Early life stages and interannual variations of fish from Canoas reservoirs, lower Paranapanema River, Brazil

Estágios iniciais de vida e variações interanuais de peixes dos reservatórios de Canoas, baixo rio Paranapanema, Brasil

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ABSTRACT

Aim: To verify variations of early fish stages through density, species composition and ecological attributes in the lower Paranapanema River. Methods: The Canoas I and Canoas II reservoirs were sampled during three reproductive periods (RP´s) between 2012 and 2015. Eggs and larvae were collected using conical-cylindrical plankton nets and juveniles by seines and sieves. After euthanasia and fixation, the samples were identified at the lowest taxonomic level and grouped according to their reproductive strategy and life history. Variations in the eggs, larvae, and juvenile's densities were tested by Kruskal-Wallis with post-hoc Dunn's test from RP´s, while Student T-test detected differences between reservoirs. Non-metric multidimensional scaling ordination (NMDS) with post-hoc analysis of similarities (ANOSIM) were employed to elucidate differences in species composition. Major results: We sampled 5,513 eggs, 3,137 larvae, and 187 juveniles in Canoas I Reservoir, and 2,709 eggs, 237 larvae, and 13 juveniles in Canoas II Reservoir. Fishes were identified in seven orders, 15 families, and 31 species, with *Pimelodus maculatus*, Anostomidae, and small-sized characids being the most abundant. There was a predominance of non-migratory reproductive strategy (46%) and periodic life history (60%), most of them opportunistic species. Differences in densities were observed between RP´s and reservoirs. A clustering of three groups were performed to larvae and juveniles, where the divergences were statistically confirmed ($p < 0.05$). Conclusions: Our findings demonstrated the decrease of early fish stages density overtime and the dominance of opportunistic species, suggesting that these species complete their life cycle in the reservoirs. Thus, *P. maculatus* can be an important species for the health of ecosystems, in addition to serving as a fishing resource in reservoirs. However, the absence of critical sites for reproduction and the climatic events, along with human responses to this, may have impaired the conclusion of life cycle from many species.

Key-words: Damming; Ichthyoplankton; Opportunistic species; Upper Paraná River

RESUMO

Objetivo: verificar as variações dos estágios iniciais dos peixes através da densidade, composição de espécies e atributos ecológicos no baixo rio Paranapanema. Métodos: Os reservatórios de Canoas I e Canoas II foram amostrados durante três períodos reprodutivos (RP´s) entre 2012 e 2015. Ovos e larvas foram coletados com redes cônico-cilíndricas e juvenis com redes de arrasto e peneiras. Após a eutanásia e fixação, as amostras foram identificadas ao menor nível taxonômico possível e agrupadas de acordo com a estratégia reprodutiva e história de vida. Variações nas densidades de ovos, larvas e juvenis foram verificadas por teste Kruskal-Wallis com teste post-hoc de Dunn por RP's, enquanto o teste T de Student detectou diferenças entre reservatórios. O escalonamento multidimensional não-métrico (NMDS) com análise post-hoc de similaridade (ANOSIM) foi empregado para elucidar diferenças na composição de espécies. Principais resultados: Foram amostrados 5.513 ovos, 3.137 larvas e 187 juvenis no reservatório Canoas I, e 2.709 ovos, 237 larvas e 13 juvenis no reservatório Canoas II. Os peixes foram identificados em sete ordens, 15 famílias e 31 espécies, sendo *Pimelodus maculatus*, Anostomidae e caracídeos de pequeno porte os mais abundantes. Houve predomínio da estratégia reprodutiva não migratória (46%) e história de vida periódica (60%), sendo a maioria espécies oportunistas. Diferenças em densidades foram observadas entre RP's e reservatórios. Foi realizado um agrupamento de três conjuntos para larvas e juvenis, onde as divergências foram confirmadas estatisticamente (p < 0,05). Conclusões: nossos resultados demonstraram a diminuição da densidade dos estágios iniciais dos peixes ao longo do tempo e a dominância de espécies oportunistas, sugerindo que essas espécies completam seu ciclo de vida nos reservatórios. Assim, *P. maculatus* pode ser uma espécie importante para a saúde dos ecossistemas, além de servir como recurso pesqueiro nos reservatórios. No entanto, a ausência de locais críticos para a reprodução e os eventos climáticos, juntamente com as respostas humanas a isso, podem ter prejudicado a conclusão do ciclo de vida de muitas espécies.

Palavras Chave: Barramento; Ictioplâncton; Espécies oportunistas; Alto rio Paraná

INTRODUCTION

The life history of freshwater fish results from the trade-offs between biological and environmental attributes, which interfere with the reproduction and fitness of the species (Winemiller, 1995). In the Paraná River, the reproductive period of fishes is regulated by the wet season between October and March, where photoperiod, temperature, and, mainly, flooding are important environmental triggers for oocyte maturation (Orsi, 2010), migration (Agostinho *et al.,* 2003), spawning (Baumgartner *et al.,* 2004; Reynalte-Tataje *et al.,* 2012a), and early fish stage development and growth (Agostinho *et al.,* 2004). Thus, for some species, the complete life cycle includes several steps and depends on the use of different habitats, with the connection between them being essential for its success (Agostinho *et al.,* 2003; Teixeira *et al.,* 2019). However, the Paraná River basin is exploited by hydropower projects (Agostinho *et al.,* 2004). For instance, the Paranapanema River is a major tributary of the upper Paraná River basin and is heavily fragmented by dams (Orsi *et al.,* 2016). Although important for the country economy, the damming promotes significant ecological impacts, causing discussions about the effects on fish fauna in the region (Britto & Carvalho, 2013).

In reservoirs, environmental alteration damages the fish reproduction and disconnects essential habitats, while the dam regulation interferes with environmental triggers (Poff & Hart, 2002; Brito & Carvalho, 2013; Orsi *et al.,* 2016). Otherwise, climate changes can create stochastic events, which are difficult to identify and repair, contributing to harm to fish reproduction (Strayer & Dudgeon, 2010; Abrial *et al.,* 2019; Zacardi *et al.,* 2020). Mitigation measures include restoration of connectivity through fish passages and flooding by engineering (Agostinho *et al.,* 2004; Pompeu *et al.,* 2012). However, some species are less dependent on environmental triggers to reproduce and do not realize movements or need specific habitats for their life cycles (Bailly *et al.,* 2008; Lima *et al.,* 2017; Abrial *et al.,* 2019). These species often dominate the early fish stages in reservoirs, becoming widespread (Lima *et al.,* 2017; Lopes & Zaniboni-Filho, 2019).

