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Article

Drifting in a free-flowing river: Distribution of fish eggs and larvae in a small tributary of a Neotropical reservoir

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Abstract: We investigated spatial and temporal variations in the distribution of fish eggs and larvae in the Guareí River, a free-flowing tributary located in the upper section of the Jurumirim Reservoir, Paranapanema River, Brazil. Fish eggs and larvae were sampled ~ fortnightly from November 2017 to March 2018 (Cycle 1), and from November 2018 to March 2019 (Cycle 2), at three sites distributed along the entire course of the Guareí River. We collected 859 fish eggs and 1,340 larvae, comprising 19 taxa. We found reproductive activity of several fish species in the Guareí River, including long-distance migrants. However, there was no spatial differences in the assemblage structure and densities of fish eggs and larvae along the channel of Guareí River. We recorded temporal differences in larvae density only in Cycle 2. The consistent capture of fish eggs and larvae in two reproductive cycles is strong evidence that this river is a spawning site for a variety of fish species. Thus, we recommend maintaining its natural flow regime.

Keywords: *Fish reproduction; Ichthyoplankton; Jurumirim Reservoir; Migratory fish; Prochilodus lineatus.*

À deriva em um rio de fluxo livre: Distribuição de ovos e larvas de peixes em um pequeno afluente de um reservatório Neotropical

Resumo: Investigamos as variações espaciais e temporais na distribuição de ovos e larvas de peixes no rio Guareí, um afluente de fluxo livre localizado na parte superior do Reservatório de Jurumirim, bacia do rio Paranapanema, Brasil. Ovos e larvas de peixes foram amostrados ~ quinzenalmente de novembro de 2017 a março de 2018 (Ciclo 1), e de novembro de 2018 a março de 2019 (Ciclo 2), em três locais distribuídos ao longo de todo o curso do rio Guareí. Foram coletados 859 ovos de peixes e 1.340 larvas, compreendendo 19 táxons. Nós encontramos atividade reprodutiva de várias espécies no rio Guareí, incluindo espécies migradoras de longa distância. Contudo, não houve diferenças espaciais na estrutura das assembleias e nas densidades de ovos e larvas e ao longo do canal do rio Guareí. Diferenças temporais foram significativas apenas para densidade de larvas no Ciclo 2. A captura consistente de ovos e larvas de peixes em dois ciclos reprodutivos é uma forte evidência de que este rio é um local para a reprodução de várias espécies de peixes. Assim, recomendamos a manutenção do seu regime de fluxo natural.

Palavras-chave: *Reprodução de peixes; Ictioplâncton; Reservatório de Jurumirim; Peixes migratórios; Prochilodus lineatus.*

Introduction

The distribution of fish eggs and larvae in freshwater ecosystems reflects the reproductive success of species. Young forms are found in most aquatic environments, such as lakes (*e.g.*, Daga et al. 2009, Tondato et al. 2010), rivers (*e.g.,* Reynalte-Tataje et al. 2011, Zacardi et al. 2017), estuaries (*e.g.,* Sarpedonti et al. 2008, Marcolin et al. 2010) and others. In rivers*,* numerous species spawn in the channel, where larvae drift with the flow toward nursery areas located downstream. Depending on the species [*e.g.*, *Salminus brasiliensis* (Cuvier, 1816)], the larvae may be carried toward downstream reaches for dozens of kilometers (Rosa et al. 2020). In this sense, spatial and temporal assessments of ichthyoplankton distribution are important to understand reproductive and recruitment dynamics in an ecosystem (*e.g.*, Castro et al. 2002, Henry & Suiberto 2014, Rosa et al. 2020). This information plays an important role to guide conservation strategies (Nakatani et al. 2001, Bialetzki et al. 2016), especially in rivers subject to human impacts (*e.g.*, river regulation, fragmentation, habitat loss, pollution, deforestation).

Accessing spatial and temporal dynamics of fish eggs and larvae in small and medium-sized rivers has become increasingly necessary in tropical regions (*e.g.*, Reynalte-Tataje et al. 2020), where hydropower expansion has affected the functioning of many lotic systems (Ferreira et al. 2016, Winemiller et al. 2016). Dams cause hydrological changes with direct and indirect negative effects on the aquatic biota (Agostinho et al. 2008, Couto & Olden, 2018). Moreover, other activities (*e.g.*, agriculture and mining) have caused additional disturbances to small systems, with significant effects on fish biodiversity (Pelicice et al. 2017; Azevedo-Santos et al. 2019, 2021). Small to large sized tributaries deserve special attention, since they may act as biodiversity hotspots in riverine networks (Vitorino Júnior et al. 2016, Silva et al. 2019), especially in areas affected by dams (Marques et al. 2018, Sanches et al. 2020). However, many small tributaries remain uninvestigated, including those that flow into reservoirs, impeding the assessment of their significance in providing critical habitats for fish recruitment.

The Guareí River is a free-flowing tributary located in the Upper Paranapanema River (Fulan et al. 2012), Upper Paraná River, Brazil. This river flows to the Jurumirim Reservoir (Azevedo-Santos et al. 2020), the first impoundment in a “cascade of reservoirs along the Paranapanema River” (Pelicice et al. 2018: p.1-12). These aspects make the Guareí River an interesting case, with potential to act as spawning site and nursery ground for the regional fish fauna. In this study, we investigated spatial and temporal variations in the distribution of fish eggs and larvae in the Guareí River. In particular, we investigated the hypothesis that the Guareí River is a breeding site for several fish species, including long-distance migratory fish (*sensu* Agostinho et al. 2003), considering that it is a free-flowing river that preserves environmental heterogeneity and habitat diversity. Moreover, adult individuals of several species have been observed in this river (Azevedo-Santos et al. 2020), many of which have been reported in Jurumirim Reservoir (see also Kurchevski & Carvalho 2014). Therefore, we investigated three predictions: (i) the presence of eggs and larvae in the Guareí River, including migratory fishes; (ii) spatial gradients in the distribution of early forms, with more eggs in the upper course of the channel, and the predominance of larvae in lower reaches, as observed in large rivers (*e.g.*, Baumgartner et al. 2004); (iii) temporal variations in the density of fish eggs and larvae, considering that reproduction is a seasonal event (*e.g.*, Reynalte-Tataje et al. 2011).

