



# Water-level fluctuations lead to changes in the diet of an omnivorous fish in a floodplain

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The hydrological regime leads to fluctuations in the availability of food resources for fish, which may reflect in their diet variation. Our main goal was to analyze the relationship between water-level fluctuations and the diet and the body condition of *Trachelyopterus galeatus* in the Upper Paraná River floodplain. The fish used in the study were sampled quarterly along nine years, at nine sampling stations. Our results showed that diet of *T. galeatus* varied in response to oscillations in the hydrometric level, with the consumption of terrestrial invertebrates being positively related to hydrometric level, while the consumption of aquatic invertebrates was negatively related. The trophic niche breadth and feeding activity were not affected by hydrometric level, but the fish body condition was positively affected. The high food plasticity allows *T. galeatus* to consume the most available resources (e.g., terrestrial invertebrates in high water levels), which probably contributed to the increase in its body condition in higher hydrometric levels. In summary, the hydrological dynamic is fundamental for the diet variation of omnivorous fish, which can take advantage of the resource availability according to the hydrometric level, increasing its body condition when allochthonous resources as terrestrial invertebrates are supposed to be more available.

**Keywords:** Body condition, Feeding activity, Hydrological cycle, *Trachelyopterus galeatus*, Trophic ecology.

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O regime hidrológico leva a flutuações na disponibilidade de recursos alimentares para os peixes, o que pode refletir na variação de sua dieta. O principal objetivo foi analisar a relação entre as oscilações do nível hidrométrico e a dieta e condição corporal de *Trachelyopterus galeatus* na planície de inundação do alto rio Paraná. Os peixes foram amostrados trimestralmente durante nove anos, em nove locais. Nossos resultados mostraram que a dieta de *T. galeatus* variou em resposta às oscilações do nível hidrométrico, com o consumo de invertebrados terrestres sendo positivamente relacionado com o nível hidrométrico, enquanto o consumo de invertebrados aquáticos foi negativamente relacionado. O nicho trófico e a atividade alimentar não foram afetados pelo nível hidrométrico, mas a condição corporal dos peixes foi positivamente afetada. A alta plasticidade alimentar permite que *T. galeatus* aproveite recursos mais disponíveis (por exemplo, invertebrados terrestres em níveis elevados), o que provavelmente contribui para o aumento da condição corporal em níveis hidrométricos elevados. Em resumo, a dinâmica hidrológica é fundamental para a variação da dieta de peixes onívoros, que podem aproveitar a disponibilidade de recursos de acordo com o nível hidrométrico, aumentando sua condição corporal quando recursos alóctones, como invertebrados terrestres, são supostamente mais disponíveis.

**Palavras-chave:** Atividade alimentar, Ciclo hidrológico, Condição corporal, Ecologia trófica, *Trachelyopterus galeatus*.

## INTRODUCTION

The natural dynamics of the hydrological cycle in river-floodplain systems are characterized by alternating periods of drought and flood. The hydrological regime is the main factor that influences the functioning of these ecosystems, changing the connections among environments, regulating the quantity and quality of habitats for fish populations (Junk *et al.*, 1989), controlling the growth of these animals (De Graaf, 2003), and changing the limnological characteristics and biological processes (Thomaz *et al.*, 2004). Hydrological cycles with regular drought and flood periods are essential for maintaining a high productivity and diversity of these ecosystems (Junk *et al.*, 1989; Agostinho *et al.*, 2004a). These seasonal changes lead to fluctuations in the availability and quality of food resources for fish (Goulding *et al.*, 1988; Luz-Agostinho *et al.*, 2008; Correa, Winemiller, 2014; Quirino *et al.*, 2017).

In low water periods, a reduction in the abundance of resources is expected (Bonvillain, Fontenot, 2020), which leads to the intensification of interactions, such as competition and predation (Junk *et al.*, 1989; Gomes *et al.*, 2012; Medeiros, Arthington, 2014), making the species diet less diversified and leading to a contraction of the trophic niche (Balcombe *et al.*, 2005; Quirino *et al.*, 2017). In contrast, in high water periods, there is an increase in the availability of food, when a large amount of terrestrial resources, such as fruits, seeds and insects are available to fishes that occupy the flooded area (Goulding, 1988; Junk *et al.*, 1989; Esteves, Galetti, 1995; Pereira *et al.*, 2011; Quirino *et al.*, 2017). Greater ecological opportunity, that is, greater availability of resources that

may be exploited, associated with the high waters period (Araújo *et al.*, 2011) contribute greatly to the diet composition, generally expanding the trophic niche breadth some fish species (Delbeek, Williams 1987; Walker *et al.*, 2013; Quirino *et al.*, 2015, 2017; Brambilla *et al.*, 2019). The inclusion of more profitable food resources that are available during the high-water period (Costa-Pereira *et al.*, 2017), may reflect in a better body condition for omnivorous fish, since the condition of a fish is affected, among other factors, by environmental and nutritional variations (Abujanra *et al.*, 2009; Jin *et al.*, 2015; Cardozo *et al.*, 2018). The inclusion of new resources may release individuals from intense intraspecific competition (Araújo *et al.*, 2011), probably favoring their well-being. Especially for floodplain systems, understanding the relationship between water-level fluctuations and the diet variability can help to clarify the mechanisms that allow the persistence and the high abundance of a species in a dynamic environment (Costa-Pereira *et al.*, 2017).

