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Changes in diet and niche breadth of a small fish species in response to the flood pulse in a Neotropical floodplain lake

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A B S T R A C T

This study tested the hypothesis that the flood pulse affects the diet composition and the niche breadth of *Moenkhausia forestii,* a small characid fish inhabiting the littoral zone of lakes. To this end, we compared the diet composition (at the population and individual levels) between hydrological periods (high and low water phases) in a floodplain lake of the Upper Paraná River. PERMANOVA revealed differences in the diet between periods (pseudo$F_{1,38} = 8.5$; $p < 0.001$), with predominant consumption of chironomid larvae and Ephemeroptera (aquatic resources) in the low-water period and an increase in the contribution of terrestrial resources (Hymenoptera, Coleoptera, and Orthoptera) during the high-water period. Based on the PERMDISP results, inter-individual variability in *M. forestii* diet also differed between periods ($F_{1,38} = 5.80$; $p = 0.02$), with higher values during the high-water period resulting in a dietary niche expansion. During the low-water period, we observed the dominance of chironomid larvae in the diets of most individuals, resulting in lower inter-individual variability and thus narrower niche breadth. The diet of *M. forestii* was affected by the flood pulse at both the population and individual levels. The most important difference was found in the origin of food items; during the low-water period, the diet consisted mainly of aquatic resources, and during the high-water period, there was a large contribution of terrestrial resources. This variation is related to the increased availability of allochthonous resources in the high period, when terrestrial areas are flooded by the overflow of the river, thereby increasing the input of resources into the aquatic environment. The increased availability of food resources during this period allowed the expansion of the trophic niche of *M. forestii*, accompanied by the highest richness (19 items) and the highest evenness of food items. Our findings demonstrated that the flood pulse affected the composition of the *M. forestii* diet at both the population and individual levels. These results support the importance of the flood pulse, which connects aquatic and terrestrial ecosystems, in providing food resources for fish.

1. Introduction

Floodplains are characterized by the dynamics of flood pulses that produce alternating periods of high waters and low waters. These pulses change the physical and chemical characteristics of water and significantly influence the dynamics, diversity and productivity of these environments (Junk et al., 1989; Thomaz et al., 2007; Junk et al., 2014). In the Upper Paraná River floodplain, although the water flow is regulates by upstream dams, hydrological regime is still the major element acting on the structure and function of communities (Agostinho et al., 2004).

River-floodplain ecosystems are formed of rivers, channels and lakes; hydrological changes should be reflected more rapidly and intensely in the latter due to their small size. Seasonally isolated marginal lakes are recognized as the preferred habitat of small-sized fish; the heterogeneity of microhabitats, food availability and connectivity degree between environments promoted by seasonal floods make such lakes favourable for the survival of these fish (Petry et al., 2004; Silva et al., 2013). However, a reduction in the intensity of periodic flooding decreases the connectivity between lakes and rivers, mainly in the lakes that are most distant from the river channel (Petry et al., 2003; Freitas et al., 2010). Thus, during low water, the chance to access other habitats decreases, due to

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the reduced area and volume of the lakes and the reduced connections with other water bodies, which generates abiotic stress and enhances competition and predation pressures (Okada et al., 2003; Magoulick and Kobza, 2003; Súarez et al., 2004; Moncayo-Estrada et al., 2011). Conversely, during high water, environments with different hydrological characteristics became connected, and the biological communities and ecological processes tend to be similar in different habitats comprising the river-floodplain ecosystems (Thomaz et al., 2007). During this period, given the increase of areas available for foraging, a relaxation of trophic interactions is expected.

Cyclical seasonal variations arising from the flood pulse influence the origin and abundance of food resources for fish, such as the availability of invertebrates (Takeda and Fujita, 2004; Lansac-Tôha et al., 2009; Colares et al., 2013), thus generating seasonal feeding patterns in fish (Mérona and Rankin-de-Mérona, 2004; Abujanra et al., 2009; Carniatto et al., 2012; Walker et al., 2013). The flood pulse is marked by cycles of abundant food resources in the flood period and limited resources in the dry period (Prejs and Prejs, 1987; Junk et al., 1989; Esteves and Galetti, 1995), with an expected higher availability of allochthonous resources during the flood period (Novakowski et al., 2008; Abujanra et al., 2009; Walker et al., 2013). The expansion of aquatic environments increases connectivity between habitats, allowing the exchange of nutrients and organisms between them (Thomaz et al., 2007), as well as the availability of new trophic niches that can be temporarily exploited by fish (Hahn and Fugi, 2007).

In addition to altering the composition of the fish diet, the flood pulse can influence the breadth of trophic niches, but there is no consensus regarding whether the niche is expanded or contracted in the presence of abundant food. Some studies on fish showed a narrow niche breadth under conditions of high abundance of resources (Walker et al., 2013), whereas others observed wider niche breadth during this period (Corrêa et al., 2009). In Amazon frugivorous fish, Correa and Winemiller (2014) reported no consistent pattern in niche breadth in response to the variation in food availability, and they suggested that this response to abundant or limited food resources depends on the taxon and ecosystem analysed. Thus, while it is clear that there are changes in food availability for fish due to the flood pulse, as described above, the degree to which these variations in availability affect the trophic niche breadth remains uncertain.