Material and Methods

1. Study area

The Guareí River (*ca.* 90 kilometers; Leite et al. 2012) is a small tributary flowing into the Jurumirim Reservoir, Upper Paranapanema River (Henry et al. 2016). Lateral lakes and pools are found along its course, especially in the middle reach (V.M. Azevedo-Santos & R. Henry, personal observation). These lentic environments are connected with the main channel during the wet season. Despite the current hydroelectric expansion in Brazil, which has boosted the construction of small-sized dams (*cf.*, Ferreira et al. 2016), the Guareí River still preserves its original lotic condition (*i.e.*, no dams). Currently, the most notable human impacts in this river are the absence of riparian forests in some stretches (Azevedo-Santos et al. 2020) and water pollution (*e.g.*, solid wastes).

The three sampling sites cover the entire course of the Guareí River (Fig. 1). Site 1 (S1: ~5 m wide and ~ 629 m asl) is located in the upper course (23°21’56.83”S, 48°10’54.47”W), within the urban perimeter of the municipality of Guareí, São Paulo, Brazil. Site 2 (S2: ~13 m wide and ~ 593 m asl) is located in the middle course (23°27’54.27”S, 48°25’18.95”W), close to the Mineiros bridge, in the municipality of Angatuba, São Paulo. Site 3 S3: ~20 m wide and ~ 579 m asl) is located in the lower course (23°27’51.44”S, 48°34’40.34”W), near Aterradinho village, also in the municipality of Angatuba, São Paulo. Site 3 is located about 5 km (straight line) upstream from the confluence of the Guareí River with the Jurumirim Reservoir.

2. Sampling and laboratory analysis

Fish eggs and larvae were sampled about fortnightly (Table S1) from November 2017 to March 2018 (Cycle 1), and from November 2018 to March 2019 (Cycle 2). The sampling period was chosen based on Henry & Suiberto (2014), who indicated a high fish reproductive activity during these months. Collections occurred under license provided by Brazilian Institute of the Environment and Renewable Natural Resources (SISBIO 57047).

Sampling took place at night, as previous studies have shown higher densities of fish eggs and larvae during this period (*e.g.*, Garcia et al. 2018). We used an ichthyoplankton net (50 cm diameter and 300 µm mesh) equipped with a flowmeter (“General Oceanics” model 2030BR). The net was positioned near the water surface (~10 cm depth), at the center of the Guareí River channel for 10 minutes (passive collection). We repeated this procedure three times at each sampling event, totaling thirty minutes of water filtered at each site and collection date. The material collected was euthanized with eugenol (procedure frequently used for adult fishes; see Vicentin et al. 2019) and fixed in formalin with CaCO3 as recommended in Nakatani et al. (2001).

In the laboratory, fish eggs and larvae were washed and separated from other materials (*e.g.*, leaves and debris) using a 50 µm sieve. The resulting sample was screened under a stereomicroscope to separate and count fish eggs and larvae. Fish larvae were determined to the lowest taxonomic level (including species) based on Nakatani et al. (2001). When necessary, a specialist confirmed the identification (see Acknowledgments section). In addition, the fish larvae were classified according to each development stage and degree of notochord flexion, following Ahlstrom & Ball (1954) and adapted by Nakatani et al. (2001; p. 33): “yolk-sac larvae”, “pre-flexion”, “flexion” or “post-flexion”.

