

Effects of flood regime on the diet of *Triportheus curtus* (Garman, 1890) in an Amazonian floodplain lake

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We analyzed the diet of *Triportheus curtus* in Lake Amapá on the Acre River (AC - Brazil), during three distinct phases of the hydrological cycle (pre-flooding, flooding, and post-flooding stages). The flooding occurred between January and June of 2009. Samples were collected monthly from October 2008 through September 2009. After collection (at 19:00, 01:00, 07:00, and 13:00 hs) and taxonomic identification, fish were eviscerated and their stomachs preserved in a 4% formalin solution for later analysis. The diet was evaluated by the Index of Relative Importance (IRI), and temporal variations (pre-flooding, flooding, and post-flooding) in the diet were summarized by an ordination technique (DCA). The diet of *T. curtus* was comprised of several orders of insects and microcrustaceans. In the pre-flooding stage, more than 62% of the diet consisted of Ostracoda. In the flooding phase, *T. curtus* fed mainly on Chaoboridae larvae (Diptera) (44.3%) and terrestrial insects (fragments) (33.7%). In the post-flooding phase, Chaoboridae comprised 80% of the diet. These results indicate that the utilization of food resources by *T. curtus* was variable, changing with alterations in the availability of resources, as influenced by the hydrological cycle. The population of *T. curtus* proved to be opportunistic, changing its diet in the course of the hydrological cycle.

Neste estudo avaliamos a dieta de *Triportheus curtus*, no lago Amapá, rio Acre (AC - Brasil), em três períodos distintos do ciclo hidrológico (pré-pulso, pulso e pós-pulso). As coletas foram realizadas mensalmente de outubro de 2008 a setembro de 2009, e o pulso de cheia ocorreu entre janeiro e junho de 2009. Após as despescas (19:00, 01:00, 07:00 e 13:00 hs) e identificação taxonômica, os indivíduos foram eviscerados e os estômagos preservados em formalina 4% para posterior análise. A dieta foi avaliada através do Índice de Importância Relativa (IRI), e as variações temporais (pré-pulso, pulso e pós-pulso) na dieta foram sumarizadas através de uma análise de ordenação (DCA). A dieta de *T. curtus* foi composta de insetos de diferentes ordens e microcrustáceos. No pré-pulso, aproximadamente 62% da dieta foi composta por Ostracoda. No pulso, *T. curtus* consumiu principalmente larvas de Chaoboridae (Diptera) (44,3%) e insetos terrestres (fragmentos) (33,7%). No pós-pulso, larvas de Chaoboridae representaram 80% da dieta. Estes resultados indicam que a dieta de *T. curtus* varia temporalmente, e que a espécie pode ser considerada oportunista, alterando sua dieta de acordo com a abundância dos recursos nas diferentes fases do ciclo hidrológico.

Key words: Acre River, Feeding plasticity, Opportunist, Seasonality, Triporthinae.

Introduction

The hydrological regime, with alternating dry and flood periods, is the most important environmental factor structuring the aquatic communities and the functioning of river-floodplain systems (Sousa & Freitas, 2008; Luz-Agostinho *et al.*, 2009; Neiff *et al.*, 2009). The seasonal floods increase the connectivity between waterbodies, allowing exchange of nutrients and organisms among habitats (Thomaz *et al.*, 2007).

During the floods, the riverbanks are inundated, forming habitats with distinct hydrological characteristics, resulting in differing ecological processes and diversified communities (Yamamoto *et al.*, 2004). These factors make floodplains ideal places for reproduction, refuge, and feeding for many species of fishes (Marçal-Simabuku & Peret, 2002; Luz *et al.*, 2009). According to Junk (1980), changes in hydrological conditions affect not only the quantity, but also the quality of available food. In this way, the availability of food resources for ichthyofauna is related to the river dynamics, and the flooded

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areas play an important ecological role, benefiting the entire drainage basin (Winemiller *et al.*, 2000).

Floodplain lakes, lentic systems formed by the main river dynamics, are important components of the river-floodplain system, which presents different degrees of connection to the main channel. Among the kinds of lakes occurring in the Amazon region are the oxbow lakes formed in abandoned meanders, which are important for the maintenance and integrity of regional biological diversity, both as natural nurseries of commercially important species of fishes, and as the preferred habitat of sedentary and small-sized species (Hamilton & Lewis, 1987; Daga *et al.*, 2009).

