



Diet of two syntopic species of Crenuchidae (Ostariophysi: Characiformes) in an Amazonian rocky stream

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Abstract: This study assessed the diet of two poorly known syntopic fish species of the family Crenuchidae, *Characidium* aff. *declivirostre* and *Leptocharacidium omspilus*, in a Presidente Figueiredo rocky stream, Amazonas, Brazil. The stomach contents were analyzed and their Frequency of Occurrence (FO %) and Relative Volume (Vol %) were combined in a Feeding Index (IAi). We examined 20 individuals of *C. aff. declivirostre* and 23 of *L. omspilus*. The Morisita-Horn Index was used to estimate the overlap between the diets of these species. Immature insects were the most valuable items consumed by both fish species. The diet of *C. aff. declivirostre* was mainly composed of larvae and pupae of Chironomidae, while *L. omspilus* predominantly consumed larvae of Hydroptilidae, Hydropsychidae and Pylalidae. Thus, both species were classified as autochthonous insectivorous. *Characidium* aff. *declivirostre* was considered a more specialized species, probably reflecting lower feeding plasticity or the use of more restricted microhabitats compared to *L. omspilus*. When the food items were analyzed at the family taxonomic level, the diet overlap between these species was considered moderate (Morisita-Horn Index = 0.4). However, a more thorough analysis, at the genus level, indicates a very low diet overlap. Therefore, we conclude that the feeding segregation between *C. aff. declivirostre* and *L. omspilus* may favor their co-existence, despite their high phylogenetic closeness.

Keywords: stream fish, co-existence, feeding overlap.

Dieta de duas espécies sintópicas de Crenuchidae (Ostariophysi: Characiformes) em um riacho rochoso amazônico

Resumo: O presente estudo investigou a dieta de duas espécies de peixes pouco conhecidas da família Crenuchidae, *Characidium* aff. *declivirostre* e *Leptocharacidium omspilus*, sintópicas de um riacho de corredeira do município de Presidente Figueiredo, Estado do Amazonas, Brasil. O conteúdo estomacal de cada exemplar foi analisado pelos métodos de Frequência de Ocorrência (FO%) e Volume Relativo (Vol%) e, posteriormente, combinados para o cálculo do Índice Alimentar (IAi). Foram analisados 20 indivíduos de *C. aff. declivirostre* e 23 de *L. omspilus*. A sobreposição entre a dieta das duas espécies foi estimada pelo Índice Simplificado de Morisita-Horn. Insetos imaturos foram os principais itens consumidos por ambas as espécies. A dieta de *C. aff. declivirostre* mostrou preferência acentuada por larvas e pupas de Chironomidae, enquanto que a dieta de *L. omspilus* concentrou-se em larvas de Hydroptilidae, de Hydropsychidae e de Pylalidae. Portanto, as espécies foram classificadas tróficamente como insetívoras consumidoras de itens autóctones. A dieta de *C. aff. declivirostre* foi mais especializada, o que pode ser reflexo de uma menor plasticidade alimentar ou do uso de microhabitats mais restritos, quando comparado a *L. omspilus*. Ao analisar os itens alimentares em nível taxonômico de família, a sobreposição alimentar foi considerada moderada (Índice de Morisita-Horn = 0,4). Entretanto, análises mais refinadas, em nível de gênero, indicaram sobreposição muito baixa na dieta. Conclui-se que tal segregação alimentar pode favorecer a coexistência de *C. aff. declivirostre* e *L. omspilus*, mesmo que sejam espécies filogeneticamente próximas.

Palavras chaves: Peixes de riacho, coexistência, sobreposição alimentar.

Introduction

The co-existence of species can be affected by their ecological niche, characterized by their diet and feeding tactics, habitat preferences, reproductive strategy, and period of activity (Hutchinson 1957). However, species with similar ecological demands (e.g., phylogenetically closely related species) might not coexist during conditions of resource limitation, because the less competitive would inevitably become extinct as defended by the theory of limiting similarity (Mac Arthur & Levins 1967) and by the competitive exclusion principles (Hardin 1960). Schoener (1974) studied the trophic relationship between syntopic species and proposed three conditions that would allow the co-existence of related species: (1) species may explore distinct microhabitats, (2) they have different diel habits, or (3) they consume distinct food items. Thus, feeding studies can be used as a valuable data source for ecological modelling research, and for the better understanding of syntopic species interaction (Schoener 1974).

Fish feeding studies in small Amazonian streams began during the 1970s (regionally called “igarapés”) (e.g., Knöppel 1970, Soares 1979), and were intensified after that (e.g., Silva 1993, Sabino & Zuanon 1998, Anjos 2005, Carvalho 2008, Zuanon & Ferreira 2008, Fernandes 2014; Barros et al. 2017). However, such information is still restricted to those streams with the typical regional geomorphology found in the Central Amazonia (i.e., with low declivity, sandy bed, the presence of stems, roots and a thick layer of humus) (Walker 1995, Mendonça et al. 2005). Moreover, few studies have been developed in areas of waterfalls and river rapids (Zuanon 1999), and to our knowledge, no studies were carried out about fish diet and resource partitioning in rapids with stony riverbed.

The region of Presidente Figueiredo is located at the southern boundary of the Guianas’ shield and is characterized by rocky streams with long rapids and waterfalls (Nogueira & Sarges 2001). Moreover, studies that are being developed in rocky streams of this same region have already recorded a high co-occurrence of two rheophilic species of the subfamily Characidiinae: *Characidium* aff. *declivirostre* Steindachner, 1915 and *Leptocharacidium omospilus* Buckup, 1993 (R.P. Leitão, unpublished data) (Figure 1). To maintain their spatial position over the rocky substratum, to find and catch preys as well as interact with individuals of the same and other species, morphological and behavioral adaptations may occur in species that inhabit high-speed rapids. Thus, our aims were to determine the diet of *Characidium* aff. *declivirostre* and *Leptocharacidium omospilus* as well as to investigate the degree of interspecific overlapping in this niche dimension.

Material and Methods

Study Area

This study was developed in Marupiará rocky stream (2° 3’ 15.41”S; