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Spatiotemporal dynamics of larvae and juveniles of two species of interest for fisheries in Itaipu: A big neotropical reservoir

Rafael Olimpio Silva[1], Tatiane Mary Gogola[1,2], Pitágoras Augusto Piana[1,2],
Dirceu Baumgartner[1,2], Paulo Vanderlei Sanches[1,2,*]

[1]Universidade Estadual do Oeste do Paraná – Centro de Engenharias e Ciências Exatas – Toledo (PR), Brazil.
[2]Instituto Neotropical de Pesquisas Ambientais – Grupo de Pesquisa em Recursos Pesqueiros e Limnologia – Toledo (PR), Brazil.
*Corresponding author: pvsanches@yahoo.com.br

ABSTRACT

The corvina (*Plagioscion squamosissimus*) and the *mapará* (*Hypophthalmus oremaculatus*) are two of the most explored fish species in the Itaipu reservoir region. However, information on the ecology and dynamics of their initial advances remains scarce. The objectives of this study were to evaluate the spatiotemporal occurrence of larvae and juveniles of these species in five arms of the Itaipu reservoir, determine the peak period of reproductive activity, identify spawning sites and initial development and evaluate the environmental effects on larval abundance. Monthly samples were collected from October to March between 2009 and 2018 in five arms in the left bank of the reservoir at sampling points distributed in the lacustrine, transition and river zones of each arm. The results demonstrated that the reproductive activity of *P. squamosissimus* peaked between January and March, while the *H. oremaculatus* one between October and January. Among all the physical and chemical variables discussed, although relevant to fish reproduction process, only temperature and pluviosity had the strongest effect on larval abundance. The highest larval density of both species was found in the lake zone in all applied arms, indicating that this zone is used as a place for spawning and initial development and is, therefore, a priority area for the conservation of the species.

Keywords: Ichthyoplankton; Itaipu reservoir; *Plagioscion squamosissimus*; *Hypophthalmus oremaculatus*.

Dinâmica espaçotemporal de larvas e juvenis de interesse para a pesca em Itaipu: Um grande reservatório neotropical

RESUMO

A corvina (*Plagioscion squamosissimus*) e o mapará (*Hypophthalmus oremaculatus*) estão entre as espécies de peixes mais exploradas na região do reservatório de Itaipu, no entanto as informações sobre a ecologia e a dinâmica dos seus estágios iniciais de desenvolvimento permanecem escassas. Os objetivos deste estudo foram avaliar a ocorrência espaçotemporal de larvas e juvenis dessas espécies em cinco braços do reservatório de Itaipu, determinar o período de pico da atividade reprodutiva, identificar locais de desova e desenvolvimento inicial e avaliar os efeitos ambientais na abundância larval. Amostras mensais foram coletadas de outubro a março entre 2009 e 2018 em cinco braços localizados na margem esquerda do reservatório em pontos amostrais distribuídos nas zonas lacustre, de transição e fluvial de cada braço. Os resultados mostraram que a atividade reprodutiva de *P. squamosissimus* atinge o pico entre janeiro e março, enquanto a de *H. oremaculatus* entre outubro e janeiro. Entre todas as variáveis físicas e químicas abordadas, embora relevantes no processo de reprodução dos peixes, somente a temperatura e a pluviosidade tiveram o efeito mais forte na abundância larval. A maior densidade larval de ambas as espécies foi encontrada na zona lacustre em todos os braços analisados, indicando que essa zona é utilizada como local de desova e desenvolvimento inicial, sendo, portanto, área prioritária para a conservação das espécies.

Palavras-chave: Ictioplâncton; Reservatório de Itaipu; *Plagioscion squamosissimus*; *Hypophthalmus oremaculatus*.

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INTRODUCTION

The construction of dams is considered an important factor that significantly modifies river ecosystems. It is accompanied by serious ecological, economic, and social impacts (Akstinas et al., 2024). The physical changes caused by dams modify the ecological regime of rivers, whose highly dynamic and complex system becomes relatively homogeneous and less productive (Winemiller et al., 2016). The flow characteristics of several Brazilian rivers have been modified by dams and artificial reservoirs of hydropower plants. After damming, the local landscape is markedly transformed from a lotic to a lentic or semi-lentic environment, altering the chemical and physical conditions of the water and the habitat of many aquatic species (Agostinho et al., 2007).

The impacts of changes to river flow characteristics in the reservoir area may alter the biological conditions of the communities, especially the reproductive dynamics of fish species (Agostinho et al., 2008). Accordingly, studies on ichthyoplankton distribution and abundance are essential to determine spawning periods and areas and identify regions important for their development. This information is crucial for understanding the entire reproductive cycle of the species.

Itaipu reservoir was formed in 1982 with 151 km in length and 1,350 km^2 of flooded area; average depth of 22.5 m, with a maximum of 170 m; water velocity lower than 0.6 m/s^{-1}; and average water resident time of 40 days, which varies from 29 days in the main water body to greater values in the arms (Oliveira et al., 2004; Thomaz et al., 2006). In addition, the reservoir is irregularly shaped, with many arms that are the flooded lower valleys of small- to medium-sized tributaries with varied spatiotemporal characteristics (Bini et al., 1999).

