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Flood pulse are the main determinant of feeding dynamics and composition of *Odontostilbe pequira* (Characiformes: Characidae) in southern Pantanal, Brazil

O pulso de inundação é o principal determinante da dinâmica e composição da dieta de *Odontostilbe pequira* (Characiformes, Characidae) no Pantanal Sul, Brasil

Andréa Fernanda Lourenço da Silva Scanferla[1] and Yzel Rondon Súarez[2]*

[1]Programa de Pós-graduação em Biologia Geral e Bioprospecção, Faculdade de Ciências Biológicas e Agrárias – FCBA, Universidade Federal da Grande Dourados – UFGD, Rod. Dourados-Itahum, Km 12, CEP 79804-970, Dourados, MS, Brazil

[2]Laboratório de Ecologia, Centro de Estudos em Recursos Naturais – CERNA, Universidade Estadual de Mato Grosso do Sul – UEMS, Rod. Dourados-Itahum, Km 12, CEP 79804-970, Dourados, MS, Brazil

*e-mail: yzel@uems.br

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Abstract: Aim: This study characterized the diet of *Odontostilbe pequira* in Porto Murtinho, Pantanal, Brazil, and evaluated the existence of spatial, temporal and ontogenetic variation in feeding. **Methods:** A total of 303 individuals were analyzed from February 2009 through January 2010, and the alimentary index was used to quantify feeding items importance. **Results:** Of the 88.7% of all stomachs analyzed that had contents, 78 prey items were identified, with a predominance of algae and microcrustaceans. Significant temporal and ontogenetic variation in diet dynamics and composition were detected. Of the prey items identified, 38.5% were associated with a specific sampling period. **Conclusion:** The food intake and composition are mainly determined by water levels followed by ontogeny of *O. pequira* in southern Pantanal.

Keywords: floodplain; macrophyte beds; microcrustacean; rotifer; fishes.

Resumo: Objetivos: O presente estudo objetivou caracterizar a dieta de *Odontostilbe pequira* no Pantanal de Porto Murtinho, Brasil e verificar a existência de variação espacial, temporal e ontogenética na obtenção do alimento. **Métodos:** Foram analisados 303 indivíduos entre Fevereiro/2009 e Janeiro/2010 e o Índice Alimentar foi utilizado para quantificar a importância dos ítens alimentares. **Resultados:** Considerando os 88,7% dos estômagos com algum alimento foram identificados 78 itens na dieta, com predomínio de algas e micro-crustáceos. Detectamos variação temporal e ontogenética significativa na dinâmica e composição da dieta. Das presas identificadas 38,5% foram associadas a um período específico de amostragem. **Conclusões:** A tomada do alimento e composição da dieta são determinadas principalmente pela variação no pulso de inundação, seguida da ontogenia de *O. pequira* no Pantanal Sul.

Palavras-chave: planície de inundação; bancos de macrófitas; micro-crustáceos; rotífera; peixes.

1. Introduction

Although some species of fish specialize in certain food items, in tropical regions the majority exhibit great plasticity in their diet, which makes it difficult to determine the structure of trophic patterns. This justify studies of spatial, seasonal and ontogenetic variations in feeding (Lowe-McConnell, 1999).

In the floodplain portion of the Pantanal wetland, small-sized species represent an important portion of the ichthyofauna, and members of Cheirodontinae are the most abundant group in different habitats (Súarez & Petrere-Júnior, 2001; Baginski et al., 2007; Milani et al., 2010; Silva & Petry, 2010; Florentino et al., 2016). The greater portion of these species live associated with large macrophyte patches, in the littoral areas of many habitat types in the Pantanal, where they are an important component of the trophic chain.

