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**ECOLOGY** 

# Life strategy of *Astyanax lacustris* (Characiformes: Characidae) in different habitats of the Upper Paraná River basin

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**ABSTRACT.** The current study was carried out in the Tibagi River basin, an important tributary of the Paranapanema River, in the southern region of Brazil. Research with fish from the Neotropical region is extremely important to understand the ecological dynamics of the region. In this context, we chose to study the reproductive variables of the species *Astyanax lacustris*, a Characiform known in the region for its reproductive plasticity and great importance in the trophic chain. The study area contained four data collection points, namely Limoeiro, Três Bocas, Congonhas I, and Congonhas II, where individuals of *A. lacustris* were collected using different capture methodologies. In total, 1553 individuals were collected, with 100% consistency in all stretches. Congonhas I and Congonhas II provided 76.3% of the total number sampled. In general, it was noted that the females of the species are more represented in the longer length classes, while males are more abundant in the shorter length classes, except for the Congonhas II stretch, where females were more abundant in all length classes. Analysis of oocytes collected from 639 females indicates that the species *A. lacustris* spawns in installments, and that its reproduction is conditioned and modified by biotic and abiotic environmental issues.

Keywords: Yellow-tailed; lambari; Tibagi River; Paranapanema basin.

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# Introduction

The Tibagi River Basin is located on the left bank of the Paranapanema River in the State of Paraná, being its largest tributary. Its waters drain an area of approximately 25000 km<sup>2</sup> that runs in a South-North direction in the state of Paraná, with its mouth in the lake of Capivara dam on the Paranapanema River (Melo et al., 2010).

The fish species *Astyanax lacustris* (Lütken, 1875) is a small characiform, known as the yellow-tailed lambari, has a wide distribution in the Upper Paraná River Basin (Langeani et al., 2007) and is known to carry out short-distance migrations (Graça & Pavanelli, 2007). Furthermore, it is an abundant species in rivers and reservoirs, being among the most widely found in the Paranapanema River Basin (Orsi et al., 2004; Jarduli et al., 2019) and demonstrating a remarkable ability to adapt to recently dammed environments (Dias et al., 2005; Hahn & Fugi, 2008).

Fish reproduction is commonly associated with environmental factors such as water temperature, precipitation, and availability of food resources (Gurgel-Lourenço et al, 2015; Maciel et al., 2011). Reproductive traits are generally adjusted to local environmental conditions, as this increases the probability of offspring survival and, thus, population persistence and growth (Alvarenga et al., 2006; Ceneviva-Bastos et al., 2015). Reproductive success can also indicate how fish use resources under different ecological conditions (Carvalho et al., 2009).

In view of this, the present study aims to understand the reproductive dynamics of *Astyanax lacustris* in the hydrographic basin region of the middle Paranapanema River, covering the final portion of its main tributary, the Tibagi River, located in the north of the State of Paraná, with the aim of determining whether different microhabitats influence the modes of reproduction of this species. An in-depth understanding of the life cycles of fish species in different aquatic environments is essential to analyze how reproductive strategies are adapted to different microhabitats, considering the different distribution areas of the species and the need to adjust to local conditions, enabling studies with the aim of conservation of native species.

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#### Materials and methods

The region studied was the lower Tibagi hydrographic basin, this river being the largest tributary of the Paranapanema River, located in the northern region of the state of Paraná, and having several important tributaries (Shibatta et al., 2002). In addition to the main channel of the Tibagi River, we selected two tributaries, Congonhas and Três Bocas, to carry out the sampling. In total we included 4 collection points: a) Main channel of the Tibagi River (Limoeiro), presenting characteristics of a large river and very fast lotic waters, with a winding stretch of approximately 2 kilometers, on average 80 meters wide and maximum depth in the channel of up to 12 meters, rocky bed with clay and sand present, having small islands and two small tributaries (Ribeirão Três Bocas and Ribeirão Apertados), native riparian vegetation is scarce and sometimes even absent, with intense agricultural activity, and the land/water transition region has a good amount of terrestrial grasses and complete absence of aquatic macrophytes; b) Três Bocas stream, a stretch located 8 kilometers from its mouth on the Tibagi River, has lotic waters with a smaller volume of water than at other points, with rapids and backwaters, a maximum depth of up to 4 meters and a width of 8 meters, it is a stretch that is impacted by urban and agricultural waste, on the banks close to the collection point there is a wider strip of riparian forest (up to 15 meters), and a large amount of aquatic macrophytes, a bed with many trunks and branches, with a large amount of periphyton; c) middle portion of the Congonhas River (Congonhas I), has lotic waters and several backwaters, with 3 shallow marginal lagoons, rugged relief, the bed and banks have a large amount of gravel, the surrounding region has great livestock activity, along the entire bank there is native riparian forest (strips of more than 50 meters), with large tree species, shrubs and others; and d) final portion of the Congonhas River (Congonhas II), a stretch located 500 meters from its mouth in the Tibagi River, a deep stretch (up to 20 meters in the main channel) with a predominance of clay, presents semi-lentic waters, 250 meters wide, representing a transition zone between two ecosystems (river and dam), its banks do not have riparian forests due to the impact caused by the damming of the Paranapanema River (UHE Escola Mackenzie), a marginal area with a high presence of macrophytes.