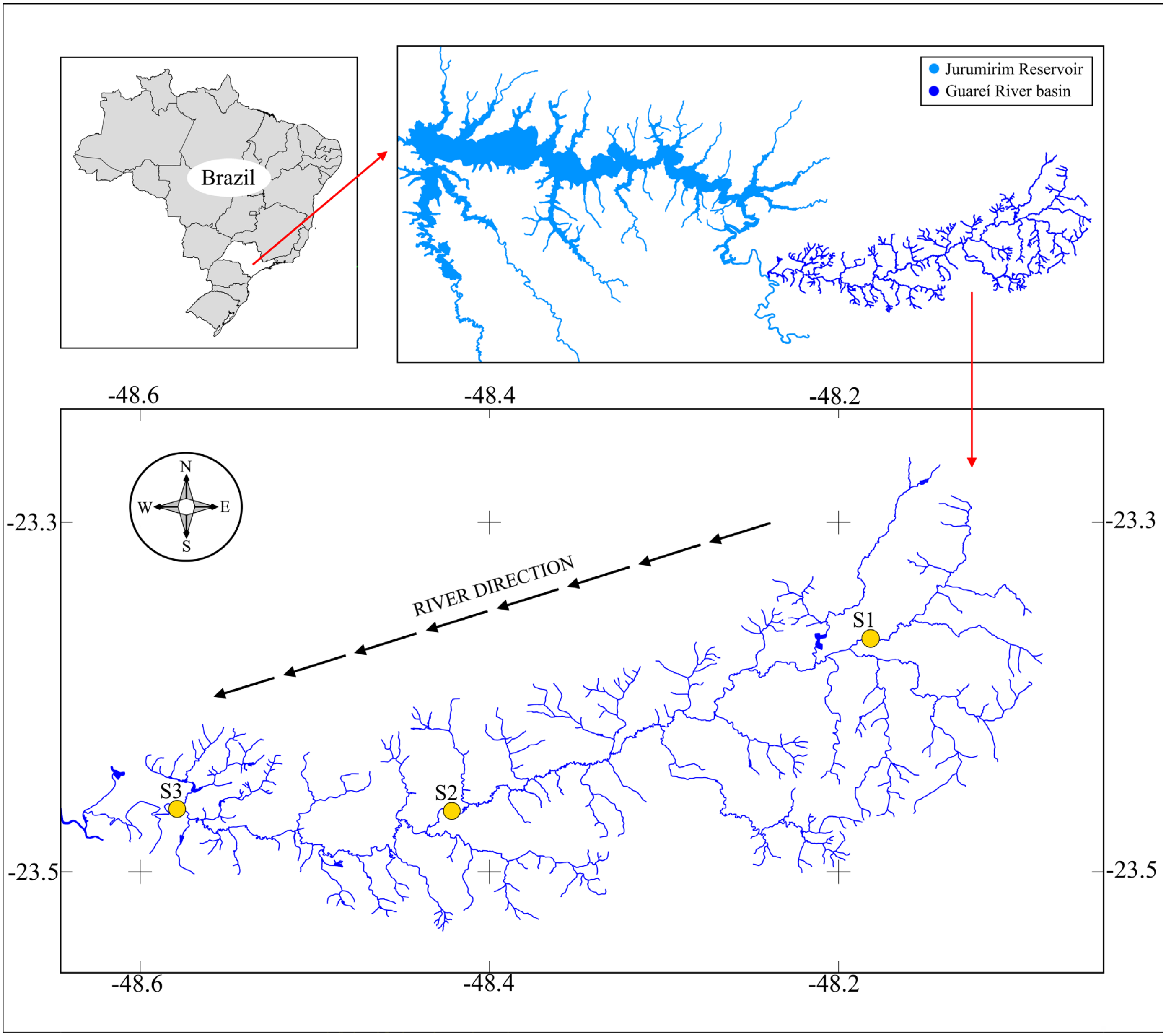

Figure 1. Location of the three sampling sites (in yellow) along the Guareí River, Paranapanema River basin (upper Paraná River system), São Paulo (modified from Azevedo-Santos *et al*., 2020).

The volume of water filtered by the planktonic net was calculated based on Nakatani *et al*. (2001). Fish eggs and larval densities (number/$10m^3$) were calculated based on Tanaka (1973) *apud* Nakatani *et al*. (2001), considering adaptations made by these last authors.

3. *Data analysis*

We ran a Non-Metric Multidimensional Scaling analysis (NMDS) (Clarke & Warwick, 2001) to investigate assemblage structure patterns among sites (S1, S2, and S3). For this analysis, fish larvae were grouped at the family level, as many individuals were not identified at the species or genus levels. Density data were log $(x + 1)$ transformed, and the analysis employed Bray-Curtis similarity (Clarke & Warwick, 2001) with the insertion of Dummy (0.01). Subsequently, a PERMANOVA was applied to test for differences in assemblage structure ($p < 0.05$) among sites. The NMDS and PERMANOVA were run in PRIMER 6.0.

Significant differences ($p < 0.05$) in egg and larval densities were investigated with non-parametric Anova (Kruskal-Wallis, H), considering sites (S1, S2 and S3) and sampling events (*e.g.*, Jan A, Jan B, so on) as factors. This same analysis was used to test differences between larval development stages in each sampling site. Data in each cycle were investigated separately. The Dunn test (Dunn, 1964) indicated differences among groups. Both tests, H and Dunn, were run in the FSA package (Ogle et al. 2019), R environment (R Development Core Team, 2018).

Results

We collected 859 fish eggs and 1,340 larvae in the Guareí River: 567 eggs and 307 larvae in Cycle 1, and 292 eggs and 1,033 larvae in Cycle 2. Captured larvae were identified up to the maximum level of class (total of one), orders (two), families (seven), genera (two), or species (seven). A total of 19 taxa was recorded (Table 1; see also Table S2): 15 in Cycle 1, and 15 in Cycle 2. Seven taxa were identified at the specific epithet level. Among them is *Prochilodus lineatus* (Valenciennes, 1837) [Prochilodontidae], a long-distance migratory fish, but these larvae were recorded only in two sites during Cycle 2 (Table 1).

Assemblage structure of larvae was similar among sampling sites in both cycles (Fig. 2a-b). Within each cycle, no significant differences in assemblage structure between sampling sites were observed (Permanova, p = 0.24 and p= 0.11).

In Cycle 1, egg density ranged between 3.3 and 12.5 eggs/10m^3, and larval density ranged between 8.7 and 14.9 larvae/10m^3 among sampling sites (Fig. 3a-b). In Cycle 2, egg density ranged between 1.8 and 7.4 eggs/10m^3, and larval density ranged between 18.0 and 46.7 larvae/10m^3 among sampling sites (Fig. 3c-d). There were no significant spatial differences in the density of fish eggs (Kruskall-Wallis, Cycle 1: p = 0.72; Cycle 2: p = 0.72) and larvae (Kruskall-Wallis, Cycle 1: p = 0.97; Cycle 2: p = 0.78) among sites in both cycles.

Temporally, egg density ranged between 0 and 36.4 eggs/10m^3, and larvae between 0.5 and 42.1 larvae/10m^3 in Cycle 1 (Fig. 4a-b). On the other hand, egg density ranged between 0 and 17.9 eggs/10m^3, and larvae between 1.1 and 158.0 larvae/10m^3 in Cycle 2 (Fig. 4c-d). Statistical differences were found only for fish larvae in Cycle 2 (Table S3).

