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FOOD RESOURCE SHARING AMONG BENTHIC AND NEKTONIC STREAM FISH SPECIES*

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ABSTRACT

Several tropical freshwater fish species are generally generalistic feeders, sometimes followed by a diet reduction during the period of decreased resource availability. This study aimed to analyze the dietary overlap between nektonic and benthic fish species. The stomachs of 82 obligatory nektonics and 52 benthic were removed. The diet composition for each individual was determined based on the analysis of the stomach content, and the contents were grouped into 11 categories. For the analysis of food items, the method of degree of food preference was used. To verify the niche overlap between benthic and nectonic, the Pianka index was applied. Benthic species consumed items across all 11 food categories and nektonic species consumed nine. The diet composition of species with nektonic and benthic habits showed a significant difference. Dietary overlapping suggests a supply of the same resources, as they are shared by both groups. The high concentration of water insect larvae in the food content of all sampled fish species, regardless of the position in the water column, shows the importance of insects in the water ecosystems. The composition of ecosystem diets is helpful towards understanding the community structure and can explain the coexistence between different fish's groups where live in different micro-habitats and how tactics used to capture food which may minimize the effects of overlapping and competitive exclusion.

Keywords: food ecology; trophic similarity; dietary overlapping; fish ecology.

COMPARTILHAMENTO DE RECURSOS ALIMENTARES POR PEIXES DE RIACHOS BENTÔNICOS E NECTÔNICOS

RESUMO

Várias espécies de peixes de água doce são generalistas, podendo seguir uma redução da dieta durante a diminuição da disponibilidade de recursos. Este estudo analisou a sobreposição alimentar entre peixes nectônicos e bentônicos. Foram retirados os estômagos de 82 indivíduos nectônicos e 52 bentônicos. A composição da dieta para cada indivíduo foi determinada com base na análise do conteúdo estomacal e os itens da dieta foram agrupados em 11 categorias. Para a análise dos itens alimentares foi utilizado o método do grau de preferência alimentar. Para verificar a sobreposição de nicho entre bentônicos e nectônicos aplicou-se o índice de Pianka. Os bentônicos consumiram 11 itens alimentares e os nectônicos, nove. A composição da dieta das espécies com hábitos nectônicos e bentônicos apresentaram diferença significativa. A sobreposição alimentar sugere a oferta dos mesmos recursos pois são compartilhados por ambos os grupos. A elevada participação de larvas de insetos aquáticos no conteúdo alimentar dos peixes, independentemente da posição na coluna d'água, evidencia a importância dos insetos para os ecossistemas aquáticos. A composição do conteúdo alimentar é importante para compreensão da estrutura das comunidades e pode explicar a coexistência entre diferentes grupos de peixes que vivem em diferentes microhabitats e como as táticas usadas para capturar alimentos podem minimizar os efeitos da sobreposição e exclusão competitiva.

Palavras-chave: ecologia alimentar; similaridade trófica; sobreposição alimentar; ecologia de peixe.

INTRODUCTION

Several tropical freshwater fish species are generally generalistic feeders (Dala-Corte et al., 2017), sometimes followed by a diet contraction during the period of decreased resource availability, but the opportunistic trophic behavior observed for neotropical fish fauna is influenced by the large variety of food and it is also related to temporal and spatial variations (Esteves et al., 2008).

In water systems, the ecosystem is a resource donor (especially in meadow areas) and headwaters are the receptor, where nutrients are of allocthonous origin, without which the primary production and food chains could not be sustained (Lobón-Cerviá et al.,

2016) and where the forest cover has an important role in the food ecology of stream fish species (Trindade et al., 2013). When riparian vegetation or channel morphology changes, the water biota is affected by the transportation of sediments, increased temperature, breaches of trophic chains, and decreased diversity of habitats (Braga and Gomiero, 2009; Dala-Corte et al., 2017).

In streams where the margins have riparian vegetation, the main source of energy comes from the vegetation itself as well as terrestrial invertebrates (Lobón-Cerviá et al., 2016). Although the contribution of autochthonous items increases with the order of streams, the main energy source comes from vegetation and allochthonous animals. In such environments, the contribution of allochthonous material is much more important for the ichthyofauna, providing food items both directly and indirectly (Rezende and Mazzoni, 2006).

Several fish species increase their diet range to take advantage of abundant resources available during the rainy season and resort to more specialized feeding during the dry season (Deus and Petrere-Junior, 2003; Silva et al., 2019), exhibiting a specialized trophic niche. The increased trophic plasticity enables neotropical fish to adjust their dietary habits according to variations in food supply (Balassa et al., 2004; Dala-Corte et al., 2017). Both stochastic and abundance processes may reduce intraspecific competition, facilitating the coexistence of species (Pinto and Uieda, 2007; Dias and Fialho, 2009). Other factors such as trophic morphology, the use of different micro-habitats, periods of activity, and tactics of capture may minimize the overlapping effects (Casatti, 2002; Cetra et al., 2011).

