chiefly use the main river, which has a milder temperature and a greater volume of water than that seen in the tributaries during the same period. Therefore, the differences in water temperature and river flow between the tributaries and the main river seem to direct reproduction to a specific river during the reproductive period.

From our results, we conclude that the mouth of the tributary is an important environment for spawning and the initial development of fish. The fish assemblages were composed mainly of species that undergo short migrations, and the dominant species of the larval assemblages varied more in a temporal than a spatial pattern because of the strong influence of temporal factors, such as photoperiod, temperature and flow. Reproductive seasonality was pronounced between October and February and was most intense in the months of November and January. Based on egg and larval distributions, we found that spawning occurred mainly in the larger tributaries and in the Uruguay River in the Chapecó section. In contrast, fish spawning in the sites downstream of dams was more restricted. Finally, the greatest reproductive activity in the tributaries occurred in periods with high flow, when the tributaries were normally dammed, and when the water temperature began to increase in the region. Conversely, the greatest reproductive activity in the main river occurred for some species during the period when the water volume was low and the water temperature was high.

The results presented in this study may be useful in guiding future management and conservation actions, especially in a river basin with a high hydroelectric potential. These preliminary results, along with other data on fish biology in this region, will help in defining special environments under the influence of dams in the upper Uruguay River region that are of particular importance for fish spawning and larval rearing (spawning and nursery grounds), and thus need to be preserved.

References

Agostinho AA, Mendes VP, Suzuki HI, Canzi C (1993) Avaliação da atividade reprodutiva da comunidade de peixes dos primeiros quilômetros a jusante do Reservatório de Itaipu. Revista UNIMAR 15:175–189

Agostinho AA, Gomes LC, Veríssimo 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, Pelicice FM, Petry AC, Gomes LC, Júlio HF Jr (2007) Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquat Ecosyst Heal Manag 10:174–186

Agostinho AA, Pelicice FM, Gomes LC (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz J Biol 68:1119–1132

Ahlstrom EH, Moser HG (1976) Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Revue des Travaux de L'Institut des Peches Maritimes 40 (3/4):379–398

Araujo-Lima CARM (1994) Egg size and larval development in Central Amazon fish. J Fish Biol 44:371–389

Bailly D, Agostinho AA, Suzuki HI (2008) Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. River Res Appl 24:1218–1229

Barletta M, Jaureguizar AJ, Baigun C et al (2010) Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. J Fish Biol 76:2118–2176

Baumgartner G, Nakatani K, Gomes LC, Bialetzki A, Sanches PV, Makrakis MC (2008) Fish larvae from the upper Paraná River: do abiotic factors affect larval density? Neotropical Ichthyology 6(4):551–558

Bialetzki 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 Fish 73:37–47

Daga VS, Gogola TM, Sanches PV, Baumgartner G, Baumgartner D, Piana PA, Gubiani EA, Delariva RL (2009) Fish larvae assemblages in two floodplain lakes with different degrees of connection to the Paraná River, Brazil. Neotropical Ichthyology 7(3):429–438

Fernandes R, Agostinho AA, Ferreira EA, Pavanelli CS, Suzuki HI, Lima DP, Gomes LC (2009) Effects of the hydrological regime on the ichthyofauna of riverine environments of the Upper Paraná River floodplain. Braz J Biol 69(2, Suppl):669–680

Godoy MP (1954) Locais de desova de peixes num trecho do rio Mogi-Guassu, vol 4. Editora Franciscana, Piracicaba

Hair JF, Anderson RE, Tatham L, Grablowski BJ (1984) Multivariate data analysis. McMillan, New York

Hermes-Silva S, Reynalte-Tataje D, Zaniboni-Filho E (2009) Spatial and temporal distribution of ichthyoplankton in the upper Uruguay River, Brazil. Braz Arch Biol Technol 52:933–944

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 Fish 56:129–151

Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74:2204–2214

Lowe-McConnell RH (1987) Ecological studies in tropical fish communities. Cambridge University Press, Cambridge

Munro AD (1990) General introduction. In: Munro AD, Scott DAP, Lam TJ (eds) Reproductive seasonality in teleosts: environmental influences. CRC, Flórida, pp 1–11

Nakatani K, Baumgartner G, Cavicchioli M (1997) Ecologia de ovos e larvas de peixes. In: Vazzoler AEAM, Agostinho AA, Hahn NS (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 (2001) Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação. Editora EDUEM, Maringá

Nascimento FL, Nakatani K (2005) Variação temporal e espacial de ovos e larvas das espécies de interesse para a pesca na sub-bacia do rio Miranda, Pantanal, Estado do Mato Grosso do Sul, Brasil. Acta Scientiarum 27 (3):251–258

OEA (Organização dos Estados Americanos) (1969) Cuenca del Rio de La Plata. Estudio para su planificación y desarrollo. Inventário de dados hidrológicos y climáticos, Roma

Oldani NO (1990) Variaciones de la abundancia de peces del valle del rio Paraná (Argentina). Revue Hydrobiologie Tropical 23(1):67–76

Peters RK (1986) The role of prediction in limnology. Limnol Oceanogr 31:1143–1159

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, Nuñer APO (eds) Reservatório de Itá. Estudos ambientais, desenvolvimento de tecnologias de cultivo e conservação da ictiofauna. Editora UFSC, Florianópolis, 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, Nuñer APO (eds) Reservatório de Itá. Estudos ambientais, desenvolvimento de tecnologias de cultivo e conservação da ictiofauna. Editora UFSC, Florianópolis, pp 95–113

Reynalte-Tataje DA, Nakatani K, Fernandes R, Agostinho AA, Bialetzki A (2011) Temporal distribution of ichthyoplankton in the Ivinhema River (Mato Grosso do Sul State/ Brazil): influence of environmental variables. Neotropical Ichthyology 9(2):427–436

Sanches PV, Nakatani K, Bialetzki A, Baumgartner G, Gomes LC, Luiz EA (2006) Flow regulation dams affecting ichthyoplankton:the case of Porto Primavera Dam, Paraná River, Brazil. River Res Appl 22:555–565

Sartori M da BG (2003) A dinâmica do clima do Rio Grande do Sul: indução empírica e conhecimento científico. Terra livre 20(1):27–49

Sato Y, Bazzoli N, Rizzo E, Boschi MA, Miranda MOT (2003) Impacto a jusante do reservatório de Três Marias sobre a reprodução do peixe reofílico curimatá-pacu (*Prochilodus argenteus*). In: Godinho HP, Godinho AL (eds) Águas, peixes e pescadores do São Francisco das Minas Gerais. PUC, Minas, Belo Horizonte, pp 327–345

Suzuki HI, Bulla CK, Agostinho AA (2005) Estratégias reprodutivas de assembléias de peixes em reservatórios. In: Rodrigues L, Thomaz SM, Agostinho AA, Gomes LC (eds) Biocenoses em Reservatórios. Padrões espaciais e temporais. RiMa, São Carlos, pp 223–242

Suzuki HI, Agostinho AA, Bailly D, Gimenes MF, Julio-Junior HF, 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, Suppl):649–660

Tanaka S (1973) Stock assessment by means of ichthyoplankton surveys. FAO Fish Tech Pap 122:33–51

Tondato KK, De F Mateus LA, Ziober SR (2010) Spatial and temporal distribution of fish larvae in marginal lagoons of Pantanal, Mato Grosso State, Brazil. Neotropical Ichthyology 8(1):123–133

Vazzoler AEAM (1996) Biologia da reprodução de peixes teleósteos: Teoria e prática. EDUEM, Maringá

Vazzoler AEAM, Lizama PHM, Inada P (1997) Influências ambientais sobre a sazonalidade reprodutiva. In: Vazzoler AEAM, Agostinho AA, Hahn SN (eds) A planície de inundação do alto rio Paraná. Aspectos físicos, biológicos e socioeconômicos. EDUEM, Maringá, pp 267–280

Vlaming VL (1972) Environmental control of teleost reproductive cycles: a brief review. J Fish Biol 4:131–140

Welcomme RL (1979) Fisheries ecology of floodplain rivers. Longman Inc, London, London

Zaniboni-Filho E, Schulz UH (2003) Migratory fishes of the Uruguay River. In: Carolsfeld J, Harvey B, Ross C, Baer A (eds) Migratory fishes of the South America: biology, social importance and conservation status. World Fisheries Trust, Victoria, pp 135–168

Zaniboni-Filho E, Meurer S, Shibatta AO, Nuner, AP de O (2004) Catálogo ilustrado de peixes do alto rio Uruguai. Ed. UFSC:Tractebel Energia, Florianópolis