Prominent among the fishes that inhabit seasonally flooded areas in the Amazon basin are species of the genus *Triportheus* Cope, 1872, commonly known as *sardinhas* (sardines). Their adaptations allow them to exploit many biotopes, and they occur from the La Plata River to the Orinoco basins and are well represented in many rivers of Amazonia (Goulding, 1980). This group of fishes is distinguished by its economic importance, constituting a valuable food resource for traditional communities (Amaral, 2005), and several species are review in Manaus (Yamamoto *et al.*, 2004) and Porto Velho (Doria & Queiroz, 2008). In recent years, species of *Triportheus* have been one of the main targets of the commercial fishery in practically the entire Brazilian Amazon basin (Batista & Petrere Jr., 2003). The fishery for *sardinhas* is seasonal, and they are harvested in the September-November period, when they migrate over long distances to breed (Doria & Queiroz, 2008). The freshwater *sardinhas* of the genus *Triportheus* are small-sized pelagic species with a superior mouth position and weak dentition, and their usual diets includes seeds, plankton, and small invertebrates (Malabarba, 2004). Their feeding habits range from omnivore to insectivore and some species are partly zooplanktivorous, in different environments (Galina & Hahn, 2003).

As the flooding makes available a series of food resources, transported by the river or by the flooding of its banks, the fish are able to take advantage of this situation to exploit these resources. The main objective of this study was to evaluate the effects of the flooding on the use of food resources by *Triportheus curtus*. Specifically, we have tried to answer the following question: does *T. curtus* show differences in the diet in the course of a hydrological cycle?

Material and Methods

Study area. Lake Amapá is located in the basin of the Acre River (Amazon basin) in the Municipality of Rio Branco, State of Acre, Brazil, between coordinates 10°02'36" S 67°50'24" W (Fig. 1). It is a typical oxbow lake, approximately 3.1 km long. Its forested shores are inundated during the flood season, with consequent large input of organic matter into the lake (Keppeler & Hardy, 2004). The lake is isolated from the river during the entire dry season, and is connected only during the flood period. The data for Acre River levels were provided

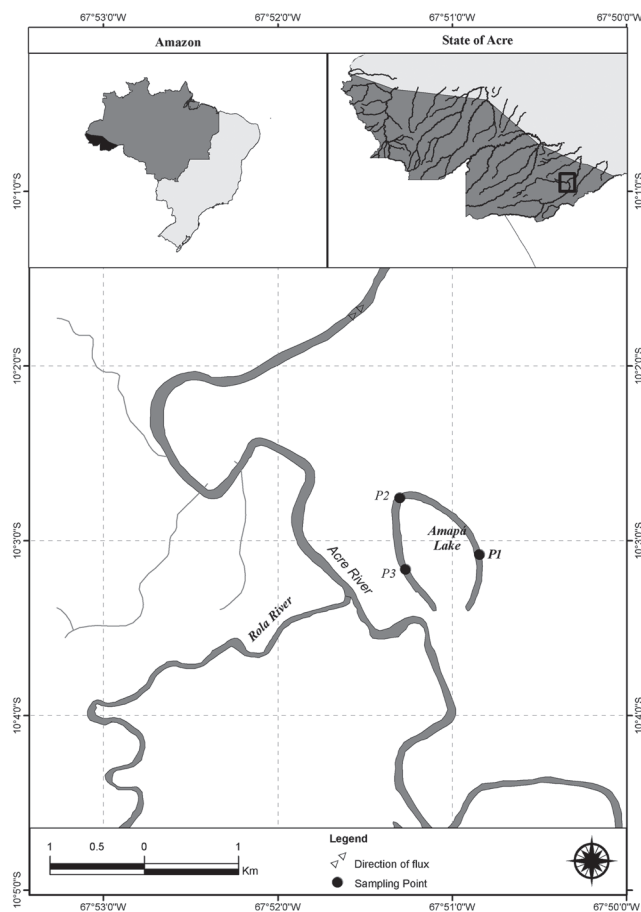


Fig. 1. Location of Lake Amapá and sampling points P1, P2, and P3.

by the Civil Defense agency of the state of Acre. The water levels in Amazon floodplain lakes are regulated by inflow from the rivers, and their depth may vary several meters during five to seven months a year, according to the hydrological regime of the rivers supplying the water (Adis & Junk, 2002).

