

# Dynamic of fish trophic guilds in the plateau-plain gradient in the Paraguay River, Northern Pantanal

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**Abstract.** This study aims to evaluate the dynamics of fish trophic guilds according to the longitudinal gradient of the Paraguay River, northern Pantanal, Brazil. Three river segments were sampled: plateau, confluence and plain. These segments have different physical and biological characteristics, with high water flow in forest areas in plateau and slow flow in meanders, with Pantanal typical vegetation. In total, 26,542 individuals distributed in 130 fish species were collected. The sampled species were characterized in seven trophic guilds. From the seven trophic guilds identified, only three were statistically related to the type of the environment; herbivores were more abundant in the plateau, piscivores in the confluence, and invertivores in the plain. According to values of corrected Akaike Information Criteria, the environmental variable that best explains the abundance of piscivorous fishes in the segments sampled in the Paraguay River was water transparency. For herbivores, the model that explained the variation in abundance was composed by temperature, altitude and dense forest proportion. The variable altitude best represented the abundance of invertivores. Water transparency, temperature, altitude, river width and dense forest proportion were determining factors for the distribution of piscivorous, herbivorous and invertivorous fishes as a response to an environmental gradient that meets its ecological requirements. Understanding the trophic relationships is fundamental for management actions, contributing to the maintenance of ecosystem services of different species. Therefore, future research must be taken into account regarding management and ecological relationships.

**Keywords.** Feeding habits; Ichthyofauna; Longitudinal gradient; Riverine landscape; Wetland.

## INTRODUCTION

The concept of the trophic guild is defined as a group of species that exploit the same class of food resources in a similar manner (Root, 1967). To obtain these resources, the organisms need to search, detect, capture, manipulate and ingest the item (Wootton, 1999). In this process, the different eating behaviours of species interfere with the use of the wide diversity of food resources available to fish in the aquatic environment (Hahn *et al.*, 1997).

In addition to the species behaviour, changes in its diets are driven by seasonal and spatial habitat modifications (Abelha *et al.*, 2001). In rivers that are seasonally influenced by flooding events, such as Brazilian ones, most of the fish species

switch the food items consumption as hydrological periods change (Dary *et al.*, 2017; Muniz *et al.*, 2019), being sometimes related to the riparian vegetation phenology (Furlan *et al.*, 2017).

Regarding spatial changes, the feeding habits of the ichthyofauna are influenced by the spatial availability of habitats, altitude, and the order of rivers and streams (Bistoni & Hued, 2002; Da Silva *et al.*, 2014). These characteristics change along the river continuum, forming a gradient of trophic interactions, that change from headwaters to floodplains (Vannote *et al.*, 1980; Wolff *et al.*, 2013; Curtis *et al.*, 2018).

Studies assessing trophic guilds, based on the differences between allochthonous resource input and primary productivity, have shown chang-

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es in the distribution of generalist (such as insectivores) and specialist (detritivores, planktophagous, and piscivores) species in longitudinal gradients (Schlosser, 1982; Angermeier & Karr, 1986; Silva *et al.*, 2014). Thus, the composition of trophic groups of aquatic communities is primarily structured according to the gradient produced by the variation of physical and biotic parameters (river discharge, channel width, and vegetation cover) and by the input and processing of organic matter and yield along the river continuum (Vannote *et al.*, 1980).

Therefore, temporal and spatial modifications lead to changes in the richness and abundance of trophic fish guilds, considering that distinct periods and environments present different abiotic conditions and food offerings (Abelha *et al.*, 2001). While the fish assemblages change according to the environmental characteristics (Súarez *et al.*, 2011), in non-transformed Amazonian wetlands, the well-structured riparian vegetation along the streams did not affect the diet of a fish assemblage, showing that the continuity of the marginal vegetation reduces the impact on fish diet (Soares *et al.*, 2020). Studies focusing on the distribution of fish trophic guilds help to understand the behaviour of these organisms in the face of environmental transformations and food availability in natural environments (Silva *et al.*, 2012).

The Paraguay River – one of the most important water sources for the Pantanal – has been highly modified, and this environmental transformation highly impacts the riparian vegetation (Damasceno-Junior *et al.*, 2005), as well as the water availability (Lázaro *et al.*, 2020). These transformations also change other environmental functionalities, such as food and habitat provision for fish under the

macrophyte beds (Da Silva *et al.*, 2010) and may consequently change the fish assemblages and the guilds.

Due to environmental changes in the river longitudinal gradient, we hypothesized that: 1) herbivorous fish are prone to be more abundant in the midreaches regions due to its dependence on allochthonous resources, and 2) while insectivores, carnivores and omnivores guilds are more abundant in the floodplain regions, mainly due to environmental heterogeneity, which enables a wide variety of food resources. Considering these aspects, this research aimed to evaluate the dynamics of trophic guilds according to the longitudinal gradient of the Paraguay River, Northern Pantanal, Brazil.

## MATERIAL AND METHODS

### Study site

The samplings were performed from July to November/2017 and August/2018 in the dry period in the upper reaches of the Paraguay River, in six sampling sites divided into two sampling areas in each segment (Fig. 1). Three segments were evaluated: 1) plateau: composed by the sampled areas in the municipalities of Barra do Bugres and Porto Estrela. These sites have similar environmental characteristics, including altitude ( $\pm 150$  m above sea level), river width ( $\pm 50$  m) and vegetation composed by forest. About 70 km downstream the plateau is the region of confluence 2) between Sepotuba, Cabaçal and Jauru Rivers with the Paraguay River, where the altitude is lower ( $\pm 120$  m above sea level) and the

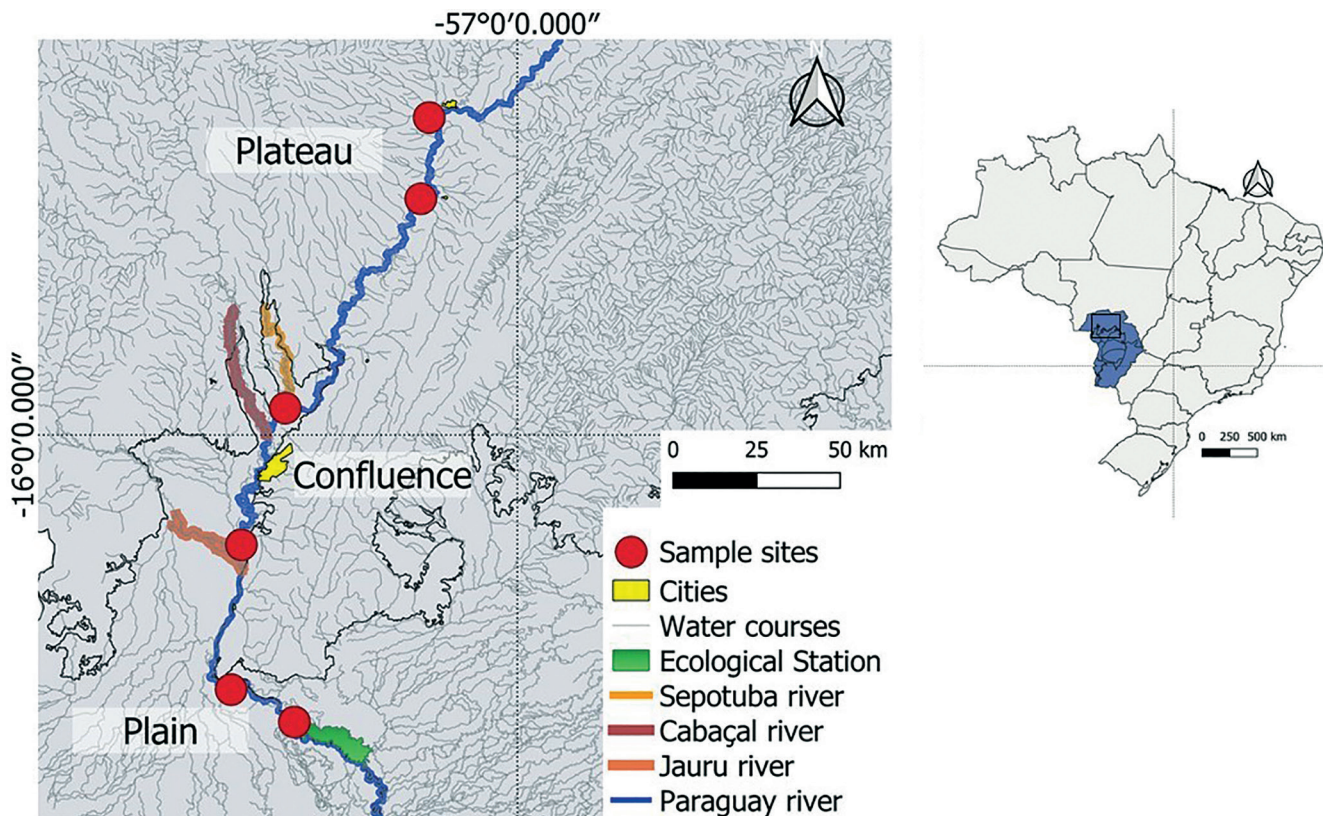


Figure 1. The sampling sites along the Paraguay River, state of Mato Grosso, Brazil.

**Table 1.** Geographic coordinates, mean altitude (m) and mean river width (m) among the sampled segments in the Paraguay River, Northern Pantanal.

Sampling site	Geographic coordinates		Mean altitude (m)	Mean river width (m)
Plateau	15°06'22.18"S	57°14'52.33"W	152.5	39.25
Plateau	15°20'06.00"S	57°16'17.80"W	146	53.84
Confluence	15°55'27.56"S	57°39'11.11"W	115.66	118.2
Confluence	16°18'33.06"S	57°46'36.00"W	125	107.66
Plain	16°43'01.61"S	57°48'20.13"W	102.66	171.87
Plain	16°48'30.02"S	57°37'39.23"W	110.33	213.32

river is wider ( $\pm 125$  m), and 3) plain: composed by areas (hills region and Taiamã Ecological Station) located in regions where the altitude was the lowest ( $\pm 100$  m above sea level) and the river was the widest ( $\pm 185$  m). Table 1 shows the mean values for altitude and river width among the sampling sites and the geographic coordination of each segment. The slow water flow in this last segment allows the colonization of the littoral area by aquatic macrophytes, occurring mainly the species *Eichhornia azurea* (Sw.) Kunth and *E. crassipes* (Mart.) Solms.

