



Changes in diet of a neotropical cichlid in response to river damming

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ABSTRACT. Changes in diet of *Laetacara araguaiae* Ottoni and Costa, 2009 were evaluated in the Sucuriú River (Upper Paraná basin, Brazil) in an area with a small hydroelectric power plant, both before and after the formation of the reservoir, in order to answer: Did the construction of the reservoir affected the diet of this species? The results showed greater change of diet composition in the upstream section of the reservoir. It was observed that before the formation of the reservoir and the first year after, the individuals from upstream section formed a group characterized by an insectivorous diet. With the dam construction and habitat change we observed that aquatic plant material, sediment, and algae predominated in the diet. These results show the opportunistic feeding habit of *L. araguaiae* and contribute to the understanding of how the impoundment of rivers can influence the trophic dynamics of the ichthyofauna.

Keywords: aquatic ecology; environmental impacts; *Laetacara araguaiae*; reservoir; Upper Paraná River; Brazil.

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Introduction

Freshwater ecosystems are among the most affected in the world by multiple and interactive pressures including pollution, water catchment, and weir and dam constructions (Ayllón, Almodóvar, Nicola, Parra, & Elvira, 2012). The main objective of weir and dam creation includes irrigation for agriculture, water supply for human use, and generation of hydroelectric power. Although most of the energy currently consumed nowadays around the world is derived from fossil fuels and nuclear power plants, 10.5% comes from so-called renewable sources, of which hydropower is the most important (Koç, 2012). However, the installation of hydroelectric power plants is one of the actions most strongly associated with impacts on aquatic ecosystems (Mérona & Vigouroux, 2006; Agostinho, Pelicice, & Gomes, 2008), because such actions alter the physical habitat and cause retention of sediments and nutrients in the reservoir, controlling the flow regime and altering the connectivity between the river and the floodplain (Agostinho et al., 2008).

Currently, about 85% of the energy produced in Brazil is generated in large and small hydroelectric plants, and almost 70% of the total energy production comes from reservoirs in the Paraná River basin (Agostinho, Pelicice, Petry, Gomes, & Julio, 2007). Small hydroelectric plants (PCHs, in Brazil) present lower cost and lower energy production capacity than conventional hydroelectric plant. Because of that, they are built in greater numbers along the same stretches breaking down-upstream connectivity, converting lotic environments into lentic environments over a short time interval (Gubiani, Gomes, Agostinho, & Okada, 2007). In addition, the barrages cause changes in the physical and chemical conditions of the water (Chellappa, Bueno, Chellappa, Chellappa, & Val, 2009) and the quality and quantity of habitats for aquatic fauna and flora, and can modify ecological and biological processes (Novaes, Moreira, Freire, Sousa, & Costa, 2014; Latini & Pedlowsky, 2016).

The higher availability of allochthonous resources in the dammed environment may cause a positive effect in the production of all trophic levels, an event known as the trophic upsurge period (Loureiro-Crippa & Hahn, 2006; Pereira, Agostinho, & Delariva, 2016). The structure of the fish communities in the first

years of damming of a river is considered decisive in the process of later colonization and seems to depend on the presence of groups that are adapted to lacustrine conditions and with great alimentary and reproductive plasticity (Olden & Naiman, 2010). Many species present wide trophic adaptability and are therefore generalists, meaning that they are potentially capable of using a broad range of food resources. In fact, in dammed rivers, many species change the

diet following changes in resource availability (Mérona, Vigouroux, & Horeau, 2003; Hahn & Fugi, 2007; Pereira et al., 2016; Wang, Li, Xu, & Gu, 2016; Oliveira et al., 2018). Thus, the study of fish feeding habits provides fundamental information about the autoecology of the species and, in impacted environments, can show how anthropogenic activities influence the systems (Delariva, Hahn, & Gomes, 2007; Souza & Lima-Junior, 2013).

Cichlids, in general, have preference for lentic environments. This characteristic, together with the well-developed parental care observed in the species of this family, provides success in the colonization of reservoirs (Baumgartner et al., 2012). *Laetacara araguaiae* Ottoni and Costa, 2009 is a cichlid abundant in the Upper Parana River system, mainly found in shallow marginal areas of streams with diverse structural conditions and even hypoxia (Casatti, Langeani, & Ferreira, 2006). Regarding the diet of the species, Souza-Filho and Casatti (2010) recorded fragments of aquatic invertebrates and aquatic insects as the most important items, indicating an invertivore diet. However, there is no study in the literature that has investigated the temporal changes in the diet of this cichlid in a river that has passed through damming.

Based on this background, the objective of this paper was to characterize the diet of *Laetacara araguaiae* in the Sucuriú River (Upper Paraná basin, Brazil) in an area with a small hydroelectric power plant, both before and after the formation of the reservoir, in order to answer the following questions: (1) did the change to a lentic environment caused by the construction of the reservoir affect the dietary composition of this species? and (2) if so, in which ways?

Material and methods

Study area and sampling procedure

This study was developed in the upper reaches of the Sucuriú River, which is an important tributary of the Paraná River (Brazil), near the current small hydroelectric power station, the so-called PCH Alto Sucuriú (19.2453°S, 52.8794°W) (Figure 1). The construction of the PCH Alto Sucuriú reservoir began in January 2005 and was concluded in September 2008.

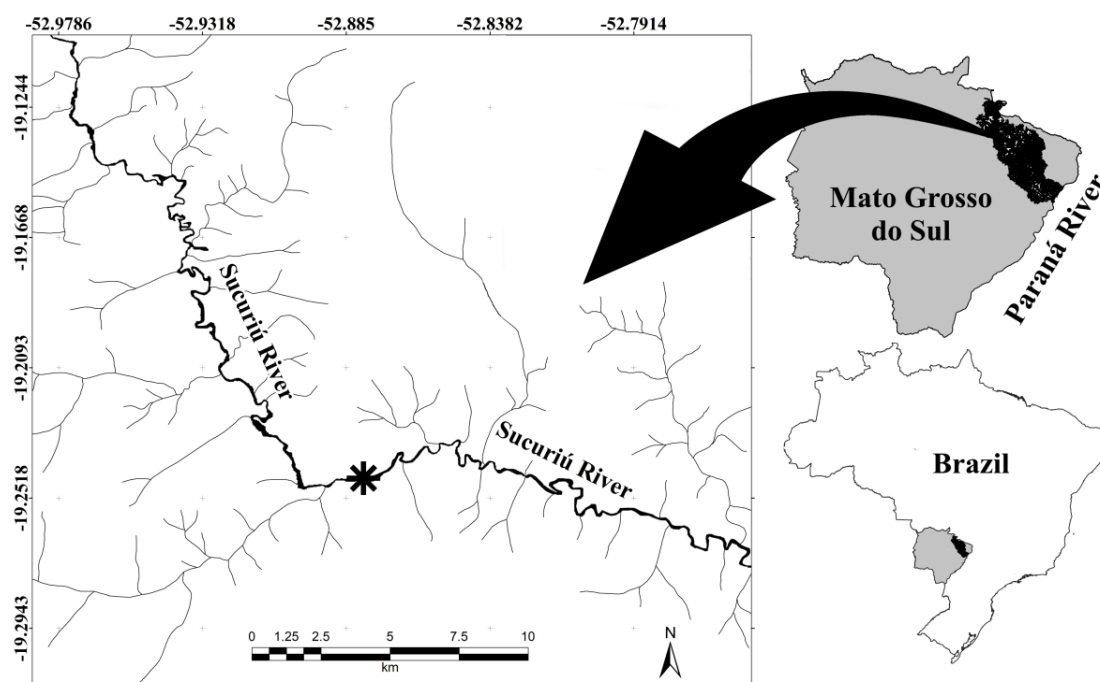


Figure 1. Location of the study area, at the Sucuriú River, Upper Paraná River, Brazil. The asterisk indicates PCH Alto Sucuriú.