In the Itaipu reservoir, artisanal fishing is vital to fisherfolk in the region (Philippsen et al., 2016). According to Itaipu Binacional (2018), approximately 800 professional artisanal fishers rely on the waters of this reservoir for livelihood. Thus, monitoring fishing and conducting research to understand the reproductive dynamics of species in the reservoir are extremely important to maintain this activity. The history of fisheries monitoring in the reservoir indicates that the most exploited species in this area are *Prochilodus lineatus* (*corimba* or *curimbatá*), *Pterodoras granulosus* (*armado*), *Plagioscion squamosissimus* (corvina), *Hypophthalmus oremaculatus* (*mapará*), and *Pinirampus pirinampu* (barbado). The combined catch of these species accounts for approximately 60% of the total fish catch (Itaipu Binacional, 2018).

In this study, we assessed the occurrence of larvae and juveniles of *H. oremaculatus* and *P. squamosissimus*, which are important species for the fisheries of this region. *H. oremaculatus* (Nani & Fuster, 1947) (Siluriformes, Pimelodidae), commonly known as *perna-de-moça* or *mapará*, is a tasty fish that reaches up to 3 kg in weight, depending on the area, with a fillet yield higher than 60% (Ribeiro et al., 2007). Before the Itaipu reservoir construction, this species was scarce, and after it, it became the most abundant species in this reservoir (Agostinho et al., 1994; Nakatani et al., 1998). Nowadays, it is one of the most caught species in professional fisheries in the reservoir.

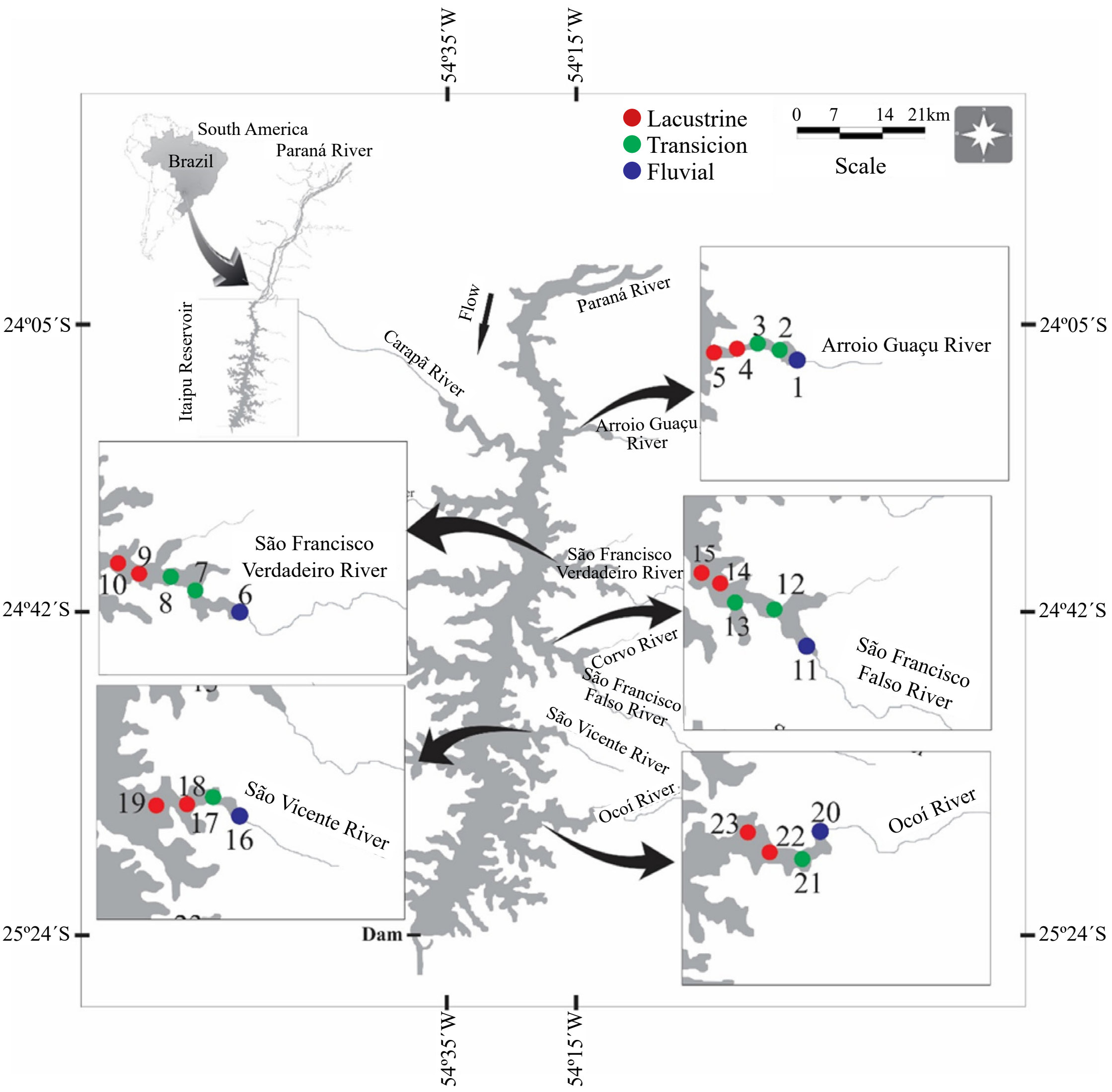
Plagioscion squamosissimus (Heckel, 1840) (Perciformes, Sciaenidae), commonly known as South American silver croaker or corvina, can reach 80 cm in length and 4.5 cm in weight (Casatti, 2003). It is highly abundant in the Itaipu reservoir and one of the most exploited fish in the area (Itaipu Binacional, 2018). This species was introduced in the Pardo River basin in 1967 (Machado, 1974; Nomura, 1984) to increase fishing income (Agostinho et al., 2007).

