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ECOSYSTEMS

Spatial variation in the trophic category of fish assemblages in longitudinal stretches in a Neotropical reservoir

THIAGO D. GARCIA, BARBARA A. QUIRINO, LUCAS R. JARDULI,
EDMIR D. CARVALHO & ANA PAULA VIDOTTO-MAGNONI

Abstract: The spatial gradients created after the installation of large reservoirs produce a great diversity of biotopes, which affects the distribution and structuring of aquatic communities, mainly fish. Thus, we hypothesized that the fishes living in the lotic stretch (river zone, closest to the natural environment) of the reservoir would have lower overlap and higher niche breadth than fishes living in the lentic stretch. Samples were collected in six sections (lentic and lotic) of the Chavantes Reservoir, middle Paranapanema River. A total of 1478 individuals distributed in 13 species were sampled in both stretches. Many resources were acquired by species, and we observed that nine species present significant differences when comparing the two stretches. Furthermore, only *Schizodon nasutus* and *Steindachnerina insculpta* showed interindividual variability. Despite the large number of food items exploited by the species, the vast majority showed preferential consumption for few food resources, evidenced by the low values of trophic niche breadth in both stretches. Furthermore, it was observed a trend towards specialization of all trophic categories indicated that the results found here, combined with a low degree of niche breadth of the species, offer a high trophic food variation among the fish species in the reservoir.

Key words: Chavantes Reservoir, dam, guilds, Paranapanema River, trophic ecology.

INTRODUCTION

In recent decades, the global electricity demand has favored the construction of many artificial reservoirs (Agostinho et al. 2007, Winemiller et al. 2016). More than half of the world's main rivers' natural flow has been interrupted by the construction of dams, while its free-flowing tributaries have been rapidly decreasing (Nilsson et al. 2005, Finer & Jenkins 2012, Zarfl et al. 2014, Winemiller et al. 2016).

Large reservoirs usually present spatial gradients in the fish assemblage (Baumgartner et al. 2018) and different strata are created along their main axes, such as transverse, vertical, and longitudinal strata (Agostinho et al. 2007, Okada et al. 2005, Affonso et al. 2016). These zoned aquatic landscapes produce a great diversity of biotopes, which affects the distribution and structuring of aquatic communities of fish species (Agostinho et al. 2007, Barletta et al. 2010, Welcomme 2011, Agostinho et al. 2015a). The longitudinal strata can be divided into a lentic stretch closer to the dam and a lotic stretch further away from the dam and more similar to the natural environment. These strata have distinct abiotic characteristics, varying in terms of flow velocity, sedimentation rate, nutrient concentration, and water transparency, which are influenced by seasonality and the functioning of the dam itself (Thornton et al. 1990, Vašek et al. 2004, Agostinho et al. 2007).

In dammed environments, a longitudinal pattern is expected in the richness and diversity of fish species, which decrease in the direction of the fluvial zone towards the lacustrine zone (Thornton et al. 1990, Okada et al. 2005, Baumgartner et al. 2018). Then, the characteristics of these environments differ from each other, for example, the lacustrine zone tends to present greater water transparency and lower nutrient concentration when compared to the fluvial zone (Agostinho et al. 2008), which mainly interferes with the water supply and food resources for aquatic biota, leading to variations in fish diets (Novakowski et al. 2007, Dias et al. 2020b). In disturbed aquatic environments, the entry of allochthonous resources tends to increase the availability of some specific resources and reduce other items (Agostinho et al. 2007, Delariva et al. 2013, Gubiani et al. 2011, Lima et al. 2018, Dias et al. 2020a, b, Oliveira et al. 2020). In this way, species that have high trophic plasticity tend to be favored because they are more tolerant to changes in the environment and they change their preference for a particular resource according to its supply (Fernando & Holčík 1991, Hahn & Fugi 2007).

Studies on food resource partition and niche overlap are essential to understand the mechanisms that lead to fish communities structuring as well as species coexistence (Schoener 1974, Gerking 1994), especially in disturbed environments such as reservoirs (Oliveira et al. 2020). Specifically, the niche breadth assesses the tendency of a given group of species to specialize in a single or more resources (Segurado et al. 2011), while niche overlap can determine the degree of segregation between species but can also provide a descriptive measure of the set organization (Winemiller & Pianka 1990). Thus, low niche overlap values indicate that species are more segregated in the environment (Corrêa et al. 2011). On the other hand, different ecological niches can minimize overlapping effects (Casatti 2002, Brasil-Sousa et al. 2009, Cetra et al. 2011).

This study aimed to assess whether diet composition in the fish assemblage tends to vary as a function of the spatial scale in the Chavantes Reservoir. Considering that the fish diet is strongly influenced by spatio-temporal factors, including the longitudinal zone formed from the damming, the diet of the fish assemblage can change between lotic and lentic stretches. The hypothesis is that the lotic stretch (fluvial zone, closer to the natural environment) of the Chavantes Reservoir would have low overlap and high niche breadth. In addition, we predicted that omnivores have high food plasticity, adjusting their diet according to the availability of food resources by the environment (Gerking 1994), piscivores benefit from the high availability of fish species in lentic and using other resources in smaller proportions as complementary resources (Luz-Agostinho et al. 2008, Pereira et al. 2016), while specialized feeders, characterized by some notable morphological adaptations (Gerking 1994) do not vary their diet, as their preferred resources are rarely limited in aquatic environments (Gido & Franssen 2007, Agostinho et al. 2015b).

MATERIALS AND METHODS

Study area

The Chavantes Reservoir (23°22'S and 49°36'W) is located between the states of São Paulo and Paraná, on the middle Paranapanema River (Nogueira et al. 2006). This reservoir is a fifth of a cascade of 11 reservoirs on the Paranapanema River, in operation since 1971. It has a drainage area of 106,500 km² and an altitude of 474 m, with a maximum depth of 80 meters near the dam (Nogueira et al. 2006, ANA 2016).