Fish collections. Sampling was carried out monthly from October 2008 through September 2009, at three points on Lake Amapá, using a set of four nets of different mesh sizes (1.5, 2.5, 3.5, and 4.0 cm between consecutive knots) and 40 m long, at each sampling point. Nets were installed for a 24-h period and were checked at 19:00, 01:00, 07:00, and 13:00 hs. All fish collected were identified, measured, weighed, and eviscerated, and their stomachs were removed and preserved in 4% formalin. Voucher specimens were deposited in the Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura da Universidade Estadual de Maringá (Nupelia-UEM) under number NUP 9114.

Diet analysis. The diet of *T. curtus* was evaluated by three methods: (1) frequency of occurrence, which is the number of times that a prey occurs in relation to the total number of

stomachs analyzed, expressed as a percentage; (2) numerical frequency, which is obtained by counting the number of prey items of each food category in the stomachs, expressed as a percentage; and (3) the point method, which was adapted so that the contribution of the food items was estimated from the area of coverage of the item on the Sedgwick-Rafter chamber or graph paper, and the volume of each item corresponds to the proportional score for the coverage area. The points method was only used to obtain the volume of food items (expressed as a percentage), whose values were used to calculate the IRI (Hynes, 1950; Hyslop, 1980). The results of these methods were combined in the Index of Relative Importance (IRI, Pinkas *et al.*, 1971), calculated by the formula: $IRI = (\%N + \%P) \%F * 100$, where: N = numerical frequency, P = percentage of points, and F = frequency of occurrence.

Temporal variations (pre-flooding, flooding and post-flooding) in the diet of *T. curtus* were summarized by an ordination technique, Detrended Correspondence Analysis (DCA - Hill & Gauch, 1980), applied to the data matrix for the diet (244 samples and 16 items; lines and columns, respectively). The input matrix summarized in the DCA contained the point's value of each food item. As some food items presented high values, we conducted a square root transformation to minimize their effect on the ordination. In addition, we opted to run the DCA algorithm giving less weight to rare food items, to also remove their effect on the ordination (for more details, see Palmer, 1993). The food items that most influenced the ordination in the diet between the sampling periods were determined from their Pearson correlation with the principal DCA matrix, using the program PC-ORD (McCune & Mefford, 1999). To evaluate the temporal differences in the diet, we tested the scores of the samples controlling the periods resulting from the DCA. The DCA scores did not conform to the assumptions of normality and homogeneity, and therefore differences in the diet were tested according to the Kruskal-Wallis non-parametric test (Zar, 1996). When the differences were significant, the *a posteriori* test (multiple comparisons of mean ranks for all groups) was used to indicate which periods differed. The significance level adopted for all analyses was $p < 0.05$.

Results

Hydrological regime. The water depth in Lake Amapá varied seasonally, influenced particularly by changes in the level of the Acre River during the flood period (January to June 2009). In the dry period, the lake's water level varied little. During the 2008-2009 hydrological cycle, three distinct periods were considered: (i) pre-flooding (October through December 2008) - the period when the water level in the lake remained relatively stable; (ii) flooding (January through June 2009) - the period beginning when the Acre River water invaded the lake until the lake again became isolated from the main river channel; and (iii) post-flooding (July through September 2009) - the period from when the lake was isolated until the water level stabilized (Fig. 2).

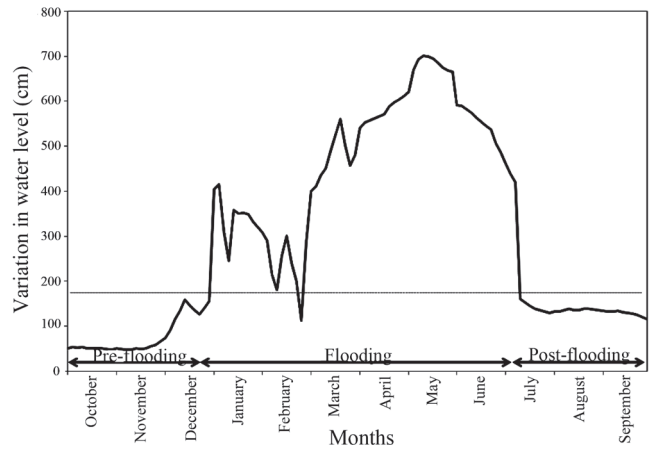


Fig. 2. Variation in river level (measured every three days) during the hydrological cycle from 2008 to 2009 in Lake Amapá. Gray line shows the threshold level for flooding from the Acre River. Main periods of pre-flooding, flooding, and post-flooding are indicated at the base of the graph.

