ECOSYSTEMS

Population biology of *Astyanax lacustris* (Pisces, Characiformes) in a Neotropical reservoir and its tributaries

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Abstract: The aging process of reservoirs has been extensively investigated; however, little is known about how fish populations are adjusted after many years of impoundment. Thus, this study aimed to compare the diet, length-weight relationship, sizes classes, variation in size, and age of *Astyanax lacustris* Lütken, 1875 collected from lotic and lentic habitats of an aging reservoir. The study group consisted of 730 captured fishes. We found that specimens collected from lotic habitats had a wider range of size classes (1.0 to 12.0 cm), were linked to a high frequency of juveniles (48.7%), and had greater feeding activity (higher stomach fullness). In contrast, fishes collected from lentic environments exhibited high rates of capture (78.4%), increased frequency of adults (87.3%), and higher values of mean standard length. The length-weight relationship indicated that lentic fishes were heavier than fish collected from lotic areas. Moreover, we observed 37 food items in *A. lacustris* diet, mainly plant material, algae, Cladocera, Hymenoptera, Coleoptera, and Ephemeroptera. Differences among the diet of fishes between sites were evidenced with Permanova (p < 0.05). *Astyanax lacustris* can be considered a persistent species in Chavantes Reservoir after aging, encountering conditions to complete its life span and adjusting to food resources.

Key words: Characidae, native species, reservoir aging, upper Paraná River basin.

INTRODUCTION

Reservoirs built to generate electricity are conspicuous components of the global landscape (Grill et al. 2015). There are over 59,000 large dams in the world (ICOLD 2018) built for multiple purposes, such as irrigation, flow containment, and water supply (Tundisi & Matsumura-Tundisi 2003), but the main use is to produce hydropower (Agostinho et al. 2016).

The construction of dams and associated reservoirs causes irreversible impacts, affecting the structure and composition of the fish fauna (Poff et al. 2007, Pelicice et al. 2015). The alterations in the dammed environments tend to reach trophic stabilization over time, *i.e.,* as its functional age progresses (Agostinho et al. 2007, Miranda & Krogman 2015, Lima et al. 2018).

Dams impact biodiversity and ecosystem services. Aquatic richness and diversity are impacted by the transformation from lotic to lentic environment, fragmentation, and success of invasive species in reservoirs (Turgeon et al. 2019). In Brazil, several studies have assessed such impacts on aquatic biodiversity (Vasconcelos et al. 2014). However, few specifically determined the influence of reservoirs on the population biology of fish species (Delariva et al. 2013), especially over several years after dam closure.

Fish species are differentially influenced by each phase of reservoir formation. After the filling phase, reservoirs undergo a heterotrophic period (upsurge period), with increase in fish abundance (Agostinho et al. 2016). During the post-heterotrophic period, environmental filters, referred as abiotic factors that prevent the establishment or persistence of species in a given location (Kraft et al. 2015) gradually remove pre-existing fluvial species (Gomes & Miranda 2001, Agostinho et al. 2016). The absence of pre-adapted species colonizing the pelagic zone of reservoirs leads to a concentrated biological diversity and abundance in the littoral zone (Mol et al. 2007, Agostinho et al. 2016), with the presence of several small and medium-sized non-migratory species and their juveniles. Their presence is due to the amounts of nutrient and food supply, and a higher spatial heterogeneity, which provides shelter to individuals (Casatti et al. 2003, Pelicice & Agostinho 2006). The proliferation of small characins has been documented immediately after the formation of several reservoirs (Agostinho et al. 1999, 2007). However, this abundance decreases sharply along time, as the age of the reservoir increases (Agostinho et al. 2007).

The presence of large tributaries, dam design, and operational procedures are some of the factors that influence the persistence of some species (Agostinho et al. 2007, 2016). Though many studies present fish ecology data (trophic and community analysis) during the initial years of reservoir formation (Loureiro-Crippa & Hahn 2006, Cantanhêde et al. 2008), few have measured the population-scale (Abelha & Goulart 2008) and the long-term ecological changes in the community (Mol et al. 2007). In this manner, it is advised to monitor fish populations to detect possible changes in community on the post-stabilization period of Brazilian reservoirs (Dei Tos et al. 2002).

In Brazil, at least 195 out of 655 reservoirs have more than 40 years of operation (ANEEL 2019). The ichthyofauna may have undergone alterations over time, and the species that persisted over the years may present different survival strategies (Agostinho et al. 2007). Since the lentic areas can become less favorable for survival with the aging of the reservoir – and some species are still abundant in old reservoirs – we hypothesize that fish species may have better conditions to complete their life span in the tributaries of the reservoir, searching for riverine conditions that rivers once had before damming.

