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Opportunistic diet of *Triportheus nematurus* (Characiformes: Triportheidae) in Southern Pantanal ponds: influences of temporal availability and abundance of resources

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ABSTRACT. The aim of this study was to investigate the diet composition and feeding strategies of *Triportheus nematurus* at the Miranda-Abobral floodplain region and evaluate if the temporal phenomenon of the flood pulse has influenced in the diet composition of the species. The fishes were sampled quarterly – between August/2014 and July/2016 – in the marginal ponds located in the Estrada Parque (MS 184). The feeding habits of *T. nematurus* was characterized as omnivorous and its opportunistic feeding behaviour, since its diet is composed of different resources along of the year. Insects and organic matter were the most important items during the drought period; plant material (leaves and roots) and Euglenophyceae algae were more expressive during the inundation period; insects and fruits were also abundant during the flood period. Through statistical analysis, it was possible to verify significant variation in the diet composition of the species. This variation in the components of the diet may be related to the availability of resources in the ponds throughout the year and reflect an already known pattern in Neotropical fish populations, which present high alimentary plasticity.

Keywords: feeding, floodplain, temporal variations, neotropical fish.

Dieta oportunista de *Triportheus nematurus* (Characiformes: Triportheidae) em lagoas do Pantanal Sul: influências da disponibilidade temporal e abundância de recursos

RESUMO. O objetivo deste estudo foi investigar a composição da dieta e as estratégias alimentares de *Triportheus nematurus* na planície de inundação da região do Miranda-Abobral e avaliar se o fenômeno temporal do pulso de inundação tem influência na composição da dieta da espécie ao longo do ano. Os peixes foram amostrados trimestralmente entre agosto/2014 e julho/2016, nas lagoas marginais situadas na Estrada Parque (MS 184). O hábito alimentar de *T. nematurus* foi caracterizado como onívoro e seu comportamento alimentar oportunista, pois sua dieta é composta de diferentes recursos ao longo do ano. Insetos e matéria orgânica foram os itens mais importantes no período de seca, matéria vegetal (folhas e raízes) e algas Euglenophyceae foram mais expressivos durante a enchente e insetos e frutos tiveram maior participação na dieta durante o período de cheia. Por meio das análises estatísticas foi possível verificar a variação temporal significativa na composição da dieta da espécie em pelo menos dois períodos. Essas alterações alimentares podem estar relacionadas à disponibilidade dos recursos nas lagoas ao longo do ano e refletem um padrão já conhecido em populações de peixes neotropicais, que apresentam alta plasticidade alimentar.

Palavras-chave: alimentação, planície alagável, variações temporais, peixe neotropical.

Introduction

The Pantanal represents the flood area of the rivers from the Upper Paraguay River basin; this extensive floodplain has about 138.183 km^2 in Brazilian territory, where approximately 65% are in the state of Mato Grosso do Sul (Silva & Abdon, 1998). As in other river basins that present floodplains, in the Pantanal, the flood pulse phenomenon plays a fundamental ecologic role in the aquatic and terrestrial communities located in floodplain regions, acting as the mechanism of interaction between these systems and being indispensable for the maintenance of diversity and conservation in these ecosystems (Junk, Bayley, & Sparks, 1989; Resende, 2008; Alho & Sabino, 2012).

In natural environments subject to seasonal alterations related to the hydrologic level, rainfall and/or temperature, it is expected that the

alimentary resources used by the fish species has been through cyclical changes, which may alter the species' feeding (Hahn & Fugi, 2007). Studies have shown that various food resources that are exploited by fish, especially of plant origin, may become available or more abundant in the aquatic environment during floods, such as fruits (Corrêa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015; Yule, Severo-Neto, Tinti-Pereira, & Costa, 2016), aquatic plants (Pott, Pott, Lima, Moreira, & Oliveira, 2011) and phytoplankton (Oliveira & Calheiros, 2000). In contrast, some resources, mainly of animal origin, such as benthic fauna, tend to present greater abundances and densities during periods of drought (Winemiller et al., 2014).

