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Importance of dam-free stretches for fish reproduction: the last remnant in the Upper Paraná River

Importância de trechos livres de represamento para a reprodução dos peixes: o último remanescente do alto rio Paraná

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Abstract: Aim: This study uses the abundance of fish eggs and larvae to evaluate the importance of the main channel of the Paraná River and the adjacent areas of the floodplain, in the last dam-free stretch in the Brazilian territory, for the spawning and development of fish of different reproductive guilds, in order to obtain subsidies to assist in the management and conservation policies of this area, focusing on the maintenance of dam-free areas. **Methods:** Data were taken quarterly from August 2013 to May 2015, in 25 sites, grouped into three biotopes: main channel, tributaries and lagoons. Possible spatial variations in fish spawning and development as well as composition and structure of larvae were evaluated. **Results:** Higher densities of eggs were found in tributaries (Paracaí and Amambai rivers) and greater densities of larvae were observed in lagoons (Saraiva). Significant differences in composition and structure of larvae were detected only between sampling stations. As for taxonomic composition, 29 taxa were recorded, mostly non-migratory. However, long-distance migratory were also widely distributed, such as *Brycon orbignyanus*, *Pseudoplatystoma corruscans*, *Prochilodus lineatus, Piaractus mesopotamicus* and *Rhaphiodon vulpinus,* as well as invasive species *Platanichthys platana* and *Hemiodus orthonops*. In turn, *Salminus brasiliensis* presented low occurrence. **Conclusions:** This study evidenced that different species spawn in the region, mainly in tributaries, and their eggs and larvae are transported to the main channel of the Paraná River and adjacent lagoons, to complete their early development. The capture of larvae of important migratory species suggests that this environment still exhibits suitable conditions for their reproduction, mainly due to the presence of dam-free tributaries. Also, they emphasize the importance of the integrity of these environments for the maintenance of the regional fish fauna, and it is extremely important the monitoring of reproduction of the most endangered species, as well as of invasive species.

Keywords: fish; egg and larvae; floodplain; breeding; unregulated tributaries.

Resumo: Objetivo: Este estudo utiliza a abundância de ovos e larvas de peixes para avaliar a importância do canal principal do rio Paraná e as áreas adjacentes da planície de inundação, no último trecho livre de barramentos em território brasileiro, para a desova e desenvolvimento dos peixes de diferentes guildas reprodutivas, a fim de obter subsídios que auxiliem nas políticas de manejo e conservação desta área, focando na manutenção de áreas livres de represamentos. **Métodos:** Os dados foram coletados trimestralmente entre agosto de 2013 a maio de 2015, em 25 estações, agrupadas em três biótopos: canal principal, tributários e lagoas. Foram avaliadas possíveis variações espaciais na desova e desenvolvimento dos peixes, assim como na composição e a estrutura das larvas. **Resultados:** Maiores densidades de ovos foram registradas nos tributários (rios Paracaí e Amambai) e de larvas nas lagoas (Saraiva). Diferenças significativas na composição e estrutura das larvas foram observadas apenas entre as estações de amostragens. Quanto a composição taxonômica, registrou-se 29 táxons, sendo a maioria não migradores. Entretanto, também foram amplamente distribuídas as larvas de migradores de longa distância como *Brycon orbignyanus*, *Pseudoplatystoma corruscans*, *Prochilodus lineatus, Piaractus mesopotamicus* e *Rhaphiodon vulpinus,* assim como as invasoras *Platanichthys platana* e *Hemiodus orthonops.* Já *Salminus brasiliensis* apresentou baixa ocorrência. **Conclusões:** Neste estudo fica evidente que diferentes espécies desovam na região, principalmente nos tributários, e seus ovos e larvas são carreados para o canal principal do rio Paraná e lagoas adjacentes, para completarem seu desenvolvimento inicial. A captura de larvas de importantes espécies migradoras, sugerem que este ambiente ainda apresenta condições adequadas para sua reprodução, principalmente, pela presença de tributários livres de represamento. Ainda, reforçam a importância da integridade desses ambientes para a manutenção da ictiofauna regional, sendo de extrema relevância o monitoramento acerca da reprodução das espécies mais ameaçadas, bem como das espécies invasoras.

Palavras-chave: peixes; ovos e larvas; planície de inundação; reprodução; tributários não regulados.

1. Introduction

The Paraná River, the main river of the La Plata basin, is the tenth largest in the world in discharge and the fourth in drainage area (5 × 108 m^3/year; 2.8 × 106 km^2, respectively) (Agostinho et al., 2007). From its source, at the confluence of the Paranaíba and Grande rivers, Brazil (lat. 20° S), to its mouth, in the estuary of the La Plata River near Buenos Aires, Argentina (lat. 34° S), this river runs about 3,780 km, draining all south-central South America, from the Andes slopes to the Serra do Mar, near the Atlantic coast (Stevaux, 1994).

The upper Paraná River (includes approximately the first third of the Paraná River basin) is entirely within the Brazilian territory, except for one stretch along the Itaipu Reservoir that borders Paraguay (Agostinho et al., 2008). Its drainage basin comprises more than 10% of the national territory (891,000 km^2) and, in terms of hydroelectric uses, this region concentrates more than a hundred reservoirs, 26 of them with more than 100 km^2 (Agostinho et al., 2007, 2008, 2013), which corresponds to almost 50% of the total dammed area in Brazil (Agostinho et al., 2008).

The only dam-free stretch of the Paraná River is restricted to 230 kilometers between the dam of Porto Primavera Hydropower Plant (officially known as Engenheiro Sérgio Motta Hydropower Plant) and the Itaipu Hydropower Plant. On the right bank of this stretch, there is an extensive floodplain, which is home to a high biological diversity (Lansac-Tôha et al., 2004; Takeda et al., 2004; Train & Rodrigues, 2004; Agostinho et al., 2005). Due to these characteristics, this area is considered of “Extreme Biological Importance” (MMA, 2002), where three conservation units are located: the Environmental Protection Area of the Islands and floodplain of the Paraná River (Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná), covering all its extension, and the areas with the most critical habitats, Ilha Grande National Park (Parque Nacional de Ilha Grande) and Ivinhema River State Park (Parque Estadual das Várzeas do Rio Ivinhema) in the state of Mato Grosso do Sul (Agostinho et al., 2013).

