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Macrophytes banks as potential fish nursery areas in small hydropower reservoirs

Bancos de macrófitas como potenciais áreas de berçário para peixes em pequenos reservatórios de hidrelétricas

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Abstract: Aim: This study verified if the macrophyte banks found in two reservoirs of small hydroelectric plants (SHPs) have a functional ecological role for the initial development of ichthyofauna. Additionally, we compared the differences in the structure of the fish assemblages along each reservoir compartment and between reservoirs. **Methods:** Sampling was performed in March 2018, in lotic, intermediate, and lentic compartments of Palmeiras and Retiro reservoirs, Sapucaí-Mirim River (SP). Three distinct macrophyte banks in each stretch (triplicates), considering the most representative in terms of composition (recurrency/dominance), were sampled, resulting in 18 samples (nine per reservoir). For fish collection we used a sieve of 1 m^2 of area, mesh size of 1 mm, which was manually hauled, from the boat, in the marginal aquatic vegetation (three hauls per sample). Simultaneously, we measured basic limnological parameters with a Horiba U-52 water probe, adjacent to the banks. **Results:** The presence of juveniles of all fish orders found in the river, Characiformes, Siluriformes, Synbranchiformes, Gymnotiformes and Cichliformes, demonstrates that, at least in certain moment of their development cycle, the macrophyte banks are used by species with different ecological requirements. It was observed significant statistical differences in the structure of the ichthyofauna along the longitudinal axes of the reservoirs, but not between reservoirs. The same was seen for the limnological data (PCA). **Conclusions:** The macrophyte banks found in the SHPs reservoirs have a potential role as nurseries for the local ichthyofauna, mainly, but not exclusively, for sedentary species and with parental care. This association is ecologically relevant, given the absence of typical lateral habitats for the initial development of the fish fauna. Additionally, despite the reservoirs small size, spatial organization was also important for the assemblage's structure, with differences in terms of composition, size and development stages along the distinct sampling stretches.

Keywords: reservoir cascade; ichthyofauna; juveniles; larvae; spatial organization.

Resumo: Objetivo: O presente estudo verificou se os bancos de macrófitas presentes nos reservatórios de pequenas centrais hidrelétricas desempenham um papel ecológico funcional no desenvolvimento inicial da ictiofauna. Adicionalmente, comparou-se a estrutura das assembleias de peixes ao longo dos compartimentos de cada reservatório e entre os reservatórios. **Métodos:** A amostragem foi realizada em março de 2018 nos compartimentos lótico, intermediário e lêntico dos reservatórios de Palmeiras e Retiro, rio Sapucaí-Mirim (SP). Três bancos diferentes de macrófitas por trecho (tréplicas), considerando os mais representativos em termos de composição (recorrência/dominância), foram amostrados, no total de 18 amostras (nove por reservatório). Para a coleta dos

peixes foi utilizada peneira de 1 m^2 de área, abertura de malha de 1 mm, introduzida manualmente, da proa do barco, sob a vegetação aquática marginal e erguida rapidamente (três lances por amostra). Simultaneamente, foram medidos parâmetros limnológicos básicos, utilizando sonda Horiba U-52, adjacente aos bancos. **Resultados:** A presença de estágios juvenis para todas as ordens de peixes encontradas no rio, Characiformes, Siluriformes, Synbranchiformes, Gymnotiformes e Cichliformes, demonstra que os bancos de macrófitas são utilizados, em algum momento do seu ciclo de desenvolvimento, por espécies com diferentes requerimentos ecológicos. Foram observadas diferenças estatísticas significativas na estrutura da ictiofauna no eixo longitudinal dos reservatórios, mas não entre os reservatórios. O mesmo foi verificado para os dados limnológicos (ACP). **Conclusões:** Os bancos de macrófitas encontrados nos reservatórios de pequeno porte das PCHs do rio Sapucaí-Mirim são berçários potenciais para a ictiofauna, principalmente, mas não exclusivamente, para espécies sedentárias e com cuidado parental. Esta associação é ecologicamente relevante, dado a ausência de habitats laterais típicos para o desenvolvimento inicial da ictiofauna. Adicionalmente, a despeito do pequeno porte dos reservatórios, a organização espacial também se mostrou importante, com diferenças em termos de composição, tamanho e estágios de desenvolvimento ao longo dos distintos trechos de amostragem.

Palavras-chave: cascata de reservatórios; ictiofauna; juvenis; larvas; organização espacial.

1. Introduction

In Brazil, the energy matrix is still highly dependent on hydropower generation, which represents around 65% of the production (EPE, 2020). In this scenario, the contribution of small hydroelectric plants (SHPs) has increased, with hundreds of generation units in operation, summing 5.5 x10^6 kW, distributed all over the country (ANEEL, 2019). The SHPs have lower construction cost, attracting more investors; losses in the energy transportation are lower, as they usually supply nearby consumers; there is also higher feasibility to be built in smaller and widely distributed rivers; with shorter implementation times and less restrictive legislation (Sharma et al., 2013). Despite the benefits hydropower brings to society in terms of energy supply, river damming may cause major changes in aquatic environments, such as fragmentation, loss of original habitats, changes in the physical and chemical water conditions, in the structure and functioning of aquatic communities and in the interactions with terrestrial ecosystems (e.g. Tundisi 1999, 2018; Agostinho et al., 2005, 2016; Soares et al., 2008; Nogueira et al., 2012). Most studies are focused on large hydropower reservoirs and the environmental impacts generated by SHPs in Brazil are still scarce (Ruocco et al., 2019).