Despite the economic and social importance of both species, information on the ecology and spatiotemporal dynamics of their early stages of development in the reservoir remains limited. Thus, given the importance of both species, primarily for the fishing sector, the objective of this study was to evaluate spatiotemporal occurrences of larvae and juveniles of *P. squamosissimus* and *H. oremaculatus* in the five arms of the left bank of the Itaipu reservoir. More specifically, based on larval occurrences at the sampled sites, we aimed to determine the period of peak reproductive activity of the species, identify the spawning and initial development sites of the species, and assess the effects of some environmental variables (pH, electrical conductivity, dissolved oxygen, temperature, and turbidity) on larval abundance.

METHOD

Study area

The study area comprised the five arms of the left bank of the Itaipu reservoir, namely Ocoí (OCO), São Vicente (SVI), São Francisco Falso (SFF), São Francisco Verdadeiro (SFV), and Arroio Guaçu (AGU) (Fig. 1), which were formed by flooded lower valleys of small- to medium-sized tributaries (Gogola et al., 2022). Itaipu reservoir (24°05'–25°33'S, 54°00'–54°37'W) was formed in 1982 by the impoundment of the Paraná River. It has a length of ~160 km, depth of 170 m near the dam, and water velocity lower than 0.6 m/s (Oliveira et al., 2004). It is a large (1,350 km^2) and deep (mean depth = 22.5 m) dendritic reservoir (Gogola et al., 2022).



Source: Adapted from Sanches et al. (2020).

Figure 1. Location of sampling points in the arms of the left bank of the Itaipu reservoir. Red dots indicate lacustrine zones; green dots indicate transition zones; and blue dots indicate fluvial zones of each arm.

For analysis purposes, each arm was divided into three zones according to the distance from the lotic section of the tributary to the reservoir body, as described in Sanches et al. (2020). Thus, the three zones sampled along the arms were named as follows:

- Fluvial zone (FLU), located the furthest from the central body of the reservoir and most strongly affected by the tributary;
- Transition zone (TRA), the intermediate area between the reservoir and the mouth of the tributary;
- Lacustrine zone (LAC), the closest to the central body of the reservoir.

All sampled arms are deep (> 15 m) and wide (600–1,150 m) in the LAC and relatively shallow (1–5 m) and narrow (30–220 m) in the FLU. Along their courses, these reservoir arms support rooted aquatic vegetation (*Egeria densa*) and floating macrophytes (*Pistia stratiotes*, *Salvinia natans*, *Eichhornia azurea*, and *Eichhornia crassipes*), submerged trunks, and natural riparian forests, mainly in the TRA and FLU (Gogola et al., 2016; Sanches et al., 2020). In their FLU, the reservoir arms are directly affected by the lotic sections of the tributaries and reach higher flow velocities.

Sampling

Monthly samplings were conducted between October and March for six periods between 2009 and 2018 (period I = 2009/2010;

II = 2010/2011; III = 2011/2012; IV = 2014/2015; V = 2015/2016; and VI = 2017/2018). The samples were collected using conical-cylindrical plankton nets with a 0.5-mm mesh size, equipped with a flowmeter (Flowmeter General Oceanics Mod. 2030R) to measure the volume of filtered water. The nets were attached to the side of the boat and operated dusk onwards in horizontal trawls along the water surface (approximately 10 cm deep) at a low speed (± 5 km/h) for 10 min.

The samples were collected using a continuous trawling system, sampling from the lentic (LAC) to the lotic (FLU) sections of each arm. For continuous trawling, a net was exposed for 10 min at the beginning of the collection event; after this period, the net was retrieved to remove the collected material, immediately exposing another net for the same time to proceed with the sampling. The sampling points were the locations where each net was initially exposed along each arm (Fig. 1).

The samples were stored in plastic bottles labelled according to the collection site and date and contained benzocaine hydrochloride (anesthetic) to euthanize captured organisms according to the guidelines of the National Council for the Control of Animal Experimentation (CONCEA, 2013), and the Animal Research Ethics Board of Universidade Estadual do Oeste do Paraná (Unioeste), and subsequently fixed in 4% formaldehyde buffered with calcium carbonate ($CaCO_3$). All captured organisms were adrift in water column, and no traps or light attractants were used during sampling.