Specimens of *L. araguaiae* were sampled upstream and downstream from the plant installation area on a quarterly basis between January 2006 and February 2012 using sieves (1x1 m, 2 mm mesh) and seine nets (8x1 m, 2.5 mm mesh). The samplings were concentrated in areas of beaches (the preferred habitat of *L. araguaiae*, as reported by Casatti et al., 2006) at a distance of up to 3km from the dam. The sampled specimens were fixed in the field using 10% formalin solution and then transferred, in the laboratory, to a 70% ethanol solution for preservation.

Dietary analysis

For the dietary analysis, the contents of the stomachs with food were weighed to the nearest 0.01 g, fixed in 10% formalin and preserved in a 70% ethanol solution until analysis. Later, the stomach content of each individual was inspected using a stereomicroscope, and each food item was given a value proportional to its abundance. The reference used for these values was the standard weight (SW), which is the approximate arithmetic mean of the stomach content weight of the sample, as proposed by Lima-Junior and Goitein (2001). Assuming that the SW is equivalent to 4 points, the stomach contents were initially assigned a total value according to the proportion of mass to the SW. Based on a visual inspection, this total value was then divided among the food items according to their relative volume.

To analyze the relative degree of dietary specialization over the studied years, the trophic niche breadth was estimated for the sampled individuals in each year and in each river section (upstream or downstream). This breadth can be defined as the diversity and the proportion of prey consumed as evaluated by the Levin's standardized index (Sá-Oliveira, Angeline, & Isaac-Nahum, 2014). The index is given by the expression:

$$B_i = [(\sum_j P^2_{ij})^{-1} - 1] (n - 1)^{-1}$$

where:

B_i = the breadth of the trophic niche;

P_{ij} = the proportion of food category j in the diet of individual i ; and

n = the total number of food categories.

Statistical analyses

From the spreadsheet obtained in stomach content analysis – where each row represents an individual and each column a food item, with the respective values assigned to each item – a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2017) was used to test for differences in the diet composition of *L. araguaiae* over the years, in a separate way to each section of the river (upstream or downstream). A post hoc test (Bonferroni-corrected p-values) was performed in order to compare the years (R Core Team, 2017). The Bray-Curtis index was used to build the similarity matrix, and the significance of the comparisons was computed from the randomization of the original matrix (9,999 permutations). In order to complement this analysis and to visualize the ordering of food items as a function of the sampling years in each section of the river, it was used a non-metric multidimensional scaling (nMDS), with Bray-Curtis index, which is available in R (R Core Team, 2017). A cluster analysis was performed from the importance indices of food items (Lima-Junior & Goitein, 2001) calculated in four groups: upstream before the formation of the reservoir (data from years 2006 to 2008), upstream after the formation of the reservoir (2009 to 2012), downstream before the formation, and downstream after the formation. For this analysis, it was used the Bray-Curtis index and the UPGMA method in R (R Core Team, 2017).

For the comparison of the trophic niche breadth (Levin's standardized index) over the years, it was used a Kruskal-Wallis test with a Dunn *a posteriori* test (since the data have no normal distribution) at a significance level of 0.05 (R Core Team, 2017), in a separate way to upstream and downstream sections.

Results

Along the years it was sampled 411 individuals of *L. araguaiae* (Table 1). The standard length of specimens sampled upstream ranged from 10.74 to 45.15 mm (mean \pm SD = 26.54 \pm 7.15 mm). For the downstream, the standard length of individuals ranged from 12.94 to 42.70 mm (mean \pm SD = 24.92 \pm 5.81 mm).

The analysis of stomachs ($n = 411$) showed that the species consumed a wide range of food resources, which were grouped into ten categories: (1) algae (branched, gelatinous and filamentous); (2) aquatic plant material (stems and leaves); (3) terrestrial plant material (stems, leaves, fruits and seeds); (4) zooplankton (Thecamoeba, Cladocera and Copepoda); (5) aquatic insects (locomotor appendages, fragments of exoskeleton, eggs and larvae of Diptera – Culicidae, Chironomidae, and Simuliidae –, Trichoptera and Coleoptera); (6) terrestrial insects (locomotor appendages, fragments of exoskeleton and wings of Ephemeroptera, Odonata, Hemiptera, Coleoptera and Hymenoptera); (7) other invertebrates (Oligochaeta, Acarina, Aranae); (8) fish remains (scales and oocytes); (9) sediment (sand, clay, gravel); and (10) unidentified material (mass of fully digested material). The diet evaluated over the years shows a clear predominance of aquatic insects in the *L. araguaiae* diet both in the upstream section (52.1% of the total values assigned to items) and in the downstream section (33.8%) in the Sucuriú river.