Biological material sampling was carried out monthly, starting in January 1997 and ending in February 1998, totaling 56 collections. Regarding the points chosen for collections, 4 stretches were selected, with distinct physical and environmental characteristics. The first stretch is located in the main channel of the Tibagi River (23°35'56"S and 50°59'58"W), called Limoeiro, the second stretch in the Três Bocas stream (23°37'39"S and 51°04'44"W), and the third and fourth stretches on the Congonhas River, Congonhas I (23°20'45"S and 50°56'28"W) and Congonhas II (22°58'45"S and 50°59'08"W), respectively.

To collect the fish, two series of gill nets were used, with meshes of 2, 3, 4, 5, and 6 cm between opposite nodes, varying the depth from 0.80 to 4.20 m, and covering a total area of 450 m<sup>2</sup>. The nets were placed for 10 hours near the banks. The use of casting nets, sieves, and dip nets was also used, with an area of 8 m<sup>2</sup>, standardized to 1 hour of successive throws and 100 meters in length.

Biometrics were performed on specimens of *Astyanax lacustris*, evaluating the total length in centimeters and the total weight in grams. To evaluate the proportion of juveniles and adults at the four collection points, the fish were classified into categories of juveniles and adults, based on the mean length of initial gonadal maturation for the species. This was carried out through the frequency of total length classes between sexes and the size composition.

To investigate the population structure, capture constancy was defined according to Dajoz (1978) methodology, classifying it as constant, accessory, and accidental. The determination of relative abundance was carried out by transforming the occurrence data into Capture per Unit of Effort (CPUE), following the methodology proposed by Agostinho (1997). The comparison of monthly CPUE means between different stretches was conducted using analysis of variance (ANOVA), which was later complemented by the Tukey test for group comparisons (Table 1).

To analyze the reproductive dynamics of *A. lacustris* in the studied stretches, oocytes with a diameter that exceeded 50 µm were selected, obtained from the gonads of females collected during biometry. The oocytes were categorized into 17 size classes. In addition to the size classes, the oocytes were also divided into different categories according to the stage of gonadal maturation. The analyzed oocytes were counted and measured under a stereomicroscope, using a millimeter eyepiece. Estimates of the parameters of the theoretical curve that relates the total length of mature females to total fecundity were used, as well as the parameters of the curve that relates the total length of mature females to batches of mature oocytes. The mean value of oocyte diameter was also calculated for each stretch sampled.

**Table 1**. Capture per unit of effort (CPUEn), absolute number captured, and relative abundance of *Astyanax lacustris*, for the four stretches in the studied period.

Stretch	Absolute number captured	Abundance (CPUE/1000m <sup>2</sup> device/day)	Relative abundance (%)
Limoeiro	159	351.0	10.2
Três Bocas	252	556.3	16.2
Congonhas I	593	1309.1	38.2
Congonhas II	549	1211.9	35.4
Total	1553	3428.3	100

To check the transparency of the water, the Secchi disk was used, with measurements obtained in centimeters. The temperature of the water and dissolved oxygen were measured using YSI-55 equipment, with values being quantified near the fishing nets, near the surface, and at the bottom, for the temperature, using the thermometer function, with an accuracy of 0.1°C. The water speed was measured using the fluctuation method, in a 10-meter stretch of river, considering the mean of three repetitions.

With the aim of evaluating the potential influences of environmental variables in the stretches under study on the biological aspects of *A. lacustris* populations, the statistical technique of Canonical Correlation Analysis was used. In this context, abiotic variables (dissolved oxygen, pH, transparency, mean temperature, and mean water velocity) and biotic variables (mean fecundity, maximum and mean diameter of oocytes, CPUEn and mean Lt) were correlated.

Since the collections were carried out before the publication of Law N° 11,794 of October 8, 2008, which regulates the use of living animals in Brazilian scientific research, this study does not have any approval from the Ethics Committee on the Use of Animals (CEUA).

# **Results**

In the 14 collections carried out in the four river stretches, 1553 specimens of *A. lacustris* were identified, with 100% consistency in all stretches. Stretches I and II of the Congonhas River together represented 76.3% of catches, while the other stretches contributed 24.7%. Figure 1 highlights the similarities in CPUEn between Congonhas I and II stretches, with a notably high catch in February 1998 in Congonhas I. In Limoeiro and Três Bocas, catches reached lowest values in July. The analysis of variance indicated statistically significant differences in the mean monthly CPUEn between the stretches (ANOVA, F = 6.095 and p = 0.0012), with greater discrepancies between Limoeiro and Congonhas I, followed by Limoeiro and Congonhas II (p < 0.05, Tukey test). This disparity is reflected in Table 2.

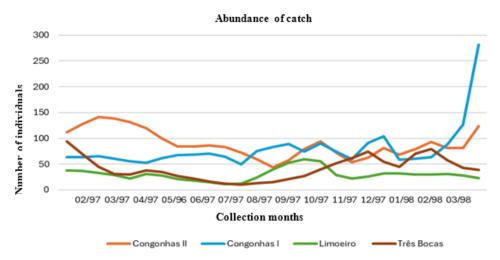


Figure 1. Capture abundance (CPUEn) of Astyanax lacustris in the four stretches sampled during the study period.