Distinct hydrological and limnological characteristics, from the original fluvial conditions, including physical compartmentalization, are the main determinants for the restructuring of the aquatic biota in reservoirs (Agostinho et al., 2008; Nogueira et al., 2008; 2010). Despite the lack of information, such longitudinal organizational pattern may also occur in SHP reservoirs. Another important aspect to be considered are the effects of reservoirs arranged in sequence – cascade systems, when several dams are present in the same river (Nogueira & Pomari, 2019). The effects of dam's sequences on fish assemblages depend on the position of the reservoirs in the river basin (Ferrareze et al., 2014; Loures & Pompeu, 2018; Pelicice et al., 2018). Negative impacts of river damming on fishes are notorious, even in SHP reservoirs (Arcifa & Esguícero, 2012; Bakken et al., 2012). The ichthyofauna affected by SHPs may exhibit reduction in abundance, average length, total weight, and condition factor (Benejam et al., 2016); interruption of the individual's free movement along the river (Bakken et al., 2012; Kucukali, 2014) and changes in ichthyoplankton dispersion (Suzuki et al., 2011; Pelicice et al., 2014, Brambilla et al., 2020).

For the neotropics it has been proven the importance of lateral habitats associated with rivers and reservoirs, such as marginal lagoons and tributaries, for fish reproduction and development (e.g. Vianna & Nogueira, 2008; Ferrareze & Nogueira, 2011; Agostinho et al., 2016). Especially in marginal lagoons, fish larvae and juveniles find refuge from predators and availability of food resource, essential conditions for early stages survival (Orsi et al., 2016). The presence of macrophyte banks, when they are not excessive in coverage and biomass (Pompêo, 2017), increases the complexity of habitats, which contributes for the maintenance of fish diversity (Agostinho et al., 2003; 2007; Pelicice et al., 2008; Dibble & Pelicice, 2010; Hermes-Silva & Zaniboni-Filho, 2012).

Nevertheless, the role of aquatic plants for the fish fauna in SHPs reservoirs is still poorly investigated. In some SHPs reservoirs, due to their small size and simplified morphometry, ecological functional connectivity with lateral environments may not properly exist. In this case, the occurrence of certain habitats, such as the aquatic macrophyte banks, can ensure the initial survival and consequently the regional maintenance of several fish species (Kirjasniemi & Valtonen, 1997; Wilzbach et al., 2002; Bulla et al., 2011; Hermes-Silva & Zaniboni-Filho, 2012).

Two SHP's reservoirs were selected in our study, located in Sapucaí-Mirim River, north of São Paulo State, Brazil. This river basin has a diverse fish fauna, with at least 105 species (Oliveira et al., 2016; Brambilla et al., 2019; Diniz et al., 2019), and it is an important direct tributary of the Grande River, upper Paraná Basin. The fish fauna is mainly represented by small and medium-size species, with only three large-sized migrators (Oliveira et al., 2016). A recent study, based on ichthyoplankton analyzes, provided consistent information about the presence of quantitatively important spawning sites, even for migratory species, in the Sapucaí-Mirim SHP reservoirs (Brambilla et al., 2020). Authors concluded that the reproductive products drift downstream, passing through the dam's physical structures, including the fish-ladders. However, it is unknown if recruitment processes are taking place along the dammed stretches, given the absence of typical nursery areas, such as lagoons and tributaries. A similar question was posed by Ávila-Simas et al. (2014), which searched for alternative spawning and nursery areas – pools and rapids, in a tributary without floodplains of the upper Uruguay River.

Based on the premise that littoral habitats are important for early fish development, the aim of this study was to verify if the macrophyte banks found in two reservoirs of small hydroelectric plants (SHPs) have a functional ecological role for the initial development of fishes. The investigation comprised the analysis of representative macrophyte banks, independent on their species composition or life-forms, distributed along the main axis of both reservoirs. We hypothesize that the aquatic plants have an important functional role as fish nursery areas. Additionally, we also searched for longitudinal differences in the structure of the plant-associated fish assemblages, as well as in the limnological variables, within each reservoir and between both reservoirs.

2. Material and Methods

2.1. Study area

The Sapucaí-Mirim River springs are located in the Atlantic Plateau (Serra da Mantiqueira), between the states of São Paulo and Minas Gerais. The river mouth is located in the left margin of Porto Colômbia Reservoir, middle stretch of Grande River (Paiva, 1982). It is a plateau river, with several rapids and small waterfalls in the upper section, becoming less turbulent with decreased water velocity in the lower section. Another distinctive characteristic of this river is the presence of several knickzones mesohabitats, bed rock (basaltic) platforms popularly known as "pedrais" (Brambilla et al., 2019; Ruocco et al., 2019). The river total length is 290 km, with its course entirely in the State of São Paulo (Paiva, 1982).