Therefore, early fish stage studies (eggs, larvae, and juveniles) are efficient tools in the diagnosing of ichthyofauna health, identifying reproductively active species and successful recruitment sites (Baumgartner

et al., 2004; Gogola *et al.,* 2010; Ferrareze & Nogueira, 2011). There have been few ichthyoplankton studies in Brazil, and these are specific to the main basins or restricted to species of economic importance (Orsi *et al.,* 2016). Studies in the upper Paraná River basin are concentrated on the last lotic stretch between the Porto Primavera Dam and Itaipu Reservoir (Gogola *et al.,* 2010; Barzotto *et al.,* 2015; Silva *et al.,* 2015). Furthermore, some studies have also evaluated early fish stages in main tributaries, such as the Grande (Suzuki *et al.,* 2013), and Paranapanema rivers (Orsi *et al.,* 2016). In the Paranapanema River basin, research is concentrated in the lower (Vianna & Nogueira, 2008; Kipper *et al.,* 2011; Garcia *et al.,* 2018), and recently, in the medium region (Azevedo-Santos *et al.,* 2021).

The Canoas I and Canoas II dams are located upstream in the lower Paranapanema River (Duke Energy, 2008) and comprise a series of two reservoirs with fish passages, linking the Capivara Reservoir and Canoas reservoirs in a stretch of approximately 130 km (Britto & Carvalho, 2013), which has been closed since 2010. The reservoirs have practically no tributaries suitable for alternative reproduction routes, and the run-of-river regime floods few lands (Duke Energy, 2008), differing from the availability of marginal lakes in the upper Paraná River floodplain (Agostinho *et al.,* 2007). The fishes that reproduce in the Canoas reservoirs support these conditions. However, in a previous study, only the early fish stages of non-migratory were recorded (Britto & Carvalho, 2013). Here, we aimed to: 1) Identify larvae and juveniles of the fish species that spawning in the Canoas reservoirs; 2) Evaluate the reproductive strategy and life history of the larvae and juveniles of the Canoas reservoirs and; 3) Verify interannual variation in the density and composition taxonomic of early fish stages.

MATERIAL AND METHODS

STUDY AREA

The headwaters of the Paranapanema River are in the Atlantic Plateau of the Serra de Paranapiacaba, São Paulo State (SP), and extend for 990 km, covering approximately 900,000 km² through the Southeast of SP and North of the Paraná State (PR) (Sampaio, 1944). Due to its unevenness of approximately 600 meters, since 1936 the river has been exploited for hydropower projects and the main channel has been transformed into a cascade of reservoirs with 11 dams (Duke Energy, 2008). From upstream to downstream, the lower Paranapanema River covers the reservoirs of Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu, and Rosana.

The Canoas I Reservoir is between the municipalities of Itambaracá (PR) and Cândido Mota (SP), and is upstream of the Capivara Dam (Figure 1). It has a flooded area of 31 km², 81 MW power, and only three tributaries, Bagre, Macuco, and Pari rivers. The Canoas II Reservoir is between the municipalities of Andirá (PR) and Palmital (SP), and is upstream of Canoas I dam (Figure 1). It has a flooded area of 22 km², 72 MW power, and has only two tributaries, the Águas Sujas and Pau de Alho rivers (Duke Energy, 2008). As the depth, width, and geomorphology of the tributaries are not appropriate for fish reproduction, and the reservoirs are without marginal lakes as in the floodplain (Britto & Carvalho, 2013), only the main channel of both reservoirs was sampled (Table 1, Figure 1).

Table 1. Sampling point's characteristics in the Canoas I and Canoas II reservoirs, lower Paranapanema River, between October 2012 and March 2015.