Habitat fragmentation promoted by the construction of dams is one of the largest and deliberate human impacts on natural systems (Dynesius & Nilsson, 1994). In addition to altering the environment at the site of the dam itself, a dam affects the riparian communities upstream, raising water levels and modifying level fluctuations, as well as downstream, by changing flow regimes (Nilsson & Berggren, 2000). These developments are associated with a global decline in the abundance and diversity of freshwater fauna in different regions of the world (Dudgeon, 2000; Bunn & Arthington, 2002; Fu et al., 2003; Agostinho et al., 2008).

For fish, the main impacts caused by the construction of reservoirs are related to changes in the composition and structure of assemblages, especially within the reservoir, and also downstream, such as changes in the seasonal flood cycle (flow control) and disruption of migratory routes of rheophilic species (Agostinho et al., 2008). Moreover, habitat fragmentation also influences the survival of eggs and larvae, since even those fish that can perform reproductive migrations upstream of a reservoir often cannot prevent their eggs and larvae from entering environments inappropriate for their development during the drift process (Dudley & Platania, 2007; Pelicice & Agostinho, 2008).

The remnant of the Paraná River floodplain is of fundamental importance in the maintenance of viable populations of species already eliminated from the upper reaches of the basin (Agostinho et al., 2013), especially due to the presence of tributaries such as Ivinheima, Ivaí, Baía, Amambai, Iguatemi and Piquiri rivers, which still maintain their original characteristics. In this context, this study uses the abundance of eggs and larvae of fish to evaluate the importance of the main channel of the Paraná River and the areas adjacent to the floodplain in the last dam-free stretch of the basin in the Brazilian territory, for the spawning and development of fish of different reproductive guilds, in order to obtain subsidies to assist in the management and conservation policies of this area, focusing on the maintenance of dam-free areas. Unlike other studies already conducted in this area (Baumgartner et al., 2004; Nakatani et al., 2004; Bialetzki et al., 2005; Daga et al., 2009; Gogola et al., 2010, 2013; Reynalte-Tataje et al., 2011, 2013; Barzotto et al., 2015), our approach in the present study allows to evaluate all biotopes (main channel, tributaries and lagoons) of this remnant at the same time, that is, a representation of how the reproductive dynamics of local species occur during reproductive events. The questions to be answered with this approach were: What are the biotopes used for spawning and development? Is there a longitudinal (upstream-downstream) gradient of distribution of fish eggs and larvae? Do species belonging to different reproductive guilds use this remnant during the reproductive process? Are larvae of migratory species found preferentially in tributaries?

2. Material and Methods

2.1. Study area

The study area is located in the floodplain of the Upper Paraná River, downstream of the dam of Porto Primavera Hydropower Plant (HPP) and upstream of the Itaipu Reservoir. This section presents a large anastomosed channel, with reduced slope (0.09 m/km), sometimes with extensive alluvial plain and large sediment accumulation on the bed, giving rise to bars and small islands (more than 300), sometimes with large islands and more restricted floodplain (Agostinho et al., 2008). The complex anastomosis also involves numerous secondary channels, lagoons, the Baía River and the lower reaches of the Ivaí, Ivinheima, Piquiri, Amambai and Iguatemi rivers, besides the floodplain (Agostinho et al., 2008).

2.2. Sampling

Samples were taken in 25 sampling stations distributed in three biotopes: main channel of the Paraná River (upstream of the mouth of tributaries); tributaries and lagoons. The names, codes and location of each sampling site are presented in Table 1

Quarterly samplings were performed from August 2013 to May 2015, always at night, around 20 hours. For the samples, conical-cylindrical plankton nets with 0.5 mm mesh size and a mouth area of 0.1104 m^2 were equipped with a flow meter to obtain the volume of water filtered; nets were exposed or dragged depending on the current velocity, for 10 minutes, in region pelagic at the subsurface (approximately 20 cm below the water surface) in all sampling stations. After, samples were stored in flasks, anesthetized and fixed with 4% formalin, buffered with calcium carbonate.

In laboratory, samples were sorted under a stereomicroscope at 10X magnification in a Bogorov chamber. After sorting, the eggs were only quantified, while the larvae were identified using the development regressive sequence, as recommended by Ahlstrom & Moser (1976) and according to Nakatani et al. (2001), which uses the shape of the body, the presence of barbels, the sequence of formation of the fins, the relative position of the anal opening in relation to the body, the number of vertebrae/myomers and the rays of the fins. After identification, larvae were taxonomically classified according to Reis et al. (2003), Britski et al. (2007) and Graça & Pavanelli (2007). Some larvae that could not be identified at least at the order level were included in the category "unidentified" (newly hatched larvae) and "unidentifiable" (damaged larvae).

In order to evaluate the type of reproductive strategy of the fish species using these environments during reproduction, the larvae identified at least at the genus level were classified according to the reproductive guild to which they belong, namely: non-migratory or short-distance migratory, with external fertilization and no parental care (NMFESC); non-migratory or short-distance migratory, with external fertilization and parental care (NMFECP); non-migratory or short-distance migratory, with internal fertilization (FI); and long-distance migratory with external fertilization (ML), classified according to Fialho et al. (2000), Suzuki et al. (2004), Smith et al. (2013) and Agostinho et al. (2015).

2.3. Data analysis

The abundance of the organisms caught was standardized to a volume of 10 m^3 of filtered water according to Tanaka (1973), modified by Nakatani et al. (2001). The mean density of the organisms (D) was obtained by the total number

Table 1. Physiographic data of the sampling stations located in the Upper Paraná River floodplain.

Site	Code	Subarea	Location	Biotope	Geographic Coordinate
1	MPARN	Paranapanema	Paraná River upstream of the mouth of the Paranapanema River	Main Channel	22°39’2.30”S/53°5’26.30”W
2	TPARN	Paranapanema	Paranapanema River	Tributary	22°38’54.00”S/53°5’2.20”W
3	MBAIA	Baía	Paraná River upstream of the mouth of the Baía River	Main Channel	22°45’38.70”S/53°19’40.60”W
4	TBAIA	Baía	Baía River	Tributary	22°45’34.40”S/53°19’42.90”W
5	MIVIN	Ivinheima	Paraná River upstream of the mouth of the Ivinhema River	Main Channel	22°59’40.60”S/53°38’41.40”W
6	TIVIN	Ivinheima	Ivinhema River	Tributary	22°59’12.00”S/53°38’56.70”W
7	MIVIH	Ivinheiminha	Paraná River upstream of the mouth of the Ivinheiminha River	Main Channel	23°14’18.50”S/53°43’3.60” W
8	TIVIH	Ivinheiminha	Ivinheiminha River	Tributary	23°14’0.30”S/53°43’24.00” W
9	MIVAI	Ivaí	Paraná River upstream of the mouth of the Ivaí River	Main Channel	23°18’11.80”S/53°41’54.20” W
10	TIVAI	Ivaí	Ivaí River	Tributary	23°18’0.50”S/53°41’32.40” W
11	MAMAM	Amambai	Paraná River upstream of the mouth of the Amambai River	Main Channel	23°21’52.30”S/53°52’47.90”W
12	TAMAM	Amambai	Amambai River	Tributary	23°20’19.90”S/53°51’24.40”W
13	MMARA	Maracaí	Paraná River upstream of the mouth Maracaí River	Main Channel	23°26’8.29”S/53°58’0.29” W
14	TMARA	Maracaí	Maracaí River	Tributary	23°25’32.03”S/53°58’13.82”W
15	MPARA	Paracai	Paraná River upstream of the mouth of the Paracai River	Main Channel	23°38’51.40”S/53°56’44.30”W
16	TPARA	Paracai	Paracaí River	Tributary	23°38’59.50”S/53°56’41.30”W
17	MPIRA	Pirajuí	Paraná River upstream of the mouth Pirajuí River	Main Channel	23°40’18.24”S/54°3’46.97” W
18	TPIRA	Pirajuí	Pirajuí River	Tributary	23°40’9.62”S/54°3’48.80” W
19	LSAJO	São João	São João Lagoon	Lagoon	23°49’01.98”S/53°59’32.62”W
20	MIGUA	Iguatemi	Paraná River upstream of the mouth of the Iguatemi River	Main Channel	23°55’27.90”S/54°9’16.60” W
21	TIGUA	Iguatemi	Iguatemi River	Tributary	23°55’37.60”S/54°11’22.00”W
22	MSARA	Saraiva	Paraná River upstream of the mouth of the Saraiva Lagoon	Main Channel	24°0’57.90”S/54°10’37.00” W
23	LSARA	Saraiva	Saraiva Lagoon	Lagoon	24°1’6.40”S/54°10’10.50”W
24	MPIQU	Piquiri	Paraná River upstream of the mouth of the Piquiri River	Main Channel	24°1’24.30”S/54°5’33.20”W
25	TPIQU	Piquiri	Piquiri River	Tributary	24°1’52.20”S/54°4’38.30”W

of organisms caught by the number of samples obtained. Later, the frequency of occurrence of each taxon was also calculated.

To evaluate the distribution of eggs and larvae in the different biotopes, an Analysis of variance (ANOVA One-way) with factor (biotope) and levels (lagoon, main channel, tributary) was used. The months of sampling were considered as replicates, total of 196 samples. When finding a significant F value, that is, when the means were significantly different in ANOVA, Tukey's post-hoc test was applied in order to detect these differences. Data were previously transformed into log10 (x + 1) to meet the assumptions of normality and homogeneity of variance (Peters, 1986).

To summarize the composition and structure of fish larvae, a Non-Metric Multidimensional Scaling (NMS) was applied using the Vegan package in R (Oksanen et al., 2012). The NMS was based on a Bray-Curtis distance matrix, calculated from the density data of the taxonomic groups found. Scores of NMS axis 1 were analyzed by one-way ANOVA in order to determine possible significant spatial variations in the composition and structure of fish larvae between biotopes and sampling stations. The assumptions of normality (Shapiro-Wilk) and homoscedasticity (Levene test) were previously checked. When ANOVA was significant, the Tukey's test was applied to determine which groups were significantly different from each other. The NMS was computed using the R software (R Core Team, 2015) and ANOVA in the Statistica™ 7.0 software (StatSoft Inc., 2005). The level of statistical significance adopted was $p < 0.05$.

3. Results

3.1. Spatial distribution

During the eight months of sampling, 592 eggs and 6,618 larvae were caught. The highest mean density of eggs was found in the tributary biotope, with 1.68 eggs/10m^3 and the lowest, in the main channel of the river, with 0.26 eggs/10m^3, although the ANOVA revealed no significant differences in egg abundance between the different biotopes (DF = 2, F = 0.78, p = 0.46) (Figure 1A). For the larvae, ANOVA evidenced significant differences between the biotopes (DF = 2, F = 4.75, p = 0.001), mainly between the lagoon, with a mean of 65.76 larvae/10m^3 and tributaries, with 3.96 larvae/10m^3 (Tukey's test, $p < 0.01$, respectively) (Figure 1B).

With respect to sampling stations, higher mean values of egg density were recorded in the Paracaí River (TPARA), with 11.45 eggs/10m^3, followed by the Amambai River (TAMAM), with 6.65 eggs/10m^3, both located in the tributary biotope (Figure 2). In the lagoon biotope, the LSARA site had the highest mean density, 1.15 eggs 10m^3, while in the main channel of the river, the site MAMAM station showed a mean density of 0.91 eggs/10m^3 (Figure 2). There were no records of eggs in MPARN, MBAIA, MPIRA and MSARA in the main channel biotope, as well as in TPIQU, in the tributary biotope (Figure 2).