Fish sampling

The collections were carried out quarterly between October/2005 and June/2006 in six locations along the Chavantes Reservoir (Figure 1, Table I), under the IBAMA/ ICMBio license: 15549-1. Gillnets (3 to 18 cm mesh between adjacent nodes), installed at dusk and exposed for 24 hours, collected the fishes. During this period, two inspections were made: at 23:00h and 6:00h.

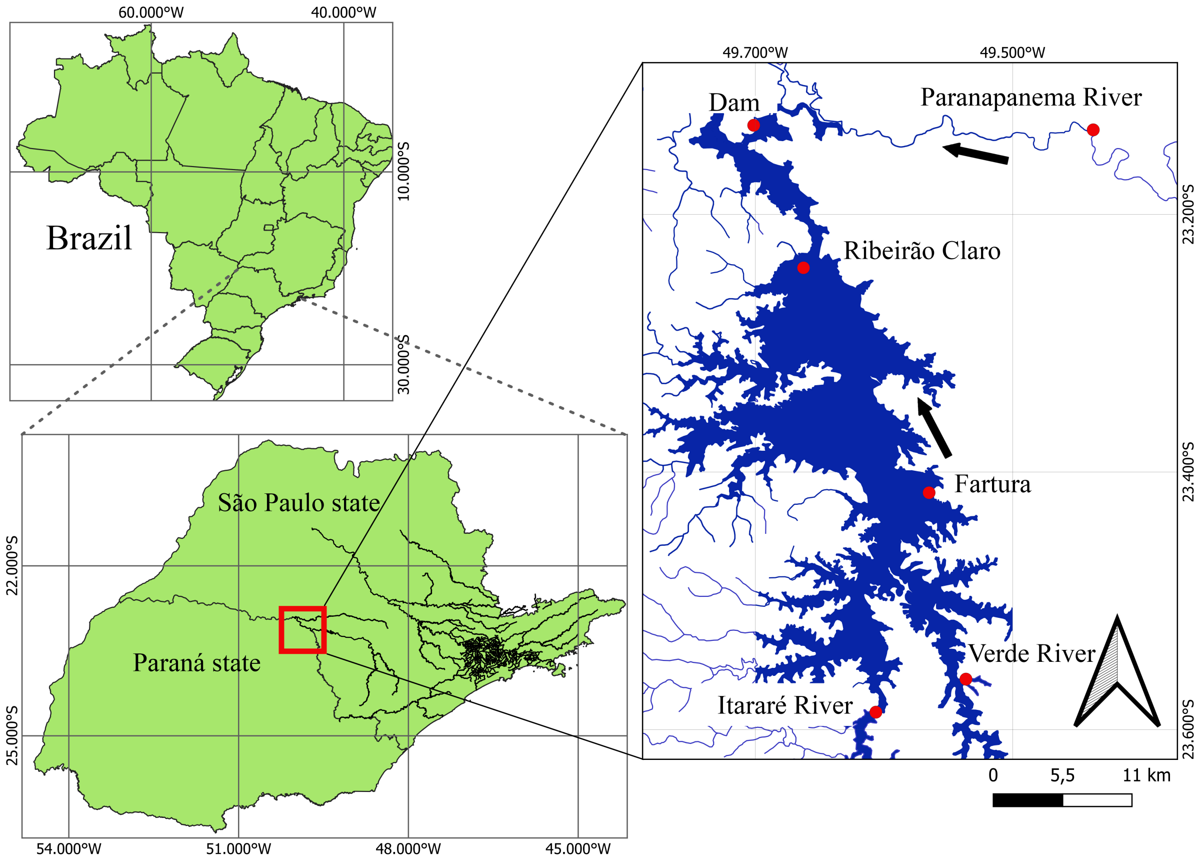

Figure 1. Map of the state of São Paulo, indicating the location of the Chavantes Reservoir, middle Paranapanema river basin, in the lentic stretch: Dam, Ribeirão Claro and Fartura, and lotic: Parapanema River, Itararé and Verde River. Black arrow = river flow.

Table I. **Description of sampled sites present in the Chavantes Reservoir, middle Paranapanema River basin.**

Site	Coordinates	Longitudinal zone	Environment description
Itararé River	23°35’11.2”S 49°36’22.9”W	lotic	The average width of 40 m and the average depth of 3.5 m. The riverbank is composed of areas of pastures and agricultural crops.
Verde River	23°33’38.9”S 49°32’10.9”W	lotic	The average width of 30 m and the average depth of 1.5 m. The riverbank is composed of areas of pastures and agricultural crops
Paranapanema River	23°08’03.3”S 49°26’14.6”W	lotic	The average width of 50 m is located upstream of the reservoir. The riverbank is composed of areas of pastures and agricultural crops.
Fartura	23°24’57.7”S 49°33’54.1”W	lentic	An approximately 4,000 m of area, it receives the influence of the Itararé River and strong winds, which favors the formation of waves that cause undermining and erosion in several points of the exposed banks. The riverbank comprises areas of pastures and agricultural crops and civil constructions.
Barragem	23°07’50.5”S 49°42’04.8”W	lentic	Depth between 50 and 80 m. This section is closer to the dam. The riverbank is dominated by The river bank is dominated by native semideciduous mesophyll forest.
Ribeirão Claro	23°14’28.9”S 49°39’45.5”W	lentic	Depth between 50 and 80 m. This section is closer to the dam. The riverbank comprises areas of pastures and agricultural crops and civil constructions.