In the main channel of the Sapucaí-Mirim River there are three SHPs arranged in a reservoir cascade system, Palmeiras, Anhanguera and Retiro, which started to operate in 2011, 2009 and 2013, respectively. For this research, two reservoirs were selected, Palmeiras and Retiro, the most upstream and the most downstream in the cascade (Figure 1). The reservoirs are similar in area, Palmeiras 2.6 km^2 and Retiro 2.8 km^2, and despite the second has a longitudinal axis (from the lotic zone to dam) which is 1.5 times larger than the first one (11 and 7.5 km, respectively), both are considered short. The average retention time is 3.3 days for Palmeiras and 3.4 days for Retiro (Brambilla et al., 2020). These reservoirs were chosen because they belong to the same stakeholder (CTG Brazil), which allowed us the access into the area, and have similar monitoring requirements determined by the Environmental Company of São Paulo State (CETESB).

2.2. Sampling

Sampling was performed in March 2018, at the end of the annual reproductive period ("piracema") for most native fish species (Vazzoler, 1982). In each lotic, intermediate, and lentic compartment of Palmeiras and Retiro reservoirs (Figure 1), three distinct macrophyte banks (nine per reservoir) were sampled in triplicates (Table 1), resulting in a total of 18 samples. The macrophyte banks were randomly chosen within each compartment, considering the recurrent/dominant species determined through visual inspection. It is important to mention that submerged macrophytes do not occur in these reservoirs, probably due to

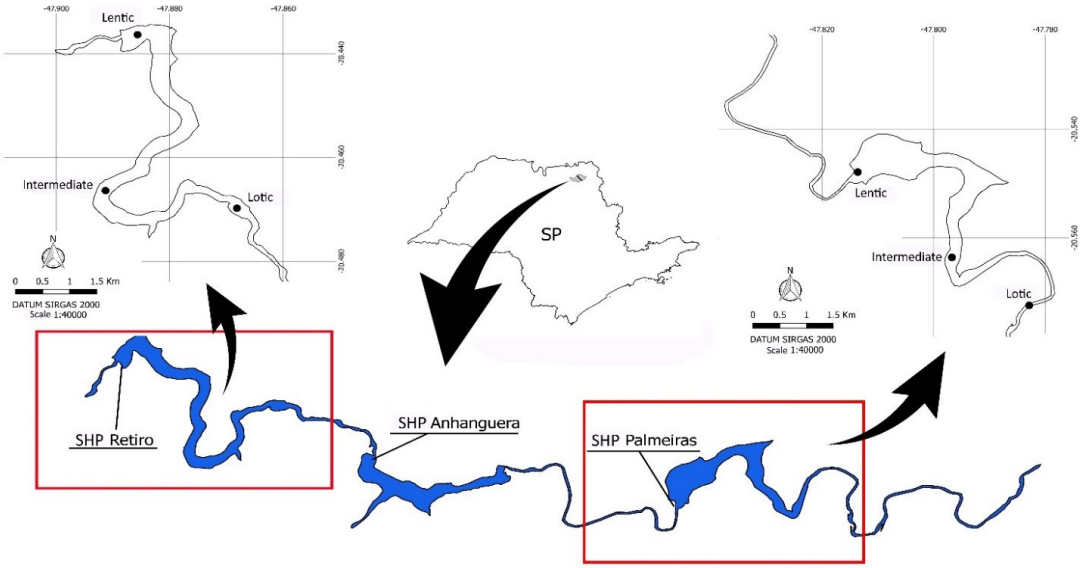

Figure 1. Map of the Sapucaí-Mirim River (SP, Brazil) stretch, where are located the studied Small Hydropower Plants (SHPs) reservoirs – Palmeiras and Retiro, with indication of the sampling sites.

the excessive water turbidity mainly observed in the summer-rainy season. For fish collection we used a sieve of 1 m^2 of area, with mesh size of 1 mm, which was manually introduced bellow the marginal aquatic vegetation and raised quickly (three times per sample). It was assumed that most fish larvae with exogenous feeding, therefore with active swimming (not in passive derive), should be captured with a 1 mm mesh size. Sampling was carried out from the forward part of the boat (bow), which was moving (engine propulsion) towards the plants. The collected material was stored in plastic bags and eugenol solution was immediately added to anesthetize the organisms. Subsequently, the samples were fixed in 4% formalin solution. Sampling was performed under the license SISBIO 13.794-1.

Simultaneously to the fish samplings, the following environmental variables were measured in the water sub-surface: temperature, pH, electrical conductivity (K), turbidity, dissolved oxygen (DO) and oxide-reduction potential (ORP), with a previously calibrated Horiba U-52 multiparameter probe.