The evaluation of the total proportion between young specimens and adults indicated a predominance of adults in all stretches (Table 2). Although the Congonhas I stretch recorded a greater number of young specimens, the predominance of adults is evident. In the Limoeiro stretch, no young specimens were captured, as confirmed by the  $\chi 2$  test, which rejected the null hypothesis (H0). The  $\chi 2$  calculated for the four stretches was consistently higher than the critical  $\chi 2$  (= 3.84), with a significance level of p < 0.05.

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**Table 2**. Proportion (%) of young and adult specimens of *Astyanax lacustris* from the four stretches studied, with the respective χ2 test, the composition of the absolute number of specimens analyzed (N), and the number of adults (na) from each stretch.

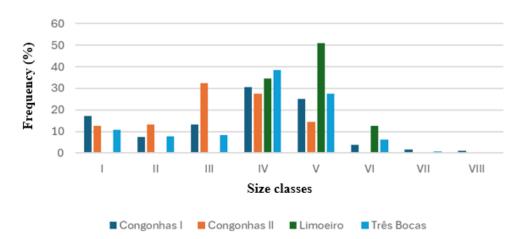
Stretches -	Development phase		·2Tost	Population structure	
Stretches -	Young Adult $\chi^2$ Test —	N	Na		
Limoeiro	0	100.0	100.0	158	158
Três Bocas	19.0	81.0	38.32	252	204
Congonhas I	24.3	75.7	26.48	549	415
Congonhas II	33.1	66.9	11.49	593	397

Table 3 shows eight total length classes, with lower and upper limits, applied to individuals from the four stretches, considering the aggregation of males and females of *A. lacustris*. These classes will be used in subsequent analyses. Figures 2 to 6 illustrate the distribution of the relative frequency (%) of the length classes for each sex, in addition to the representation for both sexes grouped in the four stretches.

**Table 3.** Total length classes (in cm) of *Astyanax lacustris*, with grouped data (males and females), in the four stretches sampled during the study period.

Full length classes	Lower limit (cm)	Upper limit (cm)
I	0.50	2.90
II	2.91	5.30
III	5.31	7.70
IV	7.71	10.10
V	10.11	12.50
VI	12.51	14.90
VII	14.91	17.30
VIII	17.31	19.70

#### Frequency distribution of size classes in each section

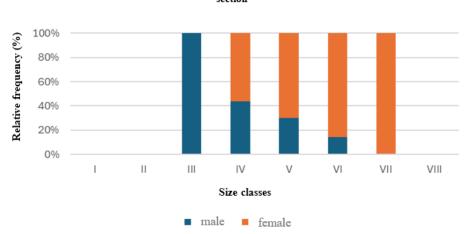


**Figure 2**. Relative frequency of grouped total length classes (males and females) of *Astyanax lacustris*, for the four stretches analyzed during the study period.

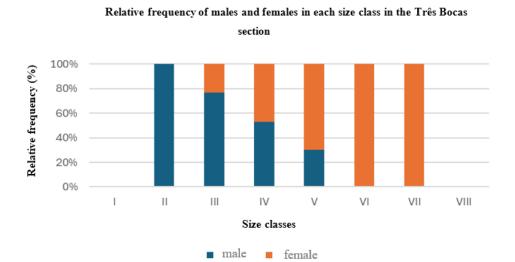
It is crucial to highlight that only the Congonhas I stretch presented individuals in the eight length classes, while the Congonhas II stretch exhibited the smallest number of total length classes (five). The highest frequency of individuals was observed in Limoeiro, concentrated in length class V. In the Três Bocas and Congonhas I stretches, class IV was the most frequent, while in Congonhas II, class III recorded the highest frequency. When carrying out a comprehensive analysis, classes IV and V were consistently the most frequent in almost all stretches.

When analyzing the frequencies of length classes by sex in the four stretches, a consistent pattern is observed in three of them - Limoeiro, Três Bocas, and Congonhas I (Figures 3, 4 and 5). In these stretches, the smaller classes, mainly II and III, presented the highest frequencies of males, while females were more frequent in the higher classes, starting from IV. The exception was in the Congonhas II stretch (Figure 6), where females were also more frequent in the smaller length classes (II and III).

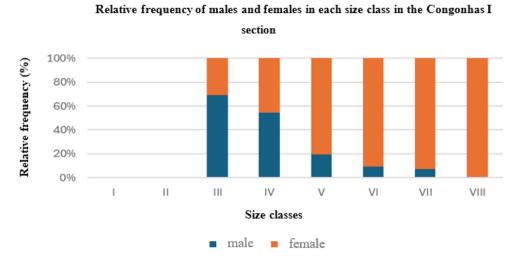
# Relative frequency of males and females in each size class in the Limoeiro section



**Figure 3**. Frequency distribution of total length classes of males and females of *Astyanax lacustris* from the Limoeiro stretch, during the study period.