Captured specimens were anesthetized by immersion in an aqueous solution with eugenol, and confirmation of death was made by checking respiratory movement. Then, the fish were fixed in 10% formalin, labeled, and more recently identified according to Ota et al. (2018). Vouchers of all species were deposited in the collection of the Laboratório de Biologia e Genética de Peixes (LBP), Universidade Estadual Paulista, Botucatu, state of São Paulo, while species of the Loricariidae family were deposited in the fish collection of Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUPELIA), Universidade Estadual from Maringá, state of Paraná, Brazil.

Diet analysis

In the laboratory, the fish had their stomachs removed, and the stomach contents were analyzed under a stereoscopic microscope and identified to the lowest possible taxonomic level, based on Hamada et al. (2014). The volume (V) of each item was obtained in two ways: i) by measuring the displacement of the water column in graduated cylinders when the volume was greater than 0.1 mL; or ii) utilizing a millimeter plate (Hellawell & Abell 1971). The volume was given in mm^3 and later transformed into milliliters when the volume was less than 0.1 ml (Hellawell & Abell 1971), the food index (IAi %) was calculated (Kawakami & Vazzoler 1980) to characterize the diet, which combines the total volume (%) and the frequency of occurrence (%) of each item (Hyslop 1980), given by the formula:

$$IAi\% = \frac{Fi * Vi}{\sum_{i=1}^{L} Fi * Vi}$$

where: Fi is the frequency of occurrence of item i (%); Vi is the relative volume of item i (%); and L is the number of items.

Foods were grouped into broader trophic categories, named: Insects (Diptera, Chironomidae, Ceratopogonidae, Chaoboridae, Lepidoptera, Trichoptera, Coleoptera, Hymenoptera, Ephemeroptera, Odonata, Dermaptera, Blattodea, Thysanoptera, Orthoptera, Neuroptera, Isoptera, Psocoptera, Plecoptera and insect eggs); Other invertebrates (Cladocera, Copepoda, Ostracoda, Tecameba, Rotifera, Decapoda, Gastropoda, Bivalvia, Mollusk, Arachnida, Aranae and Hidrudinea); Fish (fish, egg and fish scale); Plants (Superior plants, seeds and macrophytes), Algae and Others (detritus).

Trophic guilds were identified based on the volume of broad food categories. Among the various criteria adopted to classify trophic guilds (for example, De Mérona et al. 2001, Corrêa et al. 2011, Delariva et al. 2013), we determined the guilds considering an intermediate value (60% of the diet composed of a certain food category) to what is referred to in the literature. Thus, we classified them as: Herbivores - species that feed mainly on superior plants, such as leaves and seeds; Invertivores - species that explore the riverbed, selecting benthic organisms, such as: microcrustaceans, small mollusks and arachnids; Insectivores - species that predominantly ingest aquatic and terrestrial insects at different stages of development; Omnivores - species that consume two or more food categories in similar proportions, with no predominance (≥ 60%) of any of them; Piscivores - species that mainly consume fish, fish eggs and scales; Algivores – species that consume algae; and Detritivores - species that consume large amounts of detritus.

Data analysis

A permutational analysis of variance (PERMANOVA, Anderson et al. 2008) was used to verify the differences in the species' diet between the stretch (lentic and lotic) of the Chavantes Reservoir, based on a Bray-Curtis volume data similarity matrix, log-transformed (x + 1). PERMANOVA was applied to each species separately, which was common in the reservoir compartments. The pseudo-F statistic resulting from this analysis was tested by the Monte Carlo method using 999 randomizations.

Possible differences in the species' niche breadth between the different compartments of the reservoir were determined using a permutational analysis of multivariate dispersions (PERMDISP; Anderson 2004). This analysis indicates the variability of the diet among individuals of the same species in the sampled location, reflecting the niche breadth of the population (Correa & Winemiller 2014). If a population has a greater dispersion of individuals, this means that this population has a greater niche breadth. The probability values used to determine significant differences in the species' diet dispersion between compartments were calculated by residual permutation (999 permutations).

A different approach to address the trophic niche breadth variation was calculating the Levin index (Hurlbert 1978):

$$Bi = [(\sum_{i=1}^{n} {}_{j}P_{ij}^{2})^{-1} - 1](n - 1)^{-1}$$

where Bi is the standardized index of niche breadth, Pij is the proportion of food resource j in the species' diet, and y is the number of food resources. This index assumes that uniformity can estimate the diet breadth in the distribution of items among different food resources (Hurlbert 1978, Fugi et al. 2008). The value of Bi ranges from 0 (when the species consumed mainly one food resource) to 1 (when the species consumed all resources in similar proportions). Results were arbitrarily considered high when Bi > 0.6, moderate when B values were between 0.4 and 0.6, and low when Bi < 0.4 (Novakowski et al. 2008). Furthermore, to test differences between the reservoir stretches, we applied analysis of variance (ANOVA), considering the breadth values of each species as the response variable.

The trophic niche overlap between the species was calculated using the Pianka index:

$$O_{jk} = \left(\sum_{i=1}^{n} \left| P_{ij} - P_{ik} \right| \right) \ / \sum_{i=1}^{n} P_{ij}^{2} \ \cdot \ \sum_{i=1}^{n} Pic^{2}{}_{-}$$

where O $_{jk}$ = measure of Pianka food overlap between species *j* and species *k*; P $_{ij}$ = proportion of food item *i* in the total of items used by species *j*; P $_{ik}$ = proportion of food item *i* in total items used by species *k*, n = total number of food items. Interspecific overlap results were arbitrarily considered high (> 0.6), moderate (0.4 - 0.6), or low (<0.4) (Novakowski et al. 2008). We also tested differences between the reservoir compartments utilizing an ANOVA, considering the values of the overlap indices between each pair of species as the response variable.