Alongside the ichthyoplankton samples, some variables were measured using portable devices: pH, and electrical conductivity ($\mu S \cdot cm^{-1}$), measured using pH meters and conductivity meters digimed DM 3P; dissolved oxygen ($mg \cdot L^{-1}$) and temperature (°C), both measuring by oximeter YSI, 550^{a}. The turbidity (nephelometric turbidity units, NTU) was obtained from water samples analyzed in the limnology laboratory of the Limnology and Fisheries Resources Study Group (GERPEL) of Unioeste, Toledo *campus*, using the Quimis Q279 pn turbidimeter. Pluviosity data were provided by the Paraná Water Institute (Águas Paraná), and reservoir level data were provided by the National Electric System Operator (ONS).

Species characteristics

Hypophthalmus oremaculatus was initially identified as *Hypophthalmus edentatus* in the Paraná River basin but subsequently revised by Ota et al. (2018) and reclassified. Species of the *Hypophthalmus* genus are characterized by scaleless, laterally compressed body with three pairs of barbels (two mandibular and one maxillary); a small mouth and no teeth, small eyes, latero-ventrally located below the midline of the head; dorsal fin positioned around the middle of the body and a long anal fin that stretches from the anus to the anterior region of the caudal peduncle (Littmann et al., 2021; Lopez-Femandez & Winemiller, 2000). These species differ from the other catfish because they are pelagic planktophages and mainly consume cladocerans, copepods, ostracods, and microalgae, in addition to insect and shrimp larvae, fish eggs, mites, and rotifers (Abujanra & Agostinho, 2002; Cutrim & Batista, 2005; Silva & Bialetzki, 2019).

Plagioscion squamosissimus has a carnivorous generalist with ontogenetic diet shifts, consuming mostly aquatic insects during the larval and juvenile stages, while the adults predominantly feed on fish and shrimp (Neves et al., 2015). It can form large shoals and remain in the deepest zones, close to the sediment (Agostinho et al., 2007). It has an elongated body that is laterally compressed. The coloration of the body is generally silvery, with metallic reflections that can vary depending on the environment and the age of the fish. The head and eyes are relatively large, with a terminal and well-developed mouth. The scales are small and firmly attached to the body. The dorsal fin is long and composed of two parts: an anterior part with hard rays and a posterior part with softer rays. The caudal fin is truncated or slightly rounded in shape. The pelvic fins are in a thoracic position. Retaining to this day some characteristics of its marine ancestors, especially owing to the pelagic development of its eggs, this species has proliferated in several Brazilian reservoirs (Brito et al., 2020; Queiroz-Sousa et al., 2018; Orlandi Neto, et al., 2024), becoming the most successfully introduced species in the upper Paraná River floodplain in terms of abundance and biomass (Agostinho et al., 2007).

Data analysis

Larval and juvenile fish abundances were standardized for a volume of 10 m^3, according to the method described by Tanaka (1973), and modified by Nakatani et al. (2001), using Eq. 1:

$$Y = (X/V) \cdot 10 \tag{1}$$

Where: Y: number of eggs and larvae per 10 m^3; X: number of eggs or larvae collected; V: volume of filtered water.

The volume of filtered water was calculated using Eq. 2:

$$V = a \cdot r \cdot f \tag{2}$$

Where: V: volume of filtered water; a: net-mouth area (0.1104 m^2); r: number of flowmeter revolutions; f: flowmeter calibration factor (0.026873).

To determine spawning and development sites, young fish were classified into larvae and juveniles. The larval period was subdivided into four developmental stages, namely yolk-sac, preflexion, flexion, and post-flexion larval stages, according to the degree of notochord flexion and the formation of the supporting elements of the caudal fin, as proposed by Ahlstrom et al. (1976). The organisms with fully formed pectoral fin rays were included in the juvenile period (Nakatani et al., 2001).

Differences in the distribution of larvae across periods, months, and sampling points were identified using the analysis of variance (ANOVA), and tested for homoscedasticity and normality, using Levene and Shapiro-Wilk's tests, respectively (Matthews, 1998). As there is a possibility that a certain number of eggs and larvae collected at a given location within the arms come from areas above, we assume that their occurrence at that specific location indicates that it is used by the species for their initial development. Although this violates the assumption of independence between observations within the arms, which somewhat limits the conclusions for distribution within them, we believe that the results presented are consistent and important for species management actions. When ANOVA assumptions were not met, the rank transformation method was used (Quinn & Keough, 2002); if ANOVA assumptions were not met even after rank transformation, the non-parametric Kruskal–Wallis' test was applied (Zar, 1999).

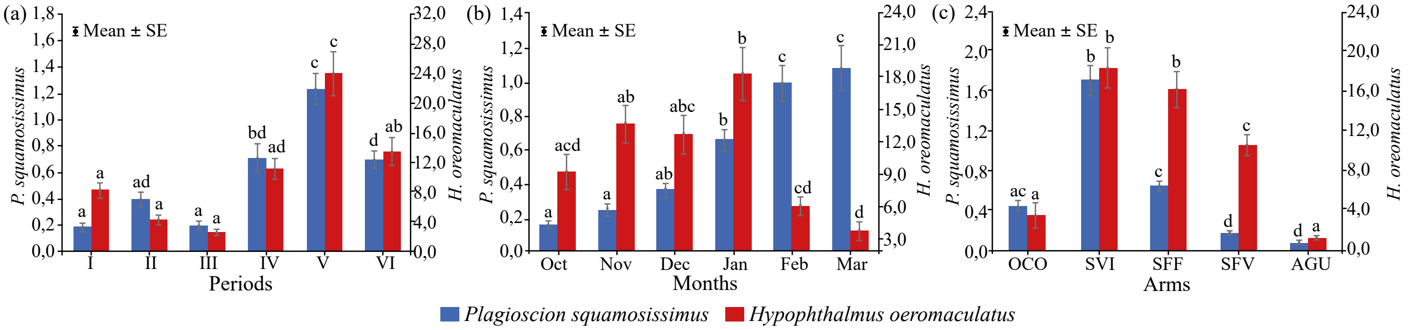
The effects of environmental factors on larval abundance were assessed using Pearson's product-moment correlation analysis, with abiotic and biotic data transformed into log (x+1) and square root, respectively (Pearson, 1901). Relationships between larval abundance and environmental factors for different periods and reservoir arms were determined using a redundancy analysis (RDA) in R software (R Core Team, 2016) by the packages Vegan (Oksanen et al., 2016) and Packfor (Dray et al., 2007). Analysis of variance was performed, and graphs were generated using the software Statistica 7.0. The significance level was set to $p < 0.05$.

RESULTS

During the sampling period, *H. oremaculatus* were predominantly caught, accounting for 94.89% of the catch volume. For both species, the catch volumes increased in period IV and peaked in period V, which significantly differed from those in the other periods (Fig. 2a). The statistical tests indicated significant differences in the occurrence of both *P. squamosissimus* ($F_{(5;\ N=3,171)}$=61.22332; p=0.00) and *H. oremaculatus* ($F_{(5;\ N=3,171)}$=64.50795; p=0.00) during period V.

The monthly occurrence of *P. squamosissimus* significantly increased ($F_{(5;\ N=3,171)}$=60.47990; p=0.00) throughout the sampling period, peaking in February and March. In these months, the catch volumes of *P. squamosissimus* significantly differed from the catch volumes in the other months (Fig. 2b). The catch volume of *H. oremaculatus* also significantly ($F_{(5;N=3,171)}$ =29.35138; p=0.00) increased over the months, but only up to January, when the catch volume of this species peaked and significantly differed from the catch volume in other months. However, this variable decreased markedly February onwards (Fig. 2b).

In terms of overall catch for each reservoir arm, SVI showed the highest densities, whereas AGU had the lowest catch densities for both species (Fig. 2c). For *P. squamosissimus*, the statistical test indicated significant differences in density between the arms during the study period ($F_{(4;\ N=3,172)}$=188.9441; p=0.00), and Tukey's *post hoc* test showed that the density

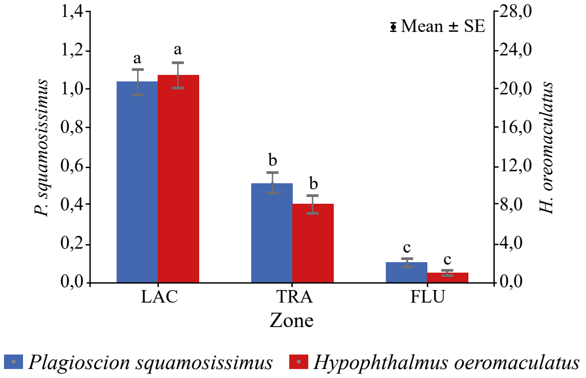


SE: standard error; OCO: Ocoí; SVI: São Vicente; SFF: São Francisco Falso; SFV: São Francisco Verdadeiro; AGU: Arroio Guaçu.

Figure 2. Mean (columns) and standard error (bars) of the abundance of *Plagioscion squamosissimus* and *Hypophthalmus oremaculatus* larval and juvenile catches by (a) period, (b) month, and (c) Itaipu reservoir arm. Letters over bars indicate significant differences (Tukey's test) for each species.

in the SVI arm significantly differed from that in all other arms. For *H. oremaculatus*, significant ($F_{(4;\ N=3,172)}$=57.0065; *p*=0.00) differences in density were also found between the arms, and Tukey's *post hoc* test revealed that the densities in SVI and SFF arms differed from those in other arms of the reservoir (Fig. 2c).

The analysis of the spatial distribution of larvae by limnological zone showed that, in general, catch densities decreased from the lentic to the lotic sections for both species in the Itaipu reservoir arms, that is, the LAC had the highest catch density, followed by the TRA and, lastly, the FLU (Fig. 3), with significant differences between these zones for both species (*P. squamosissimus*: $F_{(2;\ N\ =\ 3,174)}$=126.1377; *p*=0.00; and *H. oremaculatus*: $F_{(2;\ N=31,74)}$=166.1509), and Tukey's *post hoc* test showed that these three areas are considered different.



SE: standard error; LAC: lacustrine zone; TRA: transition zone; FLU: fluvial zone.

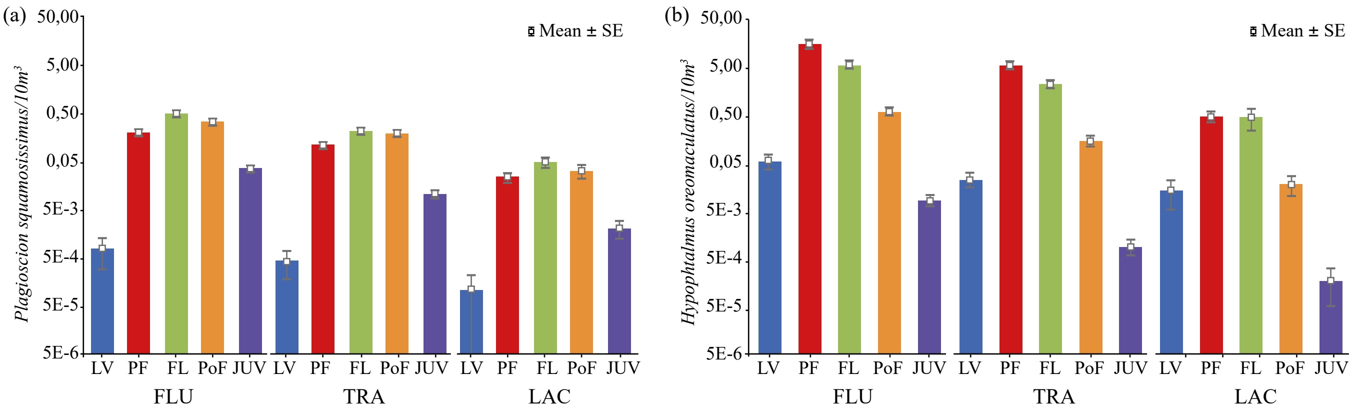
Figure 3. Mean (columns) and standard error (bars) of the abundance of *Plagioscion squamosissimus* and *Hypophthalmus oremaculatus* larval catches by limnological zones in the Itaipu reservoir arms.

All developmental stages were caught in all limnological zones (LAC, TRA, and FLU) for both species (Figs. 4a and 4b), with higher occurrences in the lacustrine and transition zones, especially for the pre-flexion and flexion stages.

The overall Pearson's product-moment correlation analysis between the mean larval density of the entire study period and environmental variables showed a significant positive correlation between *P. squamosissimus* density and water temperature (r=0.33; *p*=0.000) and pluviosity (r=0.16; *p*=0.032) and a negative correlation between larval density and dissolved oxygen (r=-0.34; *p*=0.000) and turbidity (r=-0.15; *p*=0.043) (Table 1). For *H. oremaculatus*, this test indicated a significant and positive correlation only with pluviosity (r=0.17; *p*=0.019) (Table 1).

In the RDA, only the first axis was significant ($Pr_{(<F)}$ = 0.014). This axis accounted for 46.98% of the interactions and was more strongly and negatively associated with temperature (-0.53) and pluviosity (-0.52) than with the other variables (Fig. 5). By species, *H. oremaculatus* (-1.64) was more strongly and negatively associated than *P. squamosissimus* (-0.55) in RDA1, but both species were positioned on the left side of the axis (Fig. 5).

By period (Fig. 5a), the highest concentrations were found in periods IV, V, and VI on the left side of the axis in RDA1 (negative), which was associated with the highest abundance of both species and with environmental variables such as temperature, pluviosity, pH, and dissolved oxygen. The same association was observed with respect to reservoir arms (Fig. 5b), because SVI was also concentrated on the left side of the axis.

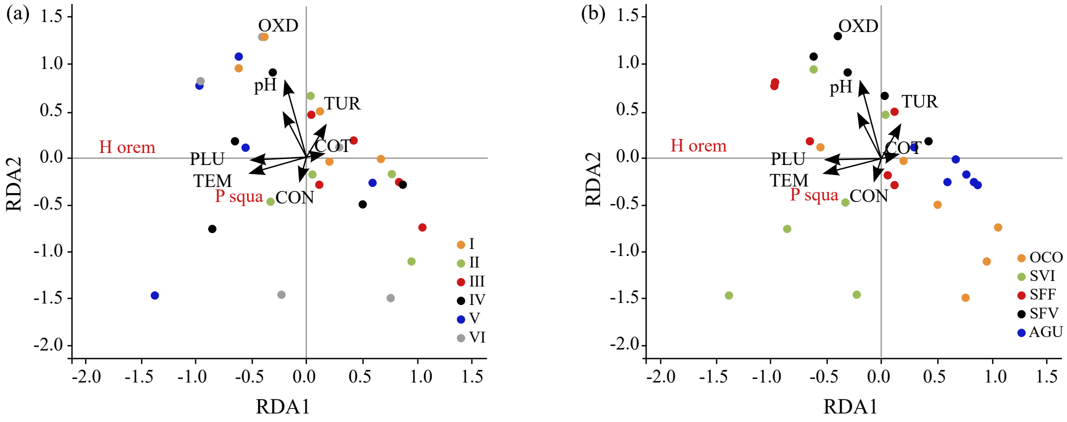


SE: standard error; LAC: lacustrine zone; TRA: transition zone; FLU: fluvial zone; LV: yolk-sac; PF: pre-flexion; FL: flexion; PoF: post-flexion larvae; JUV: juvenil.

Figure 4. Mean density of the distribution of developmental stages of (a) *Plagioscion squamosissimus* and (b) *Hypophthalmus oremaculatus* larvae by limnological zone in the Itaipu reservoir arms.

Table 1. Results of the Pearson's product-moment correlation analysis between the mean densities of *Plagioscion squamosissimus* and *Hypophthalmus oremaculatus* larvae and environmental variables. The significance level was set at $p < 0.05$. Values highlighted in bold indicate significant differences.

Variables	**Correlation values**	
	Plagioscion squamosissimus	***Hypophthalmus oreomaculatus***
Water temperature (°C)	**0.33**	0.03
Dissolved oxygen (mg·L^{-1})	**-0.34**	0.07
pH	-0.09	0.05
Electrical conductivity (µS·cm^{-1})	-0.07	0.08
Turbidity (NTU)	**-0.15**	0.03
Pluviosity (mm)	**0.16**	**0.17**
Reservoir fluviometric level (m)	-0.03	-0.04



TEM: water temperature; OXD: dissolved oxygen; CON: electric conductivity; TUR: turbidity; PLU: pluviosity; LEV: level.

Figure 5. Redundancy analysis (RDA) by (a) period and (b) reservoir arm of *Plagioscion squamosissimus* (P. squa) and *Hypophthalmus oremaculatus* (H. ore) larval abundance and environmental variables.

The RDA1 results (Fig. 5) indicated that pluviosity and temperature interacted the most with the larval densities of both species, particularly the *H. oremaculatus* one. The Pearson's product-moment correlation analysis between the overall larval density and environmental variables (Table 1) indicated that pluviosity was the only variable significantly correlated with this species. Therefore, pluviosity frequency and intensity are extremely important for its reproduction. For *P. squamosissimus*, RDA1 also indicated that temperature and pluviosity were the environmental variables most strongly correlated with larval abundance. Pluviosity and temperature were significantly correlated (Table 1), indicating that these two variables play a key role in the reproduction of these species and are directly proportionally correlated with larval abundance, that is, the higher the temperature and pluviosity, the higher the larval abundance.

RDA1 also showed that periods IV, V, and VI were correlated with both species, with most environmental factors (Fig. 5a), and with the reservoir arms SVI, SFF, and SFV (Fig. 5b), thus providing further evidence explaining the highest larval catches of both species in the last three periods, as well as the highest catch volumes and, therefore, a high preference for the SVI arm and a low preference for the AGU and OCO arms.

DISCUSSION

Occurrences of both species were recorded in all months and analyzed in this study. However, their spawning peaks differed: from October to January for *H. oremaculatus* and from January to March for *P. squamosissimus*. This temporal distinction may be associated with the increased abundance of *H. oremaculatus* in the first half of the sampling period. A lower larval abundance of this species likely reduces trophic competition, given that both species feed on the same plankton during their early developmental stages, as described by Makrakis et al. (2005).

Supporting this, Silva and Bialetzki (2019) also observed that trophic factors influenced differences in peak occurrences. They found a correlation between the abundance of *P. squamosissimus* and the availability of cladocerans and copepods–a relationship not observed for *H. oremaculatus*. This suggests that *P. squamosissimus* is more sensitive to prey availability. Such interspecific interactions can significantly affect fish growth, survival, and recruitment, particularly when behavioral dynamics create uneven resource distribution (Nunn et al., 2012; Wootton, 1990).

Although both species were found in all reservoir arms, the highest occurrences were recorded in the SVI, SFF, and SFV arms. These are located centrally in the reservoir, where more stable temperature and turbidity conditions may promote plankton proliferation, an essential food source for larvae. Conversely, the lowest occurrences in the OCO arm may be due to its proximity to the dam. This arm is most affected by hydropower plant operations (Agostinho et al., 2007; Agostinho et al., 2008), which tend to have greater impacts on freshwater biodiversity near the dam (Keppeler et al., 2022). Additionally, such areas are typically deeper and experience thermal and chemical stratification, conditions that are unfavorable for reproduction (Oliveira et al., 2004; Prchalová et al., 2009). Similar patterns in larval occurrence were also reported by Gogola et al. (2023) and Sanches et al. (2020).

In contrast, the AGU arm, situated near the remaining lotic section of the Paraná River (FLU), exhibits distinct environmental characteristics. Its conditions, such as higher flow, depth variability, input of allochthonous organic matter, turbidity, conductivity, and sediment transport, resemble those of natural riverine stretches (Agostinho et al., 2016). Combined with the low flow in this arm, these characteristics mirror floodplain lagoons, in which zooplankton densities are typically lower than in reservoirs (Portinho et al., 2016). As a result, reduced prey availability may limit feeding by *H. oremaculatus* and *P. squamosissimus*, ultimately affecting larval survival and recruitment success (Silva & Bialetzki, 2019).

