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Habitat heterogeneity on feeding habit of two sympatric and congeneric characidae fishes in two tropical reservoirs

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ABSTRACT. Food flexibility and omnivory are important features pronounced in Neotropical freshwater fish species, particularly for *Astyanax* species. Traditionally most fish diet resources are known to be originated in the aquatic environment, however recent studies have pointed to the importance of allochthonous sources. Besides, the colonization of macrophytes, common at several tropical reservoirs, may enhance insectivory in fish diet expanding or concentrating the area of available resources for feeding. Here we employed stomach contents analysis of two sympatric *Astyanax* species to access the importance of habitat differentiations as spatial complexity in two tropical reservoirs with different environmental features. The NMDS analysis indicated separation in the diet of these species between reservoirs (Stress= 8.28%). Additionally, analysis of variance revealed a significative difference in the volume of food itens ingested between the reservoirs (Anova one-way F(1, 132)=4.4446; p= 0.037). This points out the importance of environmental conditions on the composition of the diet of fishes. This study highlighted the insectivorous feeding habit of *Astyanax* species and revealed different feeding strategies between sympatric fishes despite high niche overlap in both environments. Habitat heterogeneity increasing food resources availability plays an important role in the diet strategy of these *Astyanax* species and on their constant maintenance in the two different reservoirs.

KEYWORDS. Feeding resources, land-water ecotone, trophic ecology, *Astyanax* **aff**. *bimaculatus*, *Astyanax parahybae*.

RESUMO. Heterogeneidade de habitat no hábito alimentar de duas espécies simpátricas e congenéricas de peixes caracídeos em dois reservatórios tropicais. A flexibilidade alimentar e onivoria são características das espécies de peixes de água doce neotropicais, especialmente em espécies de *Astyanax*. Tradicionalmente a maioria dos recursos na dieta de peixes é reconhecidamente originária do ambiente aquático, porém estudos recentes têm apontado para a importância das fontes alóctones. Além disso, a colonização de macrófitas, comuns em vários reservatórios tropicais, pode melhorar os aspectos de insetivoria na dieta dos peixes expandindo ou concentrando a área disponível para a alimentação. Aqui analisamos o conteúdo estomacal de duas espécies de *Astyanax* simpátricas para avaliar a importância das diferenças de habitats, como a complexidade espacial, em dois reservatórios tropicais com diferentes características ambientais. A análise NMDS indicou separação na dieta destas espécies entre reservatórios (stress = 8.28%). Além disso, a análise de variância revelou uma diferença significativa no volume de itens alimentares consumidos entre os reservatórios (Anova one-way F (1. 132) = 4,4446; p = 0.037), salientando a importância das condições ambientais na composição da dieta de peixes. O estudo destacou o hábito alimentar insetívoro das espécies de *Astyanax* e revelou diferentes estratégias de alimentação entre esses peixes simpátricos apesar da alta sobreposição de nicho nos dois ambientes. A heterogeneidade de hábitat aumentando a disponibilidade de recursos alimentares teve importância sobre a estratégia alimentar das espécies de *Astyanax* e consequentemente na manutenção constante de ambas nos dois diferentes reservatórios.

PALAVRAS-CHAVE. Recursos alimentares, ecótono terra-água, Ecologia trófica, *Astyanax* **aff.** *bimaculatus*, *Astyanax parahybae*.

Trophic interactions and quantifying spatial and temporal variability in fish diet remains a challenge for ecologists (Scheffer & Carpenter, 2003; McCann *et al.*, 2005). Food flexibility and omnivory are important features particularly pronounced in Neotropical freshwater fish species (Lowe-McConnell, 1999; González-Bergonzoni *et al.*, 2012). The food variety in the tropics can be associated with environmental conditions of the aquatic ecosystem. May be influenced directly by characteristics of land, vegetation, human activities in the drainage systems and the driving forces of dry and rainy period (Manna *et al.*, 2012; Xu *et al.*, 2012). Furthermore, the fish capacity to explore this broad food supply is directly connected with the biology of species (Abelha *et al.*, 2001).