It is noteworthy that to perform the analysis of the diet composition of the species separately, niche breadth and niche overlap, the food items were not grouped into broad food categories, which were used only for the classification of guilds and for the analysis of general community. All statistical analyzes were performed using R software (R Core Team 2019), using the "vegan" package (Oksanen et al. 2018), "spaa" (Zhang 2016), "devtools" (Wickham et al. 2021), and the plots were built using the "ggplot2" package (Wickham 2016).

RESULTS

A total of 1,478 individuals distributed in 13 species sampled in both the lentic and lotic stretches had their diet analyzed, namely: *Acestrorhynchus lacustris* (Lütken 1875), *Apareiodon affinis* (Steindachner 1879), *Astyanax lacustris* (Lütken 1875), *Galeocharax gulo* (Cope 1870), *Gymnotus carapo Linnaeus 1758*, *Hoplias malabaricus* (Bloch 1794), *Iheringichthys labrosus* (Lütken 1874), *Leporinus amblyrhynchus* Garavello & Britski 1987, *Pimelodus maculatus* Lacepède 1803, *Plagioscion squamosissimus* (Heckel 1840), *Schizodon nasutus* Kner 1858, *Serrasalmus maculatus* Kner 1858 and *Steindachnerina insculpta* (Fernández-Yépez 1948).

The observed species consumed a total of 46 different food resources (Table II). In general, the most frequent food categories in the lentic stretch were superior plants (20.86%), detritus (19.28%) and aquatic insects (19.06%). While in the lotic stretch, detritus (22.45%), superior plants (20.80%) and other invertebrates (16.70%) were consumed more frequently (Figure 2a). Fish and superior plants were the most consumed items in both stretches regarding the volume ingested (Figure 2b).

Table II. **Food resources used by the ichthyofauna (IAi %) in the lentic and lotic stretches of the Chavantes Reservoir, middle Paranapanema river basin * = IAi % < 001.**

Resources	**lentic**													**Lotic**												
	A.lac	*A.aff*	*Ast. lac*	*G. gul*	*G. car*	*H. mal*	*I. lab*	*L. amb*	*P. mac*	*P. squ*	*S. nas*	*S. mac*	*S. ins*	*A.lac*	*A.aff*	*Ast. lac*	*G. gul*	*G. car*	*H. mal*	*I. lab*	*L. amb*	*P. mac*	*P. squ*	*S. nas*	*S. mac*	*S. ins*
Insect																										
Diptera (A)	-	-	0.66	-	-	-	0.21	0.04	0.01	*	-	-	-	-	-	0.01	-	0.02	-	*	0.1	*	0.01	-	-	-
Diptera (T)	-	-	0.14	-	-	-	64.47	-	*	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
Chironomidae (A)	*	0.88	0.81	0.01	12.55	*	0.01	17.08	14.55	0.01	*	*	*	*	0.7	1.71	-	11.67	0.02	53.16	18.98	19.83	*	*	*	*
Ceratopogonidae (A)	-	-	*	-	-	-	-	-	0.03	-	-	-	-	-	-	0.01	-	0.01	-	0.01	-	0.01	-	-	-	-
Chaoboridae (A)	-	-	0.86	-	-	-	-	-	0.05	*	-	0.01	-	-	-	0.02	-	*	-	*	-	-	0.01	-	-	-
Lepdoptera (A)	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	*	-	0.05	-	*	-	0.01	-	-	-	-
Lepidoptera (T)	-	-	0.54	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-	-	-	*	-	-	-	-
Trichoptera (A)	-	*	*	-	-	-	0.14	8.84	3.38	*	-	-	-	-	*	0.01	-	0.5	-	1.23	61.02	0.23	*	-	*	-
Trichoptera (T)	-	-	*	-	-	-	-	-	*	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-
Coleoptera (A)	-	-	*	-	0.01	-	-	-	0.01	-	-	-	-	-	-	0.06	-	0.31	-	-	-	0.1	-	-	-	-
Coleoptera (T)	-	-	44.65	-	-	-	-	-	9.72	-	-	0.05	-	-	-	5.02	-	0.02	-	-	-	0.03	-	-	-	-
Hymenoptera (T)	-	-	23.8	-	-	-	-	-	0.02	-	-	-	-	-	-	19.56	-	-	-	-	-	*	-	-	-	-
Hemiptera (A)	-	-	*	-	-	-	-	0.04	0.01	-	-	-	-	-	-	0.4	-	0.03	0.4	-	-	0.04	0.04	-	-	-
Hemiptera (T)	-	-	1.55	-	-	-	-	-	0.05	-	-	-	-	-	-	0.72	-	*	-	-	-	*	-	-	-	-
Ephemeroptera (A)	-	0.01	2.68	-	45.54	-	0.81	23.29	1.16	0.77	*	0.24	-	*	0.57	2.48	-	2.75	*	0.47	1.9	0.31	-	-	0.03	-
Ephemeroptera (T)	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odonata (A)	-	-	0.01	-	-	-	-	-	3.15	1.79	-	*	-	-	-	0.03	0.34	3.04	0.3	0.95	-	2.5	0.12	-	0.01	-
Dermaptera (T)	-	-	0.22	-	-	-	-	-	*	-	-	-	-	-	-	0.06	-	-	-	-	-	-	-	-	-	-
Bllataria (T)	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thysanoptera (T)	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
Orthoptera (T)	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.11	-	-	-	-	-	-	-	-	-	-
Neuroptera (T)	-	-	*	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isoptera (T)	-	-	1.05	-	-	-	-	-	-	-	-	-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-
Psocoptera (T)	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	*	0.32	-	-	-	-	-	-	-	-	-
Plecoptera (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Insect eggs	*	-	*	-	-	-	-	-	*	-	-	-	*	*	-	-	-	-	-	*	-	*	-	-	-	-
Other invertebrates																										
Cladocera	-	0.08	0.4	-	-	-	0.1	0.04	0.01	-	-	-	*	-	0.54	3.09	-	*	*	-	-	0.19	-	*	*	*
Copepoda	*	*	0.01	-	-	*	-	-	*	-	-	-	-	-	*	0.1	-	-	*	-	-	0.01	-	*	-	-
Ostracoda	-	*	-	-	-	-	3.24	0.09	0.46	-	-	-	*	-	*	0.04	-	*	-	2.18	0.07	0.04	-	-	-	*
Tecameba	-	-	-	-	-	-	*	-	-	-	-	-	-	-	*	0.04	-	-	-	0.02	0.02	*	-	-	-	*
Rotifera	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*
Decapoda	0.14	-	0.54	16.27	-	3.94	0.01	-	0.01	2.88	-	*	-	-	-	-	-	0.01	-	-	-	-	24.16	-	-	-
Gastropoda	-	*	2.18	-	5.2	-	0.01	9.92	5.79	*	*	*	*	-	-	0.57	-	73.7	-	*	0.26	43.66	2.99	-	-	-
Bivalvia	-	-	*	-	0.29	-	4	4.09	5.5	-	-	-	-	-	-	*	-	0.08	-	17.66	0.49	6.1	-	-	-	*
Mollusk	-	-	*	-	-	-	-	20.1	-	-	-	*	-	-	-	0.01	-	-	-	-	-	-	-	-	0.01	-
Arachnida	*	*	*	-	-	-	*	0.32	0.04	-	*	-	*	-	-	0.04	-	*	-	*	0.01	0.01	-	-	-	-
Araneae	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-
Hirudinea	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Resources	**lentic**													**Lotic**												
	A.lac	*A.aff*	*Ast. lac*	*G. gul*	*G. car*	*H. mal*	*I. lab*	*L. amb*	*P. mac*	*P. squ*	*S. nas*	*S. mac*	*S. ins*	*A.lac*	*A.aff*	*Ast. lac*	*G. gul*	*G. car*	*H. mal*	*I. lab*	*L. amb*	*P. mac*	*P. squ*	*S. nas*	*S. mac*	*S. ins*
Fish	96.12	-	0.01	83.72	-	96.05	0.02	-	1.34	94.31	*	99.33	-	84.94	-	-	99.34	-	99.27	*	-	0.02	72.64	*	94.96	-
Fish eggs	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	0.13	-	-	-	0.01	-	-	-	-	-	-
Fish scale	-	-	0.01	-	-	-	-	-	0.2	*	-	0.01	-	-	-	*	-	-	-	-	-	0.08	-	-	0.21	-
Plants																										
Superior plants	0.21	13.47	3.21	-	33.81	-	0.66	8.09	23.32	0.24	58.06	-	1.98	0.03	19.22	7.77	-	4.33	-	3.45	0.3	19.71	0.03	57.1	4.77	1.83
Seed	-	*	16.16	-	-	-	-	-	11.26	-	*	-	-	-	-	47.11	-	*	-	0.01	*	0.85	-	*	-	-
Macrophyte	-	-	-	-	-	-	-	-	-	-	0.28	-	-	-	-	-	-	-	-	-	-	-	-	9.29	-	-
Algae																										
Algae	0.44	24.47	0.32	-	-	-	*	-	*	*	13.27	*	1.07	1.91	14.94	2.57	-	2.45	-	*	*	-	-	32.85	-	1.46
Others																										
Detritus	3.09	61.08	0.09	-	2.6	*	26.32	8.09	19.92	*	28.39	0.05	96.95	13.13	65.03	0.58	-	1.04	0.01	20.79	16.85	6.29	-	0.75	0.01	96.7