2.3. Sorting and identification

The sampled fish was sorted and transferred to polyethylene bottles with a 4% formalin solution and calcium carbonate for preservation of the bone structures. Larger fishes were immediately separated for posterior identification. The detailed sorting for larvae and small juveniles was made in laboratory using a Bogorov acrylic plate under stereo-microscope ZEISS (STEMI SV 6). The individuals captured were classified into three stages (larval, juvenile, and adult) and identified to the lowest taxonomic level possible. Individuals in larval phase were identified following Ahlstrom & Moser (1976) and Nakatani et al. (2001). The fish in juvenile and adult stages were identified following specialized references (Castro et al., 2004; Graça & Pavanelli, 2007; Langeani & Rego, 2014; Ota et al., 2018). The taxonomic framework followed Fricke et al. (2019).

The term "larvae" refers to the period of development between the egg hatching and the total formation of the fins (with rays) and scales (depending on the taxonomical group). The "juvenile" term refers to the period between the initial development of fin and scales and sexual maturity (Nakatani et al., 2001). For differentiation between juveniles and adults, it was used the length at first maturity (LS50) (Langeani & Rego, 2014). Using a caliper, we obtained the total length of the animals, snout tip to the end of the caudal fin. Individuals with total length smaller than LS50 described in the literature were classified as juveniles, and individuals with total length equal to or larger than LS50 were classified as adults.

Table 1. The main aquatic macrophytes present and the sampling points geographic coordinates in Palmeiras and Retiro reservoirs, Sapucaí-Mirim River (SP) (*exotic species).

Sampling area	PALMEIRAS		RETIRO	
	Main aquatic macrophytes	Geographic coordinates	Main aquatic macrophytes	Geographic coordinates
Lotic 1	Cyperaceae, *Urochloa distachya**	20°32'33.0"S 47°48'46.0"W	Cyperaceae, *Eichhornia crassipes*, *E. azzurea*	20°29'10.2"S 47°51'29.2"W
Lotic 2	Cyperaceae, *Urochloa distachya**	20°32'30.9"S 47°48'40.4"W	Cyperaceae, *Eichhornia crassipes*, *E. azzurea*	20°29'07.6"S 47°51'31.2"W
Lotic 3	Cyperaceae, *Urochloa distachya**	20°32'35.2"S 47°48'10.1"W	*Salvinia* spp., *Eichhornia crassipes*, *E. azzurea,* Cyperaceae	20°29'03.7"S 47°51'31.6"W
Intermediate 1	*Pistia stratiotes, Eichhornia crassipes*, *Salvinia* spp.	20°33'59.6"S 47°47'34.7"W	*Salvinia* spp., Cyperaceae	20°27'40.7"S 47°53'03.3"W
Intermediate 2	*Eichhornia crassipes*	20°33'59.9"S 47°47'35.2"W	Cyperaceae	20°27'42.4"S 47°53'03.6"W
Intermediate 3	Cyperaceae, *Eichhornia crassipes*	20°33'58.5"S 47°47'30.9"W	*Eichhornia crassipes, E. azzurea*, *Salvinia* spp., Cyperaceae	20°27'45.9"S 47°53'06.4"W
Lentic 1	Cyperaceae, Poaceae	20°33'47.7"S 47°46'56.5"W	*Salvinia* spp., *Pistia stratiotes, Eichhornia crassipes, E. azzurea*	20°26'03.8"S 47°53'00.2"W
Lentic 2	*Salvinia* spp., *Pistia stratiotes,* Poaceae, *Eichhornia crassipes, E. azzurea,* Cyperaceae	20°33'47.6"S 47°46'51.5"W	*Salvinia* spp., *Eichhornia crassipes, E. azzurea,* Cyperaceae	20°26'20.0"S 47°53'00.3"W
Lentic 3	*Salvinia* spp., *Pistia stratiotes*, Poaceae, *Eichhornia crassipes*, Cyperaceae	20°34'17.4"S 47°46'53.8"W	*Salvinia* spp., Cyperaceae	20°26'19.9"S 47°52'47.8"W

2.4. Statistical analysis

Initially, a descriptive approach was performed through the elaboration of graphics (SigmaPlot) of richness, absolute abundance, relative abundance by order and by development phase and size. Representations include the entire data set as well as their central (mean) and dispersion (standard deviation) descriptors. The same pattern of representation was used for limnological variables. These environmental data were tested through analysis of variance (ANOVA) for significant differences ($p < 0.05$) among compartments (lotic, intermediate, and lentic) and between reservoirs (Palmeiras and Retiro). A principal component analysis (PCA) was performed to ordinate the spatial trends in limnological conditions. Data were previously transformed using log (x + 1) (except for pH) and normalized. Finally, a Multivariate Permutation Variance Analysis (PERMANOVA), based on the Bray-Curtis similarity matrix, derived from log (x + 1) fish abundance and richness data, was used to test for differences in assemblage structure among the compartments and between the reservoirs.

3. Results

3.1. Limnology

The values of the limnological variables (temperature, pH, ORP, electrical conductivity, turbidity, and dissolved oxygen) (mean and standard deviation and statistical differences) measured in the different reservoir's compartments are presented in Table 2.

For the lentic compartment, all variables showed significant statistical differences between reservoirs. For the intermediate compartment, half of variables showed differences. For the lotic compartment, only dissolved oxygen was statistically different. Comparing lotic, intermediate, and lentic compartments, we observed difference for three variables within Palmeiras, and for four variables in Retiro.