Astyanax Baird & Girard, 1854 species are known to be highly flexible in their diets and reported as omnivorous species (Vilella *et al*., 2002; Dias *et al*., 2005; Manna *et al*., 2012). Feeding habits of several *Astyanax* species have been well studied in different Brazilian aquatic ecosystems such as in streams and rivers (Vilella *et al*., 2002; Loureiro-Crippa & Hahn, 2006; Borba *et al*., 2008; Vidotto-Magnoni & Carvalho, 2009; Manna *et al*., 2012; Moraes *et al*., 2013), floodplain (Esteves, 1996, Peretti & Andrian, 2004, 2008; Crippa *et al*., 2009) and coastal lagoons (Hartz *et al*., 1996; Aguiaro & Caramaschi, 1998). Besides feeding plasticity (Santos *et al.*, 2008), the proliferation of some species of *Astyanax*, especially *A.bimaculatus* and *A. parahybae*, in reservoirs has been associated with their reproductive strategy, including a long reproductive period, rapid maturation, prolific spawning, small eggs and high fecundity (Suzuki *et al*., 2005). *Astyanax* species have also a great ecological importance in the trophic web of fish community in reservoirs (Loureiro-Crippa & Hahn, 2006; Wolff *et al*., 2009) linking nutrients and carbon sources available in marginal areas to the limnetic food chain.

Many resources sustain fish fauna in tropical reservoirs and most of them originate in the aquatic environment (Araújo-Lima *et al*., 1995). However, morphometric features of the reservoir, such as perimeter and depth, retention time, characteristics of the area flooded and elapsed time from filling can influence the availability of the resources for fish. Recent studies have pointed to the importance of allochthonous sources for fish feeding mainly coming from marginal areas of dendritic reservoirs and with riparian forests (Araújo *et al*., 2005; Mazzoni & Rezende, 2003; Silva *et al*., 2014). Besides spatio-temporal variations in food availability strongly modulate foraging behavior (López-Bao *et al*., 2011) and seasonal variation in the quantity and also quality of the diet (Junk, 1980) may be a consequence of the hydrological regime of reservoirs (Abelha *et al*., 2001).

The colonization of macrophytes in many reservoirs may enhance aspects of invertivory in fish diet (Pelicice & Agostinho, 2006) expanding or concentrating the area of available resources for feeding. Aquatic macrophytes are important habitats for many groups of organisms as immature stages of Diptera, Ephemeroptera and Trichoptera (Carpenter & Lodge, 1986; Lalonde & Downing, 1992; Dibble *et al*., 1996; Agostinho *et al*., 2003; Casatti *et al.*, 2003) and many fish species are found in these habitats, benefiting from a diversity of food items as well as refuge from predation (Pelicice & Agostinho, 2006). Macrophytes have also been considered key components in aquatic environments, enhancing the spatial heterogeneity and increasing the number of niches (Margalef, 1983; Trivinho-Strixino & Strixino, 1993; Santos *et al*., 2008).

We employed stomach contents analysis to access the importance of habitat differences as spatial complexity for *Astyanax* feeding in two tropical reservoirs with different environmental features. This was investigated for *Astyanax* **aff.** *bimaculatus* Linnaeus, 1758 and *Astyanax parahybae* Eigenmann, 1908 (Characiformes: Characidae), which are sympatric species with frequent occurrence in both environments (Gomes *et al*., 2008; Uehara *et al*., 2015) and similar diets. Given the differences between these reservoirs, and based on aspects mentioned above we predicted that the environment where fishes inhabit will control the composition of the diet (niche width) influencing the trophic relation between the sympatric species (niche overlap) more than seasonality.

MATERIAL AND METHODS

Study area. This study was conducted in two reservoirs belonging to the complex of electrical power company Light SA (Piraí Municipality, Rio de Janeiro State, Brazil). The Ribeirão das Lajes Reservoir (Lajes Reservoir) (22°42'-22°50'S, 43°53'- 44°05'W) situated at 415-430 m above sea level, has a surface area of 30.7 to 47.8 km^2 and an average depth of 15 m and a maximum of 40 m and retention time of 300 days. The reservoir presents oligo-mesotrophic waters, used for the domestic water provision of around 1.1 million people. The high water quality of the Lajes Reservoir has been associated to the presence of a rain forest in most of its surroundings and low human influence. The dendritic shape of the lake and no abrupt fluctuations in water level impose an important ecotone between the aquatic and terrestrial areas, subject to direct exploitation by aquatic fauna.