Physiographic characteristics	Canoas I Reservoir	Canoas II Reservoir
Geographic Coordinates	22°55'52.36"S - 50°16'31.50"W	22°54'58.29"S - 49°59'32.83"W
Occupation of margins	Agriculture/pasture	Agriculture/pasture
Width riparian forest (m)	0-50	100-330
Aquatic vegetation	Mostly absent	Mostly absent
Margin (type)	Middle slope	Middle slope
Flow (type)	Lotic	Lotic
Substrate (type)	Rocky	Rocky
Length (km)	26	23
Width (m)	270	140
Depth (m)	6.1	7.2
Age (years)	23	23
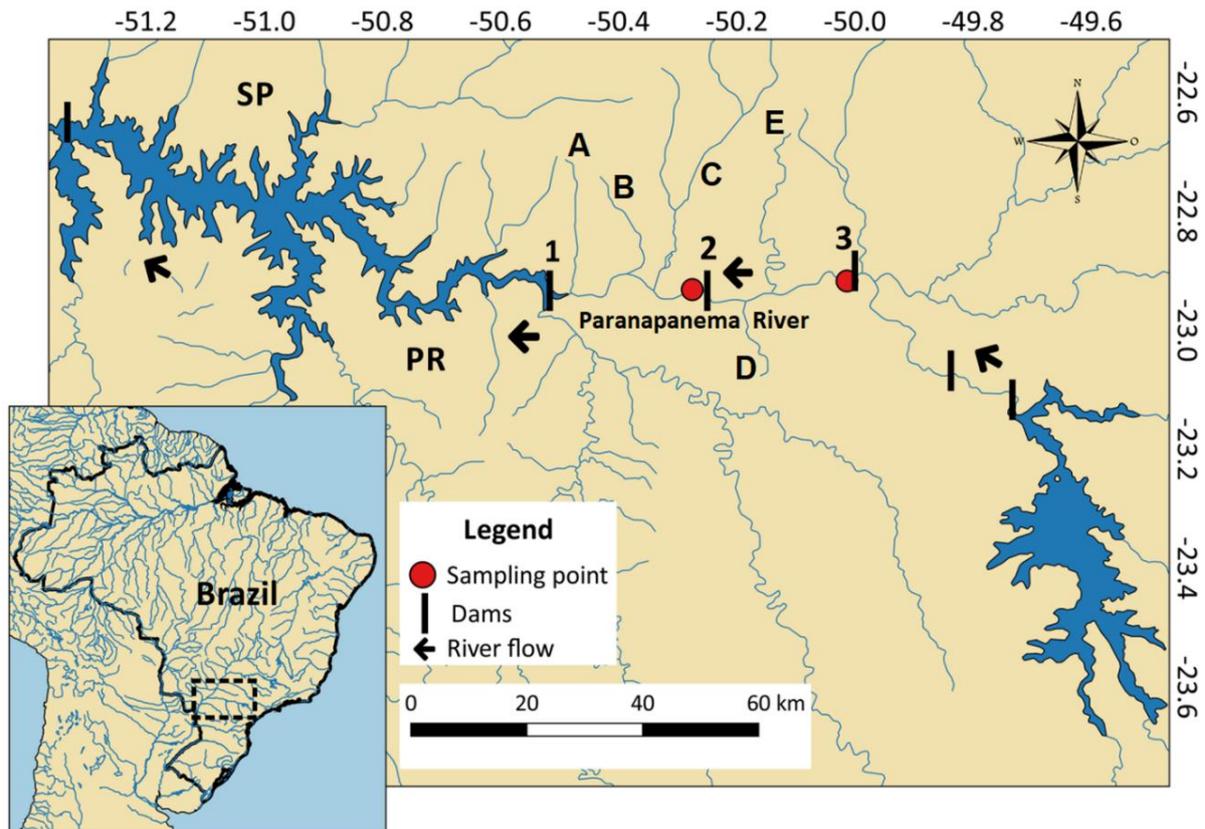
Figure 1. Sampling points in the Canoas I and Canoas II reservoirs, lower Paranapanema River. 1) Canoas I Dam, 2) Canoas II Dam, 3) Salto Grande Dam, A) Bagre River, B) Macuco River, C) Pari River, D) Águas Sujas river, and E) Pau de Alho River. PR = Paraná State; SP = São Paulo State. Arrows indicate River flow.

SAMPLINGS AND LABORATORY ANALYSIS

We used data from samples collected during three consecutive reproductive periods to assess annual variations in species. The reproductive period (RP) of fishes from the upper Paraná River ranges from October to March (Agostinho *et al.,* 2003). Thus, we sampled the reservoirs quarterly between October 2012 and March 2013 (RP1), October 2013 and March 2014 (RP2), and October 2014 and March 2015 (RP3). Eggs and larvae were collected in the limnetic zone with conical–cylindrical plankton nets, mesh size of 0.5 mm, and a flowmeter attached to the mouth of the nets to measure the volume filtered. The nets were dragged along the surface by a low-speed boat (~ 4 km/h) for 10 minutes. Four samples were collected during the day (8:00 am) and four at night (20:00 pm) eight samples/month at each sampling point. For juveniles, we used a seine (6.0 m^2, 0.5 cm mesh) and a sieve (0.4 m^2, 0.5 cm mesh) in the littoral zone, operated for one hour during daylight at each sampling point, quarterly. For the samples collected in the limnetic and littoral zones, the organisms were anesthetized and euthanized by immersion in a water solution with clove oil and fixed with 4% formaldehyde solution buffered with calcium carbonate. The collection was performed under license (SISBIO Number 16578), and the Animal Ethics Committee authorized the field sampling (CEUA number 30992.2014.33).

In the laboratory, samples were placed on a Bogorov-type plate and sorted under a stereomicroscope until identified. Individuals between hatching and total formation of fins (with rays) and scales (when present) were grouped as larvae, while those with complete fin formation and scales without sexual activity were grouped as juveniles (Nakatani *et al.,* 2001). The damaged larvae and those identified above the order level were grouped as unidentified. Larvae and juveniles were identified to the lowest possible taxonomic level (Nakatani *et al.,* 2001) and grouped according to their reproductive strategy, which followed Suzuki *et al.* (2004): long-distance migratory (LDM), migrate over 100 km; short-distance migratory (SDM), migrate less than 100 km; non-migratory (NM), do not perform migration; external fertilization (EF); internal fertilization (IF); parental care (PC), or no parental care (NPC). To the life history, we used Winemiller (1995): periodic (P), equilibrium (E), opportunistic (O), or intermediate between them.

DATA ANALYSIS

The eggs and larvae density was calculated for each point and standardized as ichthyoplankton.$10m^{-3}$ of filtered water (Nakatani *et al.,* 2001). The catch per unit effort (CPUE) of juveniles was obtained by grouped areas of seines and sieves and standardized for a total area of juvenile.$10 m^{-2}$. Density data were log transformed (x+1) and differences of eggs, larvae, and juveniles between the RP's (for both reservoirs) were investigated with non-parametric Anova (Kruskal-Wallis) with the post-hoc Dunn's test, while Student T-test detected differences between reservoirs ($p < 0.05$). Non-metric multidimensional scaling ordination (NMDS) was employed to explain the differences in species composition (*i.e.*, RP1; RP2, and RP3 between 2012 and 2015), separately for larvae and juveniles from each reservoir. Based on a matrix of distances (e.g., Bray-Curtis method), we verified the similarity between the periods following the species composition data. Thus, in our functional space, we plotted our species composition based on the first two dimensions of the NMDS. The NMDS was done using the function "metaMDS" in the Vegan package (version 2.4-1; Oksanen *et al.,* 2019). One-way ANOSIM was used to determine the significance of any clustering of replicates, within each time-periods, in NMDS ordinations (Clarke, 1993) using 999 permutations and the function "adonis" in the Vegan package (Oksanen *et al.,* 2019).