Floodplains under the influence of dams upstream, modifies the natural dynamics of the hydrological regime (Agostinho *et al.*, 2004b; Roberto *et al.*, 2009; Santos *et al.*, 2017), changing the intensity, frequency, duration, and the time when floods occur, besides reducing the seasonally flooded areas (Thomaz *et al.*, 2004; Agostinho *et al.*, 2007; Souza-Filho, 2009). The water flow in the Upper Paraná River floodplain is controlled by the presence of a cascade of reservoirs upstream and this control has become more intense with the construction of the Porto Primavera Reservoir (formed in 1998) (Souza-Filho, 2009). Although the river dynamics are still associated with the hydrological regime, and the oscillation between periods of drought and flood still define the composition of the environments in floodplains (Thomaz *et al.*, 2004; Agostinho *et al.*, 2004b; Santos *et al.*, 2017), the control of the water flow can lead to extreme droughts, which do not represent natural disturbances (Moi *et al.*, 2020).

Prolonged drought periods can promote the maximization of competitive exclusion by increasing local extinctions (Thomaz *et al.*, 2007). For example, Moi *et al.* (2020) observed that periods of extreme drought in the Paraná River, which become more frequent after the damming of the river, negatively impacted the benthic community and, consequently, the ecosystem, since macroinvertebrates are one of the main food resources for several organisms, especially fish. Likewise, the elimination of the annual flood pulse in the Barataria basin (Mississippi River floodplain) reduced the abundance of freshwater crayfish, the main prey for carnivorous fish, and potentially altered all trophic dynamics of this system (Bonvillain, Fontenot, 2020).

Based on the premises that flood pulses change the composition, amount, and quality of food resources, our main goal was to analyze the relationship between water-level fluctuations and *Trachelyopterus galeatus* Linnaeus, 1766 (Siluriformes: Auchenipteridae) diet and body condition variations. It is one of most abundant species in the Upper Paraná River floodplain (Júlio-Júnior *et al.*, 2009; Tonella *et al.*, 2018; Long Term Ecological Research (LTER) (unpublished data), a medium size omnivorous species that has a broad trophic niche breadth (Tonella *et al.*, 2018; Garcia *et al.*, 2018, 2020). Omnivory can be considered a beneficial trait for many species, once the broad feeding spectrum allows the species to exploit a high diversity of food items, which can generate a relaxation in competitive interactions (Ricciardi, Rasmussen, 1998; Ribeiro *et al.*, 2007; Nurkse *et al.*, 2016). Changes in diet associated with the water level, increasing, or reducing the trophic niche, can be considered evolutive answers to the environmental

conditions associated with water level oscillations in river–floodplain ecosystems. Thus, we hypothesize that *T. galeatus* changes its feeding habit regarding diet composition and the trophic niche breadth according to the water level once this species is able to take advantage of the different resources available in periods of increased water level. We expect that (i) the consumption of allochthonous items for *T. galeatus* is positively affected by increasing hydrometric levels; (ii) the consumption of autochthonous items for *T. galeatus* is negatively affected by increased hydrometric level; (iii) the trophic niche breadth is positively influenced by increased hydrometric level; and (iv) an increase in the feeding activity and body condition with the increase of the hydrometric level.