The Santana Reservoir is located 361-363 m above sea level (between 22°31'50"S and 43°49'15"W). It was built in 1945, has a surface area of approximately 5.23 km^2, with an average depth of 3.3m and a maximum of 12 m and a retention time of one day. The reservoir is considered eutrophic and is characterized by a high degree of human impact, since its waters receives drainage from urban, industrial and agricultural activities. The surroundings are covered by pasture and the continued nutrient input has resulted in the proliferation of macrophytes throughout the lake.

The climate of the region where the reservoirs lie is classified as high-altitude tropical with average temperatures of 20.5° C ranging from 16.6° C in July to 23.9° C in February. The months with the highest rainfall are November, December and January and the months with the least rainfall are May, June and July. The Lajes Reservoir level is maintained artificially and the highest level is reached at the end of the rainy season (April) and the lowest at the beginning of this season (November). There is no influence of seasonality on the level of the Santana Reservoir, which is managed according to operational needs and daily variations of up to 1.5 meters can occur.

Sampling. Adult fish were collected at both reservoirs in dry (May 2005, June/July 2007) and rainy (March 2004, January 2008) seasons, by means of gill-nets with mesh sizes ranging from 1.5 to 4.0 cm. The samplings followed a previously established standardized effort in the two sites, considering the amount of nets, as well as the total hours of capture. Gill-nets were placed parallel to the shore or in closed meanders and capture time was 12 hours, from dusk to sunrise. Since fishes can modify their food habits during different life stages, we selected only adult individuals based on their standard length that ranges from 6.5 to 12.5 cm (*Astyanax* **aff.** *bimaculatus*) and 7.1 to 12.5 cm (*Astyanax parahybae*). The fish were weighed, measured (standard length), and killed by freezing immediately after collection. The fish stomach content was removed at the laboratory and fixed in 10% formalin. All voucher specimens were deposited in the Collection of the Museu Nacional (Universidade Federal do Rio de Janeiro - UFRJ), under the code MNRJREG20050418.

Data analysis. The stomach content analysis was performed according to methodology proposed by (Windell, 1971; Hyslop, 1980; Branco *et al*., 1997). The food items were grouped into categories [Algae, *Egeria* (aquatic macrophyte), Terrestrial Plant, Zooplankton, Ostracoda, Nematoda, Acarina, Aranae, Gastropoda, Aquatic Insect, Terrestrial Insect, Fish Scale, Organic Matter and Sand]. The taxonomic identification of food items was done according to appropriated literature and the insects were identified to family level. Based on the data of frequency of occurrence (% F) and volume percentage (V%), the Alimentary Importance Index - IAi was calculated (Kawakami & Vazzoller, 1980) - IAi = (%F x %V)/ å (%F x %V). To examine spatial patterns in fish diet, the volumes of the diet items were ordered using non-metric multidimensional scaling (NMDS) with a Bray-Curtis dissimilarity index. A parametric one-way ANOVA was performed to test diet differences, also a similarity percentage analysis (SIMPER) was used to examine the contribution of each food item to the average dissimilarity between species in each reservoir. All the analyses were performed using the program R (R Core Team, 2013).

Niche analysis. The niche width was calculated using the MacArthur-Levins measure (MacArthur & Levins, 1967) considering $B=1/\sum(Pij)^2$ where B= measure of niche breadth, and Pij = proportion of category item "j" in the diet. Breadth niche values were set at the following levels: high (>0.6), intermediate (0.4-0.6) or low (<0.4), according to Novakowski *et al*. (2008). Feeding overlap was measured for each reservoir using the Pianka Index (Pianka, 1974) according to the formula $\alpha = \sum Pij*Pik/\sqrt{\sum Pij^2*\sum Pik^2}$ where α=Pianka measure of niche overlap from 0 to 1, Pij, Pik = proportion of item "I" used by species "j" and "k".

RESULTS

We analyzed the stomach contents of sixty-five specimens of *Astyanax* **aff.** *bimaculatus* and seventy of *A. parahybae*. The food items were gathered in 14 food items categories shown in Tab. I. Insects and organic matter were the most important category items for both species. Some changes at the importance of some categories were found between rainy and dry seasons

The ordering produced by NMDS analysis indicated separation in the diet of these species between reservoirs (Stress= 8.28%), and a slight influence of seasonality (Fig.1). This points out a higher importance of environment conditions in the composition of the diet of fishes than the seasonality. Additionally, analysis of variance revealed no significant differences in food items between the species studied (Anova one-way F(1, 133)=1.9569, p=0.164) and between rainy and dry seasons (Anova one-way F=(1,132)=0.061; p= 0.805). However, we found a significative difference in the volume of food items between the reservoirs (one-way Anova F(1, 132)=4.4446; p= 0.037).