Astyanax lacustris (early *Astyanax altiparanae*) (Lucena & Soares 2016) is highly abundant in reservoirs. This small-sized species is widely distributed in the Upper Paraná River basin (Langeani et al. 2007) and performs short-distance migration (Graça & Pavanelli 2007). Moreover, *A. lacustris* is abundant in rivers and reservoirs (Orsi et al. 2004) and can easily adapt to recently impounded rivers (Dias et al. 2005, Hahn & Fugi 2008). The species, known by its reproductive plasticity, reproduces several times in a year in both the lotic and lentic habitats (Orsi 2010). *Astyanax lacustris* is a diurnal predator, with good visual acuity (Orsi et al. 2004) and colonizes the mid-water and mid-channel habitats (Casatti 2002). The species is a generalist and opportunistic consumer of drift items (Bennemann et al. 2000, Lowe-McConnell 1999, Maroneze et al. 2011), including macroinvertebrates (Lima et al. 2018). Since *A. lacustris* can be used to investigate the aging processes of reservoirs, we aimed to characterize the population biology of *A. lacustris* in the lentic environments of the Chavantes Reservoir and its tributaries from the Middle Paranapanema River, Paraná River basin, Brazil.

MATERIALS AND METHODS

Study area

The Paranapanema River is a tributary on the East side of the Paraná River (Fig. 1) that has a drainage area of 106,500 Km² and elevation of 474 m (ANA 2016). The Chavantes Reservoir, active for 46 years of operation, is currently classified as old (according to Miranda & Krogman 2015). The Chavantes Reservoir (-49.635111; -23.380378) is located in the middle of the Paranapanema River and is 80 m deep near the dam (Nogueira et al. 2006). The water hydraulic retention time is approximately 418 days, which results in a defined thermal stratification below 20 m (Nogueira et al. 2006). The reservoir has distinct limnological characteristics and its trophic state is oligo-mesotrophic (Perbiche-Neves & Nogueira 2010) (Fig. 1). Six sampling sites were selected with distinct limnological and habitat characteristics (see Perbiche-Neves & Nogueira 2010). Three were lotic and three were lentic environments (Table I).

Sampling

Astyanax lacustris were sampled quarterly from October 2005 to July 2006 (IBAMA/ICMBio license: 15549-1). At each sampling stations, fish were captured with gillnets (five sets with five nets each, mesh sizes ranging from 3 to 7 cm between opposite knots), comprising 500 m² of the net in every sample. Gillnets were set late in the afternoon and removed the following morning (14-hour exposure). Complementarily, juveniles were caught in marginal areas with seining nets (0.6 m², 0.5 cm mesh) and sieve (0.4 m², 0.5 cm mesh), over one hour by five people.

Fish specimens were anesthetized and euthanized by immersion in a water solution with eugenol and confirmation of death was
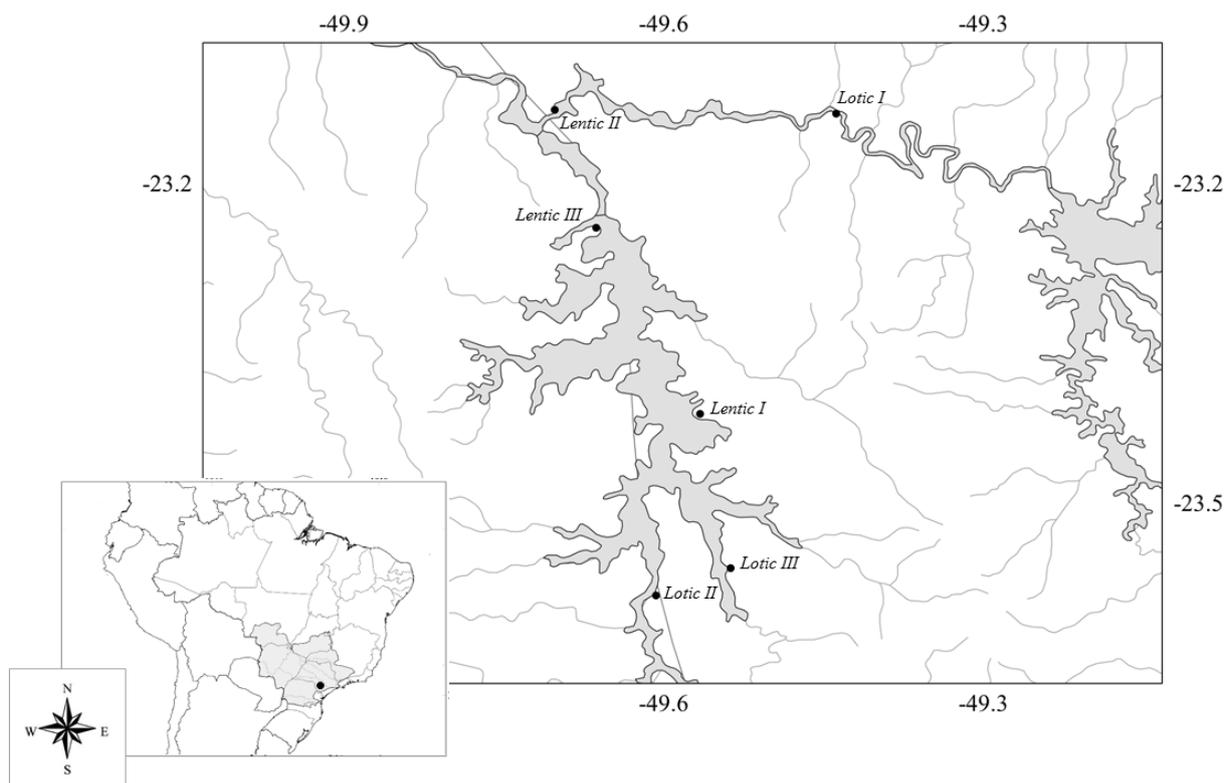
Figure 1. Map of the study area, indicating the Chavantes Reservoir and its tributaries.