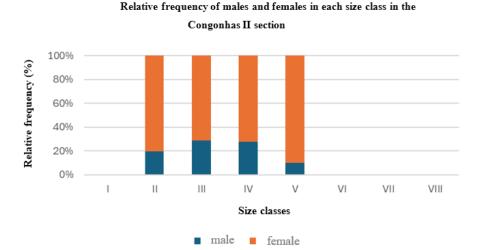


**Figure 4.** Frequency distribution of total length classes of males and females of *Astyanax lacustris* from the Três Bocas stretch, during the study period. The sex of individuals collected in size category I was not determined as the gonads are in the early stages of development.



**Figure 5.** Frequency distribution of total length classes of males and females of *Astyanax lacustris* from the Congonhas I stretch, during the study period. The sex of individuals collected in size categories I and II was not determined as the gonads are in the early stages of development.

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**Figure 6.** Frequency distribution of total length classes of males and females of *Astyanax lacustris* from the Congonhas II stretch, during the study period. The sex of individuals collected in size category I was not determined as the gonads are in the early stages of development.

In general, it is noted in these figures that males did not occur in length classes greater than class VII, indicating a predominance of larger females in the four stretches. This disparity is particularly evident in the Congonhas I stretch, where only females were recorded in class VIII.

When analyzing the size compositions obtained by the maximum, minimum, and mean values of total length (Lt) and total weight (Wt) of the species (Table 4), using analysis of variance (ANOVA - single factor), it was found that these biological variables were statistically different in all stretches (F = 46.26, p < 0.0001 and F = 38.74; p < 0.0001). It is worth mentioning that, when comparing the grouped means of these variables using the Tukey test, statistically significant differences (p < 0.05) were also evident.

**Table 4.** Size composition, mean total length (Lt), mean total weight (Wt), and respective maximum and minimum values and standard deviation of *Astyanax lacustris* specimens, from the four stretches analyzed during the study period.

Stretches	Maximum values		Minimum values		Mean values		Standard deviation	
Stretches	Lt (cm)	Wt (g)	Lt (cm)	Wt (g)	Lt (cm)	Wt (g)	Lt (cm)	Wt (g)
Limoeiro	15.60	52.01	5.5	4.02	10.93	0.88	1.49	7.22
Três Bocas	16.10	68.32	1.7	0.29	8.42	4.01	3.25	10.24
Congonhas I	18.90	82.35	0.5	0.27	8.65	14.32	3.73	12.96
Congonhas II	11.90	42.66	0.5	0.21	7.53	0.91	3.04	7.81

Individuals from Congonhas I stretch presented the highest total length and weight values, contrasting with the lowest values recorded for individuals from the Congonhas II stretch. The Limoeiro stretch, in turn, exhibited the highest mean values among the stretches studied.

When analyzing the total proportion between the sexes, with the data grouped for the period studied in the four stretches, it was observed that the number of females (absolute or relative) was always higher (Table 5). However, when using the  $\chi 2$  test, it became clear that there is a statistically significant difference between the sexes only in the Congonhas II and Limoeiro stretches. By rejecting the null hypothesis (H0,  $\chi 2 > 3.84$ ) for p < 0.05 in the specimens from these two stretches, which assumes a sex ratio of 1:1 (i.e., 50% frequency for both sexes), the highest proportions of females were found in the Limoeiro and Congonhas II stretches. These proportions indicate a ratio of 1:2 and 1:3, respectively, for each male (Table 5).

**Table 5.** Proportion between the sexes of the species *A. lacustris*, among the four stretches studied and the application of the  $\chi 2$  test.

Stretches	Absolute	Absolute frequency		Relative frequency		Sex ratio
Stretches	Males	Females	Males	Females	x² test	sex ratio
Limoeiro	52	106	32.9	67.1	11.69*	1:2
Três Bocas	89	117	43.2	56.8	1.84	1:1
Congonhas I	190	254	42.8	57.2	2.07	1:1
Congonhas II	102	314	24.5	75.5	26.1*	1:3

\* Significant for  $\chi$ 2 > 3.84 (p < 0.05).

During the reproductive period (December 1997 and January 1998), schools were observed close to the banks, exhibiting typical spawning behaviors. These schools remained close to aquatic vegetation, hiding their position through sudden movements. On some occasions, a white mass, presumably from spawning, was deposited on substrates, confirmed by stereomicroscopic analysis.

Regarding reproductive style, in visual observations carried out in aquariums and in nature, no defined pairs were observed. During fertilization, several males were seen to fertilize the eggs of a single female or to form clusters during the process. After fertilization, no parental care was observed. The eggs, attached to the substrate, were small and remained fixed, with a yellowish-white adhesive mucus, until the larvae hatched.

The results regarding the classes and frequency of oocyte diameter in the different stages of gonad maturation in the studied stretches are presented in Table 6 and in Figures 7, 8, 9 and 10. This analysis involved 639 adult females in stages B, C, and D, with 92 captured in the Limoeiro stretch, 106 in Três Bocas, 234 in Congonhas I, and 207 in Congonhas II. In general terms, females in stages B and C presented two reserve batches of oocytes in the lower classes (I, II, III, and IV), but the highest frequency peaks were evident in mature females (C). In the Limoeiro, Três Bocas, and Congonhas I stretches, the highest oocyte diameter frequency values were in classes above X (500 -  $551\mu m$ ), indicating that the release of batches of oocytes seems to occur from this class. However, for the Congonhas II stretch, females prepared for spawning released their oocytes from class VIII ( $400 - 451\mu m$ ). This analysis also suggests that *Astyanax lacustris* spawns in installments.