Table 1. Number of sampled individuals along the years in the upstream and downstream sections of the Sucuriú River, Upper Paraná River, Brazil.

Year	Upstream	Downstream
2006	33	45
2007	17	23
2008	34	4
2009	41	19
2010	60	16
2011	46	25
2012	48	0

The annual comparison of the food items by PERMANOVA indicated significant annual differences in both the upstream section (pseudo- $F = 2.93$; $p < 0.001$) and the downstream section (pseudo- $F = 3.38$; $p < 0.001$) of the river. The results of the post hoc test for comparison among years are presented in Table 2. In general, the two river sections (upstream and downstream) showed three temporal groups: Group 1, which includes 2006, 2007 and 2008, and characterizes the period prior to the formation of the reservoir; Group 2, which includes 2009 (transition); and Group 3, which includes 2010 and later, characterizing the phase with the fully formed reservoir.

Table 2. Results of the post hoc test (Bonferroni-corrected p-values) comparing the importance indices of food items consumed by *Laetacara araguaiae* over seven years before and after dam construction in the upstream and downstream sections of the Sucuriú River, Upper Paraná River, Brazil.

Upstream	2007	2008	2009	2010	2011	2012
2006	0.2184	1.0000	1.0000	0.0021	0.1953	0.0126
2007		1.0000	0.0399	0.0042	0.0210	0.0021
2008			1.0000	0.0021	0.0420	0.0021
2009				0.1407	0.1554	0.0294
2010					1.0000	1.0000
2011						1.0000
Downstream	2007	2008	2009	2010	2011	2012
2006	0.2016	1.0000	1.0000	0.0105	0.1638	-
2007		1.0000	0.0420	0.0021	0.0252	-
2008			1.0000	0.0021	0.0399	-
2009				0.1659	0.1596	-
2010					1.0000	-

The nMDS results (Figure 2) showed a higher impact on the *L. araguaiae* diet in the upstream section of the reservoir, since in this section there are more defined groupings that characterize the years before and after the dam construction. The individuals sampled in the years 2006, 2008 and 2009 (two years prior to the reservoir formation plus the first year after the reservoir formation) formed a group characterized by a diet associated with aquatic and terrestrial insects. Another group included years 2010 to 2012, whose diet is more associated with aquatic plant material, sediment and algae.

For the downstream section, there is a clear grouping of the years 2006 and 2009 that is associated with the consumption of other invertebrates and fish. However, for the other years there are no clear

groupings among the years: 2007 was characterized by the greater abundance of aquatic plant material in the diet, 2008 and 2011 by aquatic insects and sediment, and 2010 by terrestrial plant material.