Codes are: *A.lac = Acestrorhynchus lacustris, A.aff = Apareiodon affinis, Ast. lac = Astyanax lacustris, G. gul = Galeocharax gulo, G. car = Gymnotus carapo, H. mal = Hoplias malabaricus, I. lab = Iheringichthys labrosus, L. amb = Leporinus amblyrhynchus, P. mac = Pimelodus maculatus, P. squ = Plagioscion squamosissimus, S. nas = Schizodon nasutus, S. mac = Serrasalmus maculatus, S. ins = Steindachnerina insculpta*

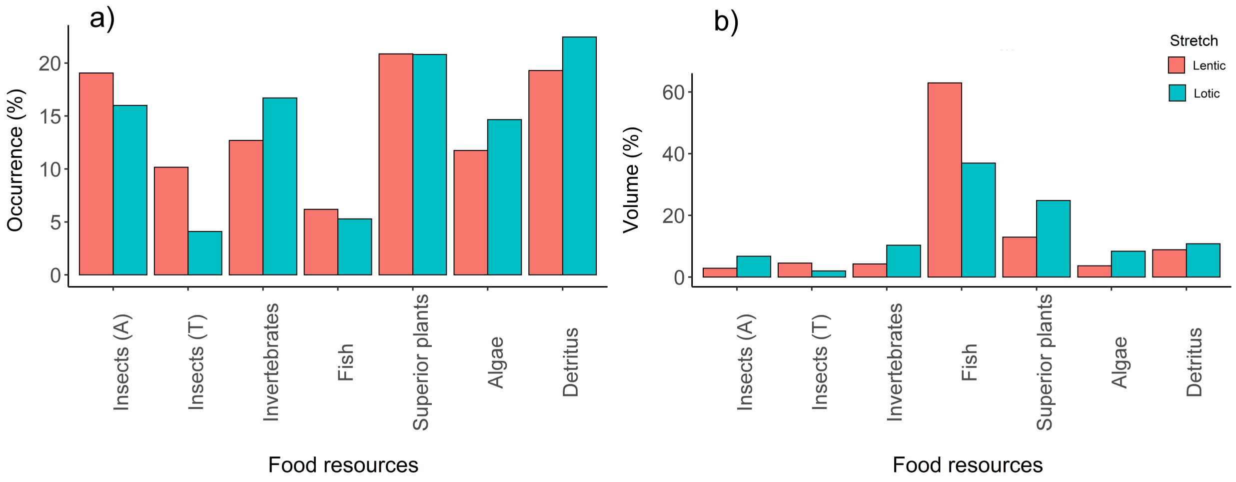

Figure 2. Percentage of a) frequency of occurrence and b) volume of trophic categories in the lentic and lotic stretch of the Chavantes Reservoir, middle Paranapanema river basin.