An interesting and contradictory fact was observed in females in stages B and C of the Congonhas I stretch, which presented only a reserve batch of oocytes (in classes I, II, and III), suggesting the possibility of total spawning also occurring and not only installments.

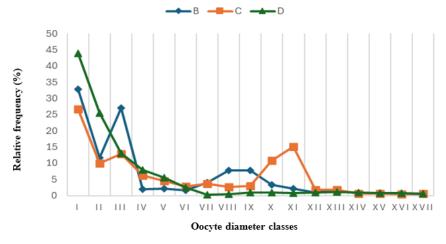
Classes	Lower limit (µm)	Upper limit (μm)
I	50	100
II	101	150
III	151	200
IV	201	250
V	251	300
VI	301	350
VII	351	400
VIII	401	450
IX	451	500
X	501	550
XI	551	600
XII	601	650
XIII	651	700
XIV	701	750
XV	751	800
XVI	801	850
XVII	851	900

Table 6. Oocyte diameter classes (µm) of Astyanax lacustris, established for females from the four stretches grouped.

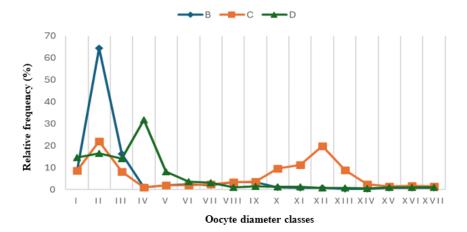


**Figure 7**. Relative frequency of oocyte diameter in classes and the respective maturation stages of *Astyanax lacustris* gonads in the Limoeiro stretch.

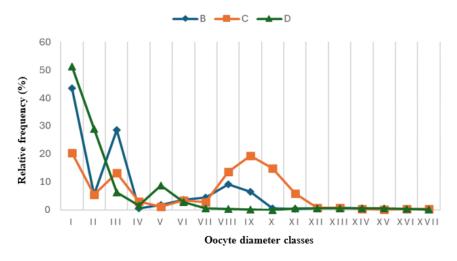
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**Figure 8**. Relative frequency of oocyte diameter in classes and the respective maturation stages of *Astyanax lacustris* gonads in the Três Bocas stretch.



**Figure 9.** Relative frequency of oocyte diameter in classes and the respective maturation stages of *Astyanax lacustris* gonads in the Congonhas I stretch.



**Figure 10**. Relative frequency of oocyte diameter in classes and the respective maturation stages of the gonads of *Astyanax lacustris* in the Congonhas II stretch.

The values of the mean and mean maximum diameters of oocytes from females that were in stage C (mature) in each stretch are presented in Table 7. The application of analysis of variance (ANOVA - single factor) for the mean diameter variable did not demonstrate statistically significant differences (p > 0.05 and F = 0.9706) between the analyzed excerpts. However, when applying this analysis to another variable, the mean maximum diameter, a statistically significant difference (F = 3.722 and P = 0.0144) was found between

the stretches. In the multiple comparison of the grouped means of this variable, using the Tukey test, it was also evident that the Congonhas II stretch presented the greatest difference between the stretches (p < 0.05), in which mature females exhibited the smallest mean maximum diameter.

**Table 7.** Number of mature females (N) and mean diameter, mean maximum diameter, and respective standard deviation of *Astyanax lacustris* oocytes, from the four stretches, during the period under study.

Stretches	N	Mean diameter (μm)	Standard deviation	Mean maximum diameter (µm)	Standard deviation
Limoeiro	15	435	76.7	809	102.3
Três Bocas	15	438	81.2	848	109.5
Congonhas I	15	478	85.2	851	92.7
Congonhas II	15	419	74.10	685	178.8

The values for the number of batches of oocytes released in the reproductive period are in Table 8, showing similarities between specimens from three of the four stretches, with emphasis on Congonhas I, where the number of batches was lower (1.5 batches). These data can be compared with the oocyte diameter frequency in Figure 9 where it is possible to verify the presence of only one batch of reserve stock.

**Table 8.** Estimation of the precise number of batches of oocytes released per reproductive period, with coefficient values ( $\phi$  and  $\theta$ ) of linear regression between fecundity (theoretical Fpr) and maximum total length (Ltm) of the species and fecundity per batch (theoretical FL) and maximum total length (Ltm), for the four stretches analyzed.

Stretches	Ltm	Fpr T	φ	θ	FL T	φ	θ	Batches
Limoeiro	15.60	10981.81	14.63	2.41	4164.41	19.10	1.96	2.6
Três Bocas	16.10	13491.35	17.61	2.39	5080.52	19.63	2.01	2.6
Congonhas I	18.90	10372.22	15.21	2.15	3449.27	17.92	1.93	1.5
Congonhas II	11.90	17609.23	15.92	2.36	6162.94	17.81	2.31	3.2

Regarding the estimate of fertility by reproductive period (Table 9), differences were identified between the stretches. Congonhas II had the highest mean value (Fpr = 14323), standing out from the others, including the highest maximum fertility value per reproductive period (Fpr = 20755). The analysis of variance confirmed the difference between the stretches (F = 10.315 and p < 0.05). The Tukey test showed that Congonhas II stood out (p < 0.001) from the others. The table also shows the results of the fecundity analysis (Fpr), corrected by the number of batches per spawning period, in the four stretches.