made by checking breathing movement. After that, fish were fixed in 10% formalin for at least 48h, transferred to 70% ethanol and identified in the laboratory (Graça & Pavanelli 2007, Ota et al. 2018).

Biometric data, such as standard length (cm) and total weight (g) of the specimens were measured. Subsequently, the fish specimens were dissected to collect their stomachs and were macroscopically analyzed to identify their stage of maturation and sex (Vazzoler 1996). The stomachs collected were fixed in 10% formaldehyde, and were transferred to 70% alcohol after thirty days. The stomach fullness was visually classified on a scale of 0 (empty), 1 (< 25% content), 2 (> 25 < 50%), 3 (> 50 < 75%) and 4 (> 75%) (Walsh & Rankine 1979). Voucher specimens were deposited in the fish collection at the Laboratory of Fish Biology and Genetics (LBP), at the Institute of Biosciences, UNESP, Botucatu, São Paulo, Brazil (LBP 9169).

The stomach content (higher than 50%) was examined using stereoscopic and optical microscopes. The food items were identified to the lowest possible taxonomic level and their weight was quantified with an analytical scale (precision 0.0001 g) (Hyslop 1980). To calculate the relative weight of algae and detritus we first weighted the total stomach content and calculated items as a percentage from the total.

Data analysis

To test for populational differences among sites, we investigated the length-weight relationship, histogram of size classes, frequencies of juveniles and adults, frequency of feeding activity and diet composition. The descriptive statistics obtained for standard length (SL) were median and quartiles (25 and 75%). The median SL values were statistically tested with the non-parametric test Kruskal-Wallis (followed by Dunn multiple comparison test) among sampled stations, as the data presented a non-normal distribution.

The length-weight relationship was determined using the linear regression: log TW = log a + b log TL, where TW is the total weight (in grams), TL is the total length (in cm), "a" is the intercept and "b" is the slope of the linear regression (Nobile et al. 2015).

The histogram of length class was plotted for the different (lotic and lentic habitats).

Table I. Characterization of the lotic and lentic sampling sites studied, influenced by the Chavantes Reservoir, Paranapanema River.

Sampling stations	Municipality	Coordinates	Maximum depth (m)	Margin (main composition)
Lotic I	Piraju (SP)	-49,437388; -23,13425	14.0	Semideciduous forest, pasture and agriculture
Lotic II	Salto do Itararé (PR)	-49,60703; -23,58613	3.5	Pasture
Lotic III	Itaporanga (SP)	-49,536676; -23,560362	1.5	Pasture
Lentic I	Carlópolis (PR)	-49,624821; -23,421889	42.0	Agriculture and urban
Lentic II	Chavantes (SP)	-49,701333; -23,130694	80.0	Semideciduous forest
Lentic III	Timburi (SP)	-49,639623; -23,23848	54.0	Agriculture and urban

The length classes were determined using the Sturges method (Sturges 1926). The analysis of the adult and young proportion for the different sampling stations was established following standard length and stage of gonadal development (Vazzoler 1996). The "chi-square" non-parametric test (χ^2) was applied in absolute frequency and represented in relative frequency of young and adults.

A covariance analysis (ANCOVA) was applied to test whether the regression lines (weight-length relationship) differed between the lentic and lotic habitat. Two null hypotheses were tested: (i) the slopes of the regression lines (b) are parallel to each other; (ii) the Y intercepts of regression lines (a) are all equal (McDonald 2014).

The differences in dietary compositions between lentic and lotic habitats were tested using permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008). The analysis was applied to a matrix of food items (individuals in rows and food items in columns). The Mahalanobis distance was selected as a measure of dissimilarity, because it corrects some of the limitations of the Euclidean distance (Linden 2009). We used 999 permutations to test the significance of the F statistic derived from PERMANOVA. Statistical analyses were conducted in the R Programming Environment and the Vegan package (The R Project for Statistical computing, http://www.r-project.org; Oksanen et al. 2017).