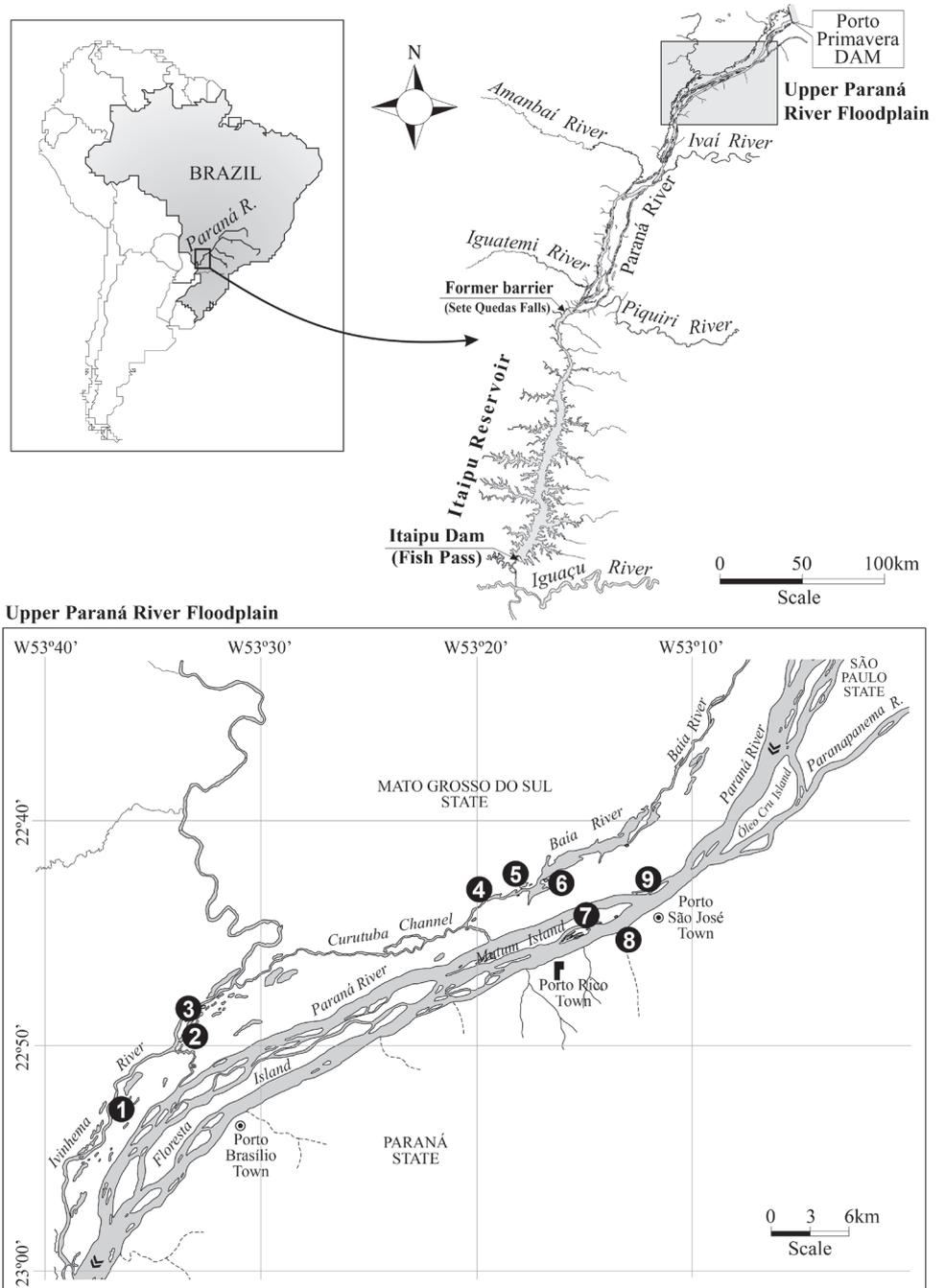
## MATERIAL AND METHODS

**Study area.** The Upper Paraná River floodplain is located between the Porto Primavera dam (upstream) and the beginning of the Itaipu reservoir (Fig. 1). This is the last undammed stretch of the Upper Paraná River in the Brazilian territory, with 230 km in length. It presents a great diversity of habitats, including the alluvial plain with numerous secondary channels, connected and isolated lakes, and the main channels of the Paraná, Baía, and Ivinhema rivers (Agostinho *et al.*, 2007). Three protected areas are located in this region: Várzeas do Rio Ivinhema State Park, Environmental Protection Area of the Paraná River Islands and Floodplains, and Ilha Grande National Park. In this study, nine environments were sampled: the main channel of the Paraná, Baía, and Ivinhema rivers (three sampling stations) and six lakes (Fig. 1).

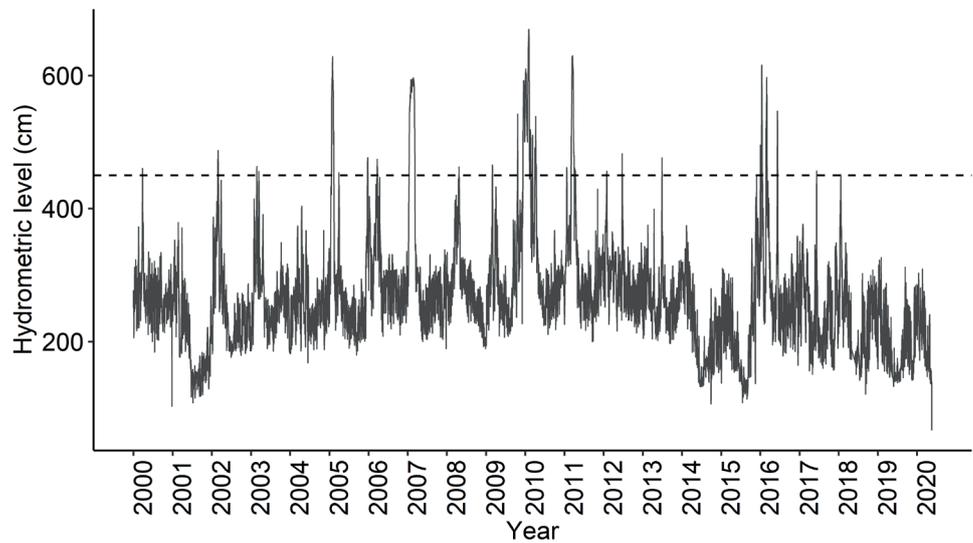
**Sampling.** The fish used in this study were sampled quarterly (March, June, September and December) along eight years (2005, 2008, 2009, 2010, 2013, 2016, 2018, 2019), and in March and September of 2017, at nine sampling stations, being three rivers (Paraná, Baía and Ivinhema) and six lakes (Fig. 1). Fish were sampled with gillnets with different mesh sizes (3 to 16 cm between opposite nodes), which were exposed for 24 h, and fish were removed at 8, 16 and 22 h. Voucher specimens are deposited at the Coleção Ictiológica of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia), of the Universidade Estadual de Maringá (NUP 11104).

**Hydrometric level.** Data from the hydrometric levels of the Paraná River were obtained from the National Water Agency (Hidroweb; [www.ana.gov.br](http://www.ana.gov.br)), measured at the fluvimetric station (64575003) located in the municipality of Porto São José, Paraná State, Brazil. The hydrological level is measured daily (Fig. 2), however, in view that fish sampling occurs quarterly, we summarize the river level in a quarterly mean.

The hydrological cycle of the floodplain has been altered due to upstream reservoirs, which was intensified after the construction of the Porto Primavera reservoir in 1998 (Souza-Filho, 2009). However, the floodplain still has a flood pulse, with the flood period usually occurring from November/December to April/May, with maximum hydrometric levels prevailing between January and March, and the drought between June and October with minimum values between July and September (Agostinho *et al.*, 2004c).



**FIGURE 1** | Location of the Upper Paraná River floodplain (downstream of the Porto Primavera dam and upstream of the Itaipu reservoir) and the nine sampling stations on the Paraná, Baía, and Ivinhema rivers.



**FIGURE 2** | Daily variation in the level of the Paraná River between 2000 and 2020 (provided by the Agência Nacional de Águas e Saneamento Básico - ANA). The horizontal line represents the 4.5 m level when the Paraná River overflows.