RESULTS

TAXONOMIC COMPOSITION

In the RP1 5,435 eggs, 3,050 larvae, and 46 juveniles were collected. The RP2 showed 584 eggs, 174 larvae and 117 juveniles, and the RP3, 2,203 eggs, 150 larvae and 37 juveniles. Of these, we captured 5,513 eggs, 3,137 larvae, and 187 juveniles in Canoas I Reservoir, and 2,709 eggs, 237 larvae, and 13 juveniles in Canoas II Reservoir. Larvae and juveniles were identified in seven orders, 15 families, and 31 species (Table 2). Of these, five species were represented by larvae and 26 by juveniles. The Canoas I Reservoir presented 19 exclusive species (59% of the richness), the Canoas II Reservoir presented four exclusive species (12%), and the reservoirs shared eight species (21%) (Table 2).

Table 2. Fishes larvae mean densities (L) (individual/$10m^{-3}$), and juveniles fishes (J) mean catch per unit of effort (CPUE) (individual/$10m^{-2}$) in the Canoas I and Canoas II reservoirs, lower Paranapanema River, between October 2012 and March 2015. *= specimens identified at the family level; **= non-native species. Reproductive and life history strategies according to Suzuki *et al.* (2004), and Winemiller (1995), respectively. NM = non-migratory; SDM = short distance migratory; LDM = long distance migratory; EF = external fertilization; IF = internal fertilization; PC = parental care; NPC = no parental care; E = equilibrium; EP = intermediate equilibrium/periodic; O = opportunistic; OP = intermediate opportunistic/periodic; P = periodic.

Taxa	Canoas I Reservoir		Canoas II Reservoir		Reproductive strategy	Life History
	L ind.$10m^{-3}$	J ind.$10m^{-2}$	L ind.$10m^{-3}$	J ind.$10m^{-2}$		
Characiformes						
Erythrinidae	-	-	-	-		
Hoplias malabaricus (Bloch, 1794)	-	0.62	0.01	-	NM, EF, PC	E
Parodontidae*	11.03	-	0.09	-		
Apareiodon affinis (Steindachner, 1879)	-	0.47	-	0.16	SDM, EF, NPC	P
Serrasalmidae	-	-	-	-		
Myloplus tiete (Eigenmann & Norris, 1900)	-	0.47	-	-	SDM, EF, NPC	P
Serrasalmus maculatus Kner, 1858	-	0.32	-	-	NM, EF, PC	E
Serrasalmus marginatus Valenciennes, 1837**	-	-	-	0.16	NM, EF, PC	EP
Serrasalmus spp.	-	0.47	-	-	NM, EF, PC	EP
Anostomidae*	810.60	-	9.19	-		
Acestrorhynchidae	-	-	-	-		
Acestrorhynchus lacustris (Lütken, 1875)	-	0.48	-	-	NM, EF, NPC	P

Characidae*	132.53	-	1.74	-		
Aphyocharax dentatus Eigenmann & Kennedy, 1903**	-	0.47	-	-	NM, EF, NPC	P
Astyanax lacustris (Lütken, 1875)	-	0.47	-	-	SDM, EF, PC	P
Hemigrammus marginatus Ellis, 1911	-	9.12	-	-	SDM, EF, NPC	P
Hyphessobrycon eques (Steindachner, 1882)**	-	2.20	-	-	NM, EF, NPC	P
Moenkhausia intermedia Eigenmann, 1908	-	2.83	-	-	NM, EF, NPC	OP
Piabarchus stramineus (Eigenmann, 1908)	-	4.45	-	-	SDM, EF, NPC	P
Psalidodon aff. *fasciatus* (Cuvier, 1819)	-	0.31	-	-	SDM, EF, NPC	P
Psalidodon aff. *paranae* (Eigenmann, 1914)	-	1.26	-	-	SDM, EF, NPC	P
Serrapinnus notomelas (Eigenmann, 1915)	-	2.52	-	-	SDM, EF, NPC	P
Gymnotiformes	-	-	-	-		
Gymnotidae	-	-	-	-		
Eigenmannia spp.	0.01	-	-	-	NM, EF, PC	E
Siluriformes	-	-	-	-		
Loricaridae	-	-	-	-		
Hypostomus ancistroides (Ihering, 1911)	-	0.31	-	-	NM, EF, PC	E
Hypostomus spp.	-	1.42	-	0.16	NM, EF, PC	E
Auchenipteridae	-	-	-	-		
Tatia neivai (Ihering, 1930)	-	0.47	0.02	-	SDM, IF, PC	P
Heptapteridae*	3.86	-	-	-		
Rhamdia quelen (Quoy & Gaimard, 1824)	15.01	-	-	-	SDM, EF, NPC	P
Imparfinis spp.	-	-	-	0.16	SDM, EF, NPC	P
Pimelodidae*	0.10	-	0.04	-		
Pimelodus maculatus Lacepède, 1803	4092.55	-	39.89	-	LDM, EF, NPC	P
Sorubim lima (Bloch & Schneider 1801)**	1.59	-	-	-	LDM, EF, NPC	P
Synbranchiformes	-	-	-	-		
Synbranchidae	-	-	-	-		
Synbranchus marmoratus Bloch, 1795	-	0.31	-	-	NM, EF, PC	E
Cichliformes	-	-	-	-		
Cichlidae	-	-	-	-		
Astronotus crassipinnis (Heckel, 1840)**	-	-	-	0.16	NM, EF, PC	P
Cichla kelberi Kullander & Ferreira, 2006**	-	0.31	-	-	NM, EF, PC	E
Crenicichla britskii Kullander, 1982	-	0.16	-	-	NM, EF, PC	E
Geophagus brasiliensis (Quoy & Gaimard, 1824)	-	0.16	-	-	NM, EF, PC	E
Cyprinodontiformes	-	-	-	-		
Poeciliidae	-	-	-	-		
Poecilia reticulata Peters, 1859**	-	-	-	0.16	NM, IF, NPC	O

Incertae sedis	-	-	-	-	
Sciaenidae	-	-	-	-	
Plagioscion squamosissimus (Heckel, 1840) **	60.06	-	8.15	0.63	SDM, EF, NPC	P
Unidentified	45.24	-	22.05	-	

Characiformes exhibit the highest number of taxa (16), followed by Siluriformes (7) and Cichliformes (4). *Pimelodus maculatus* Lacepède, 1803 (Pimelodidae) represented 78% of the total larvae density, followed by Anostomidae (15%) and Characidae (2%). For juveniles, *Hemigrammus marginatus* Ellis, 1911 represented 29% of the total CPUE, followed by *Piabarchus stramineus* (Eigenmann, 1908) (14%) and *Moenkhausia intermedia* Eigenmann, 1908 (9%). Eight non-native species were captured, representing 25% of the species richness, 28% of the larvae richness, and 23% of the juvenile richness (Table 2). *Plagioscion squamosissimus* (Heckel, 1840) was the most common of the non-natives, representing 1% of the total larvae density, while *Hyphessobrycon eques* (Steindachner, 1882) represented 7% of the total juvenile CPUE.