The gastric content analysis in neotropical fish communities has made possible to verify that, although there are species with specialized feeding habits, this ichthyofauna is characterized by a majority of species with high trophic plasticity, since they incorporate several alimentary resources in their diets (Hahn, Adrian, Fugi, & Almeida, 1997; Abelha, Agostinho, & Goulart., 2001). This plasticity is easily observed through temporal, spatial and ontogenetic variations in the species' diet (Agostinho, Hahn, Gomes, & Bini, 1997).

The *Tripotheus nematurus* sardine is a Triportheidae species that inhabits waterbodies from the Paraná and Paraguay River basins (Buckup, Menezes, & Ghazzi, 2007; Britski, Sillimon, & Lopes, 2007; Oliveira et al., 2011), being abundant in the ponds at the Pantanal subregion of the Miranda-Abobral.

Studies about the influence of hidrological phenomena on the diet of species of the *Tripotheus* spp. were carried out in some basins. Pinto, Rocha, Santos, Medeiros, and Severi (2009), reported that *T. guentheri,* in the reservoir of Sobradinho, Bahia, do not showed significant variation in their diet over the different seasons of the year or on various hidrological conditions. However, in the floodplains and igapós from Central Amazon, it was verified that the flood phenomenon directly influences the feeding of *T. elongatus*, which includes considerable quantities of seeds, such as from *Cecropia* sp.(Moraceae) and *Pseudobombax munguba* (Bombacaceae), during this period (Claro-Junior, Ferreira, Zuanon, & Araújo-Lima 2004); and in Manaus, Yamamoto, Soares, and Freitas (2004) verified that *T. angulatus* increase their consumption of fruits and seeds from several plant species during the flood periods. However, studies dealing with dietary characterization, feeding strategies and environmental variations on fish feeding are still scarce in the southern Pantanal and make it difficult to understand these ecosystems.

In this perspective, the present study sought to investigate the *T. nematurus* diet composition, in different hydrological periods and feeding strategies at the marginal ponds in the Miranda-Abobral subregion of the Pantanal and to evaluate the flood pulse influences on the diet of the species throughout the year.

Material and methods

Study site: The collections were realized quarterly from August 2014 to July 2016 in permanent and temporary ponds established in the Pantanal sub-region of the Miranda-Abobral, alongside of the Estrada Parque (MS 184), in the Corumbá municipality (Figure 1); during different hydrologic periods, such as drought, flood and, filling. The flooding are characteristic for representing the expansion, through the floodplain, of the aquatic environment (rivers, ponds, channels). Between drought and flood, it is characterized the intermediate period of filling, where the first rains occur, and that begin the processes of expansion of the water bodies.

Capture, processing of specimens and data analysis: The fishes were captured with casting and trawling nets with different meshes and kept alive, until the moment of manipulation. The necropsy was performed with the introduction of a needle in the upper part of the head, according to Eiras, Takemoto and Pavanelli (2006). Afterwards, the biometric data (weight, total length, standard length) were recorded.

The necropsy were performed through an incision along the ventral midline, exposing internal organs, which were separated in Petri dishes. The stomachs were set apart from the other organs, which were preserved in flasks with 70% alcohol for further analysis of its content. The stomachs condition were scored for the repletion degree that was visually attributed, considering the volume of the contents to the stomach's total volume, with variation.