Larvae were recorded in all the sites sampled, but the highest mean density was verified in LSARA, with 113.79 larvae/10m^3 (lagoon), followed by MMARA, with 43.42 larvae/10m^3 (main channel) and TIVIN and TAMAM, with

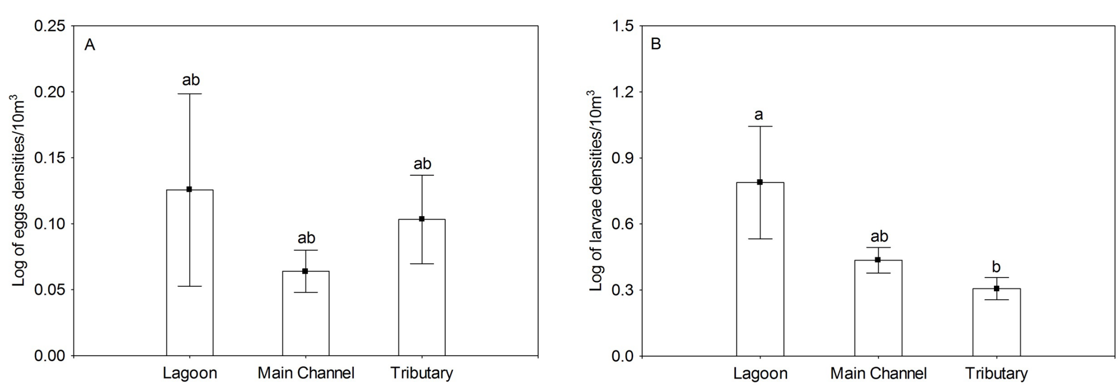

Figure 1. Density of eggs (A) and larvae (B) of fish observed in different biotopes of the Upper Paraná River floodplain between August 2013 and May 2015 (squares = mean; bars = standard error; values with different letters are significantly different).

12.52 and 11.99 larvae/10m³, respectively, both located in the tributary biotope (Figure 2).

3.2. Taxonomic composition

Throughout the samplings, we registered individuals belonging to six orders, 18 families and 29 genera and/or species. The order Characiformes presented the largest number of taxonomic groups (23 groups), followed by Siluriformes, with 11 groups (Table 2). In relation to the number of larvae in each order, more than 76% of the larvae were classified as Characiformes, 14% as Siluriformes, and the remainder divided into other orders (5%) and those that could not be identified (5%) (Table 2).

Regarding the reproductive guild, most of the groups identified belong to non-migratory (72%), divided among those with no parental

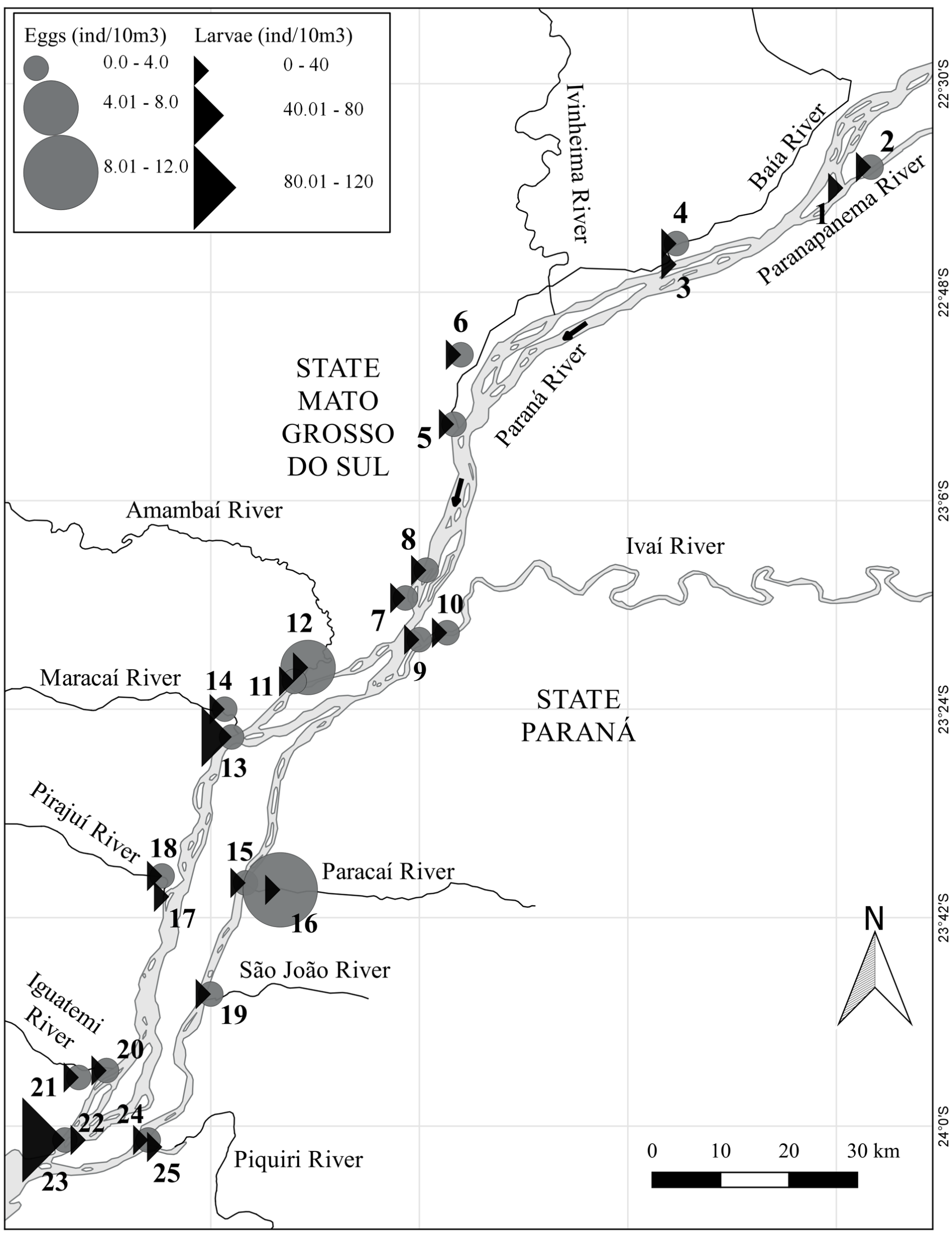

Figure 2. Spatial distribution of fish eggs and larvae (mean density) in different environments of the Upper Paraná River floodplain, between August 2013 and May 2015. 1 = MPARN; 2 = TPARN; 3 = MBAIA; 4 = TBAIA; 5 = MIVIN; 6 = TIVIN; 7 = MIVIH; 8 = TIVIH; 9 = MIVAI; 10 = TIVAI; 11 = MAMAM; 12 = TAMAM; 13 = MMARA; 14 = TMARA; 15 = MPARA; 16 = TPARA; 17 = MPIRA; 18 = TPIRA; 19 = LSAJO; 20 = MIGUA; 21 = TIGUA; 22 = MSARA; 23 = LSARA; 24 = MPIQU; 25 = TPIQU. Name of codes see Table 1.