**Table 9.** Estimated values of fecundity per reproductive period (Fpr), maximum and minimum, mean, standard deviation, and fecundity per batch, of specimens of the species *Astyanax lacustris*, in the four stretches studied, during the study period.

Stretches	N	Maximum Fpr	Minimum Fpr	Mean Fpr	Standard deviation	F batch
Limoeiro	42	15215	3386	10224	384.1	3932
Três Bocas	48	18235	4794	12013	497.3	4620
Congonhas I	93	12896	1280	9467	583.6	6311
Congonhas II	98	20755	3821	14323	647.7	4447

In general, the abiotic data demonstrated variations between the points studied, indicating that the characteristics of each chosen environment are not identical. The accumulated monthly rainfall, recorded for the Londrina region (lower Tibagi river) during the study period, showed the highest values occurred in January (621.0 mm) and February (426.3 mm) of 1997 and again in January 1998, although with lower values.

The water temperature values, sampled at the surface and at the bottom, and the monthly variation during the study period are presented in Figures 11 and 12. The analysis of variance indicated that the temperatures at the bottom for the four stretches did not present statistically significant differences for p > 0.05 (ANOVA F = 1.983 and p = 0.1280). However, the surface temperatures showed statistically significant differences for p < 0.05 (F = 4.682 and P = 0.0057), and when comparing the grouped means in the Tukey test, the stretches of Limoeiro and Congonhas II, Três Bocas, and Congonhas I, presented statistically significant results at p < 0.05, indicating different temperature patterns. Mean bottom temperatures ranged from 19.47°C in Limoeiro to 26.33°C in Congonhas II. On the surface, the variations were from 21.98°C in Limoeiro to 28.94°C in Congonhas II, with a similar trend of decreasing values from May to August and increasing from September to February, in the four stretches.

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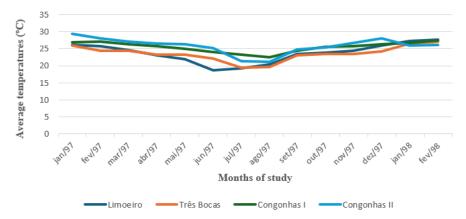


Figure 11. Mean monthly surface temperature in the four stretches analyzed, during the study period.

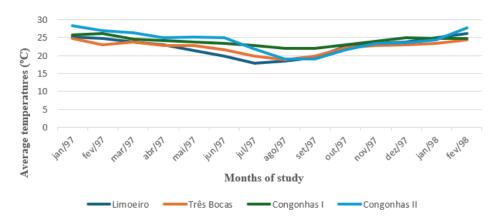


Figure 12. Mean monthly water bottom temperature in the four stretches analyzed, during the study period.

The dissolved oxygen (DO) values in the four sampled stretches also revealed statistically significant differences, as indicated by the analysis of variance (Figure 13). Monthly means ranged from 5.7 mg  $L^{-1}$  (minimum value) in Congonhas II to 9.15 mg  $L^{-1}$  (maximum value) in Congonhas I. Statistical analysis demonstrated a significant difference in the overall mean (ANOVA, F = 88.81 and p < 0.0001). In Tukey's multiple comparison test for the grouped means, no statistically significant differences were observed between the stretches of Limoeiro and Três Bocas, as well as between Limoeiro and Congonhas I. However, there was a tendency towards lower values in the stretch of Congonhas II, which showed a pronounced decrease from September to February.

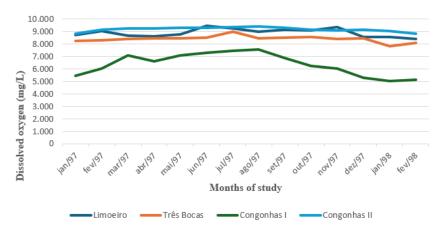


Figure 13. Mean monthly dissolved oxygen (DO) values in the water, in the four sampling stretches, obtained during the study period.

Tables 10 to 21 present the canonical correlations between abiotic and biotic variables for each sampling stretch. In Limoeiro (Table 11 and 12), canonical variable 1 shows a positive correlation between water transparency, pH, and temperature (first subset), and CPUEn and fecundity (second subset). Dissolved oxygen has a negative correlation with Lpm. In canonical variable 2, water transparency is positively related to the mean maximum diameter of oocytes and negatively to CPUEn, Lt, and fecundity.

Table 10. Analysis of canonical variables in the Limoeiro stretch.