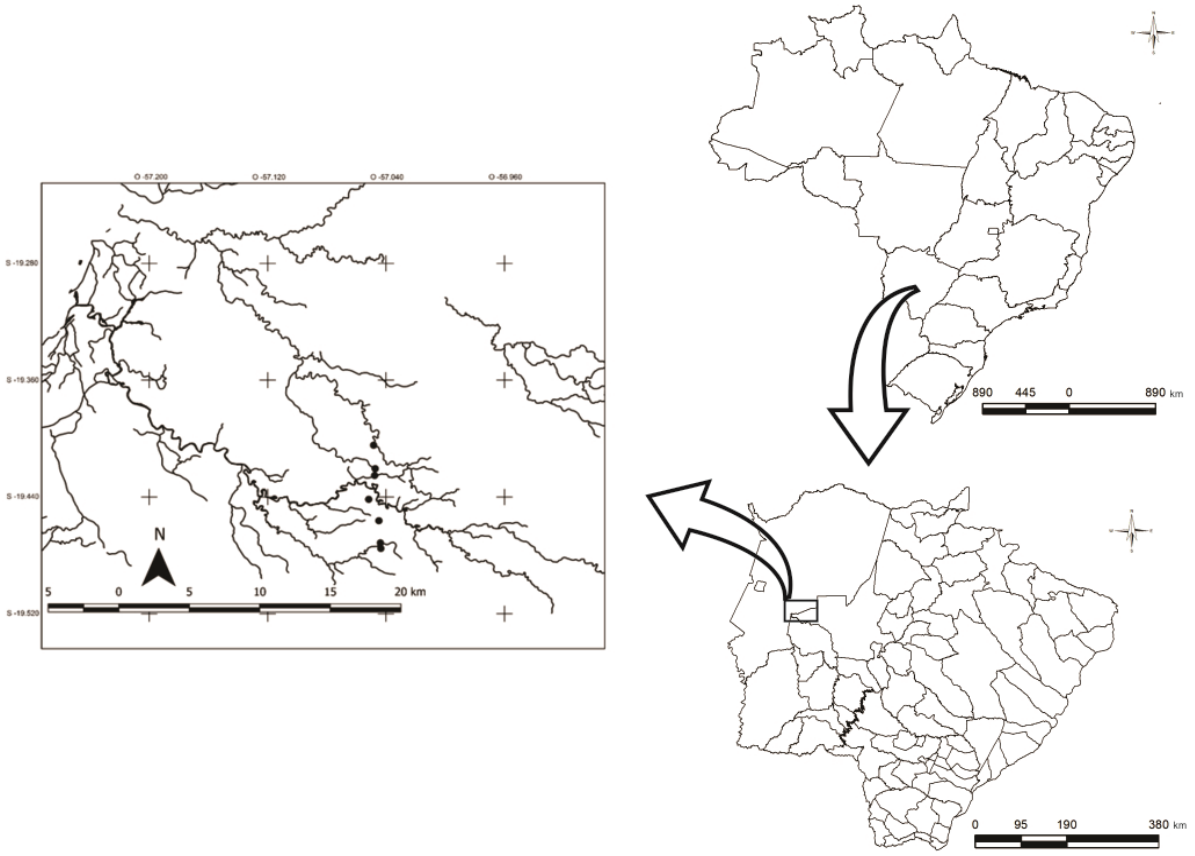

Figure 1. Sampling points along MS 184 Park Road in the Pantanal Sub-region of Miranda-Abobral.

The total stomach content was weighted, with a precision balance, and the items analyzed with the under of stereomicroscopes and light microscopes. The alimentary items were identified to the most precise taxonomic level as possible. In the analysis, the methods of frequency of occurrence (Zavala-Camin, 1996) and relative volumetric (Hyslop, 1980) were employed. The results were combined for the alimentary importance index (IAi%) (Kawakami & Vazzoler, 1980) so that the most important alimentary items could be evidenced. The volume data were submited to the Kolmogorov-Smirnov normality test and to the Kruskal-Wallis test ($p = 0,05$), using the Past 2.17c software to comparing and the significance of temporal variations in the species' diet composition during the different hydrologic periods of sampling.

Results

During the period of August 2014 and July 2016, 92 individuals of *Tripotheus nematurus* was captured. The feeding habits of the studied sample was classified as omnivorous in all periods, since it consumed animal and plant resources throughout the different hydrologic periods. Autochthonous and allochthonous resources also had different participations in the diet, in the different periods (Figure 2). The alimentary items and their respective frequency of occurrence, volumetric frequency and alimentary importance index values by sampling period are presented in Table 1.

Triportheus nematurus' diet was mainly composed of insects and organic matter during the drought period; of superior vegetables (leaves and roots) and Euglenophyceae algae during the filling period; and of insects, fruits and seeds and Xanthophyceae algae during the flood period. After checking the sample's normality by the Kolmogorov-Smirnov test, the Kruskal-Wallis test results indicated that the species' diet shows significant variations as a function of the hydrologic periods ($p > 0,05$), mainly when the drought and intermediary inundation periods are compared.

The 'allochthonous superior vegetables' resources include: leaves, stalks, roots, fruits and seeds. However, the consumption of these items occurred in a differentiated manner: during the drought and filling period, it was observed a greater importance of the leaf, root and stalk items, but during the flood, the consumption was preferentially of fruits and seeds, as shown in the Table 1.

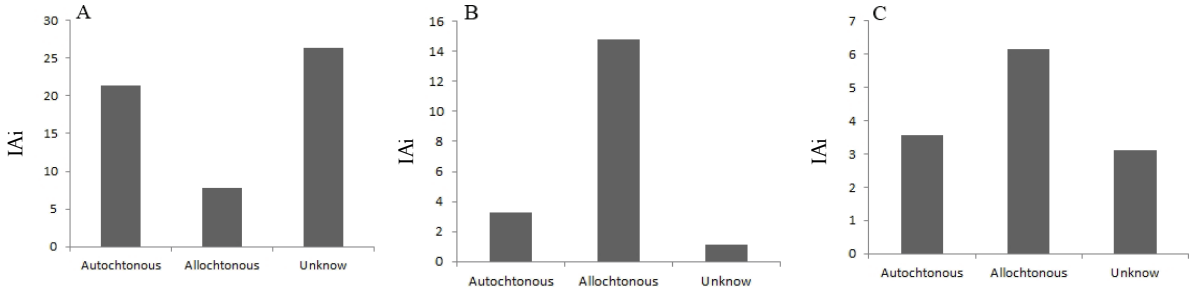

Figure 2. Relative importance of resources of different origins (IAi) in the diet of *Triportheus nematurus* in the periods sampled. A- represents dry, B- represents filling and C- represents flood.

Table 1. Alimentary items consumed by *Triportheus nematurus* in the different sampling periods and their respective FO% (relative frequency of occurrence), V% (relative item volume) and IAi (alimentary importance index) values.

Period:	Drought			Filling			Flood		
Items:	FO%	V%	IAi	FO%	V%	IAi	FO%	V%	IAi
Insects	-	-	-	-	-	-	-	-	-
Odonata (larva)	3.00	1.40	0.14	-	-	-	10.00	3.40	0.20
Ephemeroptera (larva)	10.00	8.00	2.58	-	-	-	-	-	-
Diptera (larva)	3.00	0.50	0.05	-	-	-	10.00	2.30	0.14
Chironomidae	-	-	-	2.00	0.62	0.01	-	-	-
Lepidoptera (larva)	-	-	-	2.00	2.70	0.03	-	-	-
Hemiptera	-	-	-	-	-	-	10.00	4.50	0.27
Coleoptera	-	-	-	12.00	7.90	0.56	-	-	-
Formicidae	-	-	-	2.00	0.20	0.01	10.00	4.10	0.24
Orthoptera	3.00	3.00	0.30	-	-	-	10.00	12.80	0.76
Remnants of insects	29.00	28.00	26.20	24.00	7.10	1.01	30.00	17.50	3.10
Gastropoda	-	-	-	-	-	-	10.00	5.50	0.33
Algae:	-	-	-	-	-	-	-	-	-
Chlorophyceae	10.00	8.60	2.77	2.00	8.40	0.10	-	-	-
Euglenophyceae	-	-	-	38.00	11.00	2.47	-	-	-
Xanthophyceae	-	-	-	-	-	-	30.00	16.40	2.90
Superior vegetables	13.00	14.50	6.90	52.00	45.90	14.09	30.00	10.80	1.91
Fruits and seeds	3.00	6.00	0.60	-	-	-	30.00	16.70	2.96
Scales	-	-	-	2.00	0.04	0.01	-	-	-
Feathers	-	-	-	4.00	0.19	0.01	-	-	-
Organic matter	19.00	24.00	14.70	24.00	0.60	0.08	-	-	-
Sediment	6.00	6.00	1.16	12.00	11.60	0.82	-	-	-