Table 2. Taxonomic composition of fish larvae caught in different environments of the Upper Paraná River floodplain between August 2013 and May 2015, with the respective number caught (NC), frequency of occurrence (FO), mean density (M), and original reproductive guild (RG).

Taxa	NC	FO	M	RG
Class Osteichthyes				
ORDER CLUPEIFORMES				
Family Clupeidae				
Platanichthys platana (Regan, 1917)	141	2.13	1.28	NMFESC[1+]
ORDER CHARACIFORMES*	1	0.02	0.26	
Family Parodontidae				
Apareiodon spp.	54	0.82	2.75	NMFESC[2]
Family Curimatidae**	1	0.02	0.16	
Family Prochilodontidae				
Prochilodus lineatus (Valenciennes, 1836)	52	0.79	1.18	ML[2]
Family Anostomidae**	1722	26.02	8.44	
Family Crenuchidae				
Characidium spp.	1	0.02	0.34	NMFESC[2]
Family Hemiodontidae				
Hemiodus orthonops Eigenmann & Kennedy, 1903	352	5.32	5.12	ML[4+]
Family Characidae**	502	7.59	9.72	
Astyanax lacustris (Lucena & Soares, 2016)	2	0.03	0.27	NMFESC[2]
Bryconamericus stramineus Eigenmann, 1908	1964	29.68	8.94	NMFESC[2]
Diapoma guarani Mahnert & Géry, 1987	27	0.41	1.42	NMFESC[2]
Hyphessobycon eques (Steindachner, 1882)	1	0.02	0.29	NMFESC[2]
Moenkhausia bonita Benine, Castro & Sabino, 2004	2	0.03	1.12	NMFESC[2]
Moenkhausia forestii Benine, Mariguela & Oliveira, 2009	1	0.02	0.20	NMFESC[2]
Moenkhausia cf. *gracilima* Eigenmann, 1908	154	2.33	41.18	NMFESC[2]
Salminus brasiliensis (Cuvier, 1816)	52	0.79	2.23	ML[2]
Sub-Family Bryconinae				
Brycon orbignyanus (Valenciennes, 1850)	52	0.79	0.73	ML[2]
Sub-Family Serrasalminae				
Piaractus mesopotamicus (Holmberg, 1887)	73	1.10	1.38	ML[2]
Serrasalmus spp.	3	0.05	0.21	NMFECP[2]
Sub-Family Characinae				
Roeboides descalvadensis Fowler, 1932	1	0.02	0.42	NMFESC[2]
Family Cynodontidae				
Rhaphiodon vulpinus Spix & Agassiz, 1829	16	0.24	0.50	ML[2]
Family Erythrinidae**	1	0.02	0.23	
Hoplias spp.	16	0.24	0.62	NMFECP[2]
ORDER SILURIFORMES*	66	1.00	0.92	
Family Cetopsidae				
Cetopsis gobioides Kner, 1858	6	0.09	0.33	NMFESC[3]
Family Heptapteridae**	144	2.18	2.32	
Family Pimelodidae**	199	3.01	1.63	
Hypophthalmus oremaculatus Nani & Fuster 1947	36	0.54	4.32	NMFESC[2]
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	63	0.95	1.79	ML[2]
Sorubim lima (Bloch & Schneider, 1801)	7	0.11	0.62	ML[2]
Family Doradidae**	322	4.87	7.02	
Family Auchenipteridae				
Auchenipterus osteomystax (Miranda-Ribeiro, 1918)	88	1.33	1.80	FI[2]
Tatia neivai (Ihering, 1930)	1	0.02	0.18	FI[2]
Trachelyopterus galeatus (Linnaeus, 1766)	3	0.05	0.33	FI[2]

*identified only to the order level; **identified only to the family level; NMFESC = non-migratory or short-distance migratory, with external fertilization and no parental care; NMFECP = non-migratory or short-distance migratory, with external fertilization and with parental care; FI = non-migrant or short-distance migratory, with internal fertilization; ML = long-distance migratory with external fertilization. [1]Fialho et al. (2000); [2]Suzuki et al. (2004); [3]Smith et al. (2013); [4]Agostinho et al. (2015); [+]invasive species.

Table 2. Continued...

Taxa	NC	FO	M	RG
ORDER GYMNOTIFORMES*	1	0.02	0.26	
Family Gymnotidae				
Gymnotus spp.	2	0.03	0.25	NMFESC[2]
ORDER PERCIFORMES				
Family Sciaenidae				
Plagioscion squamosissimus (Heckel, 1840)	131	1.98	0.70	NMFESC[2]
ORDER PLEURONECTIFORMES				
Family Achiridae				
Catathyridium jenynsii (Günther, 1862)	4	0.06	0.24	NMFESC[2]
Unidentified	18	0.27	0.28	
Unidentifiable	336	5.08	3.36	

*identified only to the order level; **identified only to the family level; NMFESC = non-migratory or short-distance migratory, with external fertilization and no parental care; NMFECP = non-migratory or short-distance migratory, with external fertilization and with parental care; FI = non-migrant or short-distance migratory, with internal fertilization; ML = long-distance migratory with external fertilization. [1]Fialho et al. (2000); [2]Suzuki et al. (2004); [3]Smith et al. (2013); [4]Agostinho et al. (2015); [+]invasive species.

care (NMFESC), with 16 groups, those with parental care, (NMFECP) with 2 groups and those with internal fertilization (FI), with 3 groups. Long-distance migratory (ML) represented 28% of the groups identified (Table 2).

In the lagoon biotope, the site LSARA presented the highest number of taxonomic groups, as well as the highest abundances of larvae, mainly *Bryconamericus stramineus* Eigenmann, 1908, Characidae (unidentified) and *Moenkhausia* cf. *gracilima* Eigenmann, 1908 (Table 3). In this site, we also found larvae of large migratory species, such as *Brycon orbignyanus* (Valenciennes, 1850), *Prochilodus lineatus* (Valenciennes, 1836) and *Piaractus mesopotamicus* (Holmberg, 1887), as well as the invasive species *Hemiodus orthonops* Eigenmann & Kennedy, 1903 (Table 3).