According to Krebs (1989), estimating the food niche range of a species as well as the overlap of two or more species contributes to better understanding of the shared food resources from the surrounding areas, or from the watercourse itself. Measuring the similarities in resource use of the species present within the same environment allows the ability to check the common use of resources that are linked to the maintenance of such communities.

The purpose of this study was to analyze the dietary overlap among nektonic and benthic fish species in streams. We intended to answer the following question: do fish species that occupy different parts of the water column exhibit differences in their consumption of dietary resources?

MATERIAL AND METHODS

The Claro Grande River (Figure 1) is a stream located in the State of São Paulo, Brazil, which belongs to the Alto Rio Paranapanema basin. It originates in the city of Pilar do Sul and ends at the Itapetininga River. The regional vegetation is characterized by Atlantic semi-deciduous forest with a subtropical climate.

The analyzed organisms come from Almeida and Cetra (2016). At the lab, the stomachs of 82 nektonic (*Piabina argentea* Reinhardt, 1867 and *Psalidodon paranae (*Eigenmann, 1914)) and 52 benthic individuals (*Pimelodella gracilis* Valenciennes, 1835; *Characidium schubarti* Travassos; *Characidium gomesi* Travassos, 1956) were removed. The stomach contents were observed using a stereomicroscope (OPTION; 20x and 40x magnification); identification of food items followed Mugnai et al. (2010) and Needham and Needham (1978).

We accessed each stomach by doing a ventral incision and, subsequently, we identified the food items to the lowest possible taxonomic level and quantified using stereomicroscope and optical microscope. The diet items were grouped in 11 food categories: 1- arthropods (other representatives of phylum Arthropoda); 2- Coleopterous; 3- organic debris; 4- Ephemeroptera; 5- insect fragments (of exoskeleton, legs, and antennae of a unidentified insects); 6- Coleoptera larvae; 7- Diptera larvae; 8- Ephemeroptera larvae; 9- insect larvae (other than those already mentioned); 10- Tricoptera larvae; 11- plant material (unidentified debris of leaves, flowers, and algae).

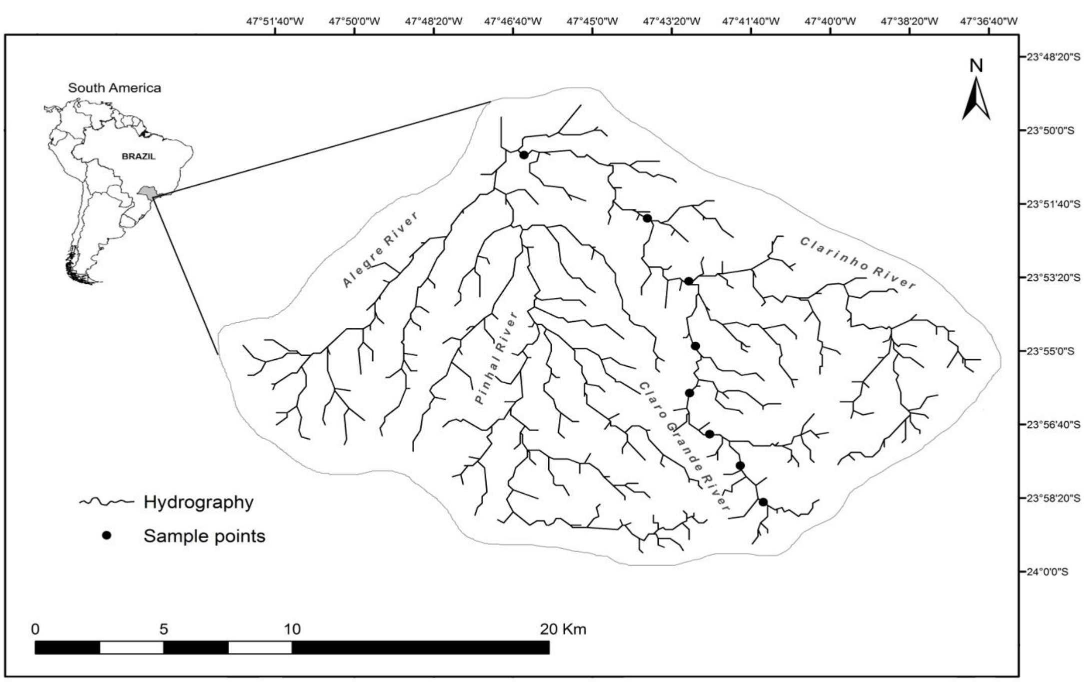

Figure 1. Alto Rio Paranapanema basin: stream stretches sampled in the Claro Grande River (black dots).