**Laboratory procedures.** Fish were measured (Standard Length = SL in mm), weighted (g) and their stomachs were visually assessed for the degree of stomach repletion using the following numerical scale: DR0 = empty stomach; DR1 = up to 25%; DR2 = 25% to 75%; DR3  $\geq$  75% (Pelicice, Agostinho, 2006; Kovalenko *et al.*, 2009). Stomachs with DR2 and DR3 were analyzed and, the food contents were identified at the lowest possible taxonomic level (McCafferty, 1983; Elmoor-Loureiro, 1997) with a stereoscopic microscope. After identification, food items were quantified using the volumetric method (Hellawell, Abel, 1971; Hyslop, 1980), in two ways: (i) by displacement of the water column, using graduated beakers; and (ii) using a gridded dish, in which the volume of the items was obtained in  $1 \text{ mm}^3$ , and later transformed into mL (Bastos *et al.*, 2013). The second method was used in cases where the items were very small in size, which makes it impossible to measure the volume in graduated cylinders. For some analysis items were grouped into large ones, which are: i) Allochthonous items: terrestrial invertebrates and plants; ii) Autochthonous items: aquatic invertebrates, detritus, and fish.

**Data analysis.** To verify whether consumption of allochthonous items for *T. galeatus* is positively affected by increased hydrometric level (prediction i), we performed a generalized mixed model (GLMM), with the Gaussian distribution, using the quarterly mean of hydrometric level as the explanatory variable (fixed effect) and the volume of allochthonous items from each sampling as the response variable. Furthermore, we performed another two models using the volume of each group of allochthonous items separately (terrestrial invertebrates and terrestrial plants) as the response variables.

To verify whether consumption of autochthonous items for *T. galeatus* is negatively affected by increased hydrometric level (prediction ii), we performed a GLMM, with the Gaussian distribution, using the quarterly mean hydrometric level as the explanatory

variable (fixed effect) and the volume of autochthonous items from each sampling as the response variable. Furthermore, we performed another three models using the volume of each group of aquatic items separately (aquatic invertebrates, detritus and fish) as the response variables.

Variations in the trophic niche breadth were assessed using the Permutation Analysis of Multivariate Dispersion (PERMDISP, Anderson, 2006), performed using the *vegan* package (Oksanen *et al.*, 2019). PERMDISP assesses the dispersion of the diet in the multivariate space, that is, the mean distance of individuals in relation to the centroid of each population. Thus, if the population has a greater mean distance from the centroid, the greater the inter-individual variability and consequently the greater the trophic niche breadth (Correa, Winemiller, 2014). To verify the influence of the hydrometric level in trophic niche breadth (prediction iii) we performed a GLMM, with the Gaussian distribution, using the hydrometric level as the explanatory variable and the mean of centroid distance (CD) from each sampling as the response variable.

The body condition was assessed through the mean of Fulton's Condition Factor for each sampling, calculated according to the equation:  $K = 100 \cdot (W/L^3)$  where  $W$  is the body weight in grams and  $L$  is the standard length in cm. Factor 100 is used to bring  $K$  close to unity (Froese, 2006). The body condition analyze is a useful tool for comparing the condition, fatness, or well-being of a fish (Tesch, 1968). We also assessed the feeding activity of *T. galeatus* by the mean degree of stomach repletion (mDR), expressed by:  $mDR = (N0 \cdot 0) + (N1 \cdot 1) + (N2 \cdot 2) + (N3 \cdot 3)/N$ , where  $N0$ ,  $N1$ ,  $N2$  and  $N3$  correspond to the number of individuals with stomach fullness of 0, 1, 2 and 3, respectively, and  $N$  is the total number of analyzed individuals in each sampling (Carniatto *et al.*, 2012, 2020). The body condition of a species can be influenced by feeding activity (Pereira *et al.*, 2016; Cardozo *et al.*, 2018). We performed a generalized mixed model (GLMM) using the Gaussian distribution in order to assess the relationship between the hydrometric level (fixed effect) and the  $K$  and mDR data of each sampling (response variable) (prediction iv).

Statistical analyses and graphs were performed with R 4.0 software (R Development Core Team, 2020), using the "lme" function from the *nlme* package (Pinheiro *et al.*, 2021) for analysis and the package *ggplot2* for graphs (Wickham, 2016). Because mixed models allow for the inclusion of a random term (Zuur *et al.*, 2009), for all GLMMs, we included the sampled years as the random effect because close years may be very similar and therefore have an influence in our analysis. In order to achieve homoscedasticity of the data, for the models of allochthonous resources (terrestrial invertebrates, terrestrial plants and detritus), the response variables were  $\log x+1$  transformed. The model assumption was visually tested for residual normality and homoscedasticity. Cook's distances were used to graphically analyze influential observations (Zuur *et al.*, 2009). In addition, the Bonferroni test was used to detect outliers (Cook, Weisberg, 1982), performed using the *car* package (Fox *et al.*, 2022) and did not show significant results (Tab. S1). Model quality was assessed using pseudo marginal  $R^2$  (the proportion of variation explained by fixed effects) and pseudo conditional  $R^2$  (the proportion of variation explained by fixed and random effects) (Nakagawa, Schielzeth, 2013). All assumptions were checked and values of  $P < 0.05$  were considered statistically significant.