Small fish are an important part of the fish fauna in floodplain lakes. Most of these species occupies littoral zones colonized by macrophytes, where they find a wide variety of food (Cunha et al., 2011; Carniatto et al., 2012). This is the case for *Moenkhausia forestii* Benine et al. (2009), a small characid fish, which reaches a maximum length of 3.8 cm (Benine et al., 2009) and occurs in lakes of the Paraná River floodplain, including Cervo Lake, where this study was conducted. *M. forestii* colonizes the littoral zone of the lake, which remains isolated from the main channel of the river during the low-water period and is connected during the high-water period, consumes invertebrates (Quirino et al., 2015) and was captured in sufficient numbers both in low and in high waters. This species therefore offers an opportunity to evaluate the immediate effect of the flood pulse, which promptly provides allochthonous resources to the fish diet upon the increase in water level. It is possible to identify the effect of hydrological pulses on the fish diet because small fish respond quickly to changes in resource availability (Hahn and Fugi, 2007).

This study tested the hypothesis that the flood pulse affects the diet composition and the niche breadth of small fish colonizing the littoral zones of lakes. To this end, we compared the diet composition of *M. forestii* between periods of high and low waters in an isolated floodplain lake of the Upper Paraná River, and we asked two questions: (i) Do the diet composition and the breadth of the trophic niche differ between periods? (ii) Does the inter-individual variation in the use of food resources differ between periods? A positive answer for either of these questions indicates that the cyclical seasonal variations resulting from the hydrological regime do influence the supply of food resources for fish.

2. Materials and methods

This study was conducted in the Upper Paraná River floodplain (22°40′–22°50′S and 53°15′–53°40′W), located in the upper region of the Environmental Protection Area of the islands and *várzeas* of the Paraná River, which is the last dam-free stretch of the Paraná River in Brazil. It is a system that includes rivers, channels and lakes belonging to the Paraná, Baía and Ivinhema systems. Sampling was carried out in Cervo Lake (22°45′29″S and 53°29′46″W), in the Ivinhema system. This is an isolated lake with no connection with the main channel of the Ivinhema River during low-water periods. It is approximately 7.8 ha in area, with an average depth of 2.0 m, and is approximately 70 m from the main river channel, to which it is connected during high-water periods. Its littoral zone is colonized by various species of aquatic macrophytes, such as *Eichhornia azurea* (Sw.) Kunth, *Eichhornia crassipes* (Mart.) Solms and *Nymphaea amazonum* Mart. & Zucc.

Sampling was carried out in September 2010 and March 2011, periods of low and high water, respectively, in the Ivinhema River (Fig. 1). According to Comumello et al. (2003), the Ivinhema River begins to overflow at a depth of 2.75 m. Fish were collected in the littoral zones in the morning (9:00 am) using seine nets of 20 m long and 0.5 cm mesh size. All fish caught were anesthetized with benzocaine, fixed in 4% formaldehyde and subsequently measured (standard length, SL). After evisceration, the stomachs were visually assessed for the degree of stomach fullness (SF): 0 = empty stomach; 1 = up to 25% SF; 2 = 25%–75% SF; 3 $\geq$ 75% SF. Stomachs classified as 2 or 3 were preserved in 4% formalin for diet analyses. Voucher specimens were deposited in the fish collection of Nupélia, State University of Maringá (http://www.nupelia.uem.br/colecao).

For diet analysis, the contents of 40 stomachs (15 individuals in the low period, SL = 2.3–3.3 cm; 25 individuals in the high period, SL = 1.8–3.4 cm) were evaluated. Food items were identified and quantified by the frequency of occurrence and by volumetric method (Hyslop, 1980; Hellawell and Abel, 1971). Temporal variations (low and high periods) in the diet of *M. forestii* were summarized using a Principal Coordinates Analysis (PCoA), applied to the data matrix for the diet, containing the volume values of each item.

Differences in diet composition between periods (low and high water) were tested using a multivariate permutation analysis of variance (PERMANOVA; Anderson, 2005), which was applied to a matrix of food items of individual fish, with volume values transformed into log + 1. This test is sensitive to differences in dispersion among the groups (Anderson, 2004). Differences between the groups (periods) detected using PERMANOVA may be due either to differences in diet composition of fish species, at the population level, or to the inter-individual variability in the diet during each period. Thus, if the PERMANOVA result showed a significant difference, a permutation analysis of multivariate dispersions (PERMDISP; Anderson, 2004) was used. The PERMDISP measures the distance between each individual and the group median (centroid) and evaluates the difference in the centroid distances between the groups (Anderson, 2004). This analysis allows the verification of which period shows a more uniform diet (smaller inter-individual variation) and whether this variability varies significantly between periods. The resulting F statistic of this analysis was tested using the Monte Carlo method with 999 randomizations. The permutational ANOVA was used to determine whether the diet differed in