### Data collection

To collect the fish specimens two sampling methods were used. A dragging net with 4 m height  $\times$  25 m width and 5 mm mesh size and a net, armed in a metallic structure of 2 m length  $\times$  1 m width  $\times$  25 cm of depth were used. In each point the limnological variables such as water transparency (cm), water temperature ( $^{\circ}$ C), water conductivity ( $\mu$ S/cm) and dissolved oxygen (mg/L) were measured using a multiparameter probe Hach HQ40D. The environment variables selected were the altitude, river width and dense forest proportion (1 km buffer), considering that this ratio directly contributes to habitat quality to the aquatic organisms.

Fish specimens' standard length (SL hereafter) (cm) and weight (g) were measured and identified following the identification keys found in Britski et al. (2007). The species valid names were checked according to Fricke et al. (2022). Specimens were fixed with formalin 10% and preserved in alcohol 70% and deposited in the collection of the Laboratório de Ictiologia do Pantanal Norte (LIPAN; see supplementary material) at the Centro de Limnologia, Biodiversidade e Etnobiologia do Pantanal (CELBE-UNEMAT).

The guilds were attributed according to the most expressive behaviour reported by the specialized bibliographies (Sazima & Machado, 1983; Lolis & Andrian, 1996; Resende et al., 1996; Resende, 2000; Hahn et al., 2002; Lonardoní et al., 2006; Ibañez et al., 2007; Corrêa et al., 2009; Brandão-Gonçalves et al., 2010; Sampaio & Goulart, 2011; Prado, 2015; Resende et al., 2016; Polaz et al., 2017; Lopes et al., 2022). The invertivores' guild was composed by invertivorous, insectivorous, invertivorous/insectivorous and zooplanktophagous species. When the species showed feeding habit alteration depending on river seasonality, it was considered the habit coincident to the period sampled in this study (i.e., dry period).

### Data analysis

Assumptions of normality of data distribution were assessed using the Shapiro-Wilk test and the Levene's test was used to assess the homogeneity of variances. The one-way ANOVA was used to evaluate the difference between guild richness and abundance in the studied areas. A *post hoc* Tukey's test was applied to verify multiple comparisons between the sampled areas. When the data did not follow the assumptions Kruskal Wallis' test and *post hoc* Dunn's test were used.

A Principal Component Analysis (PCA) was performed with limnological and environmental variables and to evaluate these variables' influence on the abundance of trophic guilds the Generalized Linear Models (GLM) analysis was used. The multicollinearity between the predictor variables was verified by the Variance Inflation Factor (VIF) of each variable, excluding those with  $VIF \geq 10$  (Lin, 2008). Thus, for each model, the values of K, AICc,  $\Delta$ AICc and weight of evidence were calculated (this measure indicates that the support level (or weight of evidence)), in favour of a given model, is the most parsimonious among the set of candidate models. Statistical analyses were conducted in the software R (R Core Team, 2019), together with the *MuMIn* (Bartoń, 2017), *modEvA* (Barbosa et al., 2013) and *vegan* (Oksanen et al., 2019) packages.

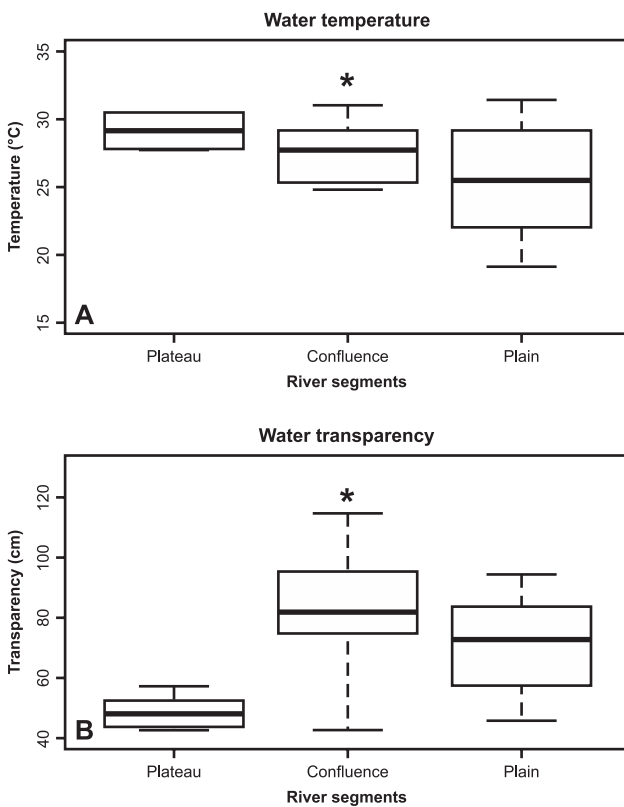
## RESULTS

### The environmental variation between segments

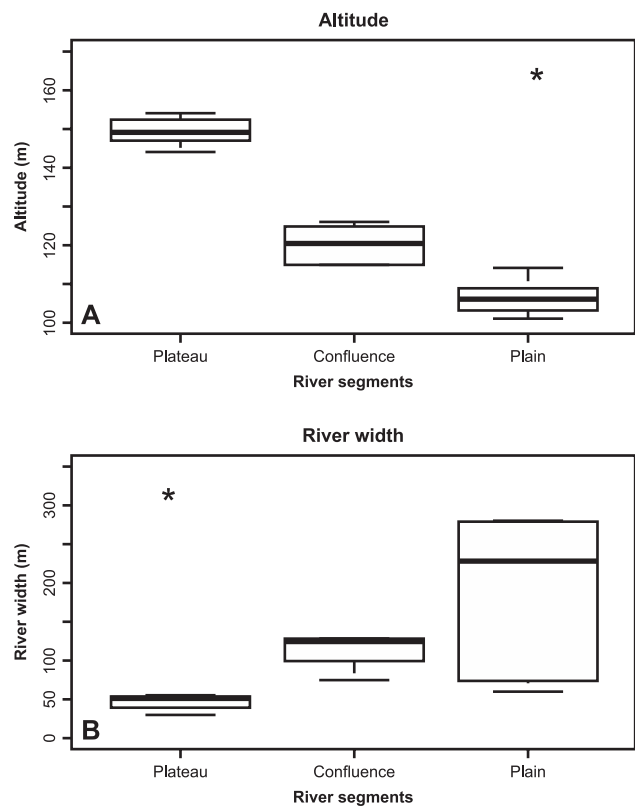
The water temperature in the sampled segments was different ( $F = 4.59$ ,  $P < 0.05$ ) and Tukey's test indicated higher temperature in the plateau ( $29.1 \pm 1.49$ ) than in the plain ( $25.4 \pm 4.88$ ) ( $P < 0.05$ ) (Fig. 2A). The water transparency variable was statistically different in the sampled segments ( $P < 0.05$ ) (Fig. 2B). Tukey's test indicated that the transparency in the plateau was lower than in confluence and plain ( $P < 0.05$ ).

Among the environmental variables, the altitude was different in the three sampled segments ( $F = 136.7$ ,  $P < 0.05$ ) and Tukey's test indicated higher values in the plateau than in confluence and plain ( $P < 0.05$ ) (Fig. 3A). The segments have different river width ( $F = 239.1$ ,  $P < 0.05$ ), being narrow in the plateau and wider in the plain ( $P < 0.05$ ) (Fig. 3B). The proportion of dense forest did not vary among the sampled segments ( $P < 0.05$ ).

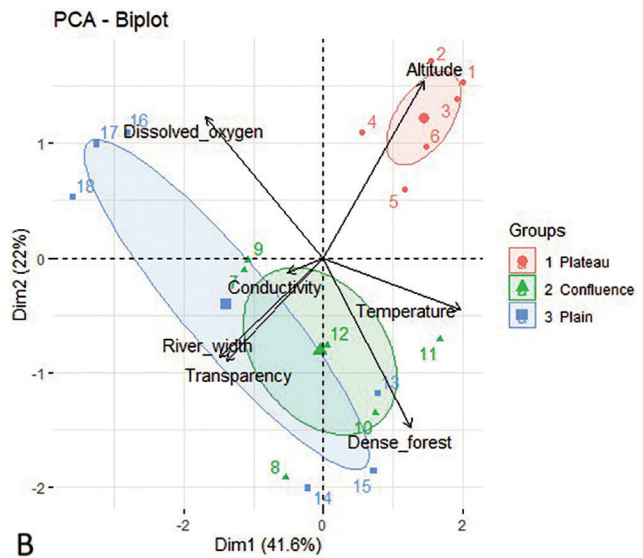
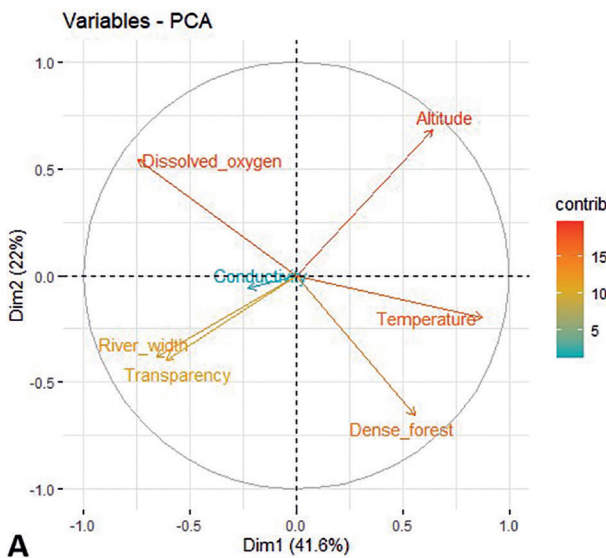
The PCA showed that the components explained 63.22% of the data variation, contributing with 41.22% and 22% of the total variance. The variables dissolved oxygen and altitude had major contribution on data variation whereas water conductivity had the minor contribution (Fig. 4A). Altitude was positively related to the Plateau and dissolved oxygen to the Plain. Temperature and proportion of dense forest had a mild contribution on data variation and were positively associated to confluence and plain (Fig. 4B).