As a result of the wide distribution of Cheirodontinae species in the main Neotropical hydrographic basins, studies about aspects of their ecology are numerous, including feeding (Luiz et al., 1998; Hirano & Azevedo, 2007; Dias & Fialho, 2009), population structure (Benitez & Súarez, 2009; Gonçalves et al., 2011; Tondato et al., 2012), reproductive ecology (Silvano et al., 2003; Azevedo et al., 2010; Tondato et al., 2014) and their effect on zooplankton density (Roche et al., 1993; Fantin-Cruz et al., 2008). However, in the Pantanal, the few existing studies did not focus on Cheirodontinae species, and are mixed with other groups (Ximenes et al., 2011). Specifically to *O. pequira*, information about feeding were available for North Pantanal (Santos et al., 2009; Lima et al., 2012), mainly describing mutilating predation behavior, and for Southern Pantanal available information is about life history traits and reproductive ecology (Tondato et al., 2012, 2014).

To understand the ecology and conservation of fishes, information on aspects of feeding, reproduction and growth of the species is essential (Andrian & Barbieri, 1996; Lowe-McConnell, 1999) and fundamental to policy-making. Studies on fish feeding are important to explain the dynamics of aquatic ecosystems, such as habitat occupancy by individual species (Loureiro-Crippa et al., 2009).

This study characterized the feeding habit of *Odontostilbe pequira* (Steindachner, 1882) and evaluated the spatial, temporal and ontogenetic variation in food selection at Southern Pantanal, Porto Murtinho, Mato Grosso do Sul State, Brazil. The hypotheses tested in the study were: 1) Are the river levels and fish standard length influence the feeding dynamics (food quantity and alimentary niche breadth) of *O. pequira* in Southern Pantanal? and 2) Is the diet composition changing among river levels and fish standard length for *O. pequira* in Southern Pantanal?

2. Material and Methods

2.1. Fish sampling

The individuals of *O. pequira* were sampled monthly from February 2009 through January 2010 in macrophyte stands, mainly along the banks of the Paraguay and Amonguijá rivers at municipality of Porto Murtinho, southern Pantanal, Brazil (Figure 1). These rivers were selected because of their differences in physical and biological characteristics. The Paraguay River is the main watercourse of the Pantanal. In the study region it is approximately 300 m wide, with macrophytes along the banks composed predominantly of *Eichhornia azurea*, *Polygonum ferrugineum* and *Urochloa subquadripara*, and flux about 0.81m.s^{-1} (±0.36 standard deviation). The Amonguijá River is a tributary of the Paraguay River. It is approximately 40 m wide, and in the dry period is almost completely covered by macrophytes, mainly *E. azurea*, *E. crassipes* and *Polygonun ferrugineum*, among others. The current is slower than in the Paraguay River (0.20±0.23 m.s^{-1}). In its lower portion, the Amonguijá has a wide flood zone, with narrow areas on great part covered by macrophyte. The higher level of the river occur in dry periods from May to July, in different period of higher rainy and temperature that occur from December to February, being this difference creates a asynchronous regime, in response by a low altimetric decrease in Pantanal wetlands.

In each month, the sampling sites were randomly defined along the riverbanks. The fish were caught with rectangular sieves measuring 0.8×1.2 m, and seine nets (1.5×5 m) with approximately 2 mm mesh. In the field, the fish were euthanized with eugenol and fixed in 10% formalin for later identification, measurements of biometric data (total weight, stomach weight, and standard length), and removal of stomachs. Voucher specimens were deposited at the Museu de Zoologia of the Universidade Federal do Rio Grande do Sul (UFRGS # 11167).

2.2. Stomach analysis

Stomach contents were assessed with the aid of an optical microscope, and quantified by the volumetric method (Hellawell & Abel, 1971).

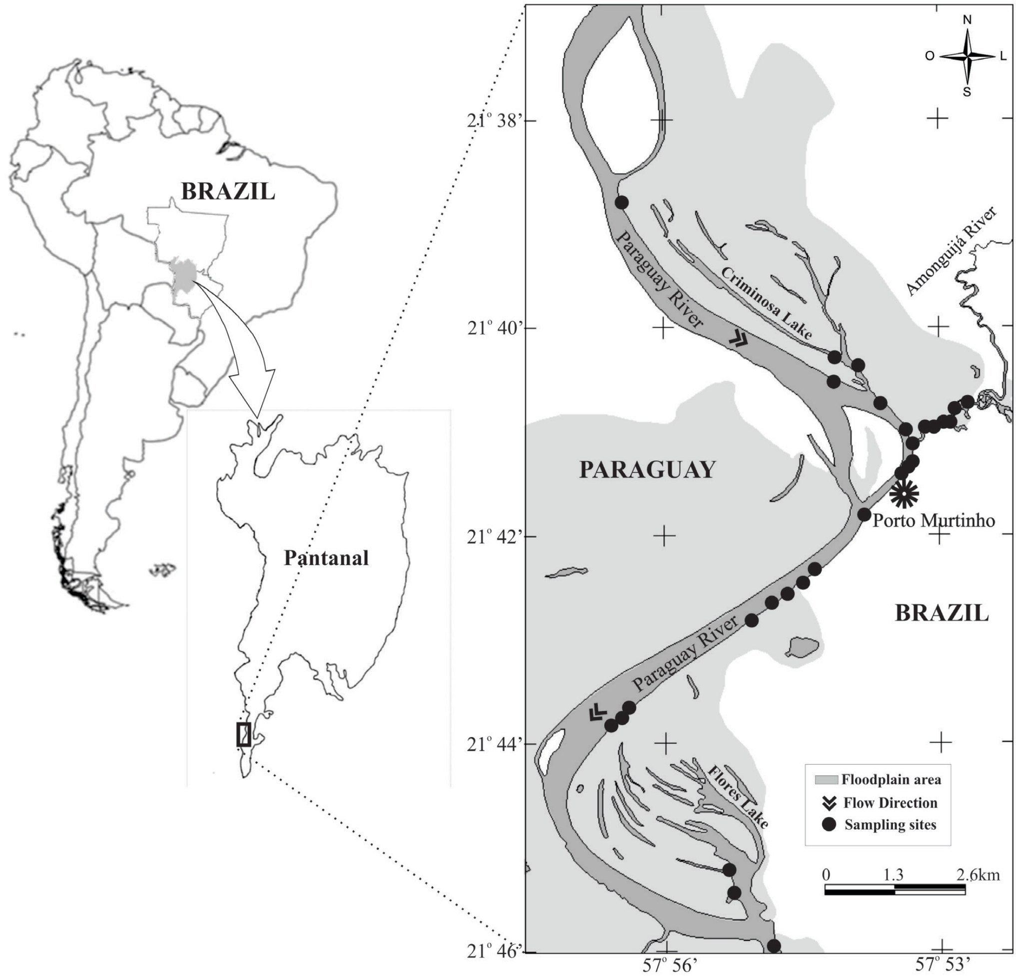

Figure 1. Sampling area at Paraguay and Amonguijá Rivers in the Southern Pantanal, Porto Murtinho, MS, Pantanal, Brazil.

The volume of each item was assigned a percentage of the total volume of all stomach contents (Hyslop, 1980), using a glass counting plate. The item volume was obtained in mm^3 and then converted to ml (Hellawell & Abel, 1971). The volume and frequency of occurrence of each group of alimentary items were used to estimate an Alimentary Index (AI), proposed by Kawakami & Vazzoler (1980).

2.3. Data analysis

The temporal variation in the frequency of each level of stomach repletion index (0=empty; 1=1/4 full; 2=up to half full; 3=3/4 full; 4=full) were evaluated using a Chi-squared test. The river levels phase were defined as rising-water (February to April); high-water (May to July); falling-water (August to October) and dry (November to January) according to historical daily river level at Porto Murtinho Navy base from 1936-2009.

To define if river level and fish size determine the feeding intensity, we conducted two co-variance analysis (ANCOVA) using stomach weight and niche breadth as the response variable, months as an explanatory variable, and standard length as a co-variable. Stomach weight were previously converted to log10, did not interaction between response and explanatory variables were detected and all presuppositions are satisfied. These analysis was realized using R package 3.2.1 (R Core Team, 2015).

To estimate the variations in dietary composition among hydrological phases and fish size classes, analyzed individuals were divided into length classes with interval of 3 mm and we used a permutational multivariate analysis of variance (PERMANOVA). The significance of the PERMANOVA was determined through a randomization procedure (9999 permutations), this analysis were carried out using an routine adonis in vegan package (Oksanen et al., 2016).

Temporal variations in feeding between the fish sampled in the Paraguay and Amonguijá rivers were compared by means of a cluster analysis, using monthly Alimentary Index and Bray-Curtis coefficient using an Unweighted Pair Group Method Average (UPGMA) as linkage method. Cophenetic correlation was obtained, to determine a good adjustment of the dendrogram obtained to the distance matrix, and 0.75 was defined as the minimum value (McGarigal et al., 2000), this analysis were carried out using an R package 3.2.1 (R Core Team, 2015).

Aiming to quantify the differences in prey occurrences along the sample period we performed an Indval analysis (Dufrêne & Legendre, 1997) using a multipatt routine in the indicspecies package (Caceres & Jansen, 2010), and a significance of indicator value was obtained for each species by a randomization procedure (9999 permutations).

3. Results

A total of 303 individuals were analyzed, of which 269 (88.7%) had stomach contents. The proportion of individuals without stomach contents varied significantly during the hydrological period (Chi^2=23.5; df=9; p=0.005) with approximately 17% empty stomachs in the dry and falling-water periods, 1.7% in the rising-water period, and 10.1% at high water. This result was corroborated by the ANCOVA, which indicated significant differences in adjusted mean stomach weight among months (r^2=0.346; F_{months}=8.18***; $F_{standard\ length}$=47.83***) and size of fish. Fish standard length was considered a main determinant of food quantity in the stomach; however, the observed temporal variations in feeding dynamics showed that the change in river level directly influenced the stomach weight. The alimentary niche breadth was also significantly related to water level (Figure 2A) and fish size (Figure 2B) (r^2=0.135; F_{months}=33.09***; $F_{standard\ length}$=7.02**) and, in relation to temporal variation, Figure 2A showed that the alimentary niche breadth reached its highest values during the rising period, while the relation with standard length is negative(Figure 2B).

The diet was composed of 78 food items; the more important in volume were algae ($AI_{amonguijá}$=34.8%; $AI_{paraguay}$=27.8%), microcrustaceans ($AI_{amonguijá}$ = 22%; $AI_{paraguay}$ =24.8%) and insect larvae ($AI_{amonguijá}$ = 1.38%; $AI_{paraguay}$ =4.1%), followed by rotifers ($AI_{amonguijá}$ = 1.44%; $AI_{paraguay}$ =0.60%), testacea ($AI_{amonguijá}$ = 0.97%; $AI_{paraguay}$ =0.73%) and non-identified digested items ($AI_{amonguijá}$ = 39.43%; $AI_{paraguay}$ =41.96%) (Table 1). Considering a general diet composition, algae were more representative in dry water for Paraguay River and have a higher importance in high-water period in Amonguijá River. In other hand, microcrustaceans have a higher importance in flood period of Paraguay River, however, in Amonguijá River they are representative along the whole year with higher values in falling period (Table 1).

Considering the whole diet composition we detected significantly variation during the sampling period (PERMANOVA F=9.99; p<0.001), among size classes (PERMANOVA F=1.66; p=0.035) and the interaction between hydrological period and size classes was also significant (PERMANOVA F=1.73; p<0.001).

The results of the cluster analyses revealed a clear temporal variation in dietary composition, with groups defined mainly according to the hydrological

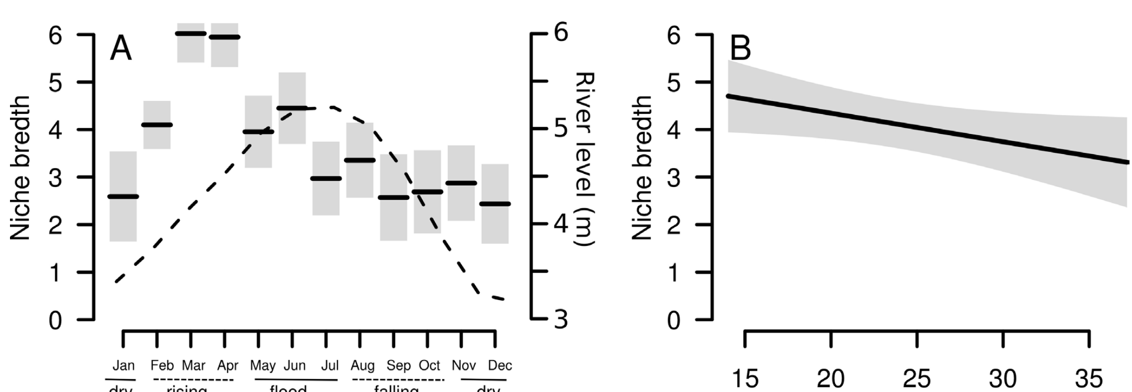

Figure 2. Temporal variation in mean adjusted niche breadth (mean±confidence interval) (A) and adjusted niche breadth (±confidence interval) in response to standard length (mm) (B) of *Odontostilbe pequira* along a sampled year in the southern Pantanal at Porto Murtinho, MS, Brazil. Doted line represent a historical mean river level of Paraguay River.

Table 1. Variation in diet composition using alimentary index among hydrological periods and rivers of *Odontostilbe pequira* in the Paraguay and Amonguijá rivers, southern Pantanal at Porto Murtinho, Brazil.

Items	Paraguay River				Amonguijá River			
	Rising Water	High Water	Falling Water	Dry	Rising Water	High Water	Falling Water	Dry
microcrustacea	28.61	21.06	-	-	20.91	23.53	40.00	17.23
aquatic insects	5.17	3.00	-	-	0.87	0.83	40.00	20.17
Algae	24.21	33.29	-	52.63	34.56	36.82	20.00	18.08
rotifera	0.19	1.68	-	-	1.27	1.90	-	0.63
tecameba	0.24	2.03	-	-	0.51	2.13	-	1.14
Others	41.59	38.94	100	47.37	41.89	34.80	-	42.75

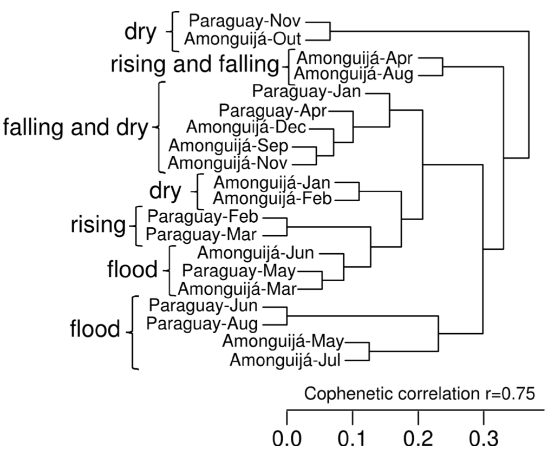

Figure 3. Similarity dendrogram (Bray-curtis coefficient) of dietary composition (Alimentary index) of *Odontostilbe pequira* in the Paraguay and Amonguijá rivers, southern Pantanal at Porto Murtinho, MS, Brazil.

phase; the samples taken in dry period, as also in flood period grouped together in both rivers. Other, less cohesive groups were composed mainly by samples from the rising and falling-water phases were partially grouped (Figure 3). Complementarily, 30 identified items (38.5%) could be used as indicators of the hydrological period (indval). Seventeen items were indicators of the rising-water period, mainly *Moina minuta*, *Ankistrodesmus* spp., Chironomidae larvae and *Ulothrix* spp. However other groups predominated in the dry phase (plant material and sediment) and fish larvae as an indicator of the dry phase, basically defining the differences between the dry and flood periods (Figure 4).

4. Discussion

Aquatic macrophyte beds support high species diversity, algae, invertebrates and vertebrates, and many fish species, juveniles, and adults of small species use this habitat as protection against predators and an ideal locale for feeding (Pelicice et al., 2005; Agostinho et al., 2007). Macrophyte roots provide an appropriate site for initial development for juveniles of larger fishes, and some small species complete their life cycles entirely in this habitat, as observed for *O. pequira* in our studies in this region.

Few information are available to *O. pequira*, being Santos et al. (2009) and Lima et al. (2012) encountered that vegetable material were the main food items consumed by *O. pequira* in North Pantanal. On the other hand Ximenes et al. (2011), also in northern Pantanal, characterized *O. pequira* as omnivorous, feeding mainly on insects, benthic fauna and plant material. Our data corroborated partially these result; then algae and zooplankton were main consumed items.

Allochthonous insects occurred in North Pantanal (Lima et al., 2012), however Santos et al. (2009) encountered only autochthonous items in Caiçara bay, also in North Pantanal. In our study allochthonous items are virtually absent in Porto Murtinho region, this difference can be explained by the smaller representativeness of arboreal vegetation in South Pantanal, once studied region is an flooded area with only some herbaceous and shrub plant species are present and show how much aquatic macrophyte beds are important for population maintenance.

A clear temporal variation in food consumption was observed in our study, with higher mean frequency of full stomach and mean weight in the rising period. Many studies of floodplain areas have suggested that increases in water level lead to higher food availability, which, associated with decreases in fish density, allow higher feeding intensity (Goulding, 1980; Abelha et al., 2001), mainly for opportunistic species. This idea corroborates the Gerking (1994) conclusions, who described the ability of fish to alter their diet in response to seasonality and food resource availability, which complicates the characterization of the trophic

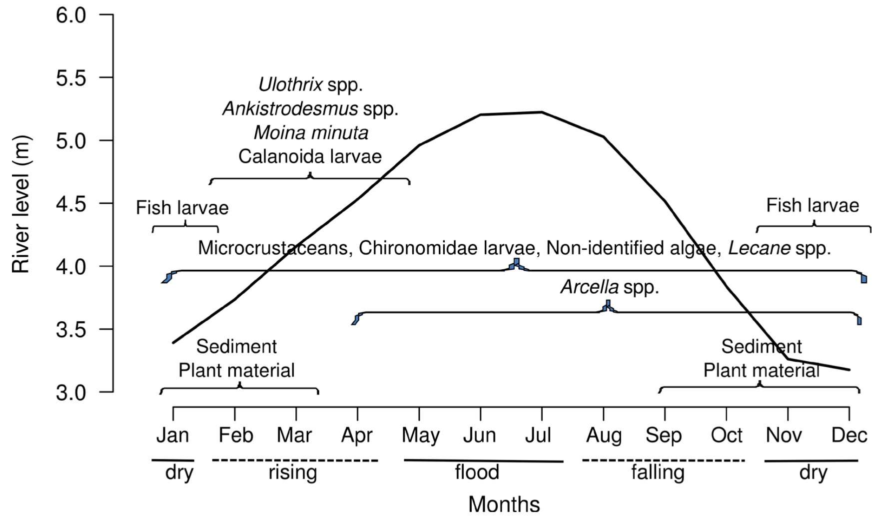

Figure 4. Temporal variation in River level and dietary composition of *Odontostilbe pequira* in the Paraguay and Amonguijá rivers, southern Pantanal at Porto Murtinho, MS, Brazil.

groups. The low frequency of empty stomachs also can be viewed as an evidence of intense feeding activity of *O. pequira*, as observed by Vitule et al. (2008) for *Deuterodon langei* in streams of Atlantic rainforest in southern Brazil.