## RESULTS

The stomachs of 295 individuals of *Trachelyopterus galeatus*, whose body length ranged from 6.1 cm to 18.3 cm, were analyzed. The *T. galeatus* diet was composed of 27 items from allochthonous and autochthonous origins, including higher plants, aquatic and terrestrial invertebrates, fish and detritus (Tab. S2). Among the resources of allochthonous origin, the invertebrates stood out, comprising a richness of 17 prey resources, among which adult Coleoptera, Orthoptera and Formicidae composed the species diet in almost all samplings (Tab. S2). Among the terrestrial plants, leaves, fruit and seeds occurred in the diet of *T. galeatus*. On the other hand, autochthonous items were composed of invertebrates, detritus and fish. Odonata nymph, Ephemeroptera larvae and Diptera pupae were the predominant aquatic invertebrates in the diet, and fish items were consumed at most samples (Tab. S2).

Considering the origin of food items consumed by *T. galeatus* as a function of the hydrometric level (prediction i), the percentage of consumption of allochthonous items showed a tendency to increase as the hydrometric level increases, but the model showed only a marginally significant result (pseudo-R<sup>2</sup>m = 0.1 - pseudo-R<sup>2</sup>c = 0.1 - p = 0.077) (Tab. 1; Fig. 3A; Tab. S3). On the other hand, when analyzing the consumption of each group of allochthonous items separately, the consumption of terrestrial invertebrates was positively affected by hydrometric level (pseudo-R<sup>2</sup>m = 0.17 - pseudo-R<sup>2</sup>c = 0.17 - p = 0.021) (Tab. 1; Fig. 3B; Tab. S4), while the percentage of terrestrial plant consumption was not affected by the hydrometric level (pseudo-R<sup>2</sup>m = 0.02 - pseudo-R<sup>2</sup>c = 0.02 - p = 0.389) (Tab. 1; Fig. 3C; Tab. S4).

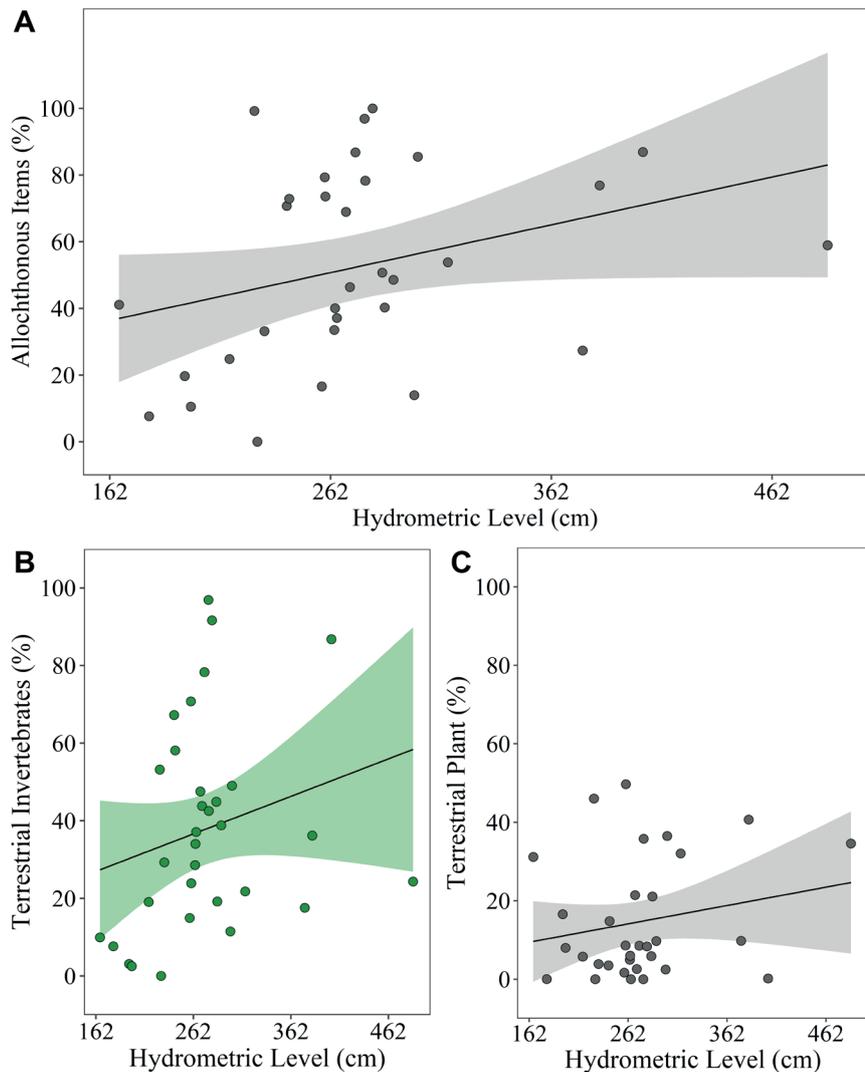
Regarding the consumption of autochthonous items, the percentage of consumption showed a negative tendency as a function of the hydrometric level, but the model only showed a marginally significant result (pseudo-R<sup>2</sup>c = 0.10 - pseudo-R<sup>2</sup>m = 0.10 - p = 0.077) (Tab. 2; Fig. 4A; Tab. S3). As for the volumetric percentage of aquatic invertebrates in the diet of *T. galeatus*, unlike the consumption of terrestrial invertebrates, it was negatively affected by the hydrometric level (pseudo-R<sup>2</sup>c = 0.17 - pseudo R<sup>2</sup>m = 0.17 - p = 0.012) (Tab. 2; Fig. 4B; Tab. S4), while for detritus consumption there was no significance of the model (pseudo-R<sup>2</sup>c = 0.05 - pseudo-R<sup>2</sup>m = 0.05 p = 0.238) (Tab. 2; Fig. 4C; Tab. S4). As well, the percentage of consumption of fish species for *T. galeatus*, was not affected by the hydrometric level (pseudo-R<sup>2</sup>c = 0.06 - pseudo-R<sup>2</sup>m = 0.06 - p = 0.354) (Tab. 2; Fig. 4D; Tab. S4).