Temporal variation in diet. A total of 244 stomachs were analyzed to characterize the feeding habits of *T. curtus*. Its diet was composed essentially of insects of different orders and of microcrustaceans (Table 1). In the pre-flooding period, the principal food resource was Ostracoda (62%), represented only by *Physocypria schubarti* (Farkas, 1958), and followed by Cladocera, which comprised 22% of the diet. In this period, Chaoboridae larvae and Algae were items of minor importance, representing 8.6% and 7.4% of the diet, respectively. In the flooding period, Chaoboridae larvae (44.3%), and terrestrial insects (fragments) (33.7%) comprised approximately 80% of

Table 1. Values of the Index of Relative Importance (%IRI) of food items in the diet of *Triporthus curtus*, in three periods of the hydrological cycle. N = number of stomachs analyzed. Values of IRI < 0.01 are indicated by an asterisk.

Items	Food resource	Pre-flooding	Flooding	Post-flooding
Ostracoda	Autochthonous	61.87	17.99	4.21
Cladocera	Autochthonous	21.85	2.08	15.31
Chaoboridae	Autochthonous	8.62	44.31	79.5
Terrestrial insects (fragments)	Allochthonous	0.27	33.7	0.88
Ephemeroptera	Autochthonous	0.01	-	*
Coleoptera	Autochthonous	-	-	*
Hymenoptera	Allochthonous	*	-	*
Hemiptera	Autochthonous	*	1.17	0.06
Plecoptera	Autochthonous	*	-	-
Trichoptera	Autochthonous	-	-	*
Rotifera	Autochthonous	*	-	-
Copepoda	Autochthonous	*	0.31	0.03
Hydracarina	Autochthonous	*	-	-
Algae	Autochthonous	7.36	0.44	*
Plant	Allochthonous	-	-	*
Scales	Autochthonous	0.01	-	-
N		169	13	62

the diet. Ostracoda was also prominent in this period, comprising 18% of the diet. In the Post-flooding, fish consumed mainly Chaoboridae larvae, responsible for approximately 80% of the diet, while Cladocera comprised 15.3% (Table 1).

The results of the data ordination for *T. curtus*'s diet indicated important temporal separations. The variation revealed by this ordination showed that on axis 1 most of the samples from the flooding and post-flooding were positioned on the right side of the graph, whereas the samples from the pre-flooding occupied the left side of the graph (Fig. 3). Along DCA axis 1 (eigenvalue=0.43), the most highly correlated food items were Ostracoda ($r = -0.53$), Algae ($r = -0.52$), and Cladocera ($r = -0.51$) negatively, and terrestrial insects (fragments) ($r = 0.62$), positively. The food items that correlated with DCA axis 2 (eigenvalue=0.19) were terrestrial insects (fragments) ($r = 0.52$) positively, and Chaoboridae larvae ($r = -0.71$) negatively (Table 2).

Significant differences among the scores for the different periods were recorded for axis 1 ($df = 2$, $H = 91.05$; $p = 0.001$). The *a posteriori* test indicated that there were differences between the periods of pre-flooding and flooding ($p < 0.01$) and between the pre-flooding and post-flooding ($p < 0.01$). No difference was observed between the periods of flooding and post-flooding ($p = 1.0$) (Fig. 4a). The differences can be explained due to greater consumption of Ostracoda and Cladocera during the pre-flooding periods, which had high correlation with the scores.

For axis 2 (Fig. 4b) ($df = 2$, $H = 63.62$; $p < 0.001$), we observed differences between the pre-flooding and post-flooding ($p < 0.01$), and between the flooding and post-flooding ($p < 0.01$), however no differences were seen between the pre-flooding and flooding ($p = 0.287$). In the post-flooding, the proportion of Chaoboridae in the diet increased sharply in relation to the pre-flooding and flooding. This difference may be due to the high negative correlation of this item with the sample scores.