Table 2. Mean values and standard deviations (into parentheses) of the limnological variables measured in the different compartments of Retiro and Palmeiras SHPs reservoirs, Sapucaí-Mirim River (SP).

Reservoir	Compartiment	Temp. (°C)	pH	ORP (mV)	Conductivity (µS cm^{-1})	Turbidity (NTU)	DO (mg L^{-1})
Palmeiras	Lotic	26.59 (0.11) (A)	7.54 (0.18) (AB)	245.33 (16.16) (A)	60 (5.77e-4) (A)	67.53 (6.26) (A)	8.95* (0.34) (A)
	Intermediate	26.48 (0.02) (A)	7.79 (0.19) (A)	229.00 (8.54) (A)	60* (5.77e-4) (B)	60.83* (2.84) (A)	9.40* (0.48) (A)
	Lentic	31.97* (0.38) (B)	8.13* (0.18) (B)	233.00* (7.54) (A)	50* (0.00) (B)	42.36* (2.74) (A)	9.47* (0.17) (A)
Retiro	Lotic	26.48 (0.03) (a)	7.56 (0.09) (a)	269.33 (5.13) (a)	50 (5.77e-4) (a)	40.33 (8.55) (a)	8.26* (0.37) (a)
	Intermediate	26.96 (0.32) (ab)	7.38 (0.28) (a)	254.33 (24.78) (a)	50* (1.15e-3) (b)	32.93* (6.82) (a)	7.48* (1.13) (ab)
	Lentic	27.28* (0.57) (b)	7.32* (0.08) (a)	261.66* (17.50) (a)	50* (0.00) (c)	65.90* (26.01) (b)	6.67* (0.58) (b)

*Indicates statistical difference between reservoirs and different letters among compartments ($p < 0.05$, ANOVA). Uppercase letters among Palmeiras compartments and lowercase letters among Retiro compartments. ORP: oxide reduction potential, NTU: nephelometric turbidity units, DO: dissolved oxygen.

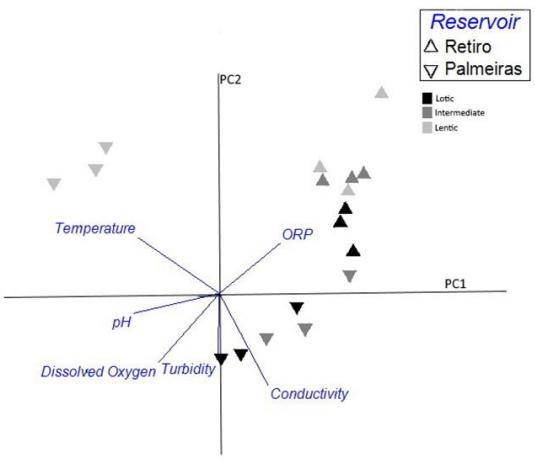

Figure 2. Graphic results of principal component analysis (components 1 and 2), based on the limnological characteristics adjacent to macrophyte banks in lotic, intermediate, and lentic compartments of Palmeiras and Retiro SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

The Principal Component Analysis (Figure 2) explained 71.1% of data variability (43.7% in the first component and 27.4% in the second component). All variables, except turbidity, showed a high correlation (> 0.4) with at least one of the two first components (Table 3). Component one separated the lentic zone of Palmeiras, which was associated with higher pH and temperature values, while other compartments were related to higher conductivity. For component two there was the separation of Palmeiras and Retiro reservoirs, the first associated with higher pH and dissolved oxygen values, and Retiro with higher ORP values.

3.2. Ichthyofauna

We collected 100 fish individuals in the macrophyte banks of Palmeiras and Retiro reservoirs, represented by 20 taxa, including 15 species, 3 genera without species discrimination and 2 individuals identified at the family level (Table 4). Limitation in identification was due to the early development stage of some sampled individuals.

In Palmeiras the fish fauna was represented by 11 taxa. The order Characiformes had five species and two families (not identified), followed by Gymnotiformes and Siluriformes with two species and two families (not identified) each, and Cichliformes and Synbranchiformes with one species and one family (not identified) each. Only four species were captured in more than one compartment. Intermediate exhibited higher richness (six taxa) and the lotic and lentic zones had five and four taxa, respectively (Figure 3; Table 4). In Retiro it was found 14 taxa, comprising nine

Table 3. Correlation values (scores) among limnological variables adjacent to macrophyte banks and components one and two of principal component analysis. Data from lotic, intermediate, and lentic compartments of Palmeiras and Retiro SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

Variable	PC1	PC2
Temperature	0.549	-0.025
pH	0.395	0.415
ORP	-0.244	-0.413
Conductivity	-0.476	0.360
Turbidity	-0.053	0.240
DO	0.160	0.595

PC1: principal component 1, PC2: principal component 2.