The SIMPER analysis showed which categories items were the most important in the differentiation of diets. On Lajes Reservoir, organic matter and insects, mainly terrestrial insect had greater importance for *Astyanax* **aff.** *bimaculatus* and aquatic insect for *A. parahybae* diet. On Santana Reservoir, organic matter and terrestrial insect were important itens for both species. The secundary items consumed by the fish were responsible for diet differences in this reservoir. *Astyanax parahybae* fed on algae and on aquatic and terrestrial vegetation probably near macrophytes patches. *Astyanax* **aff.** *bimaculatus* preyed on invertebrates associated to terrestrial vegetation, *e.g*., gastropods (Tab. II) showing different strategies on food acquision.

We also analyzed the niche width for both species that was considered low, between 0.17 and 0.35, for possible values between 0 and 1 (Fig. 2). The highest value of niche width was found for *Astyanax* **aff.** *bimaculatus* in Santana Reservoir and the lowest for the same species in Lajes Reservoir. The niche overlap for both species was higher for Lajes Reservoir (Fig. 2).

DISCUSSION

Also classified as opportunistic species (Dias *et al*., 2005), *Astyanax* display a great ability to change their prey according to environmental variations. This study confirmed the insectivorous-omnivorous habit and feeding plasticity for both *Astyanax* species, as indicated by several other authors (e.g. Nomura, 1975; Arcifa *et al*., 1991; Uieda *et al*., 1997; Bennemann *et al*., 2006; Abilhoa, 2007) and also highlighted the insetivorous feeding habit, likewise displayed by other *Astyanax* species specially in streams and rivers (see Vilella *et al*., 2002 for *A. eigenmanniorum*; Vidotto-Magnoni & Carvalho, 2009 for *A. altiparanae* and Ferreira *et al*., 2012 for *A. paranae*). At this context, diet dissimilarities between the *Astyanax* species were revealed mainly due to the source of itens consumed. Feeding strategies may differ among environments and omnivory may evolve as a response to high environmental heterogeneity (Chubaty *et al*., 2014) or food availability.

Given the habitat differences between these reservoirs, different spatial complexity and presence of macrophyte patches, we expected dissimilar diet patterns. Our results showed that *Astyanax* **aff.** *bimaculatus* diet consisted of insects, terrestrial and aquatic insects, as well as the low consumption of zooplankton, which suggest feeding habit on the water column surface and near marginal area in both reservoirs. Meanwhile, aquatic insects and zooplankton had an inexpressive importance at Santana Reservoir diet, but algae had high significance. On the other hand, *A. parahybae* exhibited different preferences in each reservoir, aquatic

Tab. I. Food items found in the diet of *Astyanax* **aff.** *bimaculatus* Linnaeus, 1758 and *A. parahybae* Eigenmann, 1908 in the Lajes (Lajes) and Santana reservoirs, state of Rio de Janeiro, Brazil in rainy and dry seasons (N, number of individuals analysed; IAi, Alimentary Importance Index; SL, range of standard length).