The frequency of stomach fullness was calculated, and the Multi-Response Permutation Procedure (MRPP) (McCune & Grace 2002) was used to test the significance of differences between the lotic and lentic habitats. MRPP provides a test statistic (T) that describes the separation between the groups (the more negative the T value, the stronger the separation), a measure of "effect size" (A) which is a measure of the degree of group homogeneity, compared to random expectation (where A_{max} = 1 when all items are identical within groups), and a p-value, which is useful for evaluating the likelihood that an observed difference is due to chance (McCune & Grace 2002). As the input distance matrix, we selected the Bray-Curtis distance, with "$n/sum(n)$" as the weighting factor.

The trophic niche breadth was calculated with corrected Levin's index (B) (Hurlbert 1978). The B value ranges from 0 (species feed on few food resources) to n (species feed on all resources in similar proportions). The statistical analyses were performed in Statistica 7.0 (Statsoft 2004) and PC-Ord v. 5.0 (McCune & Mefford 2011). For all analyses the level of significance was set to 5%.

RESULTS

We collected 730 specimens of *A. lacustris*. A higher number of individuals were caught in all the lentic sampling sites (Lotic I=53; Lotic II=47; Lotic III=61; Lentic I=339; Lentic II=112; Lentic III=118).

The lotic sample sites showed a normal standard-length distribution (Kolmogorov-Smirnov, p > 0.05), while the lentic sample sites showed non-normal distribution (Kolmogorov-Smirnov, p < 0.001). Kruskal-Wallis test showed statistically significant differences for this variable (H = 117.51, GL = 5, p < 0.0001). The highest median value was obtained for Lentic I (7.0 cm) (Dunn's test p < 0.05) and the lowest median value in Lotic II (3.6 cm) (Dunn's test p < 0.05). Dunn's multiple comparisons test showed statistically significant differences between lotic and lentic sites (Dunn's test, p < 0.001) but not within the same habitats (p > 0.05) (Fig. 2).

The sampling sites of lotic habitat showed broader frequency distribution of length classes
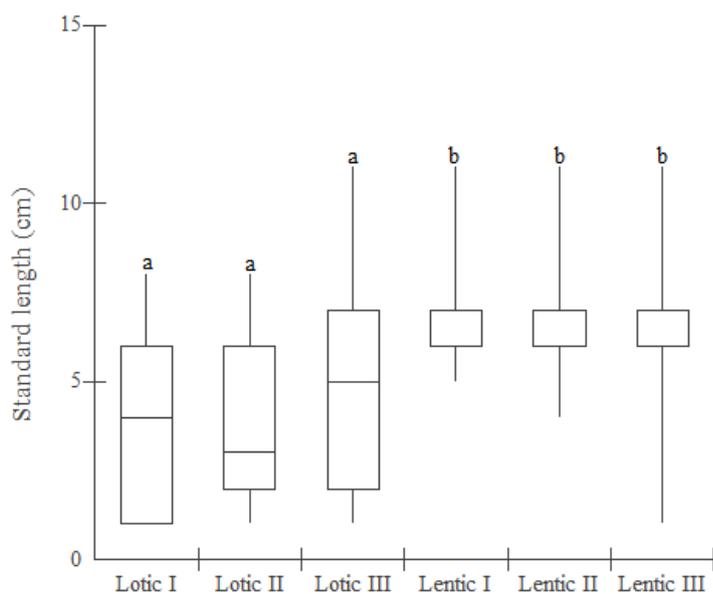
Figure 2. Median and quartiles of standard length (cm) of *Astyanax lacustris* from the lentic and lotic sites of Chavantes Reservoir, Paranapanema River. Different letters indicate the statistical difference (Kruskal-Wallis, p < 0.001).

than the lentic habitat. Lotic II presented two higher frequencies in the size class (1.1–2.0 cm and 6.1–7.0 cm), Lotic I showed peaks in size classes 2.1–3 cm and 6.1–7.0 cm and Lotic III had higher frequency of individuals from 1.1–2.0 and 8.1–9.0 cm (Fig. 3a). The lentic habitat had a high frequency of individuals in only a few size classes, with 86.5% of individuals between the size classes of 5.1– 6.0 cm and 7.1 – 8.0 cm (Fig. 3b).

The analysis of the length-weight relationship showed that the assumption of parallelism was not achieved. The null hypothesis of all slope "*b*" being equal was then rejected (interaction environment * Ls significant, F=135,23, p <0.001). The fish of the lentic areas were heavier (indicated by "a") then fish of lotic areas of the same size (Fig. 4).

Regarding the frequency of adults and young specimens, there were higher proportions of juveniles in lotic environments (Figure 5). The highest proportion of young individuals was obtained in Lotic III (59.3%) and the highest frequency of adults was obtained in Lentic I (88.8%). All lentic environments showed statistically significant differences between adult and young proportions when using the chi-square test (χ^2 Lentic I=96.46; Lentic II=10.33; Lentic III=37.23).