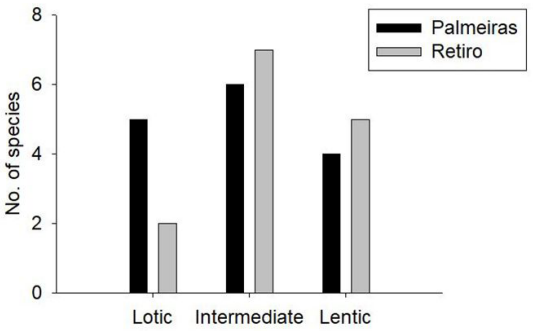

Figure 3. Richness values for the fish fauna associated to macrophyte banks in the distinct compartments of Palmeiras and Retiro SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

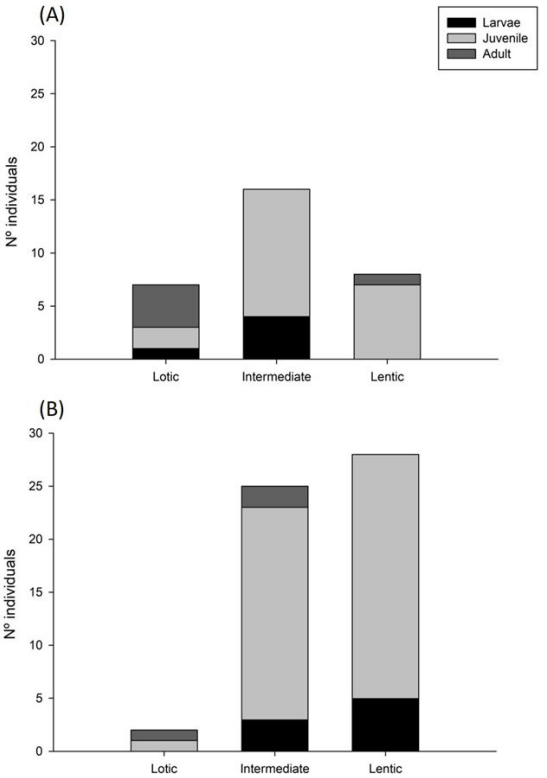

Figure 4. Abundance per development stage for the fish fauna associated to macrophyte banks in the distinct compartments of Palmeiras (A) and Retiro (B) SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

families. Characiformes also exhibited higher richness, with four species and three families (not identified), followed by Gymnotiformes and Siluriformes, both with two species and two families (not identified), Cichliformes with two species and one family (not identified), and Synbranchiformes with one species and one family (not identified). Two species were captured in more than one compartment, with the intermediate being the richest place (seven taxa) and the lotic and lentic compartments with four and five taxa, respectively (Table 4).

In Palmeiras, we collected 38 individuals and the compartment with higher abundance was the intermediate, followed by the lotic and lentic (Figure 4). In Retiro, 62 individuals were collected, with higher abundance in the lentic zone (Figure 4). Considering the abundance of each developmental stage, both reservoirs exhibited a higher number of juveniles in the intermediate and lentic compartments. In the lotic compartment, the proportion of juveniles and adults were similar in Retiro, while adults prevailed in Palmeiras (Figure 4).

Considering the relative abundance per order, in Palmeiras 42.1% were Synbranchiformes, followed by 31.5% of Characiformes, 13.1% of Gymnotiformes, 10.5% of Siluriformes and 2.6% of Cichliformes. In Retiro, 54.8% of individuals were Synbranchiformes, followed by 16.1% of Characiformes, 12.9% of Gymnotiformes, 9.7% of Siluriformes and 6.4% of Cichliformes. Figure 5 shows the relative abundance for each reservoir compartment, showing that Synbranchiformes, despite being dominant in the intermediate and lentic environments of both reservoirs, were not observed in the lotic ones.

Variation in fish size is presented in Figure 6. For Palmeiras, higher values were found in the lentic compartment, followed by lotic and intermediate. In Retiro, much higher values were found in the lentic and intermediate compared to the lotic compartment. For both reservoirs, higher sizes were influenced by the dominance of Synbranchiformes.

Table 4. Taxonomic list of fish fauna associated to macrophyte banks in the distinct compartments of Palmeiras and Retiro SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

Taxa	PALMEIRAS			RETIRO		
	Lotic	Intermediate	Lentic	Lotic	Intermediate	Lentic
Order Characiformes						
Characidae						
Astyanax lacustris (Lütken, 1875)		X				
Hyphessobrycon eques (Steindachner, 1882)					X	
Knodus moenkhausii (Eigenmann & Kennedy, 1903)	X		X	X		
Piabarchus stramineus (Eigenmann, 1908)		X				
Piabina argentea (Reinhardt, 1867)	X					
Unidentified	X			X		
Erythrinidae						
Hoplias malabaricus (Bloch, 1794)			X			
Hoplias sp.						X
Serrasalmidae						
Serrasalmus maculatus (Kner, 1858)						X
Order Cichliformes						
Cichlidae						
Cichlasoma paranaense (Kullander, 1983)					X	
Crenicichla britskii (Kullander, 1982)					X	
Oreochromis niloticus (Linnaeus, 1758)		X				
Order Gymnotiformes						
Gymnotidae						
Gymnotus sylvius (Albert & Fernandes-Matioli, 1999)	X	X			X	X
Sternopygidae						
Eigenmannia sp.					X	
Eigenmannia trilineata (López & Castello, 1966)		X				
Order Siluriformes						
Auchenipteridae						
Tatia neivai (Ihering, 1930)						X
Unidentified					X	
Loricariidae						
Hypostomus ancistroides (Ihering, 1911)				X		
Hypostomus sp.	X		X			
Unidentified				X		
Order Synbranchiformes						
Synbranchidae						
Synbranchus marmoratus (Bloch, 1795)		X	X		X	X