**Figure 2.** Limnological characteristics in the sampled segments in the Paraguay River, Mato Grosso, Brazil, from July to November 2017 and August 2018. (A) temperature. (B) water transparency. \* indicates statistical difference at the 0.05 significance level.



**Figure 3.** The difference of environmental characteristics in the segments sampled in the Paraguay River, from July to November 2017 and August 2018. (A) altitude. (B) river width. \* indicates statistical difference at the 0.05 significance level.



**Figure 4.** Principal Component Analysis (PCA) of the limnological and environmental variables in the segments in the Paraguay River, from July to November 2017 and August 2018. (A) variables contribution. (B) sampled areas ordination.

### Trophic guilds distribution along the longitudinal gradient

During the study period, 26,542 individuals distributed in 130 fish species were collected. The sampled species were characterized in six trophic guilds (Table 1 – Supplementary material). The richest guilds were invertivores (44 species), omnivores (33 species), piscivores (20

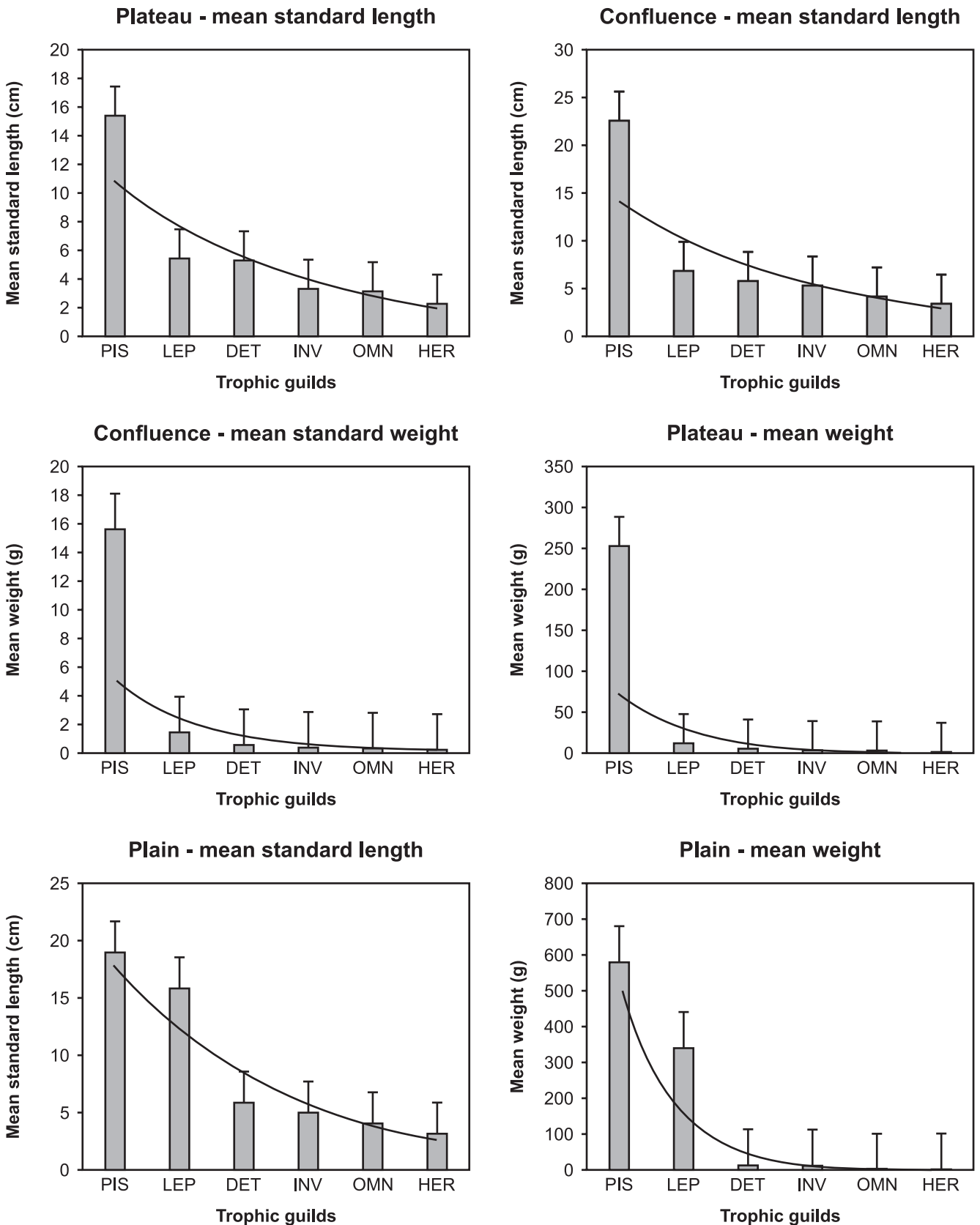
species), detritivores (22 species) and herbivores (10). The lepidophagous guild had only one species (*Roeboides prognathus* Boulenger, 1895).

The piscivores made up the group with the largest mean standard length and mean weight among the sampled segments (Fig. 5). Species such as *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *P. fasciatum* (Linnaeus, 1766) and *Salmimus brasiliensis* (Cuvier, 1816), contrib-

uted to the longest standard length (over 100 cm) and consequently the biggest weight of these guilds.

The occurrence of the species *Piaractus mesopotamicus* (Holmberg, 1887) (herbivores) and *Brycon hilarii*

(Valenciennes, 1850) (omnivores), which reach approximately 50 cm SL, were relevant for the larger length and average weight of the respective guilds. However, the invertivores and lepidophagous trophic guilds had the



**FFigure 5.** Trophic guilds mean weight and mean length in the sampled segments in the Paraguay River, from July to November 2017 and August 2018. PIS = piscivores; LEP = lepidophagous; DET = detritivores; INV = invertivorous; OMN = omnivores and HER = herbivores.

lowest mean weight and mean length, since these guilds are mainly represented by small species that live associated with aquatic macrophyte beds. Small fish species composed around 90% of the sample collected in confluence and plain segments and 96% in the plateau.

The Kruskal-Wallis test showed that the abundance of fish was distributed differently between the trophic guilds ( $X^2 = 76.26$ ,  $P < 0.05$ ). Omnivorous and invertivorous fish abundance was higher than the other guilds (9,670 and 9,228 individuals respectively). The number of guilds per sampled site varied from four to six in plateau, the mean number of collected trophic guilds was  $5.66 (\pm 0.81)$  while in the confluence and plain the mean number of trophic guilds was slightly higher ( $6 \pm 0$  both).

Along the longitudinal gradient, one-way ANOVA indicated that some trophic guilds are distributed differently. Among these, the herbivores guild ( $F = 6.17$ ,

$P < 0.05$ ), which abundance in the plateau is greater than in confluence and in the plain ( $P < 0.05$ ) (Fig. 6A). Piscivores, in turn, are more abundant in confluence ( $F = 5.54$ ,  $P < 0.05$ ) (Fig. 6B), differing from the plateau ( $P < 0.05$ ), but with similar abundance to the plain. Invertivorous species occurred in greater abundance in the plain compared to the plateau ( $X^2 = 6.75$ ,  $P < 0.05$ ), although not showing a difference with the confluence ( $P > 0.05$ ) (Fig. 6C). Albeit we hypothesised that some trophic guilds would be more abundant in plain regions due to the food availability, detritivores, lepidophagous and omnivores trophic guilds showed no significant difference between the sampled segments, which might indicate food availability for these guilds along all the river segments.

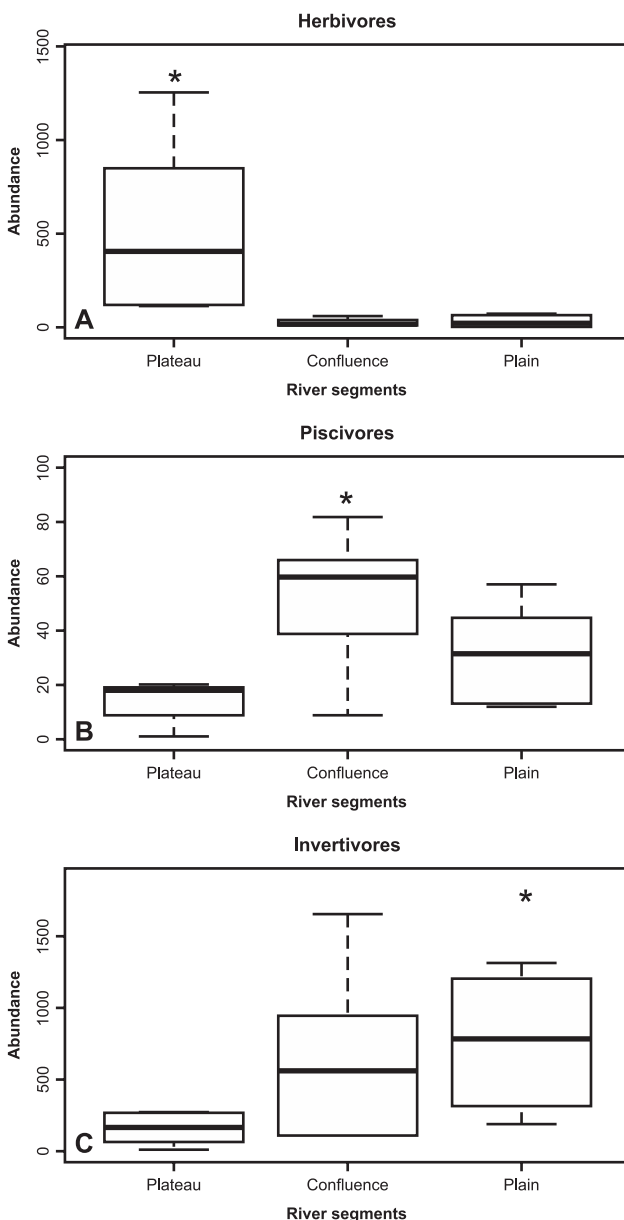
According to AICc values, the environmental variable that best explains the abundance of piscivorous fish in the segments sampled in the Paraguay River was water transparency ( $\Delta AICc = 0.00$ , weight = 0.71). For herbivores, the model that explained the variation in abundance was composed by temperature, altitude, and proportion of dense forest ( $\Delta AICc = 0.00$ , weight = 0.85). The variable altitude best represented the abundance of invertivorous ( $\Delta AICc = 0.00$ , weight = 0.78) along the longitudinal gradient (Table 2).