Despite these constraints, the presence of larvae in all developmental stages across the arms suggests that these environments serve as both spawning and nursery grounds. However, the predominance of larvae in lentic-influenced areas (LAC), particularly during the pre-flexion and flexion stages, points to a preference for these zones. This may be attributed to favorable conditions for plankton and macrophyte growth, which respectively provide food and shelter for larvae (Abujanra & Agostinho, 2002; Ambrósio et al., 2001; Ferreira et al., 2011; Gomiero & Braga, 2006).

Even so, larval accumulation in LAC may also result from both active and passive dispersion. In FLU, higher flow velocities (Genteline, 2018) can passively transport eggs and early-stage larvae, which have limited swimming ability, toward more lentic areas. Flow velocity is a key factor influencing drift dynamics, with both family- and stage-specific responses (Lechner et al., 2014; Melo-Silva et al., 2022). Active dispersion, on the other hand, likely occurs during later developmental stages (flexion and post-flexion larvae), when larvae develop stronger muscles and fins, enhancing their swimming ability and enabling them to seek out more favorable, low-flow environments in the LAC (Queiroz et al., 2022; Sanches et al., 2020).

The short duration of the yolk-sac stage may explain its low capture rates. At this stage, rapid development is critical due to the limited yolk reserve, and quicker progression enhances survival chances. Once in the flexion stage, *P. squamosissimus* larvae can prey on more mobile organisms like cladocerans and copepods (Neves et al., 2015; Silva & Bialetzki, 2019). However, post-flexion larvae and juveniles are rarely captured, likely because their advanced development, including improved sensory and swimming capabilities, enables them to avoid sampling gear (Silva et al., 2017).

The increase in larval captures from period IV onward aligns with environmental variables, particularly temperature and pluviosity, as revealed by RDA analysis. Although fish reproduction is influenced by several environmental factors, temperature and rainfall appear to be the most important factors in stimulating spawning. Temperature is a key driver of tropical fish life cycles, while pluviosity alters the limnological characteristics of aquatic systems, indirectly influencing reproductive activity (Baumgartner et al., 2003; Baumgartner et al., 2008; Bialetzki et al., 2002; Bialetzki et al., 2005). Similar effects of pluviosity on larval abundance have been documented in various ecosystems, such as the Campaspe and Broken rivers in Australia (Humphries et al., 2002) and in reservoir arms in the United States of America (Gilbert & Pease, 2019).

Statistical analyses further revealed that *P. squamosissimus* is more strongly associated with elevated environmental variables (temperature, dissolved oxygen, turbidity, and pluviosity) than *H. oremaculatus*, which was significantly associated only with pluviosity. This indicates a greater reliance of *P. squamosissimus* on favorable environmental conditions for reproduction. Carnelós and Benedito-Cecilio (2002) reported that this species only effectively colonized areas flooded by the Itaipu reservoir in spring 1986, when environmental conditions were suitable. Similar findings were reported by Baumgartner et al. (2003).

In contrast, *H. oremaculatus* appears less dependent on a wide range of environmental factors. Its reproductive period typically coincides with the rainiest months, as observed in the northern Brazil (Cintra et al., 2008; Costa et al., 2010). Ferreira et al. (2016), studying the Amazon River, found that *H. edentatus* (= *H. oremaculatus*) was significantly correlated only with pluviosity and water level, unlike other congeners. These comparatively lower environmental requirements may explain the consistently higher occurrences of *H. oremaculatus* during the sampling period.

CONCLUSION

The reproductive activity of *P. squamosissimus* peaks between January and March, whereas the *H. oremaculatus* one peaks between October and January. Temperature and pluviosity had the strongest effect on the larval abundance of *P. squamosissimus* in addition to dissolved oxygen and turbidity, whereas pluviosity was the most important environmental variable for *H. oremaculatus* reproduction.

The SVI arm stands out for the highest larval abundance of both species, indicating a preference for this location and its importance for the conservation of these species. In addition to the SVI arm, the SFF and SFV arms are also highly important for these species because the areas closest to the reservoir (LAC) have the highest densities of individuals at all stages of development. Thus, these areas are used as spawning and initial development sites of larvae and should therefore be considered a priority for protecting species and maintaining fish stocks.

CONFLICT OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

All data sets were generated or analyzed in the current study.

AUTHORS' CONTRIBUTION

Conceptualization: Silva, R.O., Sanches, P.V.; **Formal Analysis:** Silva, R.O., Gogola, T.M.; **Writing – Original Draft:** Silva, R.O.; **Writing – Editing and Review:** Silva, R.O., Gogola, T.M., Piana, P.A., Baumgartner, D.; **Data Curation:** Piana, P.A., Baumgartner, D.; **Supervision:** Sanches, P.V.; **Final approval:** Sanches, P.V.

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