Comparing the diet of each species between the reservoir stretches, it was observed that most species (9 out of 13) showed a significant difference (PERMANOVA, $p < 0.05$, Table III). Individually, *Astyanax lacustris* was classified as an insectivore in the lentic compartment, consuming mainly the insects Coleoptera terrestrial (IAi = 44.65%) and Hymenoptera terrestrial (23.80%), in addition to increasing the diet with seed (16.16%), while in the compartment lotic, the species was classified as omnivorous, consuming mainly seeds (47.11%), terrestrial Hymenoptera (19.55%), superior vegetable (7.77%) and terrestrial Isoptera (7.69%).

Table III. Results of the permutational multivariate analysis of variance (PERMANOVA) and the permutational analysis of multivariate dispersions (PERMDISP) applied to the diet data of the common species between the stretches (lentic and lotic). DC = Average distance to centroid; significant values are in bold.

Species	**PERMANOVA**		**PERMIDISP**			
	F	**p**	**Lentic (DC)**	**Lotic (DC)**	**F**	**p**
Acestrorhynchus lacustris	3.74	0.01	0.46	0.38	1.32	0.25
Apareiodon affinis	4.78	**< 0.01**	0.57	0.58	0.14	0.7
Astyanax lacustris	8.81	**< 0.01**	0.67	0.67	0.11	0.74
Galeocharax gulo	1.9	0.08	0.58	0.56	0.04	0.83
Gymnotus carapo	2.93	**< 0.01**	0.56	0.57	0.06	0.81
Hoplias malabaricus	0.4	0.93	0.57	0.58	0.01	0.93
Iheringichthys labrosus	2.49	0.02	0.52	0.5	0.21	0.64
Leporinus amblyrhynchus	1.08	0.34	0.53	0.52	0.01	0.93
Pimelodus maculatus	1.9	0.03	0.6	0.6	0.01	0.99
Plagioscion squamosissimus	4.64	**< 0.01**	0.63	0.63	0.06	0.8
Schizodon nasutus	5.62	**< 0.01**	0.56	0.64	9.64	**< 0.01**
Serrasalmus maculatus	0.88	0.51	0.61	0.61	0.04	0.83
Steindachnerina insculpta	11.24	**< 0.01**	0.27	0.38	19.05	**< 0.01**

Gymnotus carapo was classified as omnivorous in the lentic compartment, consuming aquatic Ephemeroptera (45.53%), superior vegetal (33.81%) and Chironomidae (12.54%), while in the lotic compartment, the species was classified as invertivorous, with consumption predominant of Gastropoda (73.70%). *Iheringichthys labrosus* was classified as insectivorous in the lentic compartment, consuming Chironomidae (64.46%) and detritus (26.32%) and invertivorous in the lotic compartment, consuming Chironomidae (53.16%), detritus (20.79%), and bivalvia (17.66%). *Pimelodus maculatus* was classified as omnivorous in the lentic compartment, consuming superior vegetable (23.82%), sediment (19.92%), and aquatic Chironomidae (19.85%), while in the lotic compartment, the species was classified as invertivorous, consuming Gastropoda (46.66%), Chironomidae (19.85%) and superior vegetable (19.71%) (Table II).

Astyanax lacustris, A. affinis, *P. squamosissimus*, *S. nasutus* and *S. insculpta* did not change the trophic guild, only the consumption of specific items, which contributed to the difference in diet between the stretches, as can be seen in table II. For example, the diet of *A. affinis* was composed of sediments (61.08%) and algae (24.47%) in the lentic compartment, while in the lotic compartment, the species consumed sediment (65.03%) and terrestrial plants (19.22%). On the other hand, the diet of *P. squamosissimus* was composed of fish (94.31%) in the lentic compartment, while in the lotic compartment the species consumed fish (72.64%) and complemented the diet with Decapoda (24.16%) and Gastropoda (2.99%).

The PERMDISP results showed that only two species showed interindividual variation between stretches (ANOVA: $F_{(3.353)}$ = 3.4294; p < 0.05, Table III), *Schizodon nasutus* (Average distance to centroid – Lotic DC = 0.64 and Lentic: DC = 0.56) and *Steindachnerina insculpta* (Average distance to centroid – Lotic DC = 0.64 and Lentic: DC = 0.56), with greater variability between individuals in the lotic stretch for both species.

The mean trophic niche breadth was very similar between stretch, not differing between stretches (ANOVA: $F_{(1.24)}$ = 0.02, p = 0.888; Figure 3a). In the lentic compartment, it is observed that of the 13 species, seven species exhibited high niche breadth (< 0.6), one species exhibited moderate niche breadth (< 0.4 and > 0.6) and five species exhibited low niche breadth (< 0.4). In the lotic compartment, eight species showed high niche breadth, two species showed the moderate breadth and three species showed low niche breadth (Table IV). Regarding diet overlap, 13 out of the 67 pairs formed showed high overlap (< 0.6), corresponding to 19.40% of the species pairs for the lentic compartment. As for the lotic compartment, of the 66 pairs formed, 12 showed high overlap, equivalent to 18.18% (Supplementary Material - Table SI; Figure 3b). As a consequence, there were no significant differences in trophic niche overlap between compartments (ANOVA: $F_{(1.131)}$ = 0.29, p = 0.59).