**TABLE 1** | Results of generalized linear mixed model analysis between the consumption of allochthonous items by *Trachelyopterus galeatus* in function of the hydrometric level of the floodplain. P-values < 0.05 are in bold. SE = Standard Error.

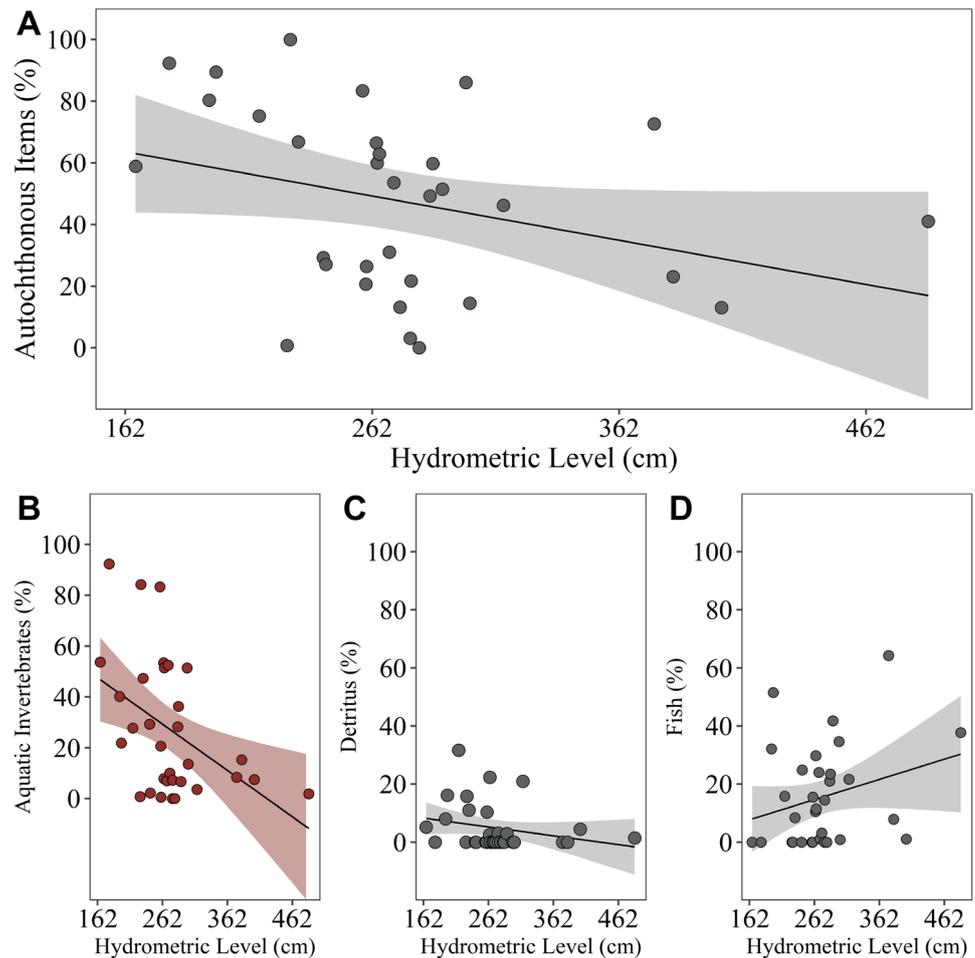
		Parameter estimate	SE	t-value	P-value
Total	Intercept	13.19	21.79	0.55	0.55
	Hydrometric level	0.14	0.08	1.85	0.07
Terrestrial invertebrates	Intercept	-7.21	4.25	-1.69	0.10
	log (level+1)	1.88	0.76	2.48	<b>0.02</b>
Terrestrial plant	Intercept	1.34	0.96	1.39	0.18
	log (level+1)	0.002	0.003	0.88	0.39

**TABLE 2** | Results generalized linear mixed model analysis between the consumption of autochthonous items by *Trachelyopterus galeatus* in the function of the hydrometric level of the floodplain. P-values < 0.05 are in bold. SE = Standard Error.

		Parameter estimate	SE	t-value	P-value
Total	Intercept	86.81	21.79	3.98	<b>&lt;0.001</b>
	Hydrometric level	-0.14	0.08	-1.85	0.07
Aquatic invertebrates	Intercept	77.14	18.84	4.09	<b>0.005</b>
	Hydrometric level	-0.18	0.07	-2.73	<b>0.01</b>
Detritus	Intercept	2.08	0.94	2.21	<b>0.03</b>
	Hydrometric level	-0.004	0.003	-1.21	0.238
Fish	Intercept	-4.49	20.81	-0.22	0.83
	Hydrometric level	0.07	0.08	0.95	0.35



**FIGURE 3** | **A.** Relationship between the hydrometric level and the consumption of all allochthonous items; **B.** The consumption of terrestrial invertebrates; **C.** And the consumption of terrestrial plants for *Trachelyopterus galeatus*. The green graphs indicate a significant positive influence of the variable as a function of hydrometric level, while grayscale graphs indicate a non-significance.