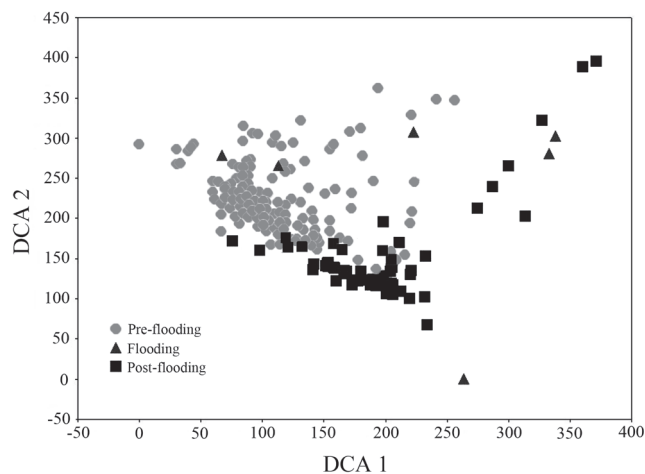


Fig. 3. Scores derived from Detrended Correspondence Analysis (DCA), considering the seasonal ordination of *Tripurtheus curtus* in the periods of the hydrological cycle of Lake Amapá.

Discussion

As a result of fluctuations in water level, the diet of *T. curtus* varied significantly among the stages of the hydrological cycle. Ostracoda was the most consumed item in the pre-flooding, Chaoboridae larvae, and terrestrial insects (fragments) in the flooding, and Chaoboridae larvae and Cladocera in the post-flooding. In lakes of Amazon floodplain and Pantanal the food spectra of species of *Tripurtheus* ranged from omnivore to insectivore (Catella & Petrere Jr, 1998; Yamamoto *et al.*, 2004).

According to Martens *et al.* (2008), Ostracoda are very common in the majority of continental waters, where they are abundant in benthic communities. In this study, these invertebrates were ingested by *T. curtus* in the largest amounts in the pre-flooding, although the IRI indicated that the ingestion of Ostracoda decreased in flooding and post-flooding, this item continued frequent in the stomachs, with about 40% and 60% respectively (Fig. 5). Although *T. curtus* is a pelagic species (Malabarba, 2004), and the majority of Ostracoda is benthic or associated with macrophytes (Higuti *et al.*, 2007), the explanation for the high consumption of these organisms may be related to the fact that some species of Ostracoda migrate upwards and swim in the water column. These include species of the genus *Physocypria* (Delorme, 2001) the only member of Ostracoda consumed by *T. curtus*.

The high consumption of terrestrial insects by the fish reflects the importance of allochthonous material as a food resource for ichthyofauna (Vidotto-Magnoni & Carvalho, 2009). The input of allochthonous material into tropical aquatic ecosystems during the flood season can explain the presence of terrestrial insects (fragments) in the diet of *T. curtus* during the flooding period, when strong rains and winds cause the insects to fall into these waterbodies. Also, insects, especially Hymenoptera, become easy prey for pelagic fish such as species of *Tripurtheus* when the riverine forests are flooded, because

Table 2. Values of Pearson's correlation (r) among food items of *Tripurtheus curtus* in Lake Amapá, on DCA axes 1 and 2. Values are listed in ascending order.

DCA 1		DCA 2	
Items	R	Items	R
Ostracoda	-0.53	Chaoboridae	-0.71
Algae	-0.52	Cladocera	-0.23
Cladocera	-0.51	Hemiptera	-0.18
Scales	-0.09	Copepoda	-0.15
Plecoptera	-0.03	Coleoptera	-0.09
Rotifera	-0.01	Trichoptera	-0.07
Ephemeroptera	0.02	Plant	-0.06
Hydracarina	0.02	Rotifera	-0.01
Copepoda	0.03	Scales	0.04
Plant	0.05	Plecoptera	0.06
Coleoptera	0.05	Ostracoda	0.08
Trichoptera	0.05	Ephemeroptera	0.11
Hymenoptera	0.17	Hydracarina	0.12
Hemiptera	0.22	Hymenoptera	0.15
Chaoboridae	0.24	Algae	0.19
Terrestrial insects (fragments)	0.62	Terrestrial insects (fragments)	0.52