REPRODUCTIVE STRATEGY/LIFE HISTORY

To reproductive strategy, there was a predominance of non-migratory species of external fertilization (46% of the richness), followed by the short-distance migratory species with external fertilization (40%), followed by long-distance migratory species with external fertilization and parental care (6%) (Figure 2A). According to life history, periodic species represented 60% of the richness, followed by equilibrium (28%) and intermediate opportunistic/periodic (6%) (Figure 2B).
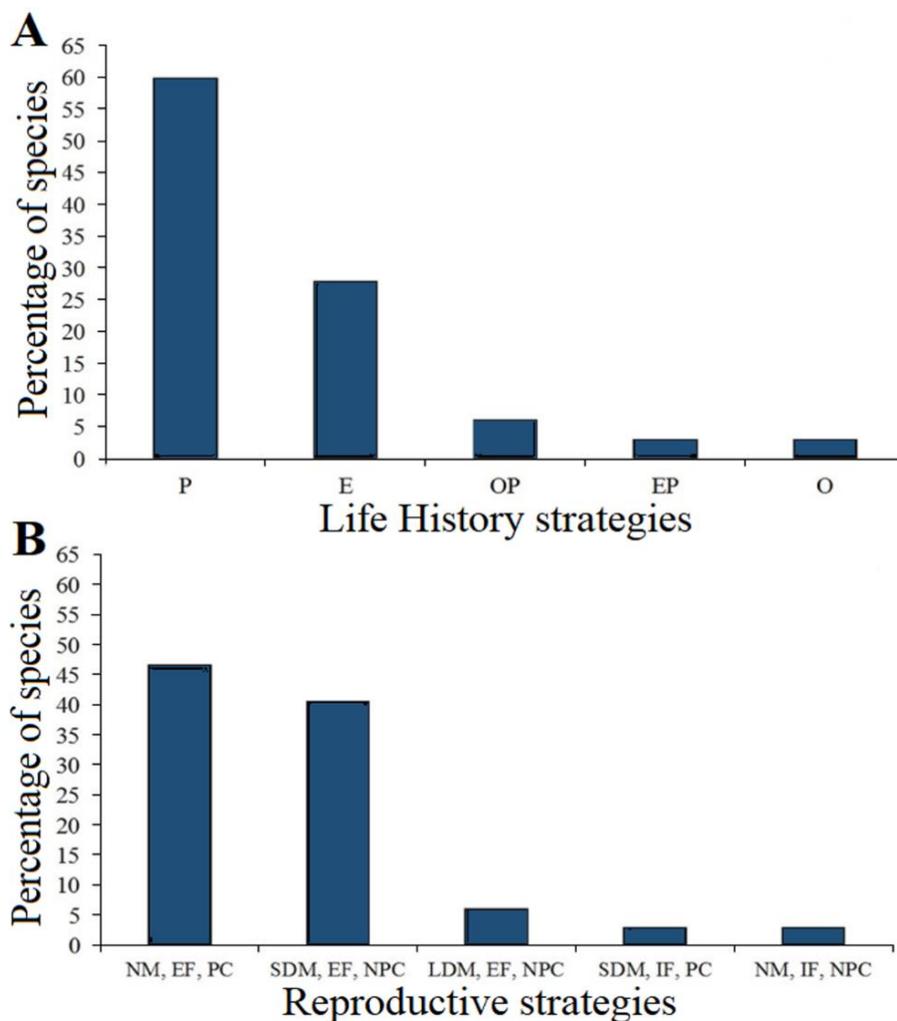
Figure 2. Frequency of species for life history (A) and reproductive strategy (B), of larvae and juveniles of fish captured in Canoas I and Canoas II reservoirs. NM = non-migratory; SDM = short distance migratory; LDM = long distance migratory; EF = external fertilization; IF = internal fertilization; PC = parental care; NPC = no parental care. P = periodic; E = equilibrium; O = opportunistic; OP = intermediate opportunistic/ periodic; EP = intermediate equilibrium/ periodic.

REPRODUCTIVE PERIOD, DENSITY AND INTERANNUAL SPECIES COMPOSITION

In the RP1, eggs mean density ranged between 1.28 and 3946.25 eggs.10m^{-3}, 3.13 and 8795.56 eggs.10m^{-3} (RP2), and 0.15 and 3.78 eggs.10m^{-3} (RP3). To larvae, mean density ranged between 3.21 and 280.99 larvae 10m^{-3} (RP1), 1.63 and 3.98 larvae.10m^{-3} (RP2), and 0.15 and 3.85 larvae.10m^{-3} (RP3). To juveniles CPUE, density ranged between 0.63 and 0.82 juveniles.10m^{2} (RP1), 0.79 and 0.90 juveniles.10m^{2} (RP2), and 0.47 and 0.50 juveniles.10m^{2} for the RP3. Differences in density were found in the RP´s (Kruskall-Wallis; eggs: p = 0.02; larvae: p = 0.012; juveniles CPUE: p = 0.03), with the RP1 being statistical difference of the other RP´s to eggs and larvae (Dunn's test; RP1 x RP2 eggs: p = 0.04; RP1 x RP3 eggs: p = 0.043; RP1 x RP2 larvae: p = 0.038; RP1 x RP3 larvae: p = 0.03). To juveniles CPUE, the RP2 was a statistical difference of the other RP´s (Dunn's test; RP1 x RP2 juveniles: p = 0.033; RP1 x RP3 juveniles: p = 0.021). Canoas I Reservoir was statistical difference of Canoas II Reservoir in eggs and larvae in the RP1 (Student T-test eggs: p = 0.045; Student T-test larvae: p = 0.048) and to the RP2 to juvenile CPUE (Student T-test: p = 0.03) (Figure 3).
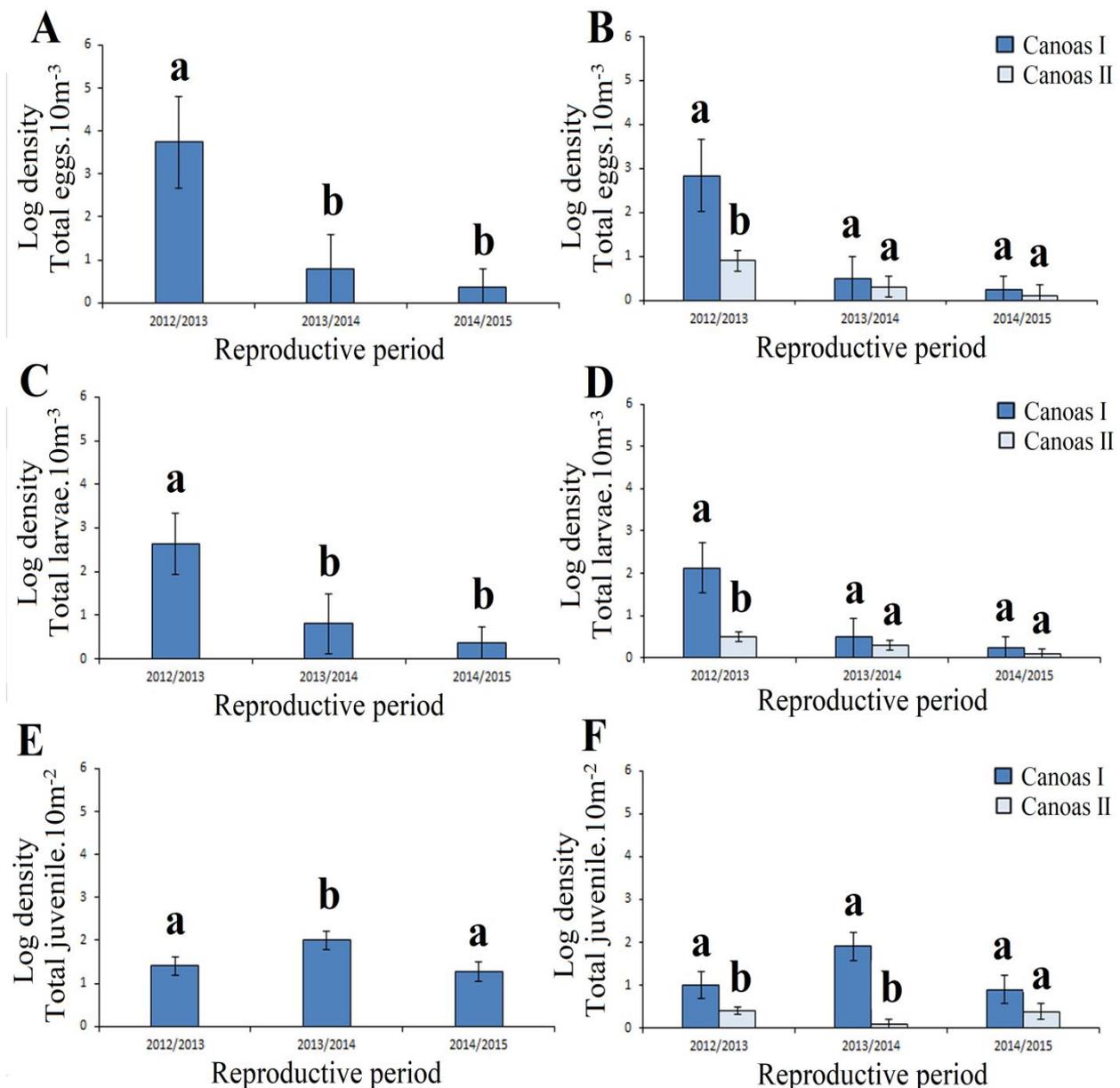
Figure 3. Variation of mean log density of fish eggs (A, B), larvae (C, D) and juveniles (E, F) per reproductive period (both reservoirs) and by reservoirs (Canoas I and Canoas II). Different letters indicate significant differences (p < 0.05).