The Grade of Feeding Preference (GFP) method was used to compute food item preferences (Braga, 1999). The diet range was quantified by applying the diversity index (H'). A randomized t-test was applied to assess whether there was a significant difference in diet range. To verify the niche overlap between two functional groups (i.e., benthic and nektonic species), the Pianka index ($O_{i,jobs}$) was used. The significance of overlap ($O_{i,jsim}$) was verified using a null model with an algorithm that keeps the niche range and randomizes the structural zeros (RA3).

We applied a nonmetric multidimensional scaling (nMDS) to obtain an ordination of food items in two axes and better represent the dissimilarity relationships among the stomachs contents from the two functional groups. Furthermore, we tested if the two functional groups have similar food items composition with a permutational multivariate analysis of variance using distance matrix (Anderson, 2001). Finally, we used the Hellinger distance as a dissimilarity index with Euclidean property (Legendre and Cáceres, 2013). All the above analyses were carried in the R environment (R CoreTeam, 2021) and RStudio Team (2019). We used the functions "niche_null_model" from the package "EcoSimR" (Gotelli et al., 2015) and "metaMDS", "betadisper", and "adonis" in the package "vegan" (Oksanen et al., 2020).

RESULTS

Benthic species consumed 11 food items, while nektonic species feeding nine items (Table 1). The benthic species niche range was significantly wider than the nektonic ($H'_{bent} = 0.79$, $H'_{nek} = 0.48$, and $p < 0.001$). The niche overlap was high and statistically significant ($O_{i,jobs} = 0.94$, $O_{i,jsim} = 0.24$, $s^2 = 0.06$, and $p = 0.001$). Food items composition from the two functional groups has significantly different compositions (Pseudo-$F_{1,138} = 12.19$, $R^2 = 0.08$, $p = 0.005$) (Figure 2).

Table 1. Mean (standard deviation) of the Grade of Feeding Preference (GFP) for benthic and nektonic species food items.

Food items	Nektonic	Benthic
Plant material	2.41 (1.33)	1.33 (1.25)
Insect fragments	1.27 (1.19)	1.34 (1.33)
Coleoptera larvae	0.21 (0.80)	0.05 (0.22)
Diptera larvae	0.18 (0.39)	0.79 (0.85)
Coleopterous	0.12 (0.53)	0.03 (0.18)
Arthropods	0.04 (0.33)	0.14 (0.61)
Tricoptera larvae	0.01 (0.11)	0.28 (0.62)
Ephemeroptera	0.01 (0.11)	0.26 (0.74)
Insect larvae	0.01 (0.11)	0.07 (0.32)
Organic debris	-	0.55 (1.14)
Ephemeroptera larvae	-	0.09 (0.28)