The diet of *A. lacustris* was composed of 37 food items (from plant material aquatic and terrestrial insects, crustaceans, mollusks, detritus, and sediment). Based on the percentage volume of the diet, plant material was the most consumed item in Lotic I, II, and III, complemented by Hymenoptera (at all Lotic sites) and Isoptera (Lotic I), Cladocera (Lotic II) and Algae (Lotic III). In the lentic sites, *A. lacustris* feed on Coleoptera (adults) and plant material (Lentic I), Hymenoptera (adults) and Decapoda (Lentic II) and Ephemeroptera (nymphs) and plant material (Lentic III) (Table II). Of the 21 comparisons performed between the six sites, nine showed p-values < 0.05 for Permanova: Lentic II vs all lotic sites, lotic I vs lotic II and III, lentic I vs lotic I and III. The diet of fishes of the lentic sites presented no statistical differences (Table III). The niche breadth (B) varied from 2.6 (Lotic II) to 5.6 (Lentic I).
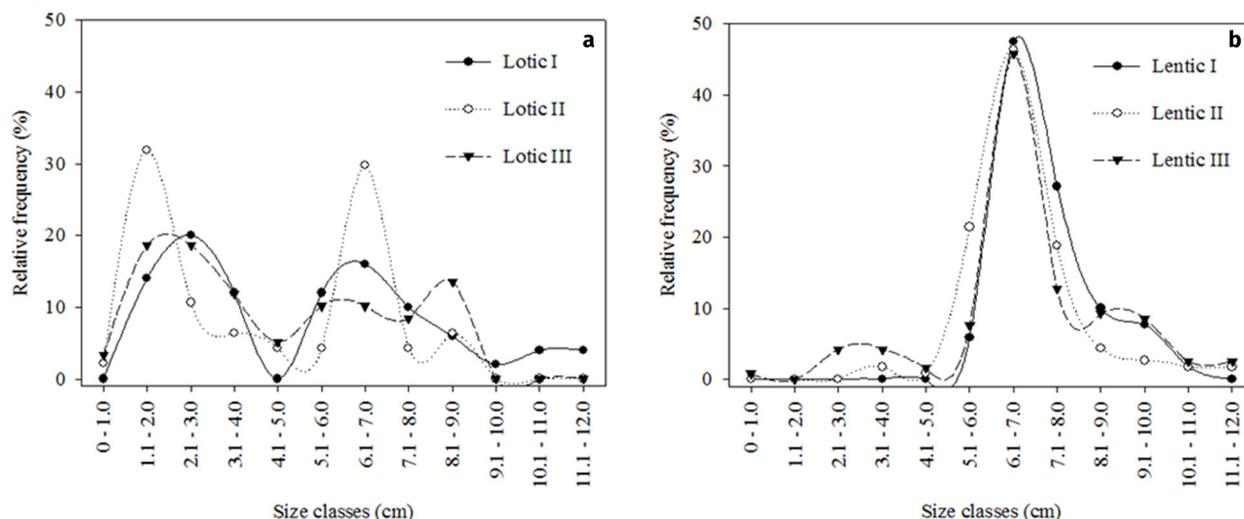
Figure 3. Histograms (size classes of standard length) of *Astyanax lacustris* individuals in the lotic (a) and lentic habitats (b) of Chavantes Reservoir, Middle Paranapanema River.

Lentic I, II and III had a higher frequency of stomachs fulness with repletion levels of 0 and 1, while Lotic I, II, and III had a higher frequency with repletion levels of 2, 3, and 4 (partially filled and full). The three lotic sites differed significantly from the three lentic sites (MRPP, T = -2.71, A = 0.21, p = 0.02).

DISCUSSION

The wider amplitude of length and distribution of adult and juvenile fishes at lotic sites indicate that fish are well adapted to these habitats. This pattern was also observed in *A. altiparanae* from another stretch of the Paranapanema River (Orsi et al. 2004), which was associated with the quality of food resources in environments with low influence of damming. The school of juveniles that generally form groups of 30 to 50 individuals (Casatti 2002, Suzuki & Orsi 2008) may encounter conditions to survive and develop at the lotic habitats. Fast-water habitats have unique ecological advantages including lower predation pressure and increased foraging efficiency (Werner et al. 1983, Lujan & Conway 2015) due to input of allochthonous material

(Orsi et al. 2004). Marginal lagoons, present in Lotic I and II, can also enhance the shelter, survival, and recruitment of young fishes (Agostinho & Zalewski 1995).

Habitat selection by fish is related to foraging profitability and predation risk (McIvor & Odum 1988), which can be exerted either by native or non-native species. In the Chavantes Reservoir, two of the most noteworthy predator fish species are non-native and widespread in lentic environments (*Cichla kelberi* and *Plagioscion squamosissimus*) (Vidotto-Magnoni 2009) and in the Tibagi River, *A. lacustris* is main prey of *P. squamosissimus* (Bennemann et al. 2000).