	LAJES		SANTANA	
Astyanax **aff.** *bimaculatus*	Rainy (N=20) SL 9.5-12.5cm	Dry (N=20) SL 7.5-9.9cm	Rainy (N=8) SL 6.9-10.5cm	Dry (N=17) SL 6.5-11.5cm
	IAi	IAi	IAi	IAi
Algae	0.02	0.00	232.49	0.00
Egeria sp.	0.00	0.00	0.00	24.92
Terrestrial plant	0.35	0.03	9.77	19.26
Zooplankton	16.58	3.36	0.31	0.00
Ostracoda	0.00	0.05	0.00	0.00
Nematoda	0.15	0.03	2.60	0.00
Acarina	0.00	0.01	0.00	0.00
Araneae	0.00	0.28	0.00	0.00
Gastropoda	0.00	0.26	260.82	0.09
Aquatic insect	510.06	116.81	0.00	6.18
Terrestrial insect	1223.08	629.55	1489.97	1038.88
Fish scale	0.35	15.97	0.00	0.00
Organic matter	849.16	1985.36	245.61	2285.68
Sand	0.00	0.00	0.00	0.23
Astyanax parahybae	Rainy (N=6) SL 10.5-12cm	Dry (N=25) SL 7.5-12.5cm	Rainy (N=14) SL 7.1-9.0cm	Dry (N=25) SL 7.5-10.5cm
	IAi	IAi	IAi	IAi
Algae	0.00	0.00	729.77	111.09
Egeria sp.	0.00	0.00	351.30	16.43
Terrestrial plant	0.00	0.29	0.00	192.10
Zooplankton	0.00	23.17	0.00	0.08
Ostracoda	0.00	0.01	0.02	0.00
Nematoda	0.00	0.68	0.13	0.00
Acarina	0.00	7.48	0.01	0.00
Araneae	0.41	0.14	0.00	0.00
Aquatic insect	2498.53	1717.18	36.66	11.07
Terrestrial insect	713.07	0.00	300.49	944.44
Fish scale	0.00	0.30	0.39	0.06
Organic matter	214.68	1710.78	298.01	1032.37

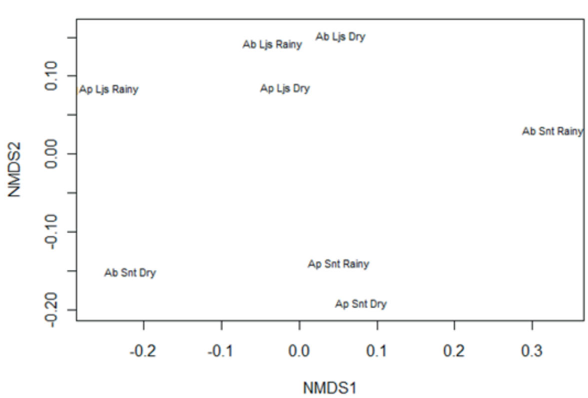

Fig. 1. NMDS plot showing relation of food item abundance found in the diet of *Astyanax* **aff.** *bimaculatus* Linnaeus, 1758 and *A. parahybae* Eigenmann, 1908 in Lajes and Santana reservoirs, state of rio de Janeiro, Brazil (Ap, *Astyanax parahybae* ; Ab, *Astyanax* **aff.** *bimaculatus*; Ljs, Lajes; Snt, Santana).

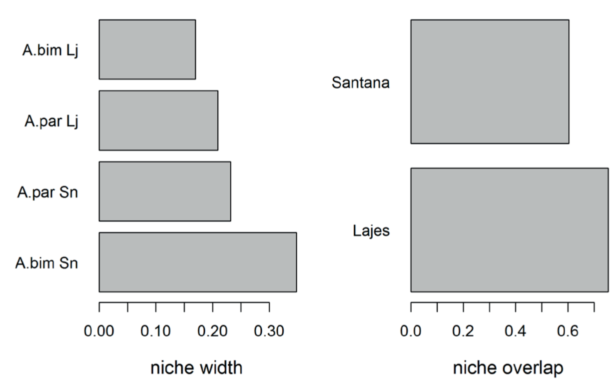

Fig. 2. Niche width and overlap of the two species in the two reservoirs, state of Rio de Janeiro, Brazil (A.bim, *Astyanax* **aff.** *Bimaculatus*; A.par, *Astyanax parahybae*; Lj, Lajes Reservoir; Sn, Santana Reservoir).

insects at Lajes Reservoir and terrestrial insects at Santana Reservoir. Besides, *A. parahybae* exhibited high consume of algae and macrophytes (*Egeria*) in this last reservoir. As exposed by others studies, environmental conditions showed great importance in the composition of the diet of fishes (Arcifa & Meschiatti, 1993; Callisto *et al*., 2002; Luz-Agostinho *et al*., 2006; Hahn & Fugi, 2007).

The diet of *Astyanax* **aff.** *bimaculatus* in the environment with less impacted surrounding vegetation (Lajes Reservoir) showed that the individuals consumed a large proportion of allochtonous items, especially insects. This high consumption of allochthonous items must be associated with preserved surrounding vegetation, essential for the input of several items in the aquatic environment

Tab. II. SIMPER analyses of item category contributing to differences in *Astyanax* **aff.** *bimaculatus* Linnaeus, 1758 and *A. parahybae* Eigenmann, 1908 diet structure in each reservoir, State of Rio de Janeiro, Brazil.