Discussion

The omnivorous alimentary habit has been described for *Triportheus nematurus* in the Upper Paraguay River basin, as demonstrated by Galina and Hahn (2003) and Novakowski, Hahn, and Fugi (2008), with a few differences, since, in some cases, the species also included microcrustaceans in its diet. However, these data may generate some confusions, since the *Triportheus* species, that inhabit the Pantanal's rivers, were revised and *T. nematurus* and *T. paranensis* were considered synonyms, besides the proposition of a new species: *T. pantanensis* (Malabarba, 2004).

In the Miranda-Abobral region, during the drought season – a period extending from May to October –, the ponds remain reduced and isolated, and many in a state of hypoxia, or even anoxia, directly influencing in the diversity of the fish community. During the rainy season – from November to April –, the full ponds interconnect themselves by exchanging waters with one another, as well as with the Miranda, Negro, and Paraguay Rivers (Resende, 2008). During this period, a most part of the Pantanal vegetation is flooded, characterizing the important phenomenon denominated flood pulse. Intermediate to these periods, it is known the period of filling, characterized by the first rains and the beginning of the expansion of the rivers and ponds by the plain.

The consumption of insects, with great importance during the drought period, may be due to the reduction of the marginal ponds, which became shallower and limited only to the lowest areas of the plain, and thus, the vegetables supply becomes less available. During this period the waters are more turbid, what also limits the development of algae. Notwithstanding, many insect species and other animals of the benthic fauna persist in these environments and are adapted to these conditions such as the larvae belonging to the Chironomidae (Aburaya & Callil, 2007; Winemiller et al., 2014).

The tendency, to herbivory, has been observed in *Triportheus* spp. that inhabit floodplains (Resende,

2000; Claro-Júnior et al., 2004; Yamamoto et al., 2004). The Euglenophyceae algae consumption, in this period, is possibly a consequence of its abundance in lentic environments, as well as in many other aquatic ecosystems (Bicudo & Menezes, 2006). Besides, in many ecosystems, they represent the main primary producers that influence all the energy flow through food webs (Begon, Townsend & Harper, 2007), what is also expected for the macrophyte plants (Pott & Pott, 2000). Studies with Pantanal producer communities have demonstrated that, both phytoplankton (Oliveira & Calheiros, 2000) and macrophytes (Pott et al., 2011), changetheir species richness and abundance as a function of hydrological periods.

The composition of the population's diet during the flood period demonstrated that, in this season, a wider range of food resources exploited by the species are available in its habitat. This fact can be highlighted through the IAi values, which were resembling for at least three of the main consumed items. Insects, Xanthophyceae algae and fruits and seeds were explored in similar proportions. The ingestion of fruits and seeds during the flood period has been discussed by some authors in order to investigate the beneficial and antagonistic interactions between fishes and vegetables. It has been suggested that in several cases, fishes and plants can interact though mutualism (Costa-Pereira, Severo-Neto, Yule & Tinti, 2011; Yule et al., 2016). Since that, when consuming fruits, this animals can remove the pulp, that involves the seeds, and act on its dormancy breaking; in addition, to transport and dispersing them and thus contributing to the diversity maintenance in vegetable communities (Souza, 2005). However, it has been observed that human influences, such as in frugivorous species overfishing regions, may disrupt mutualistic relations and still influence antagonistic relations such as herbivory (Corrêa et al., 2015).