Number	Eigenvalue	Canonical Correlation	Significance Level
1	1.0000	1.0000	0.0007
2	0.9405	0.9819	0.0013
3	0.0710	0.5428	0.6312
4	0.0499	0.2234	0.9998
5	0.0678	0.2104	0.8514

**Table 11**. Coefficients for canonical variables of the first subset (abiotic).

Variable	Canonical Variable 1	Canonical Variable 2
Water transparency	7.65452	-0.78939
PH	3.93622	-1.80678
Dissolved oxygen	-0.56221	1.31505
Water speed	-2.71523	0.46839
Temperature	1.14196	-3.16773

Table 12. Coefficients for canonical variables of the second subset (biotic)

Variable	Canonical Variable 1	Canonical Variable 2
CPUE	2.56375	-3.31508
Mean Lt	0.32145	-1.57406
Mean maximum diameter	0.65616	5.71820
Fecundity	2.38350	-1.79880
LPM	-1.82999	0.85863

In the Três Bocas stretch (Table 13, 14 and 15), only canonical variables 1 and 2 were significant. In the first subset, abiotic variables have a positive correlation with fecundity and CPUEn. In canonical variable 2, water velocity has a positive correlation with Lpm and Lt, and a negative correlation with mean maximum diameter of oocytes, fecundity, and CPUEn.

Table 13. Analysis of canonical variables of the Três Bocas section, Canonical correlation analysis.

Number	Eigenvalue	Canonical Correlation	Significance Level
1	1.0000	1.0000	0.0000
2	1.0000	1.0000	0.0031
3	0.7469	0.8102	0.7107
4	0.0214	0.3374	0.9798
5	0.0148	0.1862	0.8944

 $\textbf{Table 14}. \ \ \text{Coefficients for canonical variables of the first subset (abiotic)}.$ 

Variable	Canonical Variable 1	Canonical Variable 2
Water transparency	5.15416	-0.17663
рН	2.06878	-1.30775
Dissolved oxygen	1.78917	0.27641
Water speed	-3.61557	0.36810
Temperature	1.20454	-0.33342

Table 15. Coefficients for canonical variables of the second subset (biotic).

Variable	Canonical Variable 1	Canonical Variable 2
CPUE	1.82454	-0.23358
Mean Lt	-0.56774	1.31579
Mean maximum diameter	0.95616	-2.71830
Fecundity	3.38357	-0.79884
LPM	-0.59954	1.54461

For Congonhas I (Table 16, 17 and 18), water transparency and dissolved oxygen positively correlate with mean maximum diameter, mean total length, and fecundity. In canonical variable 2, temperature has a positive correlation with Lpm.

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<b>Table 16.</b> Analysis of canonica	al variables of the Congonha	s I stretch, canonica	l correlation analysis.
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Number	Eigenvalue	Canonical Correlation	Significance Level
1	1.0000	1.0000	0.0000
2	1.0000	1.0000	0.0008
3	0.0345	0.1894	0.8947
4	0.1849	0.1172	0.9853
5	0.0724	0.0119	0.9241

**Table 17**- Coefficients for canonical variables of the first subset (abiotic).

Variable	Canonical Variable 1	Canonical Variable 2
Water transparency	8.00649	-1.50787
pН	0.71523	-6.46837
Dissolved oxygen	2.76545	-1.78939
Water speed	-1.54465	0.59944
Temperature	-1.20454	2.16376

Table 18. Coefficients for canonical variables of the second subset (biotic).

Variable	Canonical Variable 1	Canonical Variable 2
CPUE	0.56222	-1.31505
Mean Lt	3.32143	-0.54705
Mean maximum diameter	3.78441	-1.71827
Fecundity	2.41068	-1.79279
LPM	0.61203	1.47359

In Congonhas II (Table 19, 20 and 21), canonical variables 1 and 2 are significant. In the first abiotic subset, water transparency, pH, and dissolved oxygen correlate positively with oocyte diameter, Lpm, and fecundity, and negatively with numerical abundance. In canonical variable 2, dissolved oxygen correlates negatively with abundance, oocyte diameter, and length (mean Lt and Lpm).

 $\textbf{Table 19.} \ \textbf{Analysis of canonical variables of the Congonhas II stretch, canonical correlation analysis.}$ 

Number	Eigenvalue	Canonical Correlation	Significance Level
1	1.0000	1.0000	0.0031
2	1.0000	1.0000	0.0016
3	0.2794	0.5972	0.8972
4	0.1115	0.3072	0.9394
5	0.0982	0.2359	0.9808

**Table 20.** Coefficients for canonical variables of the first subset (abiotic).

Variable	Canonical Variable 1	Canonical Variable 2
Water transparency	3.35730	0.59762
pН	2.37047	1.02377
Dissolved oxygen	1.7839	-5.80678
Water speed	-3.35730	0.78446
Temperature	-1.48445	1.58164

Table 21. Coefficients for canonical variables of the second subset (biotic).

Variable	Canonical Variable 1	Canonical Variable 2
CPUE	-3.59935	1.31548
Mean Lt	-0.89783	0.06855
Mean maximum diameter	6.64861	0.9875
Fecundity	1.89642	-1.77235
LPM	1.41021	0.36817

# Discussion

The distribution patterns of the species *A. lacustris* indicate that it uses, in a characteristic way, the space at its disposal. Preferably, it is located close to the surface in the water column and close to the banks in the coastal region, in larger environments, such as the stretch of Limoeiro and Congonhas II. In the stretches of Três Bocas and, mainly, in Congonhas I, it was observed that the species used both the surface and the mid-

water area and, to a lesser extent, the bottom, characterizing a wide variation in the occupation of spaces in environments with greater coverage. This behavior can be interpreted as a tactic to facilitate the exploitation of these habitats to reduce interspecific and intraspecific competition, whether for food or space. The differential groupings of fish can be, in terms of the use of space resources, the responsible for the diversity of use between species, associating their occupation with the type of food consumed and the availability of the location (Zeni & Casatti, 2014).