The highest stomach weights were observed in the high-water period. The alimentary niche breadth was higher in the preceding phase, suggesting that during the rising water, when the floodplain is expanding, more food items are available compared with the high-water phase. To explain this asynchrony, we suggest that despite the reduction in productivity in the high-water period (estimated by mean water conductivity), the dispersal of individuals of *O. pequira* over the floodplain allows them to access more available food items. The preceding period has higher water temperatures and nutrient availability, providing appropriate conditions for the development of more prey species and consequently higher prey richness as phytoplankton (Oliveira, 2000). Studying fish diets in a floodplain lake of the Mogi-Guaçu River, Meschiatti (1995) found the highest diversity of food items in the dry period, in response to the concentration of prey in the low water volume. The same was observed by Power (1983) for Loricariidae in streams of the upper Paraná River. Our rather unusual results can be explained by the predation effect of small characid fishes (e.g., *O. pequira* and *O. paraguayensis*, among others) on plankton density, as also observed by Fantin-Cruz et al. (2008) and corroborated by Silveira et al. (2010).

Studies in a mesocosm experiment showed that fish growth is higher when zooplankton density is also higher (Cooke et al., 2009), and also temporal abundance-occupancy relationships between fish and phytoplankton communities (Hansen & Carey, 2015). Then, considering that the increase on plankton density (phyto and zooplankton) in rising period, that still present higher temperatures and nutrient, offer more feeding resources for small fish species, explain the higher alimentary niche breadth and higher food consumption in these period.

Considering an ontogenetic variation in diet, Abelha et al. (2001) suggested that ontogenetic variation in prey selection is common in fish, and usually are associated with morphological alterations during growth (Lima-Júnior & Goitein, 2003). In this sense, our data showed higher temporal variation in diet composition when compared to ontogenetic variation. The largest individual of *O. pequira* analyzed measured 37.61 mm standard length. The small size reached for this species allow that the larger individuals still use plankton in higher representativity, once these items are not substituted by others food items; Then *O. pequira* can use the same food items throughout its life cycle, since they are continuously available. Consequently, we proposed that the seasonality in resource availability in response to environmental variations can be considered the main determinant of prey selection, as proposed by Pereira et al. (2011) analyzing seasonal diet variation in *Triportheus curtus* in Amazonian floodplain lake.

Rossa et al. (2001), studying variations in cladoceran abundance in lentic and lotic environments in the Upper Paraná river, found spatial and temporal variations in plankton density and strong correlations among the main species and limnological conditions, suggesting that different environments and hydrological periods can define the composition and abundance of these species. A study in this same region with *Aphyocharax dentatus* by Russo & Hahn (2006) found that zooplankton species had higher importance mainly in the rainy season. Our data showed a greater importance of microcrustaceans in this period; however, plant material were the main items in this period (October to February). This was probably a response to low water levels, together considering the spatial distribution of *O. pequira*, which occurs mainly in macrophyte beds near the riverside. Then, in dry period the fishes are close to the sediment and the food items consumed as ingested accidentally together with the sediment.

Considering all the 78 food items identified, approximately 38.5% can be considered an indicator of the sampling period, and 21.8% are indicators of the rising-water period. A large portion of the items occurred seasonally in the stomach analyses, corroborating the opportunism of *O. pequira*. Another interesting result is the significant indicator value of fish larvae in the dry period, when many larger fish species concentrate their reproduction. This exploitation of fish larvae suggests that small fish species can influence the reproductive success of many fish species in floodplain ecosystems.

Concluding, our data showed that algae and microcrustaceans were the basis of the diet of *O. pequira* that have temporal variation in diet dynamics and composition and whole diet vary mainly in function of temporal over ontogenetic variation mainly following the flood pulse of Paraguay River.

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