All variables showed a positive relationship with the abundance of the guilds except for dense forest proportion. Even though this variable did not show significant difference among the sampled segments, the plain region is less forested due to the floodplain characteristics, with strong effect of Taiamã Ecological Station, showing a negative relation with invertivorous fish abundance, since this guild was more abundant in the plain region.

## DISCUSSION

As this research was conducted from the plateau to the plain region, we expected to find morphophysiological environmental differences, which could result in different trophic guilds along the river corridor. Our results indicate that there is a clear trophic guilds distribution pattern along the longitudinal gradient in Paraguay River, where the guilds were more abundant. Herbivores occur mostly in the plateau region, piscivores in confluence and invertivores in the plain region. Thus, such as happens in species sorting (Leibold *et al.*, 2004), trophic guilds are also filtered by interactions and environmental characteristics in each locality in a gradient.

For instance, we found that in the plateau the water transparency is lower than in the plain, which corroborate the higher abundance of piscivorous fish in the confluence and plain that needs more visual acuity to find the prey. Turbid environments are characterized as reducers of visual efficiency, due to light dispersion by the presence of suspension particles in the water column (Utne-Palm, 2002). This fact demonstrated that foraging by piscivores on prey is highest under clearwater conditions, whilst in turbid water, it is greatly reduced (Shoup & Wahl, 2009).



**Figure 6.** Difference between trophic guilds in the sampled segments in Paraguay River. (A) herbivores. (B) piscivores. (C) invertivores. \* indicates statistical difference at the 0.05 significance level.

**Table 2.** AICc models ranking of predictor variables with the abundance of trophic guilds sampled in the Paraguay River. Predictor variables were dissolved oxygen (mg/L), temperature (°C), transparency (cm), altitude (m), river width (m) and proportion of dense forest.

Response variables	Model	K	AICc	ΔAICc	Weight
Piscivorous	<b>Transparency</b>	<b>3</b>	<b>167.93</b>	<b>0.00</b>	<b>0.71</b>
	Transparency + river width	4	170.13	2.20	0.24
	Temperature + transparency + river width	5	173.26	5.33	0.05
	Dissolved oxygen + temperature + transparency + river width	6	176.93	9.00	0.01
	Dissolved oxygen + temperature + transparency + river width + proportion of dense forest	7	182.32	14.39	0.00
	Dissolved oxygen + temperature + transparency + river width + altitude + proportion of dense forest	8	188.95	21.02	0.00
Herbivorous	<b>Temperature + altitude + proportion of dense forest</b>	<b>5</b>	<b>263.34</b>	<b>0.00</b>	<b>0.85</b>
	Dissolved oxygen + temperature + river width + altitude + proportion of dense forest	6	266.99	3.65	0.14
	Dissolved oxygen + temperature + transparency + altitude + proportion of dense forest	7	271.93	8.59	0.01
	Dissolved oxygen + temperature + transparency + river width + altitude + proportion of dense forest	8	278.64	15.30	0.00
Invertivorous	<b>Altitude</b>	<b>3</b>	<b>276.30</b>	<b>0.00</b>	<b>0.78</b>
	Altitude + temperature	4	277.90	1.60	0.19
	Altitude + river width + temperature	5	281.39	5.08	0.05
	Altitude + river width + proportion of dense forest + temperature	6	285.56	9.25	0.01
	Altitude + river width + proportion of dense forest + temperature + transparency	7	290.94	14.63	0.00
	Altitude + river width + proportion of dense forest + dissolved oxygen + temperature + transparency	8	297.63	21.32	0.00

Predator fishes presented a bigger standard length and heavier weight mean than other trophic guilds, and the fish size also influences its visual acuity, wherein bigger eyes imply an image size increasing facilitating the predation (Blaxter, 1980). Moreover, pelagic predators, such as the piscivores, are capable to swallow the entire prey due to higher body mass proportion (Nakazawa et al., 2013), corroborating to the fact that lower percentage between big fish (bigger than 10 cm SL) and small fish (smaller than 10 cm SL) was found in the confluence and the plain, indicating a prey relaxation in the plateau due to fewer piscivores (as shown in Table 1 – Supplementary material).

Piscivores naturally require more energy quantity compared to herbivores and omnivores despite the protein catabolism (Halver, 1972) and are mostly present in plain, where the high environmental heterogeneity increase the chance to find more prey diversity (Winemiller et al., 2000). The high abundance of piscivores in this segment happen once the connectivity between the main channel and its tributaries (Sepotuba, Cabaça and Jauru rivers) and bays (e.g., Caiçara bay) creates refuge habitats, such as oxbow lakes and lateral bays, promoting the fish viability and diversity (Shao et al., 2019).

The morphological characteristics of the Paraguay River change from straight in the plateau to meandric next to the confluence with other rivers (Cabaçal and Sepotuba rivers) (Silva et al., 2008). This morphologic change is also seen in the river shore vegetation diversity, which increases in the downstream reaches (Naiman & Décamps, 1997; Ward et al., 2002). The vegetation along the shore results in lower water temperature (Leach et al., 2012), affecting the fish composition.

The higher temperature observed in the plateau was considered a predictor variable for herbivorous fish. However, we consider this result due to the period of collection, where the plain region indicated a lower temperature than the plateau. Moving through a longitudi-

nal gradient from mid-reaches to downstream, the wider channels separate the riparian vegetation, increasing the sunlight incidence, consequently, resulting in higher temperature and algae productivity (Power & Dietrich, 2002).

The distribution of fish is rarely driven by only one factor (Angermeier et al., 2002), and is also associated with physiographic characteristics and biotic interactions (Leclerc & Desgranges, 2005). The high abundance of herbivorous fish in the plateau was attributed by a species that do not depend directly on riparian vegetation as a food source. *Otocinclus vittatus* Regan, 1904 represented more than 90% of the herbivores sampled and 51% of fish abundance in this river segment. Despite occurring in all segments *O. vittatus* showed dominance in the plateau segment. The lack of piscivores, the fast-running water and the submerged vegetation, like *Alchornea castaneifolia* (Willd.) A. Juss., in this segment composed a favourable environment for *O. vittatus* dominance, where it feeds on wood debris or algae (Axenrot & Kullander, 2003).

Altitude was the main predictor for the higher invertivores abundance in the confluence and plain. The result indicate that the abundance of this trophic guild increases towards the plain. In the plain region, the water flow is slow due to the larger river width, allowing the aquatic macrophytes colonization, and favouring the invertivorous fish.

The aquatic macrophyte bed, abundant in the confluence and plain, provide a detritus substrate and periphytic algae (Dudley, 1988) that feed associated invertebrates. Zooplanktons, for instance, occur in greater biomass in the littoral region of a watercourse, following the development of aquatic macrophytes (Estlander et al., 2009), floodplain important elements.

The piscivores, herbivores and omnivores represented the bigger and heavier fishes. However, the species with major length in these three trophic guilds are migratory, thus indicating more energetic requirements

due to the necessity of energy storage for migration and reproduction (Resende *et al.*, 1996).

The distribution of trophic guilds varied in the sampled segments in the Paraguay River, with more piscivores and invertivorous fish in the confluence and plain regions of the river, consequently herbivores were more abundant in the plateau region. The environmental variable water transparency is important for piscivorous fish once its predation is associated with visual acuity. The altitude, water temperature and proportion of dense forest are important to herbivores, and it was more abundant in the plateau region, where these characteristics showed higher values. Altitude is an important variable for invertivorous fish, as its abundance is higher in lower regions.

The piscivorous species are characterized as key species in aquatic ecosystems as they have an important role in energy flow in trophic webs. Although not showing big differences in SL, piscivorous fish weight in plain was the highest among the segments, indicating a good provision of food in these areas. On the other hand, forager fish such as herbivores often rely solely on the riparian vegetation as a food source, eating fruits and leaves. Both predators and foragers are favored by the hydrographic extension that allows their colonization in different environments. However, studies including the temporal scale with the spatial scale should be conducted, once it is the main drivers of feeding behavior of fish species in seasonally inundated environments.

This study provided the evidence of different distribution of trophic guilds along a portion of the Paraguay River, in Northern Pantanal. However, this area is susceptible to damming of tributaries rivers, forest loss by cattle raising, grain production, long period droughts and fires that might cause temporal and spatial alterations in local food webs, changing the dynamics along the longitudinal gradient. Therefore, future research monitoring the environment and evaluating the effect of several dangerous anthropogenic activities in the ichthyofauna must be taken into account in the Pantanal.