The NMDS evidenced a clustering of three groups (*i.e.*, RP1, RP2 and RP3) to fish larvae and juveniles of the Canoas I and juveniles of Canoas II (Figure 4), indicating divergences in the fish assembly over time. The ANOSIM confirmed that the juvenile composition of the Canoas I Reservoir between 2012 and 2015 was significantly distinct (R2 = 0.835, p = 0.01), but not to larvae composition (R2 = 0.238, p = 0.42). To Canoas II Reservoir we observed the same tendency, where juvenile composition was significantly distinct (R2 = 0.882, p = 0.03), but not to larvae composition (R2 = 0.156, p = 0.56).
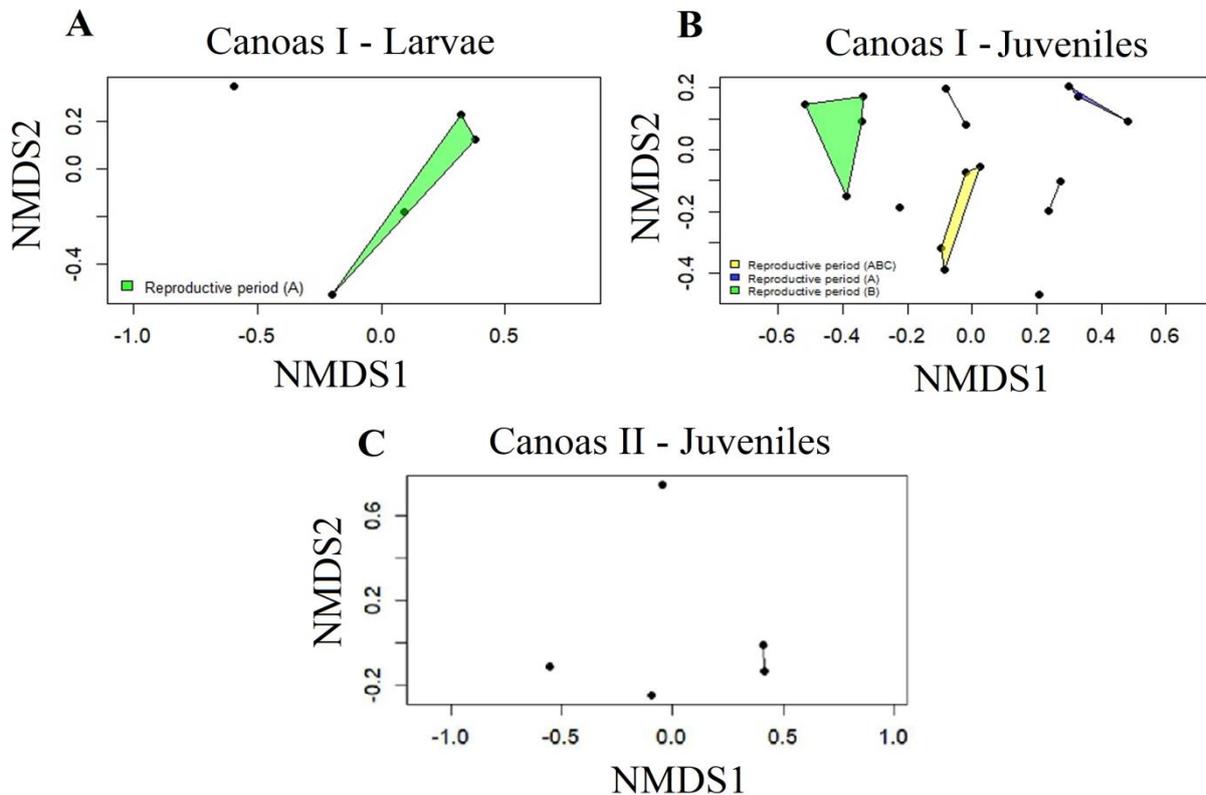
Figure 4. Non-metric multidimensional scaling (NMDS) of the fish larvae (A), and juveniles (B) composition of Canoas I Reservoir and juveniles composition (C) of the Canoas II Reservoir.

DISCUSSION

TAXONOMIC COMPOSITION AND REPRODUCTIVE STRATEGY/LIFE HISTORY

The dominance of larvae and juveniles of Characiformes and Siluriformes followed the pattern of other ichthyoplankton surveys in different Neotropical basins (Ziober *et al.,* 2012; Lopes & Zaniboni-Filho, 2019; Zacardi *et al.,* 2020). Our findings showed that the periodic life history was predominant, that is, fishes that become reproductively active later, have a short reproductive period and produce many small oocytes released in a single spawning (Winemiller, 1995). For the upper Paraná River, 19 species belonging to this life history show a long-distance migratory strategy (Suzuki *et al.,* 2004), while our results verified only the Anostomidae taxon and two species, *Pimelodus maculatus* and *Sorubim lima*. *P. maculatus* was the most abundant in larvae density, demonstrating successful reproduction and the potential for colonization in the Canoas reservoirs. The species presents unusual characteristics for migratory fishes, such as multiple spawning and short-distance movements to reproduce (Agostinho *et al.,* 2003), which provide advantages in dammed rivers. Also, the small oocytes provide greater buoyance, which increases the survival and dispersal of the early fish stages (Agostinho *et al.,* 2003). It should be noted that the previous study in the Canoas reservoirs (Britto & Carvalho, 2013) did not record *P. maculatus* in ichthyoplankton, being this an important record. Thus, the species could sustain future populations in the reservoirs, making it important for ecosystem functionality and fisheries resources (Agostinho *et al.,* 2007).

Anostomidae (the second most abundant in larvae density) are long-distance migratory fishes, but some

species present adaptations (*i.e.*, short distance movements, use of tributaries, and multiple spawning) that enable the conservation of populations in reservoirs (Orsi, 2010, Orsi *et al.,* 2016). In this way, adults of *Schizodon nasutus* Kner, 1858 and *Leporinus friderici* (Bloch, 1794) were registered in the Canoas reservoirs previously, probably populations that ascended by the fish passage of Capivara Reservoir when was still open (Britto & Carvalho, 2013). However, ichthyoplankton of Anostomidae were not recorded in the previous study (Britto & Carvalho, 2013), indicating that some species became capable of reproducing in the environment. Nevertheless, the occurrence of ichthyoplankton of migratory fishes does not guarantee viable populations in the environment (Agostinho *et al.,* 2007; Reynalte-Tataje *et al.,* 2012a), since they require critical habitats to complete their life cycles (Agostinho *et al.,* 2003; Suzuki *et al.,* 2013).

In this sense, it is important to emphasize the absence of juveniles of the most abundant species in ichthyoplankton (*P. maculatus* and Anostomidae). In reservoirs, rheophilic species spawn in tributaries upstream (Vianna & Nogueira, 2008; Suzuki *et al.,* 2013; Azevedo-Santos *et al.,* 2021), and larvae and juveniles grow in adjacent marginal lakes (Ferrareze & Nogueira, 2011; Kipper *et al.,* 2011; Garcia *et al.,* 2018). However, the tributaries of the Canoas reservoirs could be not adequate for the survival of eggs and larvae (Baumgartner *et al.,* 2004; Pompeu *et al.,* 2012; Azevedo-Santos *et al.,* 2021), and the absence of marginal lakes reduces the supply of refuge and food to juveniles (Ferrareze & Nogueira, 2011; Kipper *et al.,* 2011). This absence of critical habitats is noticeable when we compare our results with the early stage fish composition of reservoirs with extensive tributaries (Reynalte-Tataje *et al.,* 2012ab; Barzotto *et al.,* 2015; Silva *et al.,* 2015; Azevedo-Santos *et al.,* 2021) and marginal lagoons (Kipper *et al.,* 2011; Garcia *et al.,* 2018). On the other hand, the presence of adults may indicate that there is some form of juvenile's survival (Agostinho *et al.,* 2004; Reynalte-Tataje *et al.,* 2011), where recruitment areas may not have been contemplated in our sampling points.