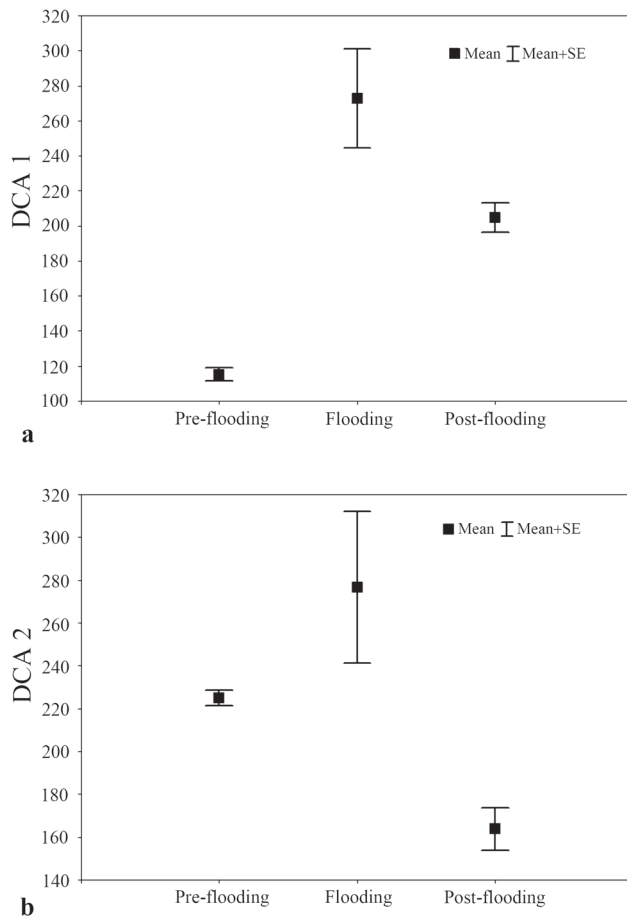


Fig. 4. Mean values for scores (\pm standard error) for axes 1 (a) and 2 (b) of the detrended correspondence analysis (DCA), in the different sampling periods.

the fish are adapted to exploit these areas (Yamamoto *et al.*, 2004). Arboreal and terrestrial forms of insects in the Amazon forests fall into the water during the flood period, where they constitute an important resource for the fish (Goulding *et al.*, 1988). This source of food is transitory but sustains many species of fishes, mainly the trophic opportunists (Hahn & Fugi, 2007). The pelagic habit of *T. curtus* facilitates the consumption of these insects, which float on the water surface.

Chaoboridae was important in the diet of *T. curtus*, especially during periods of post-flooding and flooding. These Diptera are planktonic in the larval stage, and are found in the majority of lacustrine environments (Esteves, 1988), where they carry out vertical migrations to avoid fish predation (Luoto & Nevalainen, 2009). In isolated lakes, the high organic-matter content in the bottom sediments promotes the dominance of certain groups of invertebrates, especially species of *Chaoborus* (Ezcurra de Drago *et al.*, 2007), which may have led *T. curtus* to feed intensively on this resource. Another factor that may have influenced the predation on these Diptera larvae is that in the tropics, the reproduction of Chaoboridae is

continuous, and consequently the predation pressure would also be continuous throughout the year, varying with the seasonal fluctuations in density of Chaoboridae (Arcifa, 2000), as observed by high abundance (flooding and post-flooding) in stomachs of *T. curtus*.

Cladocera was the second most important food resource of *T. curtus* when the water level of Lake Amapá was low (pre-flooding and post-flooding). Fish are important predators of zooplankton in floodplain lakes, where the zooplankton community is highly abundant and species-rich, due to the great heterogeneity of habitats created by the seasonal changes in water level (Russo & Hahn, 2006). Keppeler & Hardy (2004) studying the zooplankton of Lake Amapá, noted that there was a greater abundance of Cladocera (species of the genus *Moina* and *Diaphanosoma*) predominantly in the low water period, corroborating the results found in this study where *T. curtus* was also fed by these planktonic Cladocera.

Triporthus curtus showed seasonal variations in the composition of their diet, and is considered a carnivorous species with a preference for Ostracods in pre-flooding and Chaoboridae larvae in flooding and post-flooding. The species can be considered opportunistic, given the inclusion of different food items according to abundance in all three phases of the hydrological cycle. The predominance of opportunists in tropical riverine environments reflects the spatial and temporal oscillations in the relative abundance of food items (Abelha *et al.*, 2001). The trophic plasticity of opportunist species may result from the necessity of utilizing a variety of food items in adverse conditions, an important factor in their survival in these environments (Teixeira *et al.*, 2005).

In conclusion, the utilization of food resources by *T. curtus* was variable, changing with alterations in the availability of resources, as influenced by the flooding. The population of *T. curtus* proved to be opportunistic, changing its diet in the course of the hydrological cycle. These are characteristics of the species of Amazon fishes that show wide feeding plasticity.

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