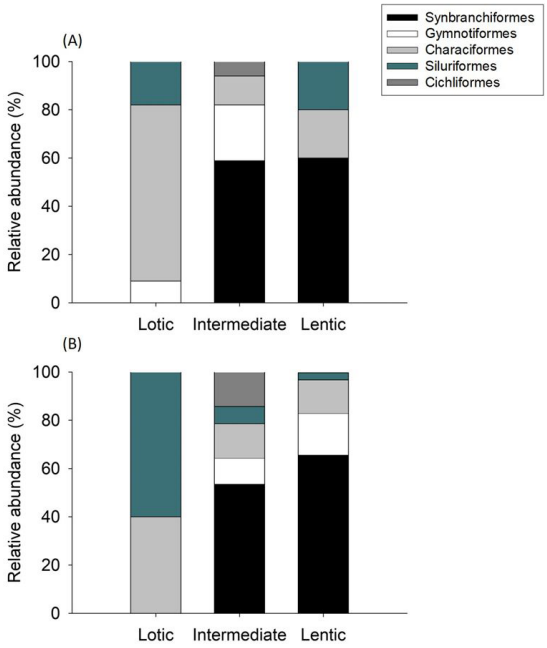

Figure 5. Relative abundance values of each order of the fish fauna associated to macrophyte banks in the distinct compartments of Palmeiras (A) and Retiro (B) SHPs reservoirs, Sapucaí-Mirim River (SP, Brazil).

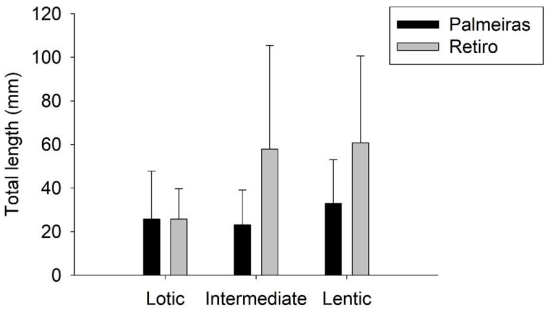

Figure 6. Values (mean and standard deviation) of the total length of the fish fauna associated to macrophyte banks in the distinct compartments of Palmeiras and Retiro SHPs reservoirs, Sapucaí-Mirim River (SP).

The PERMANOVA, based on richness and abundance, indicated a significant difference in the ichthyofauna structure when comparing the distinct compartments ($F = 4.700$; $p = 0.014$).

4. Discussion

The main hypothesis of this study was supported by the obtained data. The macrophyte banks of the SHPs reservoirs of the Sapucaí-Mirim River are used by the ichthyofauna as habitats for initial development. Most sampled fishes were juveniles, which evidences the potential ecological function of macrophytes as nursery areas. It was also observed, confirming our additional hypothesis, that assemblage structure is affected by the spatial position along the longitudinal gradient of the reservoirs, despite their small size. The macrophyte banks distributed in the SHPs reservoirs of the Sapucaí-Mirim River are particularly important, but not exclusively, for sedentary species and those with parental care. For some species that do not require long drift displacements, macrophytes may represent a functional alternative for early fish development. For a proper interpretation of the results, it must be considered that the Sapucaí-Mirim fish fauna is mainly represented by small and medium-size non-migratory species (Oliveira et al., 2016).

The number of taxa we found, at least 20 species, is comparable to other studies that also searched for fish inside macrophyte banks in Brazilian rivers and reservoirs, which varied between 22 to 26 species, but with a much higher sampling efforts – 5 to 50 times more captures (Pelicice et al., 2008; Dibble & Pelicice, 2010; Hermes-Silva & Zaniboni-Filho, 2012). In terms of composition, it is also important to mention that we sampled fish species of all orders occurring in this river (Oliveira et al., 2016; Brambilla et al., 2019; Diniz et al., 2019), namely Characiformes, Siluriformes, Gymnotiformes, Synbranchiformes and Cichliformes. This mean that fish species with distinct evolutionary histories, reproductive biology, and ecological traits (Reis et al., 2003), are using, in some way or in some period of their life cycle, the macrophyte habitats. The fact that the reservoirs have a lifetime of 7 and 5 years, Palmeiras and Retiro, respectively, was probably enough for different species to start using these areas. The order with higher number of taxa, in both reservoirs, was Characiformes, followed by Gymnotiformes. In terms of abundance, Synbranchiformes was predominant, except in the lotic stretches. Most sampled individuals belong to sedentary species, with parental care, which use these macrophyte banks as refuge against predation. In addition to fish in the early stages of development, adults of small sedentary species were also found. Similar to larvae and juveniles, they also use these banks as refuge against visual predators and feeding sites (Grenouillet & Pont, 2001; Sánchez-Botero & Araújo-Lima, 2001; Ferrareze & Nogueira, 2011).