Otherwise, the other periodic species presented a reproductive strategy of short-distance migration or non-migration, generally represented by small-sized Characidae juveniles, such as *H. marginatus*, *P. stramineus*, and *M. intermedia*. In floodplains, such as upper Paraguay (Tondato *et al.,* 2010; Ziober *et al.,* 2012), Amazon (Zacardi *et al.,* 2020), and upper Paraná basins (Suzuki *et al.,* 2004), small-sized Characiformes behave as an opportunist, which is an advantage for reproductive success and colonization of reservoirs (Orsi, 2010; Lima *et al.,* 2017). Likewise, our results confirm this reproductive behavior, demonstrating the adaptive capacity of these species. These characteristics, combined with the environmental changes from damming, were strong enough for these species to increase their distribution even in basins such as the upper Uruguay Basin, which has waterfalls and rapids where migratory species should occur (Reynalte-Tataje *et al.,* 2012a; Lopes & Zaniboni-Filho, 2019). Over time, these species may become the only ones to complete their life cycle in the Canoas reservoirs, becoming dominant in the ichthyofauna (Agostinho *et al.,* 2007).

EARLY FISH STAGES DENSITY AND INTERANNUAL VARIATIONS

The reproductive period of fishes in the upper Paraná River is regulated by the wet season, where the highest densities of eggs and larvae are recorded (Agostinho *et al.,* 2003; Vianna & Nogueira, 2008; Gogola *et al.,* 2010). Moreover, an unusual monthly rainfall in the Canoas reservoirs was observed during the samplings (ÁGUAS PARANÁ, 2020), classified as droughts in Southeastern Brazil between 2013/2014 (RP2) (Teixeira *et al.,* 2019), and related to the El Niño in South Brazil from 2014/2015 (RP3) (Terassi *et al.,* 2018). This could explain the decrease of eggs and larvae densities overtime, especially from RP2 onwards. Furthermore, between 2011 and 2017, were observed in Brazil the longest and most severe droughts of the last 30 years, especially between 2013 and 2015 in the Southeast region (RP2 and RP3) (Cunha *et al.,* 2019), suggesting the maintenance of the long-term low density of ichthyoplankton.

Beyond the climate changes that affect the reproduction of species, the human responses to these problems are additional interferences (Strayer & Dudgeon, 2010). Since fish remain in juvenile's stock from one to two years (Agostinho *et al.,* 2004), the high density of juveniles in RP2 could be the products of the reproductive effort in RP1, when the climatic events were normal. Although, we observed juvenile's density reduction from RP2 to RP3. The Canoas I Reservoir had unusual low water levels during the wet season (samplings of RP2, 2013/2014, and RP3, 2014/2015) (ONS, 2020), suggest a response of the dam (control of the water level) (Poff & Hart, 2002; Agostinho *et al.,* 2004) due to the rainfall dynamics at that moment (Terassi *et al.,* 2018; Cunha *et al.,* 2019; Teixeira *et al.,* 2019). Therefore, this can reduce the communication between the reproduction sites and prevent early fish stages from reaching growth areas (Agostinho *et al.,* 2004; Tondato *et al.,* 2010; Ferrareze & Nogueira, 2011). Consequently, this impaired the recruitment of the products of the RP2, the larvae, and juveniles of the RP3. Moreover, flow regulation provides fewer food resources for larvae and juveniles, resulting in population depletion (Agostinho *et al.,* 2007; Pompeu *et al.,* 2012).

The early fish stages are influenced by environmental conditions, so the hydrological deficit can have affected the density of specific groups (Teixeira *et al.,* 2019). For the long-distance migratory fishes, the abundance of the early fish stages is positively related to the rainfall (Agostinho *et al.,* 2004) and the duration of the flood to linking reproduction sites (Fernandes *et al.,* 2009; Tondato *et al.,* 2010), which could explain the low density of this life history. On the other hand, short-migratory fishes (Anostomidae and *P. maculatus*) or non-migratory (small-sized Characidae) showed high density, probably due to the independence of environmental triggers to reproduce (Bailly *et al.,* 2008; Lima *et al.,* 2017), as well as being less related to specific sites to spawning and growth (Abrial *et al.,* 2019). This pattern was observed in the upper Uruguay (Reynalte-Tataje *et al.,* 2012b), and middle Paraná Basins (Abrial *et al.,* 2019). Nevertheless, we found the highest density of early fish stages in the Canoas I Reservoir. Due to the similarity of the reservoirs, this could be related to the reproductive efforts of adults that ascended by the fish passages from the Capivara to Canoas I reservoirs, becoming restricted in this reservoir after the closure of passages to Canoas II in 2010 (Britto & Carvalho, 2013).

 As we verify the decrease of density over time of the early fish stages, as soon as the absence of species that present characteristic life history while others remain or rise, this scenario becomes worrying. Keeping the climatic changes, combined with the human responses (Strayer & Dudgeon, 2010; Cunha *et al.,* 2019), it can be hypothesized that there will occur a reduction of diversity of early fish stages, where only species indifferent to environmental triggers will reproduce and spread in these reservoirs (Fernandes *et al.,* 2009; Gogola *et al.,* 2010). This would not only be a problem for the ecosystem health through the ecological impacts, as well as for fisheries resources (Agostinho *et al.,* 2007; Teixeira *et al.,* 2019).

Our results showed the decrease overtime of early fish stages of the Canoas reservoirs and the dominance of opportunistic species, suggesting that these species complete their life cycle in the reservoirs. Thus, *P. maculatus* can be an important species for ecosystem health and fisheries resources in these environments. However, the absence of critical sites for reproduction and the stochastic climatic events, together with the operation of the dams in response to this scenario, could be the factors that harmed fish recruitment and the conclusion of life cycle from many species. Therefore, there is a need for constant monitoring of the ichthyofauna and its reproductive activity in the Canoas reservoirs.

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