In sites located in the main channel biotope, we observed a heterogeneous distribution of larvae. In MPARN and MBAIA, only one and two taxonomic groups were recorded, respectively (Table 3), while in MMARA (18 groups), MIVIN (15 groups) and MAMAM (17 groups), we registered the highest number of groups, mainly at the site MMARA with high abundance of larvae of Anostomidae (unidentified) and also the occurrence of larvae of six (*B. orbignyanus, Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *P. lineatus, P. mesopotamicus, Rhaphiodon vulpinus* Spix & Agassiz, 1829 and *Salminus brasiliensis* (Cuvier, 1816)) of the seven species of large migratory (Table 3). High abundance of *B. stramineus* was also observed in MIGUA, MSARA and MPIQU (Table 3). *Brycon orbignyanus* was the species that presented the broadest distribution, occurring in eight sites, while *S. brasiliensis* was recorded in only one site (MMARA). *P. corruscans*, *P. lineatus*, *P. mesopotamicus* and *R.vulpinus* also presented a considerable distribution among the sites, as well as the invasive species *Platanichthys platana* (Regan, 1917) and *H. orthonops* (Table 3).

In the tributary biotope, stood out the sites TAMAM (17 groups), TIVIN (17 groups) and TIVIH (15 groups), with the highest number of taxonomic groups, unlike TBAIA (2) and TPARA (3), where the lowest numbers were verified and TMARA none taxon was identified (Table 3). In relation to abundances, larvae of Doradidae (unidentified), Pimelodidae (unidentified) and Anostomidae (unidentified) were the most abundant in TAMAM, TIVIN and TIVIH sites, respectively (Table 3). These three sites also presented the highest abundances of larvae of migratory species, but some species were also found in TIGUA (*P. lineatus*), TIVAI (*S. brasiliensis*) and TPIQUI (*B. orbignyanus* and *P. lineatus*) (Table 3). *Platanichthys platana* and *H. orthonops* were also recorded in TBAIA, TIVIN and TIVIH (Table 3).

The non-metric multidimensional scaling (NMS) summarized the composition and structure of larvae of different fish species and indicated no differences between the biotopes (Figure 3A). A one-way ANOVA applied to NMS axis 1 scores corroborated this result ($F = 1.81$, $p > 0.05$). For sampling stations, there were significant differences in species composition (ANOVA, $F = 2.69$, $p < 0.001$, Figure 3B). The Tukey's post-hoc test indicated the sites that differed from each other (MBAIA and LSAJO, $p < 0.05$), (MBAIA

Table 3. Taxonomic composition and total density (larvae/10m³) of fish larvae found in the sampling stations of the Upper Paraná River floodplain between August 2013 and May 2015.

Taxonomic group	MPARN	TPARN	MBAIA	TBAIA	MIVIN	TIVIN	MIVIH	TIVIH	MIVAI	TIVAI	MAMAM	TAMAM	MMARA	TMARA	MPARA	TPARA	MPIRA	TPIRA	LSAJO	MIGUA	TIGUA	MSARA	LSARA	MPIQU	TPIQU
A. lacustris					+			+									+								
A. osteomystax		+				++			+	+++	+	+					+++		+		+				
Anostomidae		+			++	+++	+++	+++	+++	++	++	++	++++		+		+		+	++	++	++	+++	++	++
Apareiodon spp.																	+					+	+++	+	
**B. orbignyanus*					+	++	++	++	+		+		++				++			++			+	+	+
B. stramineus					+	++		++	+	++	+		++		++				++	+++	+	+++	++++	+++	+
C. gobioides					+							+								+			+		
C. jenynsii									+	+			+				++								
Characidae					+	++		+	+	+	+	++	+++		+				+	+++	+	++	++++	+++	++
Characidium spp.																					+				
Characiformes												+													
Curimatidae																				+					
D. guarani								+											++					+	
Doradidae						++	++				+	+++	++		+					+		+	++	+	++
Erythrinidae													+												
Gymnotiformes												+													
Gymnotus spp.											+	+													
H. eques																		+							
H. oremaculatus		++						+	++								++		++				+++		
H. orthonops					++	+		++					++		+		+			++		+++	+++	++	
Heptapteridae					++	+	+				+	++	+++							++			++	+	+
Hoplias spp.			+									++				+		++						+	
M. cf. *gracilima*															+								++++		
M. bonita																							++		
M. forestii													+												
**P. corruscans*						+++		++	+		++	+	+											+	
**P. lineatus*					++	++	+	+				++	++				+				+	+	+		+
**P. mesopotamicus*						++	+	++			+	+	+++				++						+		
P. platana				++	+	+	++	+	++		+		+++		+		++	+		++				+	
P. squamosissimus	+	++		+	+	+	+	++	++	+	++		++		++		+	++	+	++	+	+		++	

*long-distance migratory species; + 0.01 – 1.00 larvae/10m³; ++ 1.01-10.00 larvae/10m³; +++ 10.01 - 100 larvae/10m³; ++++ Higher than 100.01 larvae/10m³.

Table 3. Continued...

Taxonomic group	MPARN	TPARN	MBAIA	TBAIA	MIVIN	TIVIN	MIVIH	TIVIH	MIVAI	TIVAI	MAMAM	TAMAM	MMARA	TMARA	MPARA	TPARA	MPIRA	TPIRA	LSAJO	MIGUA	TIGUA	MSARA	LSARA	MPIQU	TPIQU
Pimelodidae		+			++	+++	++	+	+	++	++	++			+					++	+	+			+
R. descavaldensis															+		+								
**R. vulpinus*					+	++					+		+							+					
**S. brasiliensis*						++				++		+	+												
**S. lima*						+						++													
Serrasalmus spp.			+						+								+						+		
Siluriformes					+	++	+	++		+	++	++	+							+					+
T. galeatus					+																		+		
T. neivai		+																							
Unidentifiable			+		+	++	++	++	++	++	+	++	++		+	+		+		++	++	++	+++	+++	++
Unidentified					+	+	+		+		+	+		+	+	++				+	+			+	
Number of taxa identified	1	6	3	2	15	17	10	15	12	9	15	17	18	0	10	1	14	4	7	14	8	9	16	12	9

*long-distance migratory species; + 0.01 – 1.00 larvae/$10m^3$; ++ 1.01-10.00 larvae/$10m^3$; +++ 10.01 - 100 larvae/$10m^3$; ++++ Higher than 100.01 larvae/$10m^3$.