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## REFERENCES

- Abelha, M.C.F.; Agostinho, A.A. & Goulart, E. 2001. Plasticidade trófica em peixes de água doce. *Acta Scientiarum: Biological Sciences*, 23(2): 425-434. <https://doi.org/10.4025/actascibiolsci.v23i0.2696>.
- Angermeier, P.L. & Karr, J.R. 1986. Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes*, 9(1): 117-135.
- Angermeier, P.L.; Krueger, K.L. & Dolloff, C.A. 2002. Discontinuity in Stream-fish Distributions: Implications for Assessing and Predicting Species Occurrence. In: Scott, J.M.; Heglund, P.J.; Morrison, M.L.; Haufler, J.B.; Raphael, M.G.; Wall, W.A. & Samson, F. (Eds.). *Predicting species occurrences: issues of accuracy and scale*. WEashington, Island Press. p. 519-527.
- Axenrot, T.E. & Kullander, S.O. 2003. *Corydoras diphyses* (Siluriformes: Callichthyidae) and *Otocinclus mimulus* (Siluriformes: Loricariidae), two new species of catfishes from Paraguay, a case of mimetic association. *Ichthyological Exploration of Freshwaters*, 14(3): 249-272.
- Barbosa, A. M.; Real, R.; Muñoz, A.R., & Brown, J.A. 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions*, 19(10): 1333-1338. <https://doi.org/10.1111/ddi.12100>.
- Bartoń, K. 2017. *MuMIn: Multi-model inference. Version 1.40.0*. URL <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Bistoni, M.A. & Hued, A.C. 2002. Patterns of fish species richness in rivers of the central region of Argentina. *Brazilian Journal of Biology*, 62(4B): 753-764. <https://doi.org/10.1590/S1519-69842002000500004>.
- Blaxter, J.H.S. 1980. Vision and the feeding of fishes. In: Bardach, J.E.; Magnusson, J.J.; May, R.C. & Reinhart, J.M. *Fish behaviour and its use in the capture and culture of fishes*. Manila, ICLARM.
- Brandão-Gonçalves, L.; Oliveira, S.A.D. & Lima-Junior, S.E. 2010. Hábitos alimentares da ictiofauna do córrego Franco, Mato Grosso do Sul, Brasil. *Biota Neotropica*, 10(2): 21-30. <https://doi.org/10.1590/S1676-06032010000200001>.
- Britski, H.A.; de Silimon, K.Z. & Lopes, B.S. 2007. *Peixes do Pantanal. Manual de Identificação*. Brasília, EMBRAPA.
- Corrêa, C.E.; Petry, A.C. & Hahn, N.S. 2009. Influência do ciclo hidrológico na dieta e estrutura trófica da ictiofauna do rio Cuiabá, Pantanal Mato-Grossense. *Iheringia. Série Zoologia*, 99(4): 456-463. <https://doi.org/10.1590/S0073-47212009000400018>.
- Curtis, W.J.; Gebhard, A.E. & Perkin, J.S. 2018. The river continuum concept predicts prey assemblage structure for an insectivorous fish along a temperate riverscape. *Freshwater Science*, 37(3): 618-630. <https://doi.org/10.1086/699013>.
- Da Silva, A.D.R.; Santos, R.B.; Bruno, A.M.S.S.; Gentelini, A.L.; Silva, A.H.G. & Soares, E.C. 2014. Biofilter efficiency of water hyacinth on limnological variables in irrigation channels used for tambaqui farming [Eficiência do aguapé sobre variáveis limnológicas em canais de abastecimento utilizados no cultivo de tambaqui]. *Acta Amazonica*, 44(2): 255-261. <https://doi.org/10.1590/S0044-59672014000200011>.
- Da Silva, H.P.; Petry, A.C. & Da Silva, C.J. 2010. Fish communities of the Pantanal wetland in Brazil: Evaluating the effects of the upper Paraguay river flood pulse on baía Caiçara fish fauna. *Aquatic Ecology*, 44(1): 275-288. <https://doi.org/10.1007/s10452-009-9289-9>.



- Damasceno-Junior, G.A.; Semir, J.; Santos, F.A.M.S. & Leitão-Filho, H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. *Flora*, 200(2): 119-135. <https://doi.org/10.1016/j.flora.2004.09.002>.
- Dary, E.P.; Ferreira, E.; Zuanon, J. & Röpke, C.P. 2017. Diet and trophic structure of the fish assemblage in the mid-course of the Teles Pires river, Tapajós river basin, Brazil. *Neotropical Ichthyology*, 15(4): 1-14. <https://doi.org/10.1590/1982-0224-20160173>.
- Dudley, T.L. 1988. The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. *Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen*, 23(2): 1153-1158. (SIL Proceedings, 1922-2010). <https://doi.org/10.1080/03680770.1987.11899786>.
- Estlander, S.; Nurminen, L.; Olin, M.; Vinni, M. & Horppila, J. 2009. Seasonal fluctuations in macrophyte cover and water transparency of four brown-water lakes: Implications for crustacean zooplankton in littoral and pelagic habitats. *Hydrobiologia*, 620(1): 109-120. <https://doi.org/10.1007/s10750-008-9621-8>.
- Fricke, R.; Eschmeyer, W.N. & Van der Laan, R. (Eds.). 2022. *Eschmeyer's Catalog of Fishes: genera, species, references*. Available: <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Access: 18/03/2022.
- Furlan, A.O.; Muniz, C.C. & Carniello, M.A. 2017. Análise do componente vegetal na alimentação de peixes e da relação com a dispersão de sementes no Pantanal Mato-grossense. *Revista Brasileira de Ciências Ambientais*, 45: 61-70. <https://doi.org/10.5327/z2176-947820170176>.
- Hahn, N.S.; Agostinho, A.A. & Goiten, R. 1997. Feeding ecology of curvina *Plagioscion squamosissimus* (Hechel, 1840) (Osteichthyes, Perciformes) in the Itaipu reservoir and Porto Rico floodplain. *Acta Limnologica Brasiliensia*, 9: 11-22.
- Hahn, N.S.; Fugi, R.; Peretti, D.; Russo, M.R. & Loureiro-Crippa, V.E. 2002. Estrutura trófica da ictiofauna da planície de inundação do alto rio Paraná. In: *A Planície de Inundação do Alto rio Paraná*. Maringá, Area de Pesquisas Ecológicas de Longa Duração, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura-Nupelia, Universidade Estadual de Maringá. p. 123-126.
- Halver, J.E. 1972. *Fish nutrition*. New York, Academic Press.
- Ibañez, C.; Tedesco, P.A.; Bigorne, R.; Hugueny, B.; Pouilly, M.; Zepita, C.; Zubieta, J. & Oberdorff, T. 2007. Dietary-morphological relationships in fish assemblages of small forested streams in the Bolivian Amazon. *Aquatic Living Resources*, 20(2): 131-142. <https://doi.org/10.1051/alr:2007024>.
- Lázaro, W.L.; Oliveira-Júnior, E.S.; Da Silva, C.J.; Castrillon, S.K.I. & Muniz, C.C. 2020. Climate change reflected in one of the largest wetlands in the world: an overview of the Northern Pantanal water regime. *Acta Limnologica Brasiliensia*, 32: 8. <https://doi.org/10.1590/S2179-975X7619>.
- Leach, J.A.; Moore, R.D.; Hinch, S.G. & Gomi, T. 2012. Estimation of forest harvesting-induced stream temperature changes and bioenergetic consequences for cutthroat trout in a coastal stream in British Columbia, Canada. *Aquatic Sciences*, 74(3): 427-441. <https://doi.org/10.1007/s00027-011-0238-z>.
- Leclerc, J. & Desgranges, J.L. 2005. Exploratory multiscale analysis of the fish assemblages and habitats of the lower St. Lawrence River, Québec, Canada. *Biodiversity and Conservation*, 14(5): 1153-1174. <https://doi.org/10.1007/s10531-004-7839-y>.
- Leibold, M.A.; Holyoak, M.; Mouquet, N.; Amarasekare, J.M.; Chase, J.M.; Hoopes, M.F.; Holdt, R.D.; Shurin, J.B.; Law, D.; Tilman, D.; Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7(7): 601-613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>.
- Lin, F.J. 2008. Solving multicollinearity in the process of fitting regression model using the nested estimate procedure. *Quality and Quantity*, 42(3): 417-426. <https://doi.org/10.1007/s11135-006-9055-1>.
- Lolis, A. & Andrian, I.F. 1996. Alimentação de *Pimelodus maculatus* Lacépède, 1803 (Siluriformes, Pimelodidae) na planície de inundação do Alto rio Paraná, Brasil. *Boletim do Instituto de Pesca*, 23: 187-202.
- Lonardoni, A.P.; Goulart, E.; de Oliveira, E.F. & Abelha, M.C.F. 2006. Hábitos alimentares e sobreposição trófica das raia *Potamotrygon falkneri* e *Potamotrygon motoro* (Chondrichthyes, Potamotrygonidae) na planície alagável do alto rio Paraná, Brasil. *Acta Scientiarum. Biological Sciences*, 28(3): 195-202. <https://doi.org/10.4025/actascibiolsci.v28i3.208>.
- Lopes, T.M.; Ganassin, M.J.; Oliveira, A.G.D.; Affonso, I.P. & Gomes, L.C. 2022. Feeding strategy of the introduced *Astronotus crassipinnis* (Cichlidae) in upper Paraná river floodplain. *Iheringia. Série Zoologia*, 112: e2022001. <https://doi.org/10.1590/1678-4766e2022001>.
- Muniz, C.C.; Flamini, A.C.; Kantek, D.L.Z.; Lázaro, W.L.; Souza, A.R. & Oliveira-Junior, E.S. 2019. Stress hídrico determina a dieta de *Tetragonopterus argenteus* (Cuvier, 1816) no Pantanal Norte. *Revista Ibero-Americana de Ciências Ambientais*, 10(4): 209-218. <https://doi.org/10.6008/cbpc2179-6858.2019.004.0016>.
- Naiman, R.J. & Décamps, H. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics*, 28(102): 621-658. <https://doi.org/10.1146/annurev.ecolsys.28.1.621>.
- Nakazawa, T.; Ohba, S.Y. & Ushio, M. 2013. Predator-prey body size relationships when predators can consume prey larger than themselves. *Biology Letters*, 9: 1-5. <https://doi.org/10.1098/rsbl.2012.1193>.
- Oksanen, J.; Guillaume Blanchet, F.; Friendly, M.; Kindt, R.; Legendre, P.; McGinn, D.; Minchin, R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Szoecs, E. & Wagner, H. 2019. *vegan: Community Ecology Package. R package version 2.5-6*. <https://CRAN.R-project.org/package=vegan>.
- Polaz, C.N.M.; Ferreira, F.C. & Petrerre-Junior, M. 2017. The protected areas system in Brazil as a baseline condition for wetlands management and fish conservancy: the example of the Pantanal National Park. *Neotropical ichthyology*, 15(3): e170041. <https://doi.org/10.1590/1982-0224-20170041>.
- Power, M.E. & Dietrich, W.E. 2002. Food webs in river networks. *Ecological Research*, 17(4): 451-471. <https://doi.org/10.1046/j.1440-1703.2002.00503.x>.
- Prado, A.V.R. 2015. *Ecomorfologia e uso de recursos alimentares: relações inter e intraespecíficas da ictiofauna associada a bancos de macrófitas aquáticas*. (Doctoral Thesis). Universidade Estadual de Maringá, Maringá.
- R Core Team. 2019. *R: A language and environment for statistical computing*. Vienna, R Foundation for Statistical Computing. URL <https://www.R-project.org>.
- Resende, E.K. 2000. Trophic structure of fish assemblages in the lower Miranda river, Pantanal, Mato Grosso do Sul State, Brazil. *Revista brasileira de Biologia*, 60(3): 389-403.
- Resende, E.K.; Ferreira, L.; Mônico, I.D.A. & Cruz, L.D.S. 2016. *Aspectos bioecológicos dos peixes associados à macrófitas aquáticas na Baía Tuiuiú, Rio Paraguai, Pantanal Sul*. Corumbá-MS, EMBRAPA Pantanal. (Boletim de Pesquisa e Desenvolvimento INFOTECA-E).
- Resende, E.K.; Pereira, R.A.C.; Almeida, V.D. & Silva, A.D. 1996. *Alimentação de peixes carnívoros da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil*. Corumbá-MS, EMBRAPA-CPAP.
- Root, R.B. 1967. The Niche exploitation pattern of the Blue-Gray Gnatcatcher. *Ecological Monographs*, 37(4): 317-350.
- Sampaio, A.L.A. & Goulart, E. 2011. Cíclídeos neotropicals: ecomorfologia trófica. *Oecologia Australis*, 15(4): 775-798. <https://doi.org/10.4257/oeco.2011.1504.03>.
- Sazima, I. & Machado, F.A. 1983. Hábitos e comportamento de *Roeboides prognathus*, um peixe lepidófago (Osteichthyes, Characoidei). *Boletim*