The presence of small sedentary species, especially in the lotic compartment of Palmeiras reservoir, may be associated with the proximity

with a knickzone, located immediately upstream, where 82% of the species were of small size, representing 98% of total abundance observed in this macrohabitat (Brambilla et al., 2019). The higher abundance of individuals of the Synbranchidae family in the macrophyte banks, as well as the presence of the order Gymnotiformes, can be explained by the adaptations they have such as the elongated body shape, easily camouflaged between plants, insectivorous feeding behavior, and tolerance to low oxygen concentrations (Henderson & Hamilton, 1995; Crampton & Hopkins, 2005; Bulla et al., 2011). In case of Gymnotiformes, an intensive study of Hermes-Silva & Zaniboni-Filho (2012), comparing the ichthyofauna of macrophyte and non-macrophyte areas, found the species *Gymnotus carapo* only inside macrophyte banks.

The fact that we found a low abundance of fish larvae, including those of migratory fish, probably is related to the sampling period (late March), which correspond to the end of the seasonal reproductive period ("Piracema"). Another possibility to be checked in future studies is that the reproduction of migratory fish is happening further upstream of this sequence of reservoirs.

The sampled macrophyte banks were randomly chosen to represent the distinct reservoirs and their respective compartments. They had a mixed composition of plant species. Therefore, it was not possible to discriminate if any specific type of plant had a direct influence on the composition of the associated fish fauna. However, independent on the species composition or their life-form, it has already been proven that macrophyte banks can support high abundance of individuals and species of fish due to their role as spawning substrate, refuge against predators and high food availability (Dibble et al., 1996; Agostinho et al., 2003, 2007; Pelicice et al., 2005, 2008; Dibble & Pelicice, 2010). Commonly, there is a high abundance of insects and other aquatic invertebrates associated with the roots and leaves of aquatic plants, which potentially serve as food for most fish species (Neiff & Carignan, 1997; Padial et al., 2009; Ferrareze et al., 2015). According to Rossi & Parma de Croux (1992), these plants can also be used directly as food, as well the associated periphyton and organic detritus. However, it is important to note that excessive macrophyte growth can disrupt the ecological functioning of aquatic ecosystems and cause major problems in terms of hydropower reservoir management (Thomaz & Bini, 2003; Pompêo, 2008; 2017).

The limnological characterization indicates a tendency of differentiation between the reservoirs due to their positioning (opposite extremes in the dam cascade), as well as the longitudinal intra-reservoir variability. Significant differences for limnological variables such as temperature, turbidity, pH, and electrical conductivity were determined between reservoirs and among intra-reservoir compartments.

Studies show the relationship between the composition and structure of the ichthyofauna along dammed rivers (Ferrareze et al., 2014; Nobile et al., 2019). The lotic, intermediate, and lentic environments have distinct environmental conditions, with particular limnological features as function of differential water flow and its effects on suspended particles (Nogueira et al., 1999, 2012; Nogueira & Pomari, 2019). Despite of the lack of limnological studies for SHP´s reservoirs, the theoretical model of spatial compartmentalization should be investigated in these systems. For Palmeiras, the PCA showed a clear separation of the lentic compartment compared to the lotic and intermediate ones. In case of Retiro, the same analysis indicated a gradient of conditions between lotic, intermediate, and lentic compartments. Probably the different kind of separation among compartments observed in each reservoir must be associated with the relatively higher extension of Retiro longitudinal axis when compared to Palmeiras. Therefore, the influence of the spatial organization on the fish fauna cannot be neglected, directly, through the limnological variables and passive drift of eggs and larvae, or indirectly, through the macrophytes composition and abundance.

In this study, the larger number of individuals, mainly juveniles, was found in the intermediate zone of Palmeiras Reservoir and in the lentic zone of Retiro Reservoir. This shows that these compartments may have better biological, physical and chemical characteristics for the initial development of fish than lotic zones, especially for sedentary species, such as *Synbranchus marmoratus*, which was the most abundant species. These conditions include food availability, relatively low water velocity compared to the lotic stretches, higher temperatures, shallow depth (littoral), high microhabitat heterogeneity, and shelter availability (Silva et al., 2012; Price et al., 2013). In turn, lotic environments are more likely to function as spawning areas (Brambilla et al., 2020), due to low water transparency and high velocity, which

minimize sedimentation rates and protect the offspring (mainly egg stages) from visual predators (Pompeu et al., 2012).

Our findings are relevant for the local and regional context, considering that typical habitats for the initial development of fishes do not exist in the study area, such as tributaries and marginal lagoons. Furthermore, there was a statistically significant difference in the limnological conditions among the lotic, intermediate, and lentic compartments, which should contribute to the differential distribution of the ichthyofauna, including the species associated with aquatic vegetation. Our results point to the need of future studies to evaluate in detail the effects of the SHPs reservoirs on the distribution of early life stages, as well as the longitudinal compartmentalization and position in relation to the cascade (upper, intermediate, and lower), phases of the reproductive cycle and particularities in terms of macrophyte composition.

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