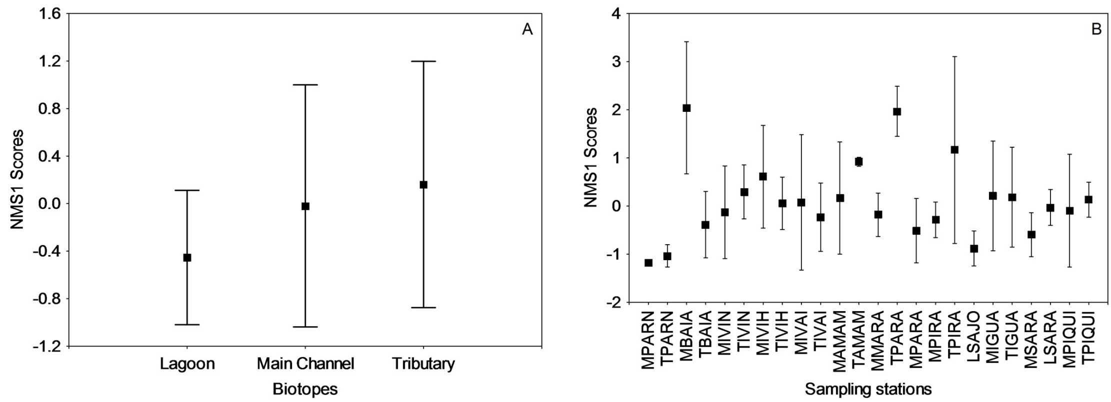

Figure 3. Mean variation of NMS axis 1 scores (two-dimensional solution, stress: 0.14) for spatial analysis: biotopes (A) and sampling sites (B) in relation to the structure and composition of fish larvae sampled between August and May 2015 in the Upper Paraná River floodplain (squares = mean; bars = standard error).

and TPARN, $p < 0.001$) and (TPARA and TPARN, $p < 0.05$).

4. Discussion

Floodplains are characterized by the presence of different biotopes (e.g. main channel, tributaries and lagoon) that are used by species with different ecological requirements during their life cycle (Paiva, 1982; Junk et al., 1989). In particular, in the Upper Paraná River floodplain, although we have adopted a design with few samplings and only one equipment, the capture of eggs and larvae was considerable (592 eggs and 6,618 larvae) when compared, for example, to the study by Gogola et al. (2010) developed exclusively during the reproductive period (October to March), in tributaries and lagoon of the Ilha Grande National Park, in which the authors found 8,029 eggs and 25,190 larvae. This result indicates that despite the fact that it is under several human impacts, the only dam-free stretch in the Upper Paraná River can still be considered an important breeding site for fish species, corroborating the results found by Baumgartner et al. (2004), Bialetzki et al. (2005), Gogola et al. (2010, 2013), Reynalte-Tataje et al. (2011, 2013), Barzotto et al. (2015) and Silva et al. (2016), which sampled some of the stations here evaluated, with most of the samples performed during the reproductive period.

Fish spawning habitats, in general, are the large tributaries of the Paraná River (Agostinho et al., 2003). Our results partially confirm this pattern, since no significant differences were detected between the biotopes and in occurrence of eggs, although the greatest abundances were found in the tributaries. Among the sampled sites, the main routes used for spawning were the Amambai and Paracaí rivers, both located within the Ilha Grande National Park, on the right and left banks of the main channel of Paraná River, respectively. These tributaries, in addition to maintaining the reproduction events, have still contributed with the input of larvae to the downstream stretches. Numerous studies carried out in this basin (Baumgartner et al., 2004; Daga et al., 2009; Gogola et al., 2010; Reynalte-Tataje et al., 2011, 2013; Da Silva et al., 2015; Silva et al., 2016) and in the basins of the rivers Uruguay (Reynalte-Tataje et al., 2008, 2012a, b; Hermes-Silva et al., 2009; Corrêa et al., 2011) and São Francisco (Sato et al., 2005; Weber et al., 2013; Normando et al., 2014; Nunes et al., 2015), as well as in other parts of the world (Bottcher et al., 2013; Webber et al., 2013; López-Casas et al., 2016), have argued for the importance of free-flowing tributaries upstream of regulated rivers as alternative migratory routes. Nevertheless, it is important to emphasize the need for an adequate distance between the spawning site and the complete early embryonic and larval development, preventing the drift of larvae to inappropriate places, such as reservoirs, where they can be preyed upon or settle to the substrate (Pelicice & Agostinho, 2008; Olden, 2016). In the case of dorado (*S. brasiliensis*), for example, Rosa et al. (No prelo) estimated with based on the Ivinheima river flow rate and the time (hours) between stages of development, the distance traveled between the hatching and the post-flexion stage, when the larvae already have the caudal, anal and dorsal fins partially or fully developed and can perform swimming movements, was just over 100 kilometers.

The marginal lagoons of river-floodplain systems are widely recognized for the importance in the maintenance and integrity of regional biodiversity, either as natural breeding grounds for commercially important species, most of which are long-distance migratory (Welcomme, 1979, 1985; Agostinho et al., 1993, 2000), or as a preferential habitat for sedentary and small species. In the lagoon biotope, larvae are highly abundant in the Saraiva Lagoon, which is permanently connected to the Paraná River. This lagoon presented sixteen taxa among the thirty-nine found in the study, among the non-migratory species stand out *B. stramineus* and *M.* cf. *gracilima* and among the migratory species, *B. orbygnianus, P. lineatus* and *P. mesopotamicus.* A study carried out in the same lagoon by Daga et al. (2009) found twenty-five taxa, including the migratory species *S. brasiliensis, P. corruscans, Pterodoras granulosus* (Valenciennes, 1821) and *Pimelodus* spp. For Petry et al. (2003), fish species diversity and the size of stocks of migratory species depend largely on the conservation and integrity of marginal ponds.

The sites located in the main channel of the Paraná River also stood out in relation to larval abundance and the number of taxonomic groups, including important migratory species (*B. orbignyanus, P. corruscans, P. lineatus, P. mesopotamicus, R. vulpinus* e *S. brasiliensis*). This result may be due to larval drift, in which species would use the main channel of the river as a transport corridor between spawning grounds and growing sites. In this case, eggs and larvae could be transported to (i) low flow areas and macrophytes, (ii) marginal lagoons or (iii) reach the Itaipu Reservoir, to complete their development as suggested by Baumgartner et al. (2004). The larval drift could occur either in the middle of the channel or near the banks, taking advantage of the decrease in current velocity or taking advantage of the proximity to floodplain lagoons (Araujo-Lima & Oliveira, 1998).