Lentic habitats presented higher abundance of individuals and fish heavier than the lotic ones. Similar results were observed by Abelha & Goulart (2008) with *A. paranae* from Alagados Reservoir, in state of Paraná and by Orsi et al. (2004) for *A. lacustris* in lentic areas of Tibagi River near to Capivara Reservoir. The marginal areas of lentic habitats are often occupied by species pre-adapted to lacustrine condition (Agostinho et al. 2016). However, a small feeding activity was observed in specimens collected
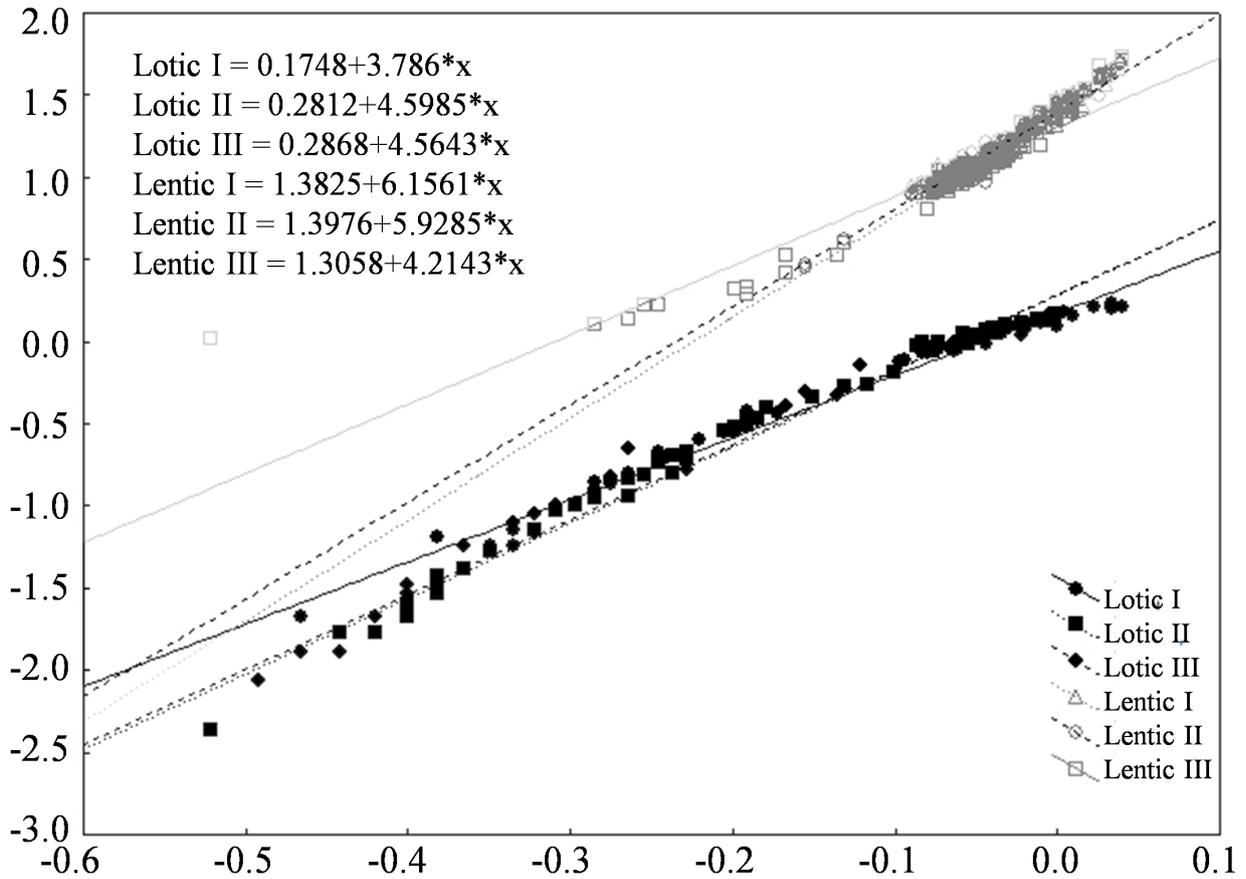
from the lentic sites, indicating that damming could be affecting the offer of preferential food resources. Pereira et al. (2016) attributed the reduction in feeding activity of *A. lacustris* to the piscivory displayed by the species after the damming of Salto Caxias, Iguaçu River. Carnivorous fish usually have higher rate of empty stomachs, which can be associated to the faster digestion (Gerking 1994), as observed in lentic areas.

The feeding behavior of species from genus *Astyanax* corresponds to what Gerking (1994) describes as switching from one food source to a more advantageous source, which occurs in opportunistic species over a given period of time, both from the bottom (Abelha et al. 2006) and the surface of the water (Cassemiro et al. 2002). This opportunistic behavior was observed by Lobón-Cerviá & Bennemann (2000) in *Astyanax altiparanae* in Tibagi River and by Castro & Carvalho (2014) in Jurimirim Reservoir (Paranapanema River). The differences in the diet of *A. lacustris* among the lotic and lentic sites and the trophic niche breadth indicates that these species exhibit an opportunistic behavior. Plant material, the primary food resource in Lotic sites, is a preferential food item of *A. lacustris* in the large rivers (Bennemann et al. 2005) and reservoirs (Lima et al. 2018), which is also a common feeding resource for other species of the genus, such as *A. taeniatus* (Manna et al. 2012). An herbivorous feeding habit is an adaptation to the use of vegetation on river margins, reservoirs, and cultivated pastures and was observed for this species in Iguaçu River before the closure of Salto Caxias Dam (Pereira et al. 2016). Terrestrial insects