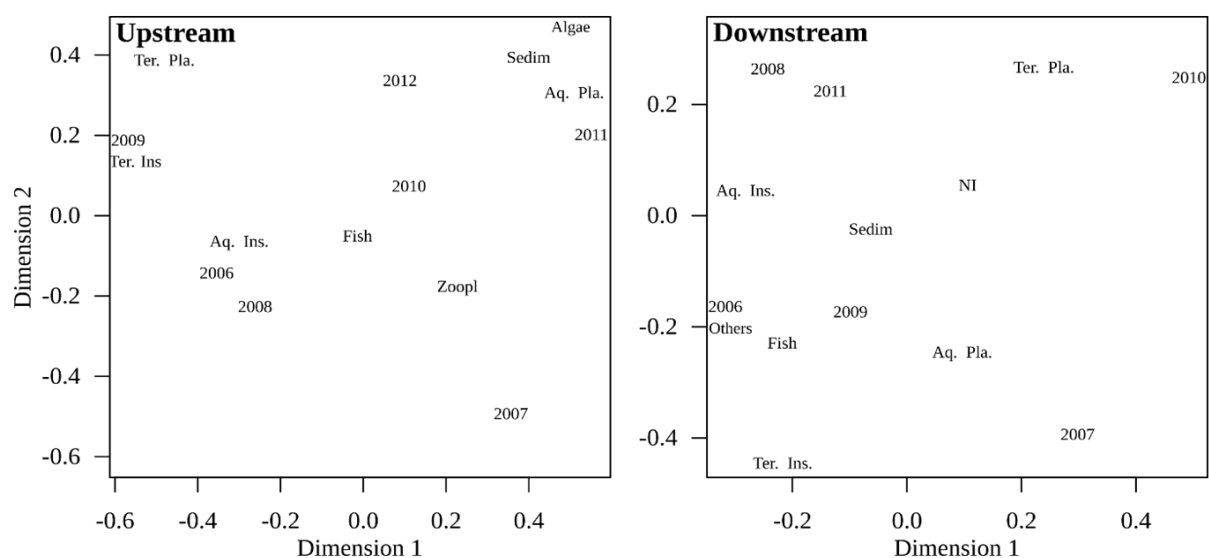


Figure 2. Results of the nMDS for the food items consumed by *Laetacara araguaiae* over seven years before and after dam construction in the upstream ($r^2 = 0.95$) and downstream ($r^2 = 0.76$) sections of the Sucuriú River, Upper Paraná River, Brazil.

The cluster analysis performed using the importance indexes of food items consumed by *L. araguaiae* over the years in the upstream and downstream sections of the Sucuriú River (Figure 3) shows more evident differentiation of the group formed by the data obtained from the period after the formation of the reservoir, in the upstream section, compared to the other groups.

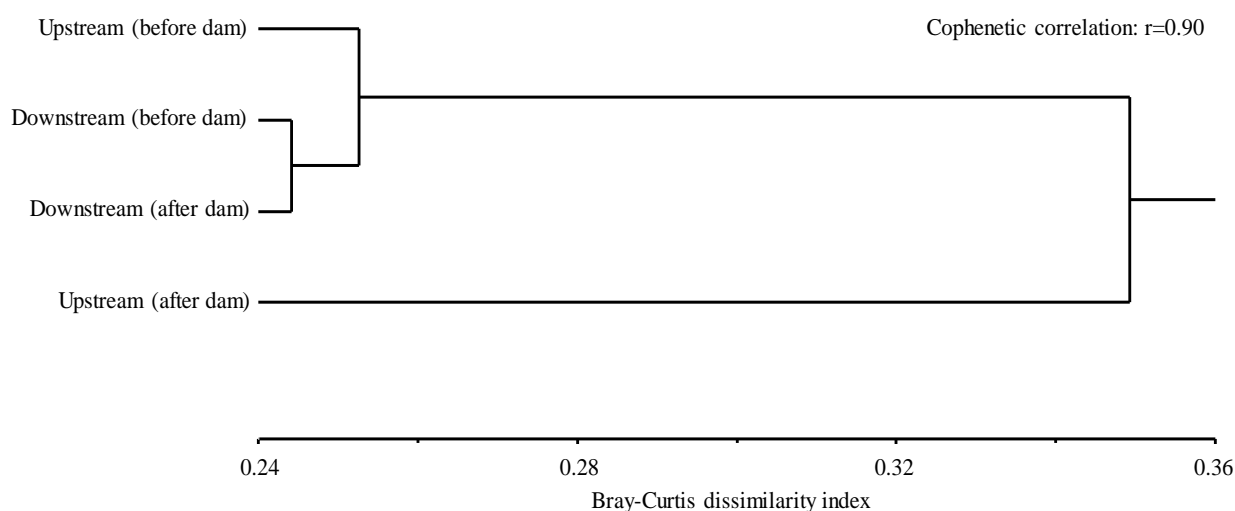


Figure 3. Results of the cluster analysis for the food items consumed by *Laetacara araguaiae* in the upstream and downstream sections of the Sucuriú River, Upper Paraná River, Brazil, before and after the formation of the hydroelectric dam reservoir.