The main channel of the Paraná River may also be used for the spawning and growth of some species. Galat & Zweimüller (2001) state that fluvial specialist species can complete their entire life cycle in this biotope, using areas near the banks as growing sites. Nannini et al. (2012) suggests that larval fish show habitat specialization, similar to adults, indicating that both the backwater lakes and the main channel are important for larval fish and preserving the diversity of fish assemblages in large floodplain rivers. However, the use of these areas by the larvae still needs to be better investigated, with the aid of complex analysis of development stages and complete habitat structure.

In general, we did not find an expected longitudinal pattern of distribution of eggs and larvae, that is, where eggs would be more abundant in upstream reaches and larvae in downstream areas. On the contrary, our results show that the eggs were caught in several sampling stations, indicating that the spawning may be occurring within the tributaries and the eggs drifting to the Paraná River channel, but may also be occurring in the Paraná River itself, as already discussed above. Another interesting result is the low abundance and also the reduced number of taxa found in MPARN, TPARN, MBAIA and TBAIA sites, located near the HPPs of Porto Primavera (Paraná River) and Rosana (Paranapanema River). This may be the direct result of the oligotrophication that the Paraná River has been suffering over the past twenty years, caused by reservoir cascades in the basin and aggravated by the formation of Porto Primavera Reservoir (Roberto et al., 2009). Turbid waters are essential for the survival of fish eggs and larvae as they decrease visual predation (Agostinho et al., 2002). In the Uruguay River basin, Reynalte-Tataje et al. (2012a) reported similar results and suggested that low densities downstream of dams indicate low reproductive activity influenced by water quality and flow control, with an abundance improvement only one hundred and thirty kilometers downstream of the dam. In the Upper Parana River, this effect also seems to be minimized near the Ivinheima River, about ninety kilometers downstream of Porto Primavera, where the abundances were comparatively greater, confirming the importance of this river for this stretch of the basin.

In almost all sites downstream of the Ivinheima River, there were considerable catches of eggs or larvae or both. These results can support the Serial Discontinuity Theory (SDC) (Ward & Stanford, 1995), which assumes that smaller rivers, as well as floodplain, represent lateral interference in rivers, contributing with the input of organic and inorganic particulate matter, restoring the natural attributes that were degraded with flow regulation by upstream reservoirs (Stanford & Ward, 2001). The theory further argues that the river, according to lateral, vertical and longitudinal gradients, presents an innate tendency to recovery, including the aquatic communities, that is, the river channel downstream of Porto Primavera, as well as environments adjacent to this remnant are capable of offering biotic and abiotic conditions for reproduction of the regional fish fauna.

As for the taxonomic categories, it was not possible to identify the eggs collected, due to the lack of information on the morphology of these eggs in the literature. Among the larvae, there were a significant number of taxonomic groups identified between genera and species, which accounted for approximately 16% of the total number of species recorded by Graça & Pavanelli (2007) for the region. The predominance of Characiformes and Siluriformes larvae reflects the species richness of these two orders in the region. According to Langeani et al. (2007), these two orders account for about 80% of the species and comprise the dominant groups in most of the lotic environments of the Upper Paraná River.

Most of the larvae recorded are of non-migratory or short-distance migratory species with external fecundation and with no parental care. Suzuki et al. (2004) reported that more than 83% of the species in the region are sedentary or migrate short distances to reproduce, while other species (little more than 16% or nineteen species) perform reproductive migrations. In this study, larvae of seven migratory species were found, *B. orbignyanus P. corruscans, P. lineatus, P. mesopotamicus, R. vulpinus, S. brasiliensis* and *S. lima*, evidencing the key role of this remnant in the maintenance of these fish with specific requirements for reproduction. However, the low abundance verified may be a direct consequence of the changes in the environment and/or the strong pressure on fish stocks in the region (Sanches et al., 2006). According to the Red Book of the Threatened Fauna in the State of Paraná (Livro Vermelho da Fauna Ameaçada no Estado do Paraná) (Abilhoa & Duboc, 2004), migratory species such as *P. corruscans* and *S. brasiliensis* are already very rare throughout the Paraná River basin, being found in small size and number, while *B. orbignyanus* was classified as "endangered" in the Ordinance 445 of December 17, 2014 by the Ministry of the Environment (Brasil, 2014), decree 445. It is also important to consider in this result the reduced number of samplings made in the reproductive period of the species.

The presence of larvae of invasive species such as *H. orthonops* and *P. platana* was a worrying result. According to Agostinho et al. (2015), *H. orthonops*, a migratory species from the Paraguay and Paraná rivers basin, invaded the Upper Paraná River in 2002, through the "Piracema Canal (ITAIPU)" transposition mechanism, and is currently established. In turn, *P. platana*, whose origin is still unknown, is probably already established as well (Langeani et al., 2007). Meanwhile, its invading potential can be measured by its high dispersal potential, since it was found in all sampled biotopes (lagoons, main channel and tributary) and, practically, in the whole plain, as well as its opportunism in relation reproduction and characteristics of the environment, which probably favored its establishment.

The results found in this study reinforce the importance of the integrity of this remnant and its biotopes (main channel, tributaries and marginal lagoons) for the maintenance of the fish fauna, mainly of migratory species and those with importance for regional fishing. However, the existence of three conservation units in the floodplain does not rule out the risk of new hydroelectric projects being built in this remnant, especially in tributaries that still maintain intact their original characteristics. The Piquiri and Ivaí rivers would be the most affected in the short term (EPE, 2013; Affonso et al., 2015), in the case of new constructions (HPPs and Small Hydropower Plants). In this sense, Affonso et al. (2015) demonstrated the importance of join local communities, law experts and universities in the search for joint actions to impede the construction of new dams in the basin. Nonetheless, broader actions could also involve the state sphere, for example the State of Minas Gerais, which created, through Law 15082 of April 27, 2004, a type of conservation unit not provided for in the National System of Conservation Units, called "Permanent Preservation Rivers", constituting an important initiative for the conservation of fish in their respective basins (Pompeu, 2012) and also of sites already impacted and vulnerable to new interventions, such as the Paraná River basin.

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