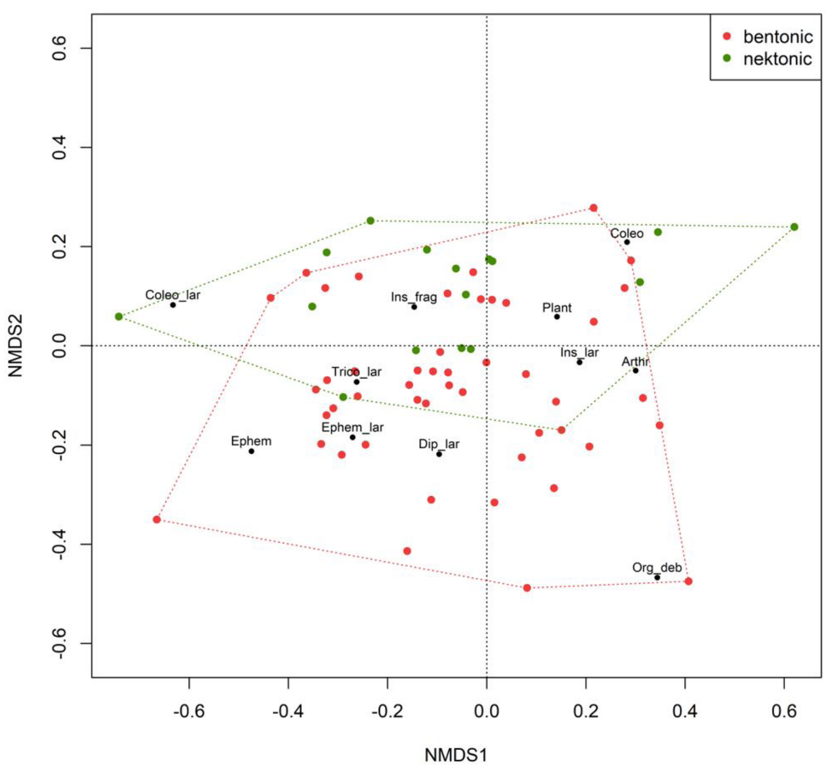

Figure 2. nMDS biplot of the stomachs contents from the two functional groups (Hellinger-transformed and Euclidean distance matrix). Stress = 0.11. Food items: Plant material (Plant); Insect fragments (Ins_frag); Coleoptera larvae (Coleo_lar); Diptera larvae (Dip_lar); Coleopterous (Coleo); Arthropods (Arthr); Tricoptera larvae (Trico_lar); Ephemeroptera (Ephem); Insect larvae (Ins_lar); Organic debris (Org_deb); Ephemeroptera larvae (Ephem_lar).

DISCUSSION

In this study, segregation patterns were observed in the use of food resources which may be explained by differences in micro-habitats, morphology, feeding, and foraging tactics. For example, in the case of micro-habitat usage, *P. paranae* and *P. argentea* live in the water column where they capture the food transported by the current and available on the water surface, such as terrestrial insects and plants. On the other hand, the benthic species *Pimelodella gracilize*, *Characidium schubarti* and *Characidium gomesi* have a distinct feeding tactic, mainly consuming resources such as macroinvertebrates and insect larvae present in streambeds (Casatti et al., 2005; Oliveira et al., 2006; Dias and Fialho, 2009). The high consumption of immature and adult Ephemeroptera, Diptera, and Coleoptera larvae is probably related to their high abundance from the connected Claro Grande River, thus making a great number of resources available for mainly benthic species.

The plant material originating from riparian forests is the basis of the trophic chain of many water ecosystems (Melo et al., 2004). According to Casatti et al. (2012), changes in the composition and structure of riparian vegetation may lead to changes in food availability and may consequently change the dietary habits of generalist fish species, as this energetic and resource-input flow is typical of headwaters that present low primary productivity and what makes water organisms dependent on allochthonous food resources.

The increased participation of water insect larvae in the food composition of fish species, regardless of their position in the water column, evidences the importance of insects for the proper functioning of ground systems adjacent to streams and to the water bodies themselves (Roque et al., 1990; Silva et al., 2019). We believe that changes in the environmental conditions of riparian vegetation would change the supply of resources, thus resulting in changes to the relationships among species which could trigger competitive exclusion and decreases in species variety (Villéger et al., 2010; Lobón-Cerviá et al., 2016).

Generally, stream fish species, especially for small Characidae as previously reported, are opportunistic feeders and may change their diet according to spatial variations and interactions with other species (Dala-Corte et al., 2017). Fish species with nektonic and benthic habits require external resources (Teresa and Carvalho, 2008), as evidenced by the presence of adult terrestrial insects as well as riparian plant fragments found in stomach contents in this study. Therefore, a well-structured riparian forest is capable of protecting the water environment and preserving water quality (Sonoda et al., 2011; Lobón-Cerviá et al., 2016), including providing allocthonous organic matter which serves as food as well as shelter and habitat for aquatic species (Casatti et al., 2009).

Food items found in the stomachs of the studied fish species were different, implying distinct foraging activities for benthic and nektonic species. These results may explain the variety and diversity of species found (Villéger et al., 2010). Assuming that two communities have the same number of resources, the increase in niche overlap enables the occurrence of greater variety. In addition, using the approach across different trophic groups as well as analyzing the use of habitat, i.e., species with different roles in the dynamics and structure of the community, may provide more precise information on the environmental integrity thanks to detailed analyses of the food resources available in the environment. According to Peressin and Cetra (2014), fish species may be used as bio-indicators of the environmental conditions in which the community finds itself.

The high dietary overlap observed may be a result of the collection period, i.e., in the dry season. Studies suggest that, during the dry season, the overlapping level is greater due to the lack of resources available during this period (Deus and Petrere-Junior, 2003; Silva et al., 2019). During the dry season, the increased consumption of allocthonous plant material is caused by the low water current flow, which enables leaves and tree trunks to accumulate along the stream, making them more available to the water community (Aquino et al., 2009). Sabino and Castro (1990) found numerous cases of dietary overlapping in the diets of several fish species and noted that they exhibited differences in spatial distributions and dietary periods.

CONCLUSION

The studied nektonic and benthic fish species exhibited niche overlapping, i.e., they share resources. A possible explanation for this coexistence would be the usage combination of different micro-habitats, periods of activity, and tactics used to capture food, all which may minimize the effects of overlapping and competitive exclusion.

Information about dietary composition may be used to produce a precise diagnosis of the similarity and overlap in the use of resources and is important for understanding community structure. This study showed that nektonic and benthic fish exhibited differences regarding the food resources used. However, because of the high dietary overlapping, many of those resources are shared by both groups.

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