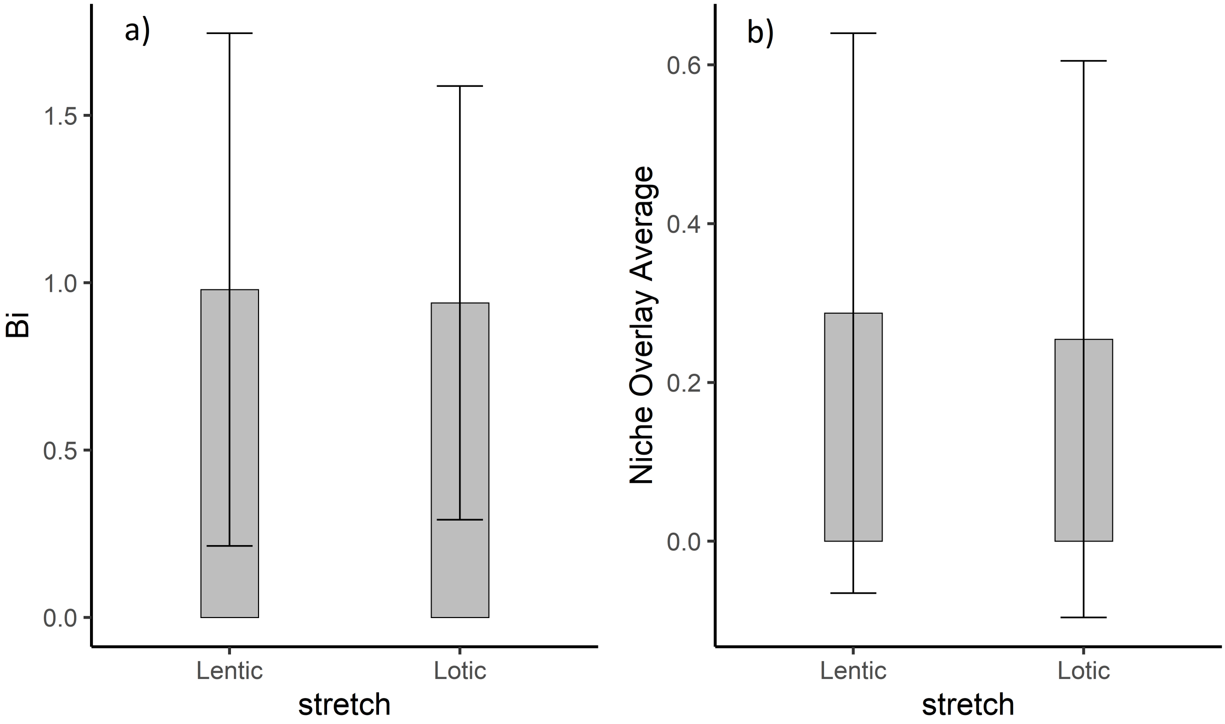

Figure 3. a) Trophic niche breadth and b) trophic niche overlap of fish species in each stretch of the Chavantes Reservoir, middle Paranapanema river basin.

Table IV. **Trophic niche breadth values (B) of fish species in the lentic and lotic stretches of the Chavantes Reservoir, middle Paranapanema River, state of São Paulo, Brazil.**

Species	**Lentic**	**Lotic**
Acestrorhynchus lacustris	0.25	0.51
Apareiodon affinis	1.09	1.04
Astyanax lacustris	2.38	2.15
Galeocharax gulo	0.4	0.14
Gymnotus carapo	1.14	1.28
Hoplias malabaricus	0.35	0.15
Iheringichthys labrosus	1.2	1.55
Leporinus amblyrhynchus	1.75	1.1
Pimelodus maculatus	2.22	1.76
Plagioscion squamosissimus	0.34	0.89
Schizodon nasutus	1.17	1.09
Serrasalmus maculatus	0.23	0.3
Steindachnerina insculpta	0.21	0.24

DISCUSSION

In general, the ichthyofauna from the Chavantes Reservoir exploited a large number of different food resources. Food items such as plants, detritus and invertebrates were the most consumed resources in both the lentic and lotic reaches of the reservoir, reflecting the high trophic plasticity of most Neotropical fish species (Abelha et al. 2001). Almost 70% of the species had significant changes in diet composition when compared between the lentic and lotic stretches, which indicates the consumption of different food items and/or different proportions of these resources. On the other hand, no differences were found in the diet overlap and trophic niche breadth between the stretches. Although damming can affect the availability of the species' preferred food resources due to spatial variation, such as differences between river size, width, depth and flow (Vidotto-Magnoni et al. 2021), other factors such as foraging behavior and the lifestyle of the species, can interfere with the consumption of resources (Vazzoler 1996, Zavala-Camin 1996, Quirino et al. 2015).

Some species maintained the same feeding habits in both stretches: *G. gulo*, *H. malabaricus* and *S. maculatus* classified as piscivorous and *L. amblyrhynchus* as invertivore. These results are explained by the specialist behavior that these species present (Deus & Petrere-Junior 2003, Mendonça et al. 2004, Peretti & Andrian 2008) since they maintain their food preference for a certain type of resource regardless of the environment. The determination of the trophic guild of *Astyanax lacustris* as an insectivore in the lentic stretch and omnivore in the lotic stretch is consistent with the opportunistic behavior of most species of the genus *Astyanax* (Gerking 1994, Abelha et al. 2008, Vidotto-Magnoni et al. 2021) and was demonstrated in this study by the high consumption of Coleoptera and Hymenoptera in the lentic stretch and seed and higher plants in the lotic stretch. It is worth mentioning that leaves, fruits and seeds are common in lotic environments, being these items of preference in the diet of *A. lacustris* (Bennemann et al. 2005, Lima et al. 2018, Garcia et al. 2021, Vidotto-Magnoni et al. 2021). Other items such as Coleoptera were the main resources in the species' diet in the lentic stretch and are well documented for *Astyanax lacustris* in rivers and reservoirs (Casatti 2002, Bennemann et al. 2005, Bonato et al. 2012, Delariva et al. 2013).

Gymnotus carapo and *Pimelodus maculatus* had an omnivorous diet in the lentic stretch and invertivorous in the lotic stretch, mainly of Gastropoda, demonstrating an opportunistic feeding habit. The consumption of molluscs by typically omnivorous species (Hahn et al. 1998, Oliveira et al. 2005) may be associated with the increase in invasive invertebrates such as *Corbicula fluminae* (Müller, 1774) and *Limnoperna fortunei (Dunker, 1857)*, already recorded in the Chavantes Reservoir and with high abundance in other downstream reservoirs (Takeda et al. 2005, Kudo et al. 2006), and used as food by fish in this watershed (Fugi et al. 2005). *Iheringichthys labrosus* was characterized by an insect-based diet, with Diptera composing more than 64% of its diet in the lentic stretch. Chironomidae and bivalve were the main resources in the lotic stretch, and these resources are very common in the diet of fish species in several Neotropical reservoirs (Fugi et al. 1996, Abes et al. 2001, Callisto et al. 2002).

Acestrorhynchus lacustris and *P. squamosissimus* were classified as piscivorous due to their diet predominated by fish in both locations. However, the consumption of complementary items in smaller proportions, such as sediments and algae by *Acestrorhynchus lacustrine* and Decapoda by *P. squamosissimus* in the lotic stretch, caused their diets to present significant differences between the stretches. In addition, *P. squamosissimus* is considered a non-native species, and although its feeding habit is generalist (Stefani & Rocha 2009), the species has preferences for Decapoda, when this resource is available in the environment (Bennemann et al. 2006, Neves et al. 2015, Kliemann et al. 2022).

Apareiodon affinis and *S. insculpta* had their diets based on detritus for both stretches. This finding may be related to the low depth of the rivers, high values of suspended material, and low water transparency (Personal observation). According to Hahn et al. (1998), a high abundance of this trophic group is expected in the fluvial zones of reservoirs, as they use the detritus that accumulates in unconsolidated bottoms as a food resource. Its wide distribution in the reservoir indicates that the species has wide environmental tolerance, adapting to the different conditions of the studied locations, such as depth, width and flow.

On the other hand, *S. nasutus* and *S. insculpta* were the only ones to present an interindividual variation in the diet between the stretches, this variation was greater in the lotic stretch for both species, when there was high consumption of macrophytes and algae by *S. nasutus* and different items of invertebrates and algae by *S. insculpta*. The fact that the other species do not show inter-individual variation indicates that even though they can exploit different resources available in the environment, they present the same pattern of inter-individual variation in the use of resources (Brasil-Sousa et al. 2009, Quirino et al. 2015).

Despite the large number of food items exploited by the species, the vast majority showed preferential consumption for few food resources, evidenced by the low values of trophic niche breadth in both stretches. Furthermore, it was observed that trophic segregation was very similar but slightly higher in the lentic stretch, indicating trends in trophic specialization (Mérona & Rankin-de-Mérona 2004, Novakowski et al. 2008). Trophic segregation is considered a key factor for the coexistence of fish species (Schoener 1974, Silva et al. 2017), which may explain the low overlap of the diet in both stretches, preventing interspecific competition. Furthermore, the results found here, combined with the low niche breadth of all species, suggest a high degree of food partitioning between species, common to other fish communities in the Neotropical region (Uieda et al. 1997, Mérona & Rankin-de-Mérona 2004, Esteves et al. 2008, Novakowski et al. 2008).

It is observed that the Chavantes Reservoir presents a mosaic of characteristics both concerning the environmental gradient and to the local characteristics inherent to its forming rivers (Paranapanema, Itararé and Verde Rivers). However, differences between the stretches were evidenced in the consumption of the main food resources by the species in the different compartments, and in their trophic organizations, indicating that the longitudinal gradient is an important factor in the structure of fish assemblages in the Chavantes Reservoir.

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SUPPLEMENTARY MATERIAL

Table SI.

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THIAGO D. GARCIA[1]
https://orcid.org/0000-0001-6330-0068

BARBARA A. QUIRINO[3]
https://orcid.org/0000-0002-7734-3795

LUCAS R. JARDULI[4]
https://orcid.org/0000-0002-5796-6434

EDMIR D. CARVALHO[5*]

ANA PAULA VIDOTTO-MAGNONI[2]
https://orcid.org/0000-0003-1819-7019

[1]Programa de Pós-Graduação em Ciências Biológicas, Universidade Estadual de Londrina, Rodovia Celso Garcia Cid. PR, 445 Km 38° PR, 86057-970 Londrina, PR, Brazil
[2]Universidade Estadual de Londrina, Laboratório de Ecologia e Comportamento Animal, Rodovia Celso Garcia Cid. PR, 445 Km 38° PR, 86057-970 Londrina, PR, Brazil
[3]Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá, Avenida Colombo, 5790, 87020-900 Maringá, PR, Brazil
[4]Centro Universitário das Faculdades Integradas de Ourinhos, Rodovia BR 153, Km 338+420m, Água do Cateto, 19909-100 Ourinhos, SP, Brazil
[5]Universidade Estadual Paulista - Júlio de Mesquita Filho, Av. Prof. Mário Rubens Guimarães Montenegro, 18618-000 Botucatu, SP, Brazil
in memoriam

Correspondence to: **Thiago Deruza Garcia**

E-mail: thiago.deruza@hotmail.com

Author contributions

APVM and EDC designed the study; TDG, BAQ and LRJ analyzed the data; APVM and TDG led the manuscript writing and all of the authors contributed with ideas and writing.