Analysis of the trophic niche breadth over the years in the upstream area revealed a significant annual difference only in the comparisons between the years 2006 and 2010, 2006 and 2012, and 2008 and 2010. There is no consistent pattern of significant differences between the years before and after the formation of the reservoir. In other words, although the species altered its diet due to river damming, the trophic niche breadth of the population remained basically unchanged (Figure 4 and Table 3).

For the downstream section, it was observed significant differences between the years (Figure 4 and Table 3). However, we did not observe a pattern that could be clearly associated with the impact caused by the formation of the reservoir.

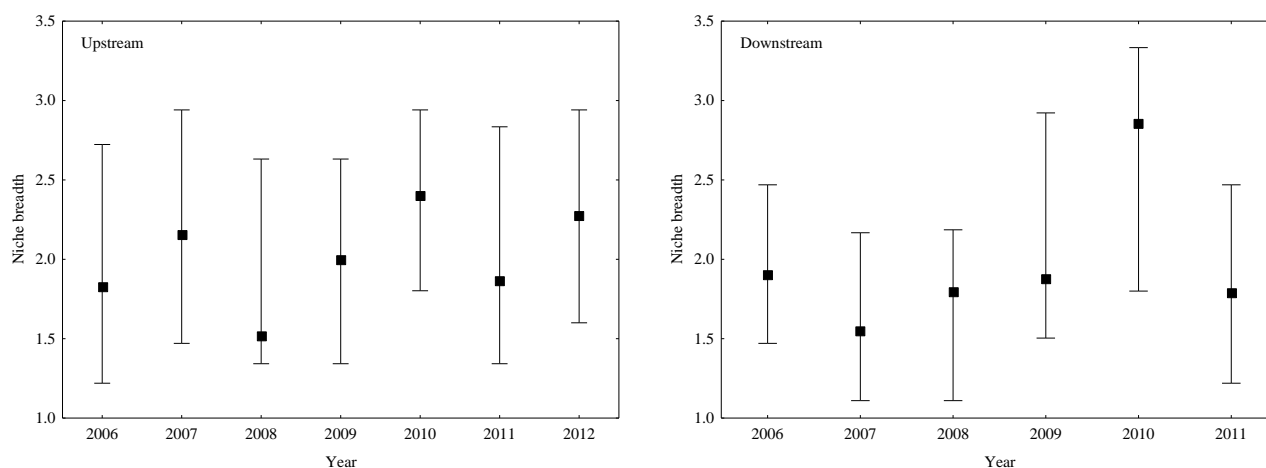


Figure 4. Trophic niche breadth (median and interquartile range) of *Laetacara araguaiae* over seven years upstream and downstream of the Sucuriú River, Upper Paraná River, Brazil.

Table 3. Results of the post hoc test (Dunn p-values) comparing *Laetacara araguaiae* individual trophic niche breadth over seven years before and after dam construction in the upstream and downstream sections of the Sucuriú River, Upper Paraná River, Brazil.

Upstream	2007	2008	2009	2010	2011	2012
2006	0.1637	0.7678	0.3481	0.0028	0.3721	0.0369
2007		0.1664	0.5584	0.3196	0.5472	0.6791
2008			0.3174	0.0131	0.3333	0.0603
2009				0.0544	0.9775	0.2509
2010					0.0555	0.5221
2011						0.2474
Downstream	2007	2008	2009	2010	2011	2012
2006	0.2781	0.4158	0.9640	0.0593	0.6235	-
2007		0.7542	0.2904	0.0105	0.4891	-
2008			0.4257	0.0151	0.7013	-
2009				0.0917	0.6229	-
2010					0.0195	-

Discussion

According to the River Continuum Concept, proposed by Vannote, Minshall, Cummins, Sedell, and Cushing (1980), the lotic system is a gradient presenting increased volume along the watercourse in which the importance of allochthonous organic matter input decreases from the head to the mouth. Matter entering the system in the higher reaches, that is not processed locally, must be carried downstream and fully utilized by the communities along the river so that the dynamics of the system as a whole remain in equilibrium. Thus, the construction of dams along a river changes the natural dynamics of the system causing disturbances that alter the trophic chain, and only the species with higher dietary plasticity can adapt to the new conditions (Pereira et al., 2016; Oliveira et al., 2018). In this context, *L. araguaiae* – like other cichlids (Baumgartner et al., 2012) – is the species that seems to be relatively well adapted to the impacts caused by the formation of the reservoir. The wide variety of food items recorded in this research supports this assertion, since it demonstrates that the species has an omnivorous diet and displays opportunistic feeding behavior.