- de Zoologia, 7(7): 37-56. <https://doi.org/10.11606/issn.2526-3358.bolzoo.1983.122032>.
- Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological monographs*, 52(4): 395-414. <https://doi.org/10.2307/2937352>.
- Shao, X.; Fang, Y.; Jawitz, J.W.; Yan, J. & Cui, B. 2019. River network connectivity and fish diversity. *Science of the Total Environment*, 689: 21-30. <https://doi.org/10.1016/j.scitotenv.2019.06.340>.
- Shoup, D.E. & Wahl, D.H. 2009. The Effects of Turbidity on Prey Selection by Piscivorous Largemouth Bass. *Transactions of the American Fisheries Society*, 138(5): 1018-1027. <https://doi.org/10.1577/t09-015.1>.
- Silva, A.; Souza Filho, E. & Cunha, S.B. 2008. Padrões de canal do rio Paraguai na região de Cáceres (MT). *Revista Brasileira de Geociências*, 38(1): 167-177. <https://doi.org/10.25249/0375-7536.2008381167177>.
- Silva, D.A.; Pessoa, E.K.R.; Costa, S.A.G.L.; Chellappa, N.T. & Chellappa, S. 2012. Ecologia Reprodutiva de *Astyanax lacustris* (Osteichthyes: Characidae) na Lagoa do Piató, Assú, Rio Grande do Norte, Brasil. *Biota Amazônia*, 2(2): 54-61. <https://doi.org/10.18561/2179-5746/biotaamazonia.v2n2p54-61>.
- Silva, M.R.; Fugui, R.; Carniatto, N. & Ganassim, M.J.M. 2014. Importance of allochthonous resources in the diet of *Astyanax aff. fasciatus* (Osteichthyes: Characidae) in streams: a longitudinal approach. *Biota Neotropica*, 14(3): e20130016. <https://doi.org/10.1590/1676-06032014001613>.
- Soares, B.E.; Benone, N.L.; Rosa, D.CO. & Montag, L.F.A. 2020. Do local environmental factors structure the trophic niche of the Splash Tetra, *Copella arnoldi*? A test in an Amazonian stream system. *Acta Amazonica*, 50(1): 54-60. <https://doi.org/10.1590/1809-4392201802681>.
- Suárez, Y.R.; Souza, M.M.; Ferreira, F.S.; Pereira, M.J.; Silva, E.A., Ximenes, L.Q.L.; Azevedo, L.G.; Martins, O.C. & Lima-Júnior, S.E. 2011. Patterns of species richness and composition of fish assemblages in streams of the Ivinhema River basin, Upper Paraná River. *Acta Limnologica Brasiliensia*, (23)2: 177-188. <https://doi.org/10.1590/s2179-975x2011000200008>.
- Utne-Palm, A.C. 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Marine and Freshwater Behaviour and Physiology*, 35(1-2): 111-128. <https://doi.org/10.1080/10236240290025644>.
- Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R. & Cushing, C.E. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1): 130-137.
- Ward, J.V.; Tockner, K.; Arscott, D.B.; & Claret, C. 2002. Riverine landscape diversity. *Freshwater Biology*, 47(4): 517-539. <https://doi.org/10.1046/j.1365-2427.2002.00893.x>.
- Winemiller, K.O.; Tarim, S.; Shormann, D. & Cotner, J. B. 2000. Fish Assemblage Structure in Relation to Environmental Variation among Brazos River Oxbow Lakes. *Transactions of the American Fisheries Society*, 129(2): 451-468. [https://doi.org/10.1577/1548-8659\(2000\)129<0451:fasirt>2.0.co;2](https://doi.org/10.1577/1548-8659(2000)129<0451:fasirt>2.0.co;2).
- Wolff, L.L.; Carniatto, N. & Hahn, N.S. 2013. Longitudinal use of feeding resources and distribution of fish trophic guilds in a coastal Atlantic stream, southern Brazil. *Neotropical Ichthyology*, 11(2): 375-386. <https://doi.org/10.1590/S1679-62252013005000005>.
- Wootton, R.J. 1999. *Ecology of teleost fish*. Dordrecht, Springer.

## SUPPLEMENTARY MATERIAL

**Table 1.** List of trophic guilds with species. **PLT:** plateau **CON:** confluence e **PLA:** plain.

Voucher	Trophic guilds, species	Authors	PLT %	CON %	PLA %	Length range (cm)	Weight range (g)
<b>Piscivores</b>			<b>0.85</b>	<b>2.86</b>	<b>2.01</b>	<b>0.9-80.4</b>	<b>0.01-13300</b>
LIPAN052	<i>Acestrorhynchus pantaneiro</i> Menegalezes, 1992	Resende et al. (1996)	0.212	0.371	0.042	8.5-22.1	5.8-202.8
LIPAN265	<i>Ageneiosus ucayalensis</i> Castelnau, 1855	Corrêa et al. (2009)	—	—	0.010	3.5	0.74
LIPAN272	<i>Ageneiosus valenciennesi</i> Bleeker, 1864	Hahn et al. (2002)	—	0.018	0.010	19-27.8	71.5-156.1
LIPAN012	<i>Catathyridium jenynsii</i> (Günther, 1862)	Hahn et al. (2002)	—	0.009	—	5.6	6.8
LIPAN294	<i>Cichla</i> sp Block & Schneider, 1801	Hahn et al. (2002)	—	0.009	—	21	277.95
LIPAN266	<i>Galeocharax humeralis</i> (Valenciennes, 1834)	Corrêa et al. (2009)	—	0.168	0.366	1.9-4.2	1.18-1.12
LIPAN149	<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)	Hahn et al. (2002)	0.018	0.415	0.031	16.8-52.1	67.2-2142
LIPAN050	<i>Hoplias malabaricus</i> Bloch, 1794	Resende et al. (2016)	0.460	1.042	0.418	0.9-10.8	0.01-1090
LIPAN267	<i>Pinirampus pirinampu</i> (Spix & Agassiz, 1829)	Hahn et al. (2002)	—	—	0.052	33.1-68.4	22-4390
LIPAN047	<i>Plagioscion ternetzi</i> Boulenger, 1895	Resende et al. (1996)	—	0.035	—	18.1-18.5	111.17-118.2
LIPAN117	<i>Potamotrygon falkneri</i> Castex & Maciel, 1963	Lonardoní et al. (2006)	0.071	0.018	—	20.5-53	35.42-1770
LIPAN293	<i>Pseudoplatystoma corruscans</i> (Spix & Agassiz, 1829)	Resende et al. (1996)	—	0.026	0.105	25.8-108.1	31.10-13300
LIPAN120	<i>Pseudoplatystoma fasciatum</i> (Linnaeus, 1766)	Resende et al. (1996)	—	0.062	0.052	14.6-77.8	153.6-6410
LIPAN053	<i>Pygocentrus nattereri</i> Kner, 1858	Resende et al. (1996)	0.018	0.238	0.324	10.5-29.5	49.34-860
LIPAN268	<i>Roeboides bonariensis</i> Steindachner, 1879	Resende et al. (2016)	0.018	0.009	0.094	2.5-7	0.19-6.11
LIPAN292	<i>Salminus brasiliensis</i> (Cuvier, 1816)	Corrêa et al. 2009	—	0.009	—	50.5	2210
LIPAN051	<i>Serrasalmus maculatus</i> Kner, 1858	Corrêa et al. (2009)	0.018	0.177	0.157	1.2-23.5	0.03-506.3
LIPAN177	<i>Serrasalmus marginatus</i> Valenciennes, 1837	Corrêa et al. (2009)	0.035	0.124	0.167	1.5-19.9	0.06-480
LIPAN125	<i>Serrasalmus spilopleura</i> Kner, 1858	Resende et al. (2016)	—	0.035	0.105	9.6-23.7	33-638
LIPAN123	<i>Sorubim lima</i> (Bloch & Schneider, 1801)	Hahn et al. (2002)	—	0.026	0.031	14.5-47.8	20-1040
<b>Detritivores</b>			<b>11.84</b>	<b>17.34</b>	<b>10.27</b>	<b>1-55</b>	<b>0.01-810</b>
LIPAN133	<i>Apareiodon affinis</i> (Steindachner, 1879)	Hahn et al. (2002)	0.478	—	0.209	2.7-9	0.20-12.5
LIPAN073	<i>Curimatella dorsalis</i> (Eigenmann & Eigenmann, 1889)	Polaz et al. (2017)	1.026	1.625	0.178	3.1-8.1	0.68-7.1
LIPAN063	<i>Curimatopsis myersi</i> Vari, 1982	Resende et al. (2016); Polaz et al. (2017)	0.035	1.042	0.679	1.2-4	0.03-1.81
LIPAN036	<i>Cyphocharax gillii</i> (Eigenmann & Kennedy, 1903)	Resende et al. (2016); Polaz et al. (2017)	—	0.088	0.031	2.5-10	0.36-28.59
LIPAN144	<i>Farlowella paraguayensis</i> Retzer & Page, 1997	Polaz et al. (2017)	—	—	0.021	5-6.2	0.14-0.20
LIPAN151	<i>Hypoptopoma inexpectatum</i> (Holmberg, 1893)	Resende et al. (2016)	7.415	11.171	2.759	1.7-7	0.14-7.6