Reservoir	Item	Mean volume (mm³)		Cumulative contribution (%)
		Astyanax **aff.** *bimaculatus*	*Astyanax parahybae*	
Lajes				
	Organic matter	135.94	95.10	34
	Aquatic insect	87.97	168.00	67
	Terrestrial insect	96.72	24.19	95
Santana				
	Organic matter	151.72	179.43	33
	Terrestrial insect	132.14	150.76	60
	Algae	13.33	96.21	74
	Egeria sp.	7.80	45.79	86
	Terrestrial plant	11.84	42.17	93
	Gastropoda	25.00	0.00	98

by rain, wind or simply falling into the water. *Astyanax parahybae* diet, also at Lajes reservoir, is more focused on autochthonous items such as aquatic insects. Besides the contribution of allochthonous items, riparian vegetation also provides the permanence of aquatic insect larvae that feed, directly or indirectly, on allochthonous organic material imported from riparian vegetation (Castro, 1999; Abilhoa, 2007). This may emphasize the importance of ecotone land-water zone for fish forraging behavior (Dias *et al*., 2005; Barreto & Aranha, 2006; Casatti, 2010).

Dropping the riparian vegetation, as found in Santana Reservoir, would lead to a reduction of allochthonous resources. However, *Astyanax* **aff.** *bimaculatus* and *A. parahybae* diets revealed ingestion of large amounts of allochthonous items, such as terrestrial insects in this reservoir. Besides, we found a great proportion of algae, macrophytes and gastropods in fish diets in such reservoir. The presence of macrophytes patches apparently enhances the diversity and richness of animal groups at littoral zone and interfering with the dynamics of communities at the lake ecosystem as a whole (Margalef, 1983; Trivinho-Strixino & Strixino, 1993; Duncan & Kubecka, 1995; Peiró & Alves, 2006; Vidotto-Magnoni & Carvalho, 2009). For example, Ephemeroptera, the order of insects most consumed by *A. parahybae* in this reservoir, according to Casatti *et al.* (2003) can be associated to aquatic macrophytes. Thus, we can infer that the macrophytes pacthes probably influences the items used by *Astyanax* species at Santana Reservoir, even as the operational actions with daily level variations (Gomes *et al*., 2008) that enhance the input of allochtonous items at fishes diet (Abujanra *et al*., 2009).

Our results revelead similarities between *Astyanax* species food resources. The niche overlap can be considered high for both environments, which would be associated with the high abundance of the same resources. Despite the availability of resources was not measured in the present study, we assume that the preyed items were abundant based in high dominance by few resources (Novakowski *et al*., 2008). Other factors such as the combination of different microhabitats, periods of activity and strategies of foraging can allow coexistence when species present high niche overlap. This resource sharing represent a situation commonly found in tropical streams (Aranha *et al*., 1998; Casatti, 2002). A previous study at Lajes Reservoir also revealed high trophic niche overlap of *Astyanax* species and suggested ecomorphological differences as a way to probably decrease competition (Silva-Camacho *et al*., 2014).

Although the two species of *Astyanax* had have a high niche overlap, *A.* **aff.** *bimaculatus* showed a narrow niche breath at Lajes Reservoir. These findings may indicate that *A.* **aff.** *bimaculatus* are better adapted to lentic environments (Silva-Camacho *et al*., 2014). Also, this can show some strategy to avoid diret competition between these species at Lajes Reservoir. On Santana Reservoir, an extremely variable flood system under more antropic influence, they had to explore different habitat and feeding resources resulting in a wider niche breath. Besides the similar basic diet for these two species and high niche overlap, they drew a slight different diet for both reservoirs. These findings corroborate the importance of trophic plasticity in *Astyanax* species leading to a reduced competition in these environments (Araújo-Lima *et al*., 1995).

In conclusion, this study showed that these sympatric fishes despite presenting a similar diet can coexist with a low feeding competition over the reservoirs studied. Whether competition for food occurs, it is minimized by trophic plasticity and spatial segregation. Habitat heterogeneity plays an important role on food resource consumed by these *Astyanax* species. However, further studies are needed to allow the detection of possible changes over time, mainly to explore temporal effects of anthropogenic habitat modifications, as frequently found at reservoir environments.

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