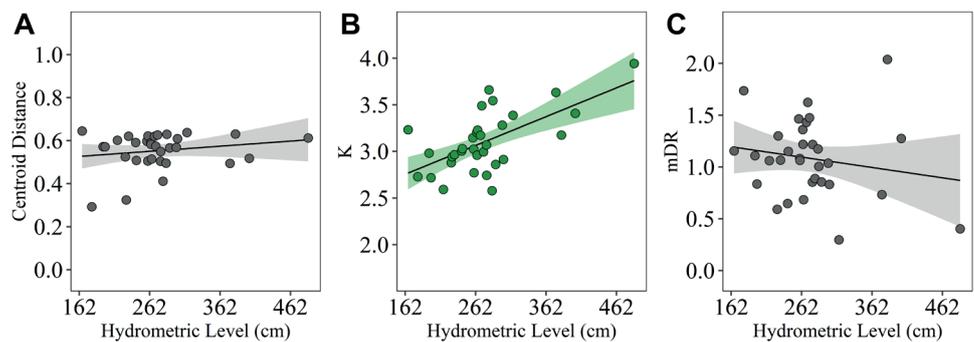


**FIGURE 4 |** A. Relationship between the hydrometric level and the consumption of all autochthonous items; B. The consumption of aquatic invertebrates; C. The consumption of detritus; D. And the consumption of fish for *Trachelyopterus galeatus*. Red graphs indicate a significant negative influence of the variable as a function of hydrometric level, while grayscale graphs indicate a non-significance.

The values of the trophic niche breadth, evaluated through the PERMDISP, ranged from 0.3 to 0.6, remaining above 0.5 in 87.5% of samplings. The results did not show any tendency, furthermore, the linear model did not show any significant effect of the hydrometric level on trophic niche breadth (adjusted- $R^2 = 0.04$  -  $p = 0.371$ ) (Fig. 5A; Tab. 3), rejecting our third prediction. The GLMM model for the body condition (Fig. 5B) showed a significant and positive relationship for K and the hydrometric level ( $p < 0.01$ ; Tab. 3), however, the data varied greatly between the levels of the random effects (years sampled - pseudo- $R^2_m = 0.28$  - pseudo- $R^2_c = 0.52$ ). We did not find any evidence that the feeding activity of fish (mDR; Fig. 5C) increased with the hydrometric level, rather it presented a slight decline. The model did not show any significant effect of the hydrometric level on feeding activity and the data varied greatly with the increase of the hydrometric level (Tab. 3). This model also varied greatly between the levels of the random effects (years sampled - pseudo- $R^2_m = 0.02$ ; pseudo- $R^2_c = 0.08$ ).

**TABLE 3** | Results of generalized linear mixed model analysis for Centroid Distance (CD), K and mDR values of *Trachelyopterus galeatus* with hydrometric level. SE = Standard Error.

		Parameter estimative	SE	t-value	P-value
CD	Intercept	1.999	0.223	8.959	<0.0001
	Hydrometric Level	-0.00069	<0.0001	-0.894	0.371
K	Intercept	2.394	0.197	12.123	<0.0001
	Hydrometric Level	0.002	0.0006	3.692	0.0013
mDR	Intercept	1.326	0.292	4.533	0.0002
	Hydrometric Level	-0.00088	0.001	-0.853	0.4024

**FIGURE 5** | **A.** Relationship between the hydrometric level and the trophic niche breadth; **B.** Body condition; **C.** And the feeding activity of *Trachelyopterus galeatus*. The green graphs indicate a significant positive influence of the variable as a function of hydrometric level, while grayscale graphs indicate a non-significance.

## DISCUSSION

Our results show that the diet of *Trachelyopterus galeatus* varied in response to oscillations in the hydrometric level, with the consumption of different food resources or different proportions of them. The consumption of allochthonous resources tends to increase with the increase of the hydrometric level, while the consumption of autochthonous resources tends to decrease. The terrestrial invertebrates were positively influenced by the hydrometric level, while the aquatic invertebrates were negatively influenced by the hydrometric level, both showing significant relationships. However, variations of the hydrometric level showed no influence on the trophic niche breadth, which hardly varied in most of the samplings. As expected, fish body condition was positively affected by the increase in the hydrometric level, while the feeding activity was not influenced by such increase. These results indicate that different hydrological conditions could influence the availability of resources in the environment, and it is likely that fish with trophic opportunism change their diet as a consequence.

The diet of *T. galeatus* was composed of many food items (27), including fish, plants (leaves, seeds and fruits), detritus, and invertebrates (mainly insects). A broad diet allows the exploitation of different resources according to availability, providing a competitive advantage (Courant *et al.*, 2017). *Trachelyopterus galeatus* has an omnivorous habit (Tonella *et al.*, 2018; Garcia *et al.*, 2020), and our result showed that it presents different diet patterns according to river level fluctuations, changing it according to the availability of allochthonous and autochthonous resources provided by the hydrological dynamics (Prejs, Prejs, 1987; Winemiller, Kelso-Winemiller, 2003; Quirino *et al.*, 2017). Some omnivorous species can change their trophic position according to variations in the hydrometric level (*e.g.*, Quirino *et al.*, 2015; McMeans *et al.*, 2019). In our study, the consumption of these basal resources (*e.g.*, fruits and seeds) did not show a significant relationship with the hydrometric level, but there was a trend to replace autochthonous resources with allochthonous ones. Terrestrial invertebrates may represent a high quality food resource because of their high energy density compared to aquatic ones (Sullivan *et al.*, 2014) and may also justify the high consumption of terrestrial invertebrates by *T. galeatus*, once they were higher in relation to the consumption of plants.

As expected, there was a trend to increase the consumption of allochthonous items with the increase in the hydrometric level (prediction i), which was particularly significant for the consumption of invertebrates. Several studies suggest an increase in the consumption of allochthonous resources, such as invertebrates, in high water periods compared to low water periods (Quirino *et al.*, 2017; Heng *et al.*, 2018; Castello *et al.*, 2019). The high consumption of terrestrial items by *T. galeatus* is related to the flooding of terrestrial environments as the hydrometric level increases. In these conditions, fish occupy newly flooded areas, where they find allochthonous resources in greater proportions and for a longer time, which is an advantage. In fact, there was a trend to replace aquatic invertebrates with terrestrial ones in the diet, once these resources have a higher energy density when compared to autochthonous resources (Junk, 1983; Francis, Schindler, 2009; Sullivan *et al.*, 2014).