The constant temporal variations in *T. nematurus* diet, occurred as a function of the availability of a few alimentary resources, such as vegetables, insects, algae and organic matter; corroborating with a pattern that was proposed by Lowe-McConnell (1999) to the Neotropical region after trophic structure comparisons in ecosystems of continental waters from different continents. In turn, this availability of resources varies mainly as a function of hydrological change, which unleashes a series of abiotic and biotic phenomena (Lake, 2003). According to Winemiller and Jepsen (1998), these temporal changes in the food availability affect the communities trophic relations, since they alter the supply of resources throughout the year.

The temporal variations in *T. nematurus* diet evidenced an opportunistic feeding strategy for the species, where autochthonous items tend to be most abundant and important in the drought and more important allochthonous items during filling and flood. This fact corroborates with Mortillaro et al. (2015) that observed that several species of omnivorous and insectivorous fish present this characteristic of the feeding behavior in floodplains of Central Amazonia, which was verified through isotope analysis stable. Opportunistic behaviors have also been observed in Rivulidae species and are probably related to the sexual dimorphism of these animals and the instability of the environment in which they live (Gonçalves, Souzam & Volcan, 2011). This feeding strategy was also observed in an omnivorous Characiformes and Siluriformes species in the Upper Paraná River basin, which began to consume mainly fish after the formation of the Salto Caxias reservoir, which provided a considerable increase in the abundance of small species (Pereira, Agostinho & Delariva, 2016). For *T. nematurus* in the marginal ponds of the Miranda-Abobral Pantanal, the presence and abundance of resources in the environment, influenced by the flood pulse, seem to be the determining factor for opportunistic feeding behavior.

These data indicate that the study of the feeding ecology of *T. nematurus* can be an interesting tool for the conservation biology, since the natural changes of the environment are determinant for the diet of the species, which although it has an omnivorous habit, demonstrates trends in the different hydrological periods. A series of hydropower projects, which can alter water flow and nutrient discharge in the Pantanal (Calheiros, Arndt, Rodriguez, & Silva 2009, Alho & Sabino, 2012) are planned for the plateau-plain interface areas of the Upper Paraguay River basin. These alterations can interrupt a series of seasonal phenomena that influence ecohydrological functioning in the lowlands and consequently affect the species. Hydrological changes are cited as the cause of reduced abundance of various functional groups of ichthyofauna in a floodplain in Central Amazonia, including a species of *Triportheus* (Röpke et al., 2017). Vidotto-Magnoni and Carvalho (2009) also found that *T. nematurus* in a reservoir environment in the Lower Tietê River has a predominantly insectivorous habit and mainly consumes Chironomidae larvae, which present high plasticity as the environment in (Aburaya & Callil, 2007) and therefore can be indicators of low environmental quality.

These results demonstrate feeding habit at a population level for *T. nematurus* and how it behaves in face of the temporal variations unleashed by the flood pulse in the plain of the Pantanal subregion of the Miranda-Abobral. Future studies may concentrate on investigating dietary aspects at an individual level of the species, exploring more complex intraspecific and behavioral aspects, as has been proposed by Bolnick et al. (2003) and Araújo et al. (2010), thus being an important tool in the comprehension of the Pantanal ecology.

Conclusion

Triportheus nematurus is a species with omnivorous habit and opportunistic feeding strategy. The temporal hydrological variations of the Pantanal influence the availability and abundance of autochthonous and allochthonous resources in the aquatic environment that are reflected in the qualitative and quantitative composition of the species diet.

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