(Hymenoptera and Coleoptera) were the main food resources of *A. lacustris* in Lentic I and II and are well documented for this species in rivers and reservoirs (Casatti 2002, Bennemann et al. 2005, Bonato et al. 2012, Delariva et al. 2013). The differences observed between lotic sites (Paranapanema, Itararé and Verde rivers) can be inferred by the differences in conditions (size, width, depth) that may interfere in the composition and availability of different food items.

Species that persist many years after reservoir formation may have the behavioral personality of boldness (a trait where individual are prone to take risks and explore the environment faster when exposed to novelty). Boldness has implications for survival, reproduction, and many other behavioral and life-history traits (Budaev 1997, Binoy 2015, Ariyomo & Watt 2015), especially for those like *A. lacustris* that form schools (Suzuki & Orsi 2008). A variation in the boldness spectrum may influence the risk of predation, diet, and consequently growth and fitness of the species (Wilson et al. 1994). Understanding the boldness spectrum of species should be subject of future research.

Our hypothesis was partially corroborated, since *A. lacustris* encountered superior conditions for recruitment in lotic habitats, adjacent to reservoir. Moreover, this species showed an ability to adapt to the impoundments using different food resources at the lentic sites and colonizing littoral areas.

Lotic I = 0.1748+3.786*x
Lotic II = 0.2812+4.5985*x
Lotic III = 0.2868+4.5643*x
Lentic I = 1.3825+6.1561*x
Lentic II = 1.3976+5.9285*x
Lentic III = 1.3058+4.2143*x

Lotic I
Lotic II
Lotic III
Lentic I
Lentic II
Lentic III

Figure 4. Slope and equations for data of length and weight of fishes in lotic and lentic habitats of Chavantes Reservoir, Middle Paranapanema River (see Table I for more details).
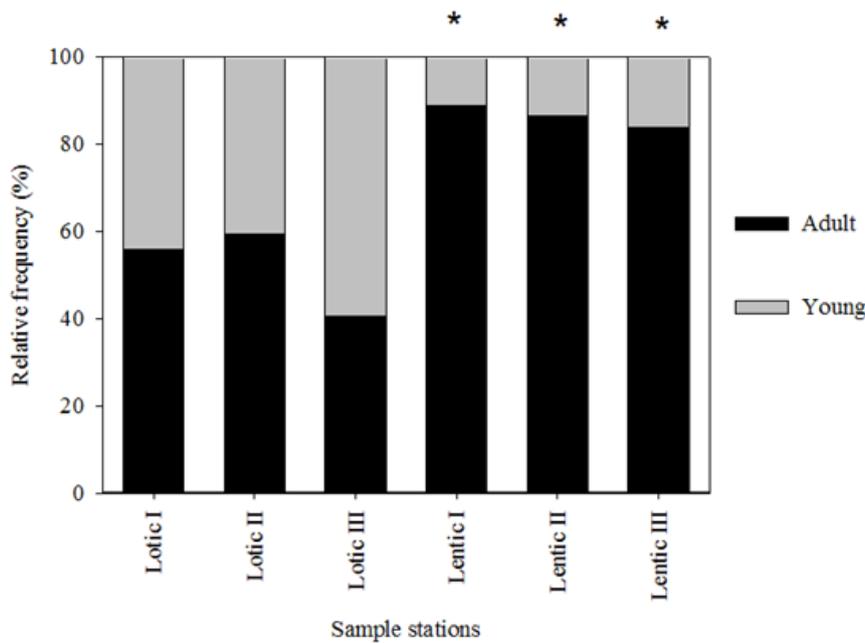
Figure 5. Adult and young proportion of *Astyanax lacustris* in lotic and lentic habitats of Chavantes Reservoir, Middle Paranapanema River. * = statistically significant differences based on the chi-square test.

Table II. Variation in standard length range and number of individuals (N) selected for diet analysis; the number of items found in the diet, trophic niche breadth (B), and diet composition (% weight) of the food resources consumed by *Astyanax lacustris* in lotic and lentic sites influenced by the Chavantes Reservoir, Paranapanema River.