As expected, the diet of *T. galeatus* in low water levels was mainly composed of detritus, fish and aquatic invertebrates, being the latter significantly consumed in lower hydrological levels. Although autochthonous resources are abundant throughout the year, they are most accessible during periods of low water (Abujanra *et al.*, 2009) – when the area, water volume, depth and connectivity between aquatic environments are reduced (Gomes *et al.*, 2012; Medeiros *et al.*, 2014) – which leads to a concentration of aquatic organisms, facilitating predation (Wantzen *et al.*, 2002). In order to persist during extreme levels of drought, *T. galeatus* was able to consume energy-dense food items, such as aquatic invertebrates and fish, which are more cost-effective prey than plants or detritus (Dorenbosch, Bakker, 2011). *Trachelyopterus galeatus* also consumed detritus, mainly at lower hydrological levels. Although very abundant, this food item usually has a low energy value (Barrera-Oro, 2002; Pyrzanowski *et al.*, 2019). Nevertheless, the habit of consuming detritus and fish in different hydrometric levels may help to explain the high abundance of *T. galeatus* in the studied environment. Even though this fish is not a native species of this floodplain (Ora *et al.*, 2018), it is able to exploit resources that are rarely limited (Moyle, Light, 1996), even in periods of scarcity of more energy-efficient resources.

The trophic niche breadth did not vary significantly regarding changes in the hydrometric level. In trophic ecology studies, there is no consistent pattern of trophic niche breadth for fish (Correa, Winemiller, 2014). While some studies show an expansion of the trophic niche of invertivorous fish in the flood season, when there is an increase in food abundance (Correa *et al.*, 2009; Quirino *et al.*, 2017), a contraction of the niche breadth was also observed in this period (Walker *et al.*, 2013). However, species response to the abundance or limitation of resources in different hydrological seasons depends on the taxa and environments (Correa, Winemiller, 2014). In this way, the opportunistic diet of *T. galeatus* can explain its persistence throughout the entire hydrological cycle, regardless of water level fluctuation, because it can prey on the most profitable prey types (terrestrial or aquatic). This leads to improvements in their diet based on the abundance and availability of resources, causing low variation in trophic niche breadth across the hydrometric level.

As expected, the condition factor was associated significantly with the hydrometric level. This increase with the increase in the hydrometric level may be associated with access to new food sources due to the high connectivity between the aquatic and terrestrial environments, in contrast to low hydrometric levels, when food resources are restricted (López-Rodríguez *et al.*, 2019). Despite the significant increase in body condition in periods of high hydrometric levels, our results showed a constancy in the degree of stomach repletion. Luz-Agostinho *et al.* (2008) also found that a piscivorous species, *Hoplias aff. malabaricus*, showed feeding activity regardless of the flood regime while body condition improved during periods of high water. The authors pointed out that the different patterns observed for feeding activity and body condition may be associated with different energy costs for searching for prey. Generally, a temporal influence on fish feeding activity is expected (Gelós *et al.*, 2010), but specifically in relation to the dry and flood periods, there is also no consensus, as it has already been observed that periods of high water promote a more intense feeding or a null effect, depending on the fish feeding habit (Luz-Agostinho *et al.*, 2008; Abujanra *et al.*, 2009). In our study, *T. galeatus* did not show significant changes in its feeding activity, in this case, keeping it almost constant at different hydrometric levels. This demonstrates that this species maintains its efficient foraging skills regardless of the water level. This is also another favorable characteristic for this species, as it guarantees adaptation to different environmental conditions (Garcia *et al.*, 2020) and, probably, the stability of the population.

In summary, our results showed that variations in hydrological levels affect fish diet and even their body condition, as they likely change food availability, favoring species capable of taking advantage of such different resources. Although other factors can influence fish feeding, *e.g.*, degree of connectivity between environments, vegetation, and others aspects in the landscape scale, the sampling sites are located in an environmental protection area and are very similar considering land cover, in addition to connecting in high water periods (Thomaz *et al.*, 2007). Our results reinforce the fundamental role of hydrological dynamics in diet composition, generating important implications for omnivorous fish feed behavior in the environment. A species with high food plasticity is likely to become a successful invader (Nurkse *et al.*, 2016; Courant *et al.*, 2017; Tonella *et al.*, 2018), which is one of the reasons why *T. galeatus* is currently the third most captured species in this floodplain (Tonella *et al.*, 2018). Hence, the

high food plasticity, and trophic opportunism allows *T. galeatus* to take advantage of the most available resources, consuming predominantly aquatic invertebrates with a decrease in the hydrometric level; and terrestrial invertebrates with an increase in the hydrometric level which probably contributed to the increase in its body condition in this situation, while it kept similar trophic niche breadth and feeding activity regardless of hydrological condition.

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**Kátia Yasuko Yofukuji:** Investigation, Methodology, Writing-review and editing.

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**Rosemara Fugi:** Conceptualization, Investigation, Methodology, Supervision, Writing-review and editing.

#### ETHICAL STATEMENT

Fish were anesthetized with benzocaine and euthanized according to the protocol approved by the Ethics Committee on the Use of Animals at the Universidade Estadual de Maringá (CEUA/UEM n° 1420221018 - ID 001974).

#### COMPETING INTERESTS

The author declares no competing interests.

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