Voucher	Trophic guilds, species	Authors	PLT %	CON %	PLA %	Length range (cm)	Weight range (g)
LIPAN273	<i>Hypostomus cochlodon</i> Kner, 1854	Polaz et al. (2017)	—	—	0.052	1.5-4.9	0.07-3.9
LIPAN056	<i>Hypostomus</i> sp (Lacepède 1803)	Polaz et al. (2017)	0.867	0.433	2.822	1-7.5	0.01-7.5
LIPAN269	<i>Liposarcus anisitsi</i> (Eigenmann & Kennedy, 1903)	Resende et al. (2016)	—	0.071	0.052	20.5-34.5	223.9-770
LIPAN274	<i>Loricaria</i> sp Linnaeus, 1758	Polaz et al. (2017)	—	—	0.010	1.6-8.7	0.09-6.9
LIPAN124	<i>Loricariichthys labialis</i> (Boulenger, 1895)	Resende et al. (2016); Polaz et al. (2017)	—	—	0.010	15	18.4
LIPAN156	<i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979	Resende et al. (2016); Polaz et al. (2017)	0.035	0.035	0.031	7.2-26	0.23-127.5
LIPAN270	<i>Megalancistrus aculeatus</i> (Perugia, 1891)	Hahn et al. 2002	—	0.026	—	3-4.3	0.85-2.04
LIPAN004	<i>Potamorhina squamoralevis</i> (Braga & Azpelicueta, 1983)	Polaz et al. (2017)	0.018	0.062	0.512	1.2-23.7	0.04-369
LIPAN091	<i>Prochilodus lineatus</i> (Valenciennes, 1836)	Polaz et al. (2017)	—	0.274	0.010	8.7-33	19-810
LIPAN069	<i>Psectrogaster curviventris</i> (Eigenmann & Kennedy, 1903)	Polaz et al. (2017)	—	0.194	0.449	4.2-55	1.62-226
LIPAN130	<i>Rineloricaria parva</i> (Boulenger, 1895)	Resende et al. (2016); Polaz et al. (2017)	0.301	2.119	1.829	1.6-8.7	0.09-6.9
LIPAN018	<i>Satanoperca papaterra</i> (Heckel, 1840)	Sampaio & Goulart 2011	0.053	0.071	0.010	8-16.5	26.8-167
LIPAN178	<i>Spatuloricaria evansii</i> (Boulenger, 1892)	Polaz et al. (2017)	0.212	0.018	0.010	3-31	0.11-227.2
LIPAN179	<i>Steindachnerina brevipinna</i> (Boulenger, 1902)	Resende et al. (2016)	1.363	0.018	0.439	2.5-10.7	0.24-38.2
LIPAN076	<i>Steindachnerina conspersa</i> (Holmberg, 1891)	Resende (2000)	—	0.053	0.021	3.2-10.5	0.73-41.4
LIPAN116	<i>Sturissoma barbatum</i> (Kner, 1853)	Polaz et al. (2017)	0.035	0.044	0.136	5.8-11.4	0.55-71.73
<b>Herbivores</b>			<b>53.91</b>	<b>1.31</b>	<b>2.0</b>	<b>1.3-46.7</b>	<b>0.07-3720</b>
LIPAN132	<i>Abramites hypselonotus</i> (Günther, 1868)	Polaz et al. (2017)	0.177	0.044	0.073	1.7-9.3	0.09-21.52
LIPAN005	<i>Mesonauta festivus</i> (Heckel, 1840)	Polaz et al. (2017)	—	0.088	0.125	2.5-10	0.20-56.1
LIPAN287	<i>Myloplus levis</i> (Eigenmann & McAtee, 1907)	Polaz et al. (2017)	—	0.044	0.167	7.5-25.2	19.2-270
LIPAN286	<i>Mylossoma paraguayensis</i> (Norman, 1928)	Resende et al. (2016)	—	—	0.010	14.5	102.3
LIPAN071	<i>Mylossoma duriventre</i> (Cuvier, 1818)	Polaz et al. (2017)	—	0.009	0.659	2.8-22.2	3.9-490
LIPAN161	<i>Otocinclus vittatus</i> Regan, 1904	Polaz et al. (2017)	53.61	0.318	0.042	1.3-5	0.07-0.60
LIPAN074	<i>Piabucus melanostoma</i> Holmberg, 1991	Polaz et al. (2017)	0.088	0.283	0.303	4.9-8.5	0.39-3.9
LIPAN164	<i>Piaractus mesopotamicus</i> (Holmberg, 1887)	Polaz et al. (2017)	0.035	0.009	0.366	12-40.8	72.6-2420
LIPAN288	<i>Schizidon borelli</i> (Boulenger, 1900)	Polaz et al. (2017)	—	0.230	0.240	4.6-15.5	0.56-702.1
LIPAN092	<i>Schizidon isognathus</i> Kner, 1858	Polaz et al. (2017)	—	0.283	0.010	3.2-22.8	0.68-250.2
<b>Invertivores</b>			<b>11.43</b>	<b>34.01</b>	<b>44.06</b>	<b>0.09-9.7</b>	<b>0.01-9.01</b>
LIPAN279	<i>Apistogramma trifasciata</i> (Eigenmann & Kennedy, 1903)	Resende et al. (2016)	—	0.645	1.850	0.8-4.6	0.01-1.4
LIPAN037	<i>Aphyocharax anisitsi</i> Eigenmann & Kennedy, 1903	Resende et al. (2016)	1.380	0.406	1.087	1.3-3	0.03-7.13
LIPAN289	<i>Aphyocharax paraguayensis</i> Eigenmann, 1915	Resende et al. (2016)	—	0.009	0.387	1.5-3	0.03-0.47
LIPAN087	<i>Apistogramma commbrae</i> (Regan, 1906)	Polaz et al. (2017)	0.425	0.115	0.136	1.2-3.1	0.04-1.93
LIPAN070	<i>Apteronotus albifrons</i> (Linnaeus, 1766)	Polaz et al. (2017)	—	0.009	0.261	4.3-19.8	0.34-19.9
LIPAN097	<i>Astronotus crassipinis</i> Heckel, 1840	Polaz et al. (2017)	—	0.044	—	16.5-22	125.5-461
LIPAN021	<i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1918)	Hahn et al. (2002)	—	0.009	—	3.9	0.91
LIPAN111	<i>Brachyhypopomus</i> sp Mago Leccia, 1994	Resende et al. (2016)	0.088	0.636	2.216	4.7-22.1	0.05-22
LIPAN028	<i>Bryconamericus exodon</i> Eigenmann, 1907	Polaz et al. (2017)	0.088	0.177	0.125	1.3-5.7	0.08-2.76
LIPAN136	<i>Bryconamericus stramineus</i> Eigenmann, 1908	Polaz et al. (2017)	0.991	0.009	0.031	1.2-4.8	0.05-2
LIPAN011	<i>Bujurquina vittata</i> (Heckel, 1840)	Resende et al. (2016)	0.053	0.159	0.063	1.1-6.9	0.03-14.5
LIPAN030	<i>Characidium</i> aff. <i>zebra</i> Eigenmann, 1909	Resende et al. (2016)	2.442	2.464	1.725	1.2-4.7	0.02-2.32
LIPAN290	<i>Characidium laterale</i> (Boulenger, 1895)	Polaz et al. (2017)	—	0.018	0.125	2.2-3.3	0.21-0.53
LIPAN072	<i>Charax leticiae</i> Lucena, 1987	Resende et al. (2016)	0.053	0.062	0.157	4.9-9.4	1.38-15.95
LIPAN112	<i>Crenicichla lepidota</i> Heckel, 1840	Resende et al. (2016)	—	0.062	0.021	11-33.1	35-525.6
LIPAN140	<i>Corydoras aeneus</i> (Gill, 1858)	Brandão-Gonçalves et al. (2010)	0.230	—	—	2-3.5	0.40-1.9
LIPAN027	<i>Corydoras hastatus</i> Eigenmann & Eigenmann, 1888	Polaz et al. (2017)	0.124	0.265	0.084	1.2-2	0.04-0.46
LIPAN055	<i>Crenicichla vittata</i> Heckel, 1840	Resende et al. (2016)	0.319	2.181	2.028	2-16.8	0.12-113.7
LIPAN024	<i>Eigenmania virescens</i> (Valenciennes, 1847)	Polaz et al. (2017)	—	0.106	5.676	1.7-18.7	0.03-11
LIPAN025	<i>Eigenmania trilineata</i> Lopes & Castello, 1996	Resende et al. (2016)	0.018	5.175	10.996	2.5-31.5	0.03-39.6
LIPAN46	<i>Entomocorus benjamini</i> Eigenmann, 1917	Resende et al. (2016)	—	0.026	1.631	2-4.9	0.08-12.9
LIPAN145	<i>Gasteropelecus sternicla</i> (Linnaeus, 1758)	Polaz et al. (2017)	0.672	0.212	0.010	2-6	0.23-3.7
LIPAN060	<i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)	Polaz et al. (2017)	0.053	0.168	0.345	4.4-90	0.34-1370
LIPAN107	<i>Gymnotus paraguayensis</i> Albert & Crampton, 2003	Polaz et al. (2017)	—	0.018	—	9.9-11.7	2.1-3.7
LIPAN022	<i>Hemigrammus ulreyi</i> (Boulenger, 1895)	Resende et al. (2016)	0.566	6.323	2.530	1.5-3.4	0.06-1.1
LIPAN146	<i>Hemigrammus marginatus</i> Ellis, 1911	Brandão-Gonçalves et al. (2010)	0.035	—	—	2.5-2.7	0.27-0.33
LIPAN058	<i>Hemiodontichthys acipenserinus</i> (Kner, 1853)	Polaz et al. (2017)	—	0.009	—	9	3.26
LIPAN032	<i>Hyphessobrycon eques</i> (Steindachner, 1882)	Polaz et al. (2017)	0.672	7.144	6.930	0.9-9.7	0.01-2.2
LIPAN034	<i>Ituglanis herberti</i> (Miranda Ribeiro, 1940)	Polaz et al. (2017)	0.177	2.874	—	1.3-3.2	0.01-12
LIPAN291	<i>Ituglanis eichorniarum</i> (Miranda Ribeiro, 1912)	Polaz et al. (2017)	0.009	0.010	—	1.5-3.4	0.05-0.45
LIPAN081	<i>Ossancora eigenmanni</i> (Boulenger, 1895)	Polaz et al. (2017)	0.238	0.146	—	3.3-6	0.87-5.67
LIPAN045	<i>Pimelodella mucosa</i> Eigenmann & Ward, 1907	Resende et al. (2016); Polaz et al. (2017)	1.274	1.872	1.913	2.7-9	0.35-15.8
LIPAN167	<i>Poptella paraguayensis</i> (Eigenmann, 1907)	Polaz et al. (2017)	1.345	3.214	0.157	2-6.9	0.38-8.7