Table 1. Taxa and their respective average densities (fish larvae/10m^3) at each site during each sample cycle (classification of taxa in Table S2). Larvae identified up to the level of class^1, order^2, family^3, genus^4, and species^5.

Taxon	Cycle 1			Cycle 2		
	S1	S2	S3	S1	S2	S3
Actinopterygii^1	3.4642	0.3287	1.9238	0.8437	0	0
Anostomidae^3	0	0.1018	0.1130	0	1.0089	3.9260
Apareiodon affinis (Steindachner, 1879)^5	0	1.3641	1.6488	0	0	1.0414
Astyanax spp.^{4}	0.7436	0	0.1141	0	0.6668	0
Bryconamericus aff. *iheringii* (Boulenger, 1887)^5	3.7678	0.2609	0.1959	0.6946	0.1830	0
Bryconamericus spp.^{4}	1.1463	2.5315	1.2926	3.3124	2.1812	12.0052
Callichthyidae^3	0	0	0	0.0194	0	0
Characidae^3	5.4966	2.2468	1.0301	10.7488	29.3673	3.6576
Characiformes^2	0.0279	1.6250	1.0529	0	0.5408	0.2719
Curimatidae^3	0	0	0	1.6467	6.8202	0
Heptapteridae^3	0.2549	0.3304	0.1223	0.7615	4.0958	0
Hoplias malabaricus (Bloch 1794)^5	0	0.0407	0	0	0	0
Hoplosternum littorale (Hancock 1828)^5	0.0208	0.0121	0	0	0	0
Parodontidae^3	0	0	0.0235	0	0	0
Pimelodidae^3	0	0.0339	0.0222	0	0	0
Prochilodus lineatus (Valenciennes, 1837)^5	0	0	0	0	0.0609	0.0057
Schizodon nasutus Kner, 1858^5	0	4.5731	1.1937	0	1.7162	3.4945
Serrasalmus maculatus Kner, 1858^5	0	0	0	0	0.0852	0.3362
Siluriformes^2	0	0	0.0128	0	0	0.0029

We recorded four different developmental stages for fish larvae (Fig. 5). In Cycle 1, the yolk-sac larvae stage was predominated (Fig. 5b; Table S4).

Discussion

Our results support the hypothesis that the Guareí River is a reproductive area for rheophilic and migratory fishes. We expect the same pattern in other small rivers flowing to hydroelectric reservoirs in Brazil. In general, the role of small tributaries in areas affected by impoundments — like the Guareí River — as spawning areas for fishes are often overlooked. In fact, studies usually focus on medium or large-sized rivers (e.g., Silva et al. 2019). Therefore, we fill an important knowledge gap concerning the distribution of fish eggs and larvae in these small watercourses.

We recorded larvae of the migratory fish *Prochilodus lineatus*, although in low density. This species is able to migrate hundreds of kilometers to spawn (Agostinho et al. 1993, Agostinho et al. 2003), but dams block migration routes and affect spawning dynamics — and populations usually decline in the impoundment and adjacent areas. The presence of preserved tributaries (*i.e.*, free-from-dams) can sustain populations (*e.g.*, Agostinho et al. 2003, Lopes et al. 2019), and the Guareí River seems to offer conditions for spawning. Our sampling also detected the presence of *Schizodon nasutus* Kner, 1858, a medium-sized rheophilic fish (maximum ~ 30 cm) (Nobile et al. 2015), that migrates small distances to spawn (Carvalho et al. 1998). Other species found were *Apareiodon affinis* (Steindachner, 1879), *Bryconamericus* aff. *iheringii* (Boulenger, 1887), *Hoplias malabaricus* (Bloch, 1794), *Hoplosternum littorale* (Hancock, 1828), and *Serrasalmus maculatus* Kner, 1858, non-migratory fishes (*sensu* Vazzoler 1996) with populations in the Jurumirim Reservoir (Kurchevski & Carvalho 2014). The reproduction of these species — which include several with commercial importance (see Novaes

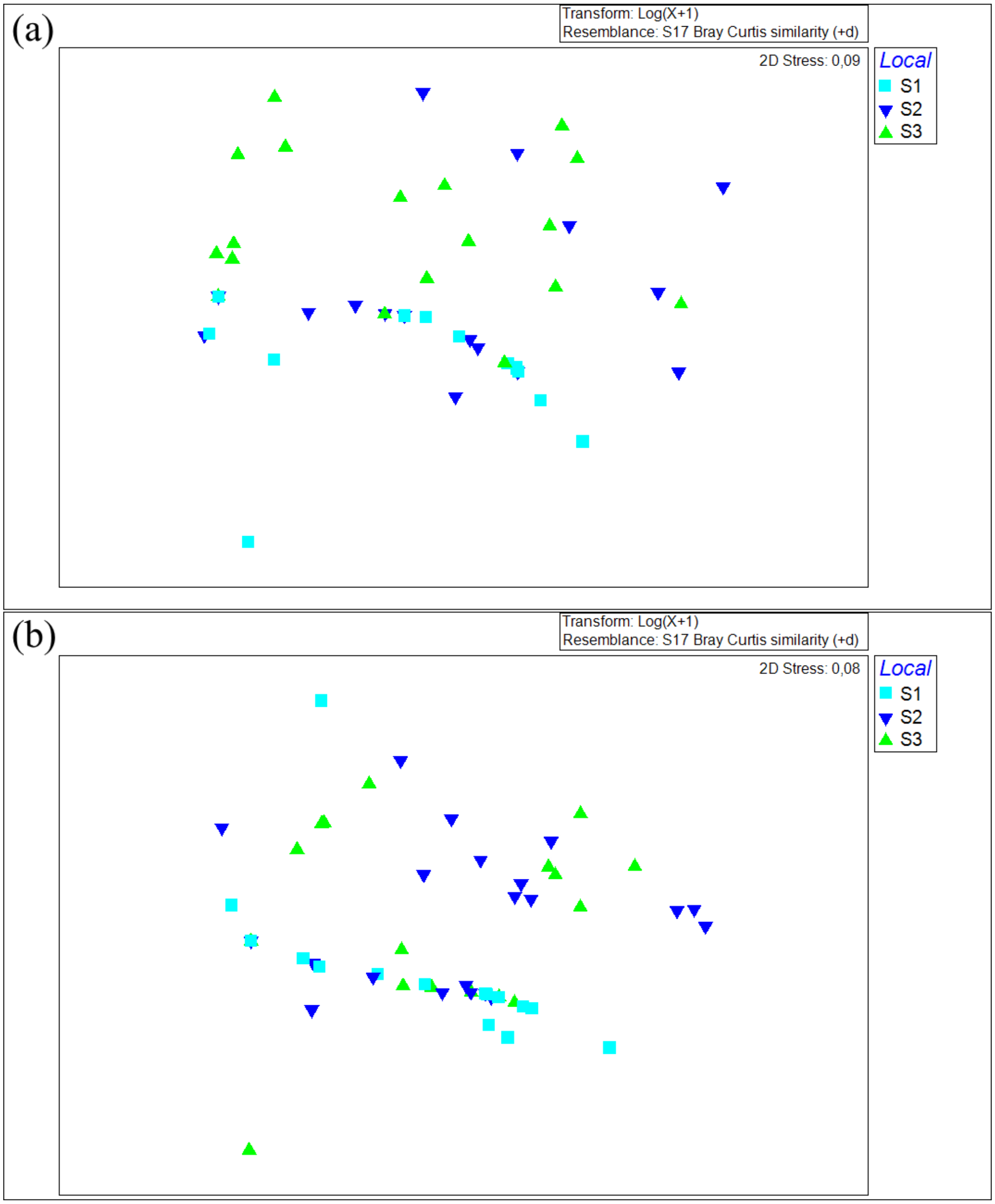

Figure 2. NMDS depicting spatial variation in fish larvae structure (Family level) in sampled sites along the Guareí River, Paranapanema River basin (upper Paraná River system), São Paulo, Brazil, in the: (a) Cycle 1; (b) Cycle 2.

& Carvalho 2009) — is indication that the Guareí River serves as a spawning ground for fishes with different reproductive strategies.

The fish larval structure was similar among sampling sites. However, it should be noted that the analyses were carried out mostly at the family level, since the identification of species is difficult (see Bialetzki et al. 2016, for a broader discussion on this issue). This aspect may have precluded the observation of differences in structure among sites. For example, representatives of Characidae may be widely distributed along the river, but with different species occupying the gradient headwater-mouth (Azevedo-Santos et al. 2020).

Contrary to our prediction, we observed no spatial gradient in the distribution of fish eggs and larvae along the Guareí River. The predominance of non-migratory fish in this river (Azevedo-Santos et al. 2020) may explain this pattern. Non-migratory fish release eggs in different localities along the river (Baumgartner et al. 2004), probably in the confluence with streams; they do not need to reach upper stretches to spawn, which is a common behavior among migratory fishes (Agostinho et al. 2003, Baumgartner et al. 2004). Our results show that in small rivers like the Guareí River (with few migratory species), different reaches may provide adequate conditions for spawning.

Contrary to our prediction, no significant temporal differences were found during Cycle 1, as reproduction occurred in all sampling months. Significant differences between peaks were found only for fish larvae in November A and December A during Cycle 2, reflecting the increased reproductive activity in these occasions. Our results suggest that small rivers like the Guareí do not present a clear temporal pattern

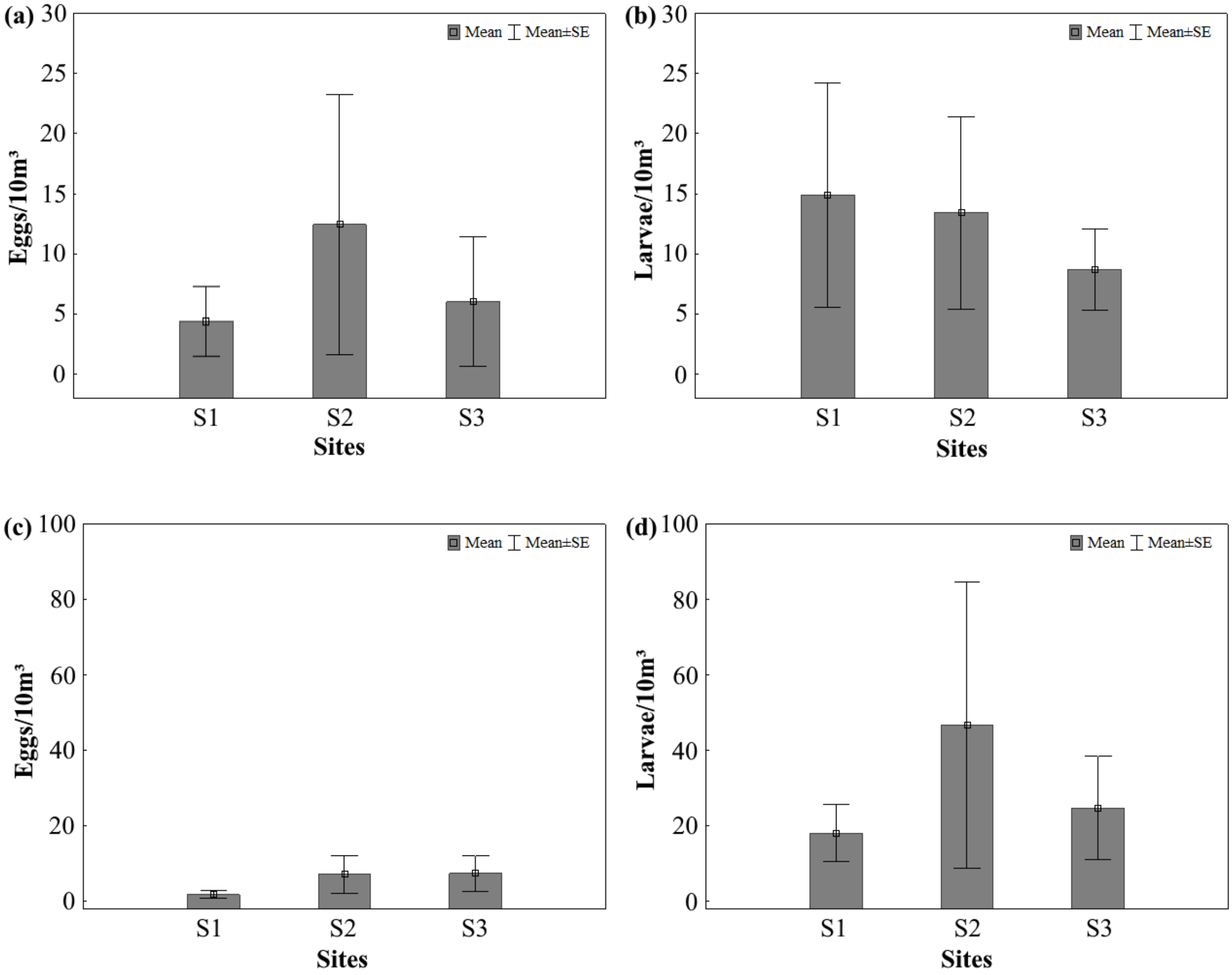

Figure 3. Average density and standard deviation of the ichthyoplankton collected at each site along the Guareí River: (a) eggs and (b) larvae, Cycle 1; and (c) eggs and (d) larvae, Cycle 2.

of reproduction peaks. Other possible explanation is that sampling occurred only in six months, when most species in the region reproduce (Henry & Suiberto 2014). Therefore, the detection of fine scale patterns and spawning peaks would require a different sampling design (*i.e.*, considering samplings in all months of the year).

At each site, the larval development stage was variable. In general, after hatching, the fish larvae develop during the drifting process in the river (Baumgartner et al. 2004). Then, results indicate that the river channel is an area of dispersion and growth. Considering the two cycles, fish larvae in more advanced development stages (*i.e.*, flexion and post-flexion) had lower densities when compared to the other stages (*e.g.*, yolk-sac larvae). As we used passive collection, we believe that larvae in flexion and post-flexion stages show some type of mobility (se also Sanches et al. 2020), impeding them to drift with the river flux up to the ichthyoplankton net. Another possibility is that fish larvae in these more advanced stages are able to remain in areas less affected by the current (*i.e.*, backwaters, including those close to vegetation), or in lateral lakes and ponds, which offer favorable conditions for feeding and survival.

A number of studies (*e.g.*, Nunes et al. 2015, Silva et al. 2015, Marques et al. 2018, Silva et al. 2019, Sanches et al. 2020) have shown or suggested the importance of tributaries for the maintenance of fish diversity in impounded areas. Therefore, the data presented here indicate that the Guareí River is important to the maintenance of fish assemblages in the Jurumirim Reservoir, given the connectivity between the two areas (*i.e.*, free-flowing river and dam). First, it is possible that migratory species (short or long distance) found in the Guareí River, and that also occur in the Jurumirim Reservoir (*e.g.*, *S. nasutus*, *P. lineatus*; Kurchevski & Carvalho 2014), are using this tributary as a route to complete their reproduction; since this affluent has important characteristics that many species require for spawning (*e.g.*, rapids, free-flow). Secondly, is possible that larvae of migratory or sedentary species that reproduce in the Guareí River may reach the Jurumirim Reservoir through drift; and in viable development stages for feeding and displacement. For example, Rosa et al. (2020) estimated that fish larvae can drift long distances until they reach growth areas. In the case of the Guareí River, larvae of *P. lineatus* (especially in stages more susceptible to drift, *e.g.*, pre-flexion) may reach the Jurumirim Reservoir

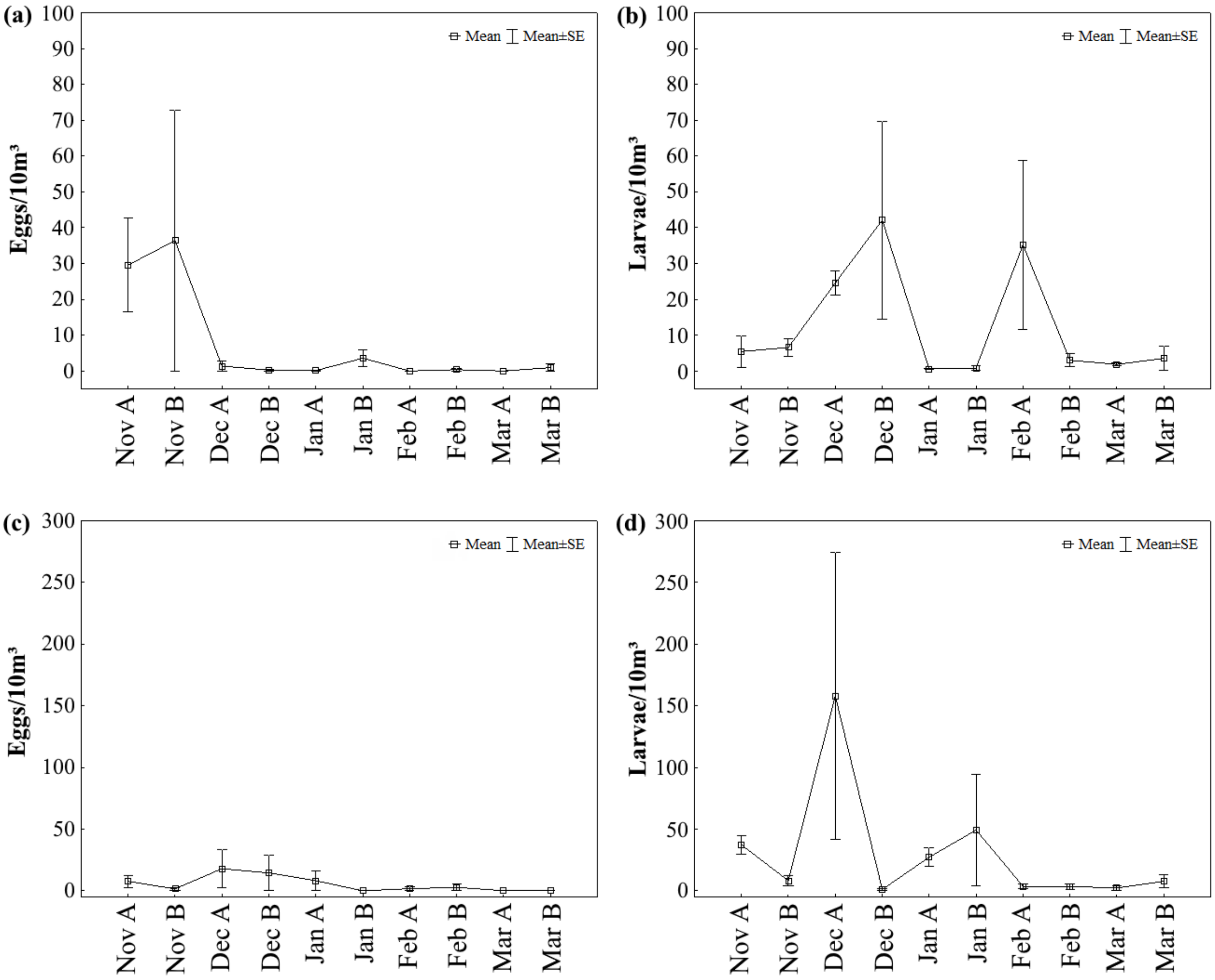

Figure 4. Average density of the ichthyoplankton collected at each sampling occasion in all sites along the Guareí River: (a) eggs and (b) larvae, Cycle 1; and (c) eggs and (d) larvae, Cycle 2.

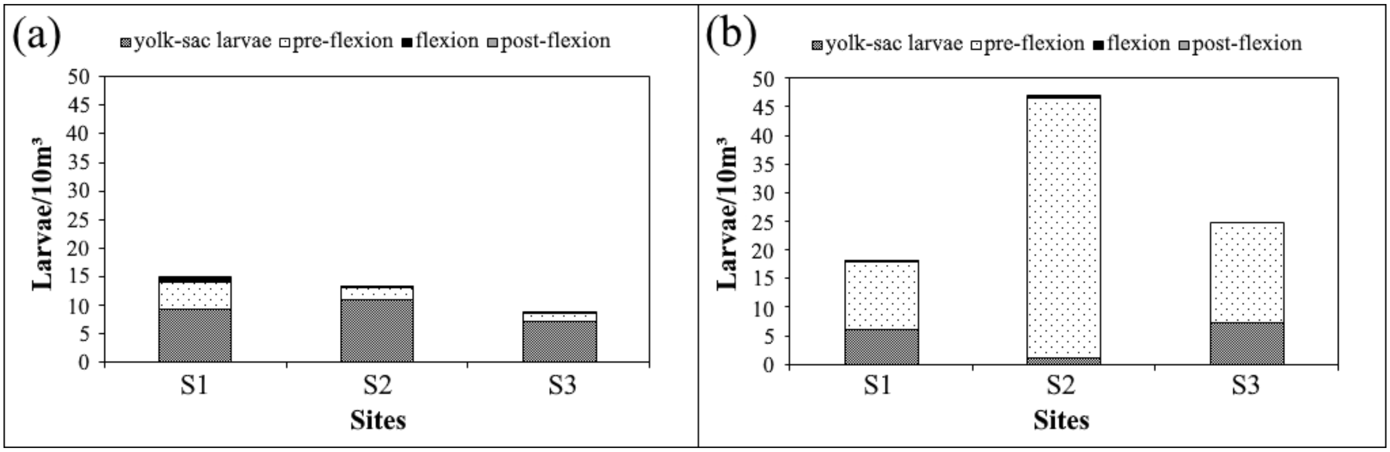

Figure 5. Average density of each larvae stages collected in (a) Cycle 1 and (b) Cycle 2 in each site of the Guareí River.

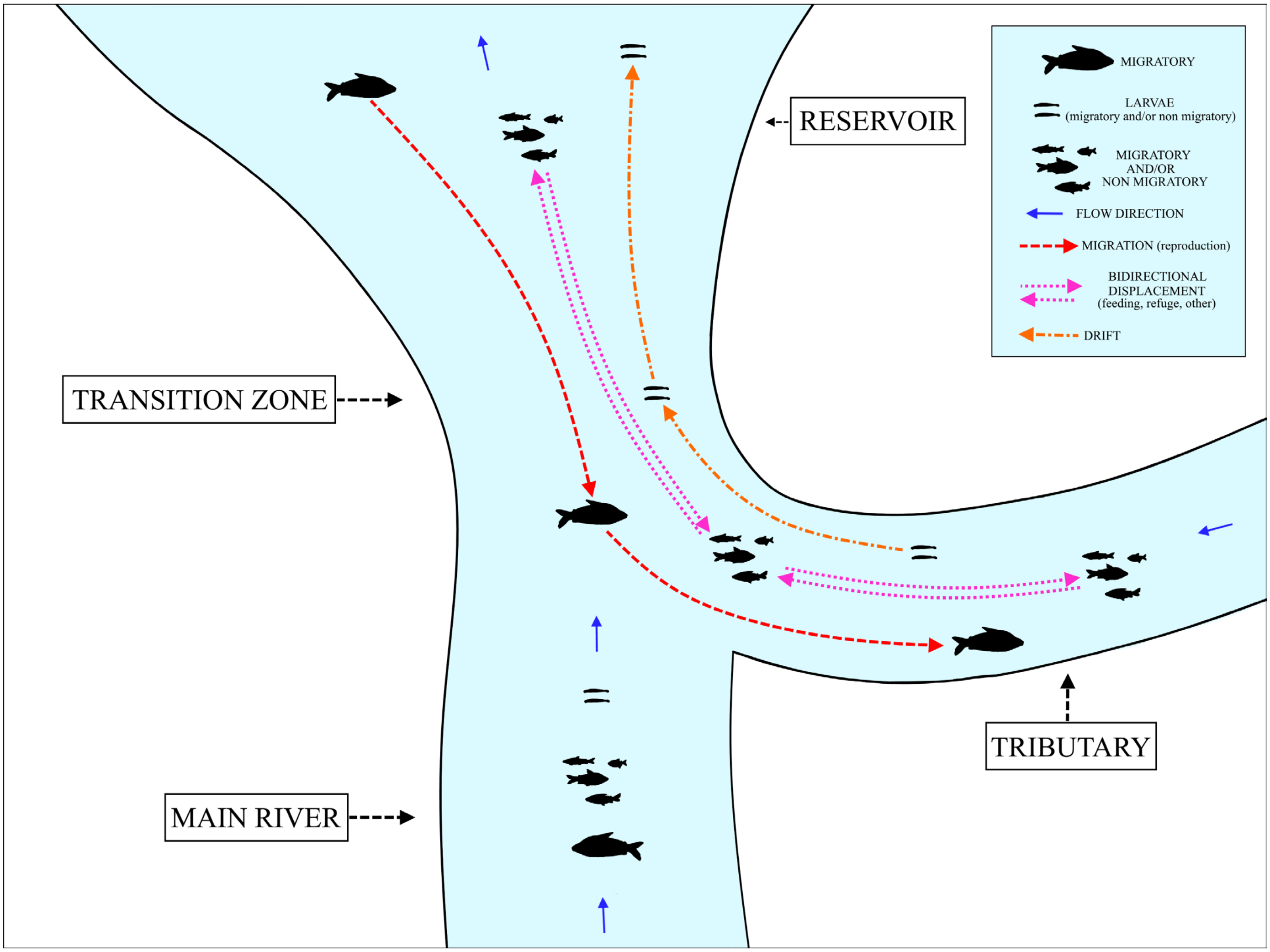

Figure 6. Conceptual model showing how the Guareí River may serve as a "biodiversity source" for the Jurumirim Reservoir, São Paulo, Brazil.

and, once in it, individuals will be able to find growth areas with food such as zooplankton, a resource present in dammed environments and freshwater areas adjacent to them (*e.g.*, Arcifa 1984, Nogueira 2001, Casanova & Henry 2004, Coelho & Henry 2021). This second explanation is reinforced by the data of Henry & Suiberto (2014), who showed the presence of *P. maculatus* larvae and other species at the confluence of the Guareí River with the Jurumirim Reservoir. Third, species may reproduce in the Guareí River, grow in this tributary, and then move to the Jurumirim Reservoir in short (seasonal) or long term (years) for different reasons, especially in search of food, space, or refuge (*e.g.*, macrophytes) (Fig. 6). In other words, we believe that the Guareí River may serve as a "biodiversity source" to the Jurumirim Reservoir. Thus, due to its importance for the reproduction of several fish species — and because it is a lotic tributary of a reservoir —, we emphasize the need to maintain its natural flow regime.

Conclusion

Our results confirmed the hypothesis that the Guareí River is a spawning area for several species, including long-distance migratory fish. However, we detected no spatial differences in assemblage structure or in the densities of fish eggs and larvae along the Guareí River. In addition, we recorded temporal differences in densities of fish larvae only in Cycle 2. As an important watercourse for fish reproduction, we recommend maintaining natural flow regime.

Supplementary Material

The following online material is available for this article

Table S1 - Detailed information about the months, their acronyms, and dates of collections at the three sample sites along the Guareí River, São Paulo, Brazil.

Table S2 - Classification (*sensu* Fricke *et al.,* 2018a, Fricke *et al.,* 2018b) of each taxon captured in the Guareí River, São Paulo, Brazil.

Table S3 - Significant results of Dunn's test for larvae collected in the Cycle 2 in the Guareí River, São Paulo, Brazil.

Table S4 - Results of the statistical analysis of the larval stages.

Acknowledgments

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Author Contributions

Valter M. Azevedo-Santos: performed the collection and identified taxa, performed data analysis, interpretation of data, wrote the first version, led the reviews and writing.

Vanessa S. Daga: performed data analysis, interpretation of data, and collaborated with writing.

Fernando M. Pelicice: performed data analysis, interpretation of data, and collaborated with writing.

Raoul Henry: performed collection of taxa, data analysis, interpretation of data, and collaborated with writing.

Conflicts of Interest

None.

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