It is extremely necessary to point out the need to compare communities along a river course due to the fact that there are geomorphological and physicochemical differences during the course of a river that may require morphological and behavioral adaptations (Saldaña & Ibáñez, 2007). The complexity of this type of study is great, given the diversity of species in inland water ecosystems in Brazil and the large extension of its river basins. It was possible to demonstrate that, in an environment with better conditions, such as Congonhas I, the species *A. lacustris* was able to explore spaces in a more comprehensive way, covering both the water column and the area perpendicular to the banks of this ecosystem.

The length of first maturation in fish is closely related to the genotype-environment interaction and directly to growth, presenting intraspecific spatial and temporal variations linked to the abiotic and biotic environmental conditions prevailing in the occupied area, or in the period in which the population is subjected to them (Koons et al., 2008; Vazzoler, 1997). In the present study, some situations were observed regarding this parameter related to reproduction:

The stretches known as Limoeiro and Três Bocas showed oocyte maturation lengths that were statistically similar to each other, which indicates comparable environmental conditions or similar genetic influences. In Congonhas II, individuals were found with maturity at a shorter total length, possibly being related to specific environmental conditions that promote rapid development. The Congonhas I stretch had the latest maturation process observed, indicating possible adaptations to an environment that favors slower maturation. This variation in reproductive tactics can be explained if it is correlated with the different environmental conditions found in each stretch. Furthermore, sexual maturity in relation to the length of the individual may vary in different rivers of the Paraná River basin (Agostinho et al., 1984; Bailly et al., 2008)

Fecundity, which refers to the number of eggs produced by a female, is a crucial indicator of a species' reproductive strategy. The high fecundity in *A. lacustris* compared to other species of the characiform group may be associated with the opportunistic reproduction strategy, in which the species invests in a large number of eggs to maximize the chances of offspring survival (Súarez et al., 2017). This strategy is common in variable and unpredictable environments (Vasconcelos et al., 2011).

The distribution of oocyte diameters prompts considerations about the oocyte maturation process and the reproductive synchrony of the population. The presence of different diameter classes suggests staggered spawning, where different groups of females release their eggs at different times. This pattern may be an adaptation to optimize reproductive success, ensuring that spawning takes place at different times, which can be beneficial in dynamic environments.

Understanding these aspects of reproductive dynamics is fundamental to understanding the population biology of the species and its ability to adapt to different environmental conditions. The reproductive plasticity observed in *A. lacustris* may be an evolutionary strategy that contributes to the success of the species in different environments, allowing adjustments in reproduction in response to the specific conditions of each location.

In summary, we were able to show how the fecundity of the species *A. lacustris* varies between different stretches. In Três Bocas and Limoeiro, fecundity patterns and spawning type are similar, suggesting shared environmental influences. On the other hand, Congonhas II exhibits larger oocyte diameters, indicating possible single spawning due to more stable environmental conditions, while Congonhas I exhibits smaller diameters but greater fecundity and number of oocyte batches, possibly adapting to unfavorable conditions.

Regarding the distribution of oocyte diameters, the species demonstrates split spawning, with Limoeiro, Três Bocas, and Congonhas I releasing oocytes from 500  $\mu$ m, and Congonhas II releasing smaller oocytes, from 400  $\mu$ m, indicating environmental influence. Although Congonhas I suggests concentration of spawning in one batch, histological studies could provide additional details.

These adaptations in reproductive dynamics may be crucial for the survival of the species in different environments, reflecting its ability to adjust reproductive tactics according to the specific conditions of each stretch. The study provides valuable input to understand the reproductive biology and ecology of the species, contributing to management and conservation strategies. The results presented by Súarez et al. (2017) and

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Merçon et al. (2022) also corroborate our hypothesis that the species *A. lacustris* presents a varied range of reproductive strategies, shaped according to perennial and seasonal characteristics and environmental requirements.

# Conclusion

Analysis of reproductive dynamics provides valuable information about the population biology of *A. lacustris*, highlighting the ability of this species to adapt to different environments. The opportunistic reproduction strategy, evidenced by high fecundity, suggests an adaptive response to variable and unpredictable environmental conditions. This strategy is advantageous in environments subject to fluctuations, allowing the species to maximize the chances of reproductive success in the face of uncertain environmental conditions.

The presence of different oocyte diameter classes, indicating staggered spawning, highlights the complexity of the reproductive strategy of *A. lacustris*. This adaptation can offer benefits in dynamic environments, where reproductive synchronization can increase the chances of offspring survival. The ability to adjust reproduction in response to specific environmental factors demonstrates the reproductive plasticity of the species.

Understanding these reproductive characteristics not only contributes to knowledge of the species' biology but is also crucial for the management and conservation of natural populations. The information obtained about reproductive dynamics aids in the development of more effective conservation strategies, considering the species' adaptive response to different environmental conditions.

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