	Lotic I (N = 45)	Lotic II (N = 38)	Lotic III (N = 51)	Lentic I (N = 200)	Lentic II (N = 67)	Lentic III (N = 63)
Standard length range (cm)	1.2–11.5	1.0–8.7	1.0–8.9	5.5–10.8	4.0–11.4	1.0–11.5
Number of items	27	20	22	34	22	26
Trophic niche breadth (B)	4.6	2.6	4.1	5.6	3.5	4.5
Tecameba	0.01	0.12	0.04	0.00	0	0
Rotifera	0	0	0	0.0008	0	0
Cladocera	0.01	12.54	4.11	9.29	0.25	1.41
Copepoda	0.01	0.58	0.08	0.00	0.0008	0.30
Ostracoda	0	0.33	0.07	0	0	0
Decapoda	0	0	0	1.53	24.21	0.10
Acari	0	1.93	0	0	0	0
Araneae	0.16	0	0	0.05	0.09	0.30
Hymenoptera (Adult)	26.58	10.85	11.32	8.77	45.99	6.47
Coleoptera (Adult)	8.74	0.38	0.43	32.39	5.17	10.30
Hemiptera (Adult)	1.80	0.05	0.93	1.94	1.99	0.38
Diptera (Adult)	0.03	0	0	0.61	0	0.07
Lepidoptera (Adult)	0	0	0	0.20	0	0.20
Dermaptera (Adult)	1.71	0	0	1.64	0	0
Blataria (Adult)	0	0	0	0.79	0	0.02
Tysanoptera (Adult)	0	0	0.01	0.01	0	0
Orthoptera (Adult)	0	0	7.67	1.19	0	0
Ephemeroptera (Adult)	0	0	0	0.01	0	0
Neuroptera (Adult)	0	0	0	0	0	0.02
Trichoptera (Adult)	0.12	0	0	0	0.18	0.18
Isoptera (Adult)	25.93	0	0.13	5.42	0	0
Psocoptera (Adult)	0	0	0	0.14	0.05	0.06
Terrestrial Insect (Non identified)	0.54	1.96	0.97	3.16	4.73	3.56
Diptera (Larvae/Pupa)	1.15	0.68	1.56	2.52	5.34	3.32
Ephemeroptera (Nymph)	0.20	4.16	8.46	7.78	3.26	31.56
Odonata (Larvae)	0	0.68	0.06	0.16	0	0.10
Hemiptera (Adult/Aquatic)	0.55	0.16	0.06	0.05	0.06	0
Trichoptera (Larvae)	0.14	0.03	0	0	0	0.07
Coleoptera (Larvae)	0.43	0.03	0.01	0.05	0	0.06
Lepidoptera (Larvae)	0.08	0	0	0	0	0
Aquatic Insect (Non identified)	0.78	0.12	0.04	0.05	0.07	0.04
Mollusk (Gastropoda; Bivalvia)	0.99	0	0	0.05	0.11	0
Invertebrate Egg (Non identified)	0	0	0	0.01	0.01	0
Fish	2.82	0.08	0.02	0.20	0.71	0.25
Plant Material	26.78	59.84	40.91	21.23	7.01	30.45
Algae	0	4.73	21.58	0.47	0.07	10.40
Detritus/Sediment	0.42	0.76	1.50	0.30	0.68	0.39

Table III. Permanova results comparing *Astyanax lacustris* diet from lotic and lentic sites of Chavantes Reservoir, Middle Paranapanema River. p-values <0.05 are shown in bold.

Pairs	F Model	R^2	p-value
Lentic III vs Lentic II	1.191581	0.009223	0.108
Lentic III vs Lotic I	1.567429	0.016231	**0.001**
Lentic III vs Lotic II	1.075321	0.010745	0.296
Lentic III vs Lentic I	1.593026	0.006067	0.06
Lentic III vs Lotic III	1.219092	0.010768	0.223
Lentic III vs Lotic I	0.927694	0.012721	0.563
Lentic II vs Lotic I	2.128092	0.021044	**0.001**
Lentic II vs Lotic II	2.023161	0.019264	**0.001**
Lentic II vs Lentic I	1.647233	0.006178	0.038
Lentic II vs Lotic III	2.605537	0.021968	**0.001**
Lentic II vs Lotic I	1.284684	0.016623	0.229
Lotic I vs Lotic II	1.65333	0.023074	**0.001**
Lotic I vs Lentic I	2.219409	0.009476	**0.01**
Lotic I vs Lotic III	2.082982	0.024482	**0.001**
Lotic I vs Lotic I	1.012475	0.023004	0.429
Lotic II vs Lentic I	1.288611	0.005431	0.226
Lotic II vs Lotic III	0.71877	0.008194	0.821
Lotic II vs Lotic I	1.237847	0.025661	0.203
Lentic I vs Lotic III	1.802821	0.007188	**0.029**
Lentic I vs Lotic I	0.449709	0.002147	0.696
Lotic III vs Lotic I	0.85688	0.01408	0.568

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APVM contributed in the concept of the study; data collection; data analysis and interpretation; manuscript preparation; critical revision, adding intellectual content. GK contributed to data analysis and interpretation; manuscript preparation; critical revision. FPL, ABN, DAZG and ACRC contributed to manuscript preparation and critical revision, adding intellectual content. ADP contributed to data analysis and interpretation; manuscript preparation; critical revision, adding intellectual content. MLO contributed to critical revision, adding intellectual content.