Dipterans of the Chironomidae family are among the aquatic invertebrates most consumed by fish, and this is associated with the high abundance of this group in many aquatic environments, including impacted environments (Delariva et al., 2007; Souza & Lima-Junior, 2013), since these Diptera have adaptations that enable them to become the first settlers of newly flooded areas (Rossaro, 1991). In fact, it was observed that aquatic insects, mainly Chironomidae, represented the most important item of the diet of *L. araguaiae* in the Sucuriú River, both in upstream and downstream sections (about 50% of the total values assigned to items).

In addition to the changes associated with water flow, the flooding of terrestrial areas due to reservoir formation leads to a greater input of organic material during and after the reservoir filling phase (Loureiro-Crippa & Hahn, 2006). Along the reservoir formation, the riparian vegetation is removed, causing increased

input of inorganic sediments, branches, trunks and leaves (Nakamura & Yamada, 2005; Sá-Oliveira et al., 2014). In fact, in the years 2010 to 2012 (after the reservoir formation), it was observed that aquatic plant material, sediment and algae became more abundant in the diet of *L. araguaiae* upstream from the dam.

The formation of a reservoir strongly influences several environmental conditions and leads to an increase in the diversity and abundance of algae (Bini, Thomaz, Murphy, & Camargo, 1999; Thomaz & Bini, 2003). Corroborating this assertion, in the Itaipu reservoir (Paraná River, between Brazil and Paraguay), Hahn, Agostinho, Gomes, and Bini (1998) observed that herbivorous species consumed primarily filamentous algae in the first five years after damming. The present results are in agreement, as there were differences observed in the diet of *L. araguaiae* in the upstream section of the dam after the formation of the reservoir compared to other spatio-temporal groups; this was also shown in the cluster analysis, as this cited group was clearly separate from the others, indicating that impacts from the dam influenced the dietary changes in the studied fish species, mainly at upstream of the hydroelectric plant.

Regarding the trophic niche breadth, we did not observe a consistent pattern to indicate increased or decreased diversity of food items consumed by *L. araguaiae* due to the impoundment of the Sucuriú River. Similar results were observed by Gandini, Boratto, Fagundes, and Pompeu (2012) for fish in the Rio Grande, downstream of the Itutinga hydroelectric plant, in the Upper Paraná River, Brazil. This result reinforces the opportunistic nature of this species, as it was able to change its diet as a function of environmental change without restricting the diversity of the consumed items.

Considering the optimal foraging theory (Charnov, 1976), the prey use is based on availability and return of energy to a predator. Then, considering that hydrological changes can affect prey availability and composition (Loureiro-Crippa & Hahn, 2006; Pereira et al., 2016), it is expected that a polyphagous predator alter the feeding composition to equalize its energy and nutrient needs. In this context, our results corroborate the presuppositions of adjust of feeding for *L. araguaiae* in response to environmental change caused by river damming, as observed for many other fish species (Mérona et al., 2003; Hahn & Fugi, 2007; Pereira et al., 2016; Wang et al., 2016; Oliveira et al., 2018). In the same way, the maintenance of niche breadth pattern along studied time reinforces that the changes in diet composition is not accompanied by diversity of used prey. These changes probably are only possible due to feeding plasticity of this species and cannot be inferred to others species, however they can serve as a basis to species that occupy similar niches.

Conclusion

Before the formation of the reservoir and the first year after, the individuals from upstream section were characterized by an insectivorous diet. With the dam construction and habitat alteration, aquatic plant material, sediment, and algae predominated in the diet. These results demonstrate the opportunistic feeding habit of *L. araguaiae* and contribute to the understanding of how the impoundment of rivers can influence the trophic dynamics of the ichthyofauna.

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