Voucher	Trophic guilds, species	Authors	PLT %	CON %	PLA %	Length range (cm)	Weight range (g)
LIPAN061	<i>Potamorhaphis eigenmanni</i> Miranda Ribeiro, 1915	Ibañez et al. (2007)	—	—	0.021	11.3-24	15.1-24.88
LIPAN122	<i>Potamotrygon motoro</i> (Müller & Henle, 1841)	Lonardoni et al. (2006)	—	0.018	—	30.5-50.7	158-278.63
LIPAN105	<i>Pseudotylorus angusticeps</i> (Günther, 1866)	Resende et al. (2016)	0.106	—	—	21-26	11.4-21.2
LIPAN029	<i>Pyrhulina australis</i> Eigenmann & Kennedy, 1903	Resende et al. (2016); Polaz et al. (2017)	0.035	0.971	2.216	1.4-4.2	0.06-2.47
LIPAN285	<i>Rhamphichthys hahni</i> (Meinken, 1937)	Resende et al. (2016); Polaz et al. (2017)	—	0.035	0.178	1.5-44.3	0.02-177.1
LIPAN049	<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	Resende et al. (2016)	0.018	0.742	1.056	2.4-52.5	0.60-380
LIPAN106	<i>Synbranchus marmoratus</i> Bloch, 1795	Polaz et al. (2017)	0.142	0.026	0.052	4.5-22.9	0.11-10.60
LIPAN019	<i>Tatia neivai</i> (Ihering, 1930)	Polaz et al. (2017)	—	0.009	—	2.7	0.49
LIPAN065	<i>Tetragonopterus argenteus</i> Cuvier, 1816	Resende et al. (2016)	—	0.212	0.314	4.5-11.1	0.73-57.3
LIPAN180	<i>Thoracocharax stellatus</i> (Kner, 1858)	Resende et al. (2016); Polaz et al. (2017)	0.142	0.424	0.031	2.9-10.8	0.56-4.7
LIPAN119	<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	Resende et al. (2016)	0.159	0.353	0.199	4.9-16.4	0.70-123
<b>Lepidophagous</b>			<b>0.33</b>	<b>0.28</b>	<b>0.52</b>	<b>2.5-20.5</b>	<b>0.19-6.11</b>
LIPAN176	<i>Roeboides prognathus</i> Boulenger, 1895	Sazima & Machado (1983)	0.336	0.380	0.523	2.5-20.5	0.19-6.11
<b>Omnivores</b>			<b>21.63</b>	<b>43.43</b>	<b>37.66</b>	<b>1-57.8</b>	<b>0.01-2600</b>
LIPAN066	<i>Aequidens plagiozonatus</i> Kullander, 1984	Polaz et al. (2017)	—	0.795	0.188	1.1-6.7	0.02-13.1
LIPAN101	<i>Anadoras weddellii</i> (Castelnau, 1855)	Resende et al. (2016); Polaz et al. (2017)	0.142	0.751	0.324	2.5-9.5	0.06-19
LIPAN283	<i>Aphyocharax dentatus</i> Eigenmann e Kennedy, 1903	Polaz et al. (2017)	3.840	1.210	0.575	1.5-6.7	0.07-6.4
LIPAN282	<i>Apteronotus caudimaculosus</i> de Santana, 2003	Polaz et al. (2017)	—	—	0.042	9.4-12.7	2.40-5.93
LIPAN102	<i>Astyanax asuncionensis</i> Géry, 1972	Resende et al. (2016); Polaz et al. (2017)	—	0.362	0.251	5-18.3	2.72-12.10
LIPAN001	<i>Brycon hilarii</i> (Valenciennes, 1850)	Polaz et al. (2017)	—	0.035	0.084	18.7	136.1-630
LIPAN110	<i>Ctenobrycon alleni</i> (Eigenmann & Mcate, 1907)	Polaz et al. (2017)	—	0.026	0.105	6.5-8.9	5.8-16.9
LIPAN033	<i>Gymnocorimbis ternetzi</i> Boulenger, 1895	Resende et al. (2016)	0.018	0.018	0.220	2-4	0.17-2.2
LIPAN083	<i>Gymnogeophagus balzanii</i> (Perugia, 1891)	Resende et al. (2016)	0.142	0.018	0.063	3.3-13.5	1.34-131.9
LIPAN148	<i>Hemiodus orthonops</i> Eigenmann & Kennedy, 1903	Polaz et al. (2017)	0.088	0.124	0.669	3-26.6	0.28-242.3
LIPAN062	<i>Jupiaba acantogaster</i> (Eigenmann, 1911)	Polaz et al. (2017)	3.327	0.442	6.345	1.1-3.5	0.01-0.46
LIPAN093	<i>Laetacara dorsigera</i> (Heckel, 1840)	Polaz et al. (2017)	0.035	0.026	0.084	2-7.3	0.37-20.1
LIPAN100	<i>Leporinus friderici</i> (Bloch, 1794)	Resende et al. (2016); Polaz et al. (2017)	0.035	0.424	0.491	3.5-25.5	0.48-380
LIPAN020	<i>Leporinus lacustris</i> Campos, 1945	Polaz et al. (2017)	—	0.185	0.178	3.5-25.5	0.79-244
LIPAN154	<i>Leporinus macrocephalus</i> Garavello & Britski, 1988	Resende et al. (2016); Polaz et al. (2017)	0.088	0.009	0.010	20-48	210-2600
LIPAN155	<i>Leporinus striatus</i> Kner, 1858	Resende et al. (2016); Polaz et al. (2017)	0.018	0.318	0.376	1.7-7.4	0.12-7.6
LIPAN157	<i>Moenkhausia dichroua</i> (Kner, 1858)	Polaz et al. (2017)	4.229	12.390	12.899	1-4.6	0.01-2.33
LIPAN035	<i>Moenkhausia sanctaefilomenae</i> (Steindachner, 1907)	Resende et al. (2016)	1.522	2.746	2.080	1.6-5.7	0.07-5.3
LIPAN280	<i>Odontostilbe calliura</i> (Boulenger, 1900)	Resende et al. (2016)	5.256	5.961	4.097	1-3	0.01-4.81
LIPAN281	<i>Odontostilbe pequirá</i> (Steindachner, 1882)	Polaz et al. (2017)	2.265	14.509	6.042	1-4.1	0.01-0.86
LIPAN075	<i>Oxydoras kneri</i> Bleeker, 1862	Polaz et al. (2017)	—	0.026	0.021	31-38.8	458.9-980
LIPAN284	<i>Pimelodella gracilis</i> (Valenciennes, 1835)	Resende et al. (2016)	—	—	0.010	8.1	7.7
LIPAN65	<i>Pimelodus argenteus</i> Perugia, 1891	Resende et al. (2016); Polaz et al. (2017)	—	0.009	—	17	100.68
LIPAN042	<i>Pimelodus maculatus</i> Lacépède, 1803	Lolis & Andrian (1996)	—	0.406	0.220	3.9-31.3	0.5-550
LIPAN166	<i>Pimelodus ornatus</i> Kner, 1858	Hahn et al. (2002)	0.018	0.009	0.031	22-39.3	180-1810
LIPAN275	<i>Platydoras armatulus</i> (Valenciennes, 1840)	Polaz et al. (2017)	—	0.088	0.073	4-6.1	2.1-7.36
LIPAN026	<i>Prionobrama paraguayensis</i> (Eigenmann, 1914)	Polaz et al. (2017)	0.248	0.627	0.042	2.2-3.9	0.13-1.78
LIPAN006	<i>Psellogrammus kennedyi</i> (Eigenmann, 1903)	Polaz et al. (2017)	0.053	0.565	0.941	1.4-5.8	0.05-2.46
LIPAN276	<i>Pterodoras granulosus</i> (Valenciennes, 1821)	Hahn et al. 2002	—	—	0.021	28-57.8	5.3-22.8
LIPAN278	<i>Rhamdia</i> aff. <i>quelen</i> (Quoy & Gaimard, 1824)	Polaz et al. (2017)	—	0.026	0.010	2.3-23.5	0.12-241.5
LIPAN277	<i>Trachelyopterus coriaceus</i> Valenciennes, 1840	Polaz et al. (2017)	—	—	0.073	5.5-12.5	5.9-65.5
LIPAN064	<i>Trachydoras paraguayensis</i> (Eigenmann & Ward, 1907)	Resende et al. (2016)	0.283	0.450	0.470	3.7-7.6	1.4-28.4
LIPAN003	<i>Triportheus paranensis</i> (Günther, 1874)	Resende et al. (2016)	0.018	0.874	0.627	3.5-20.5	2.5-172.4
<b>Total</b>			<b>100</b>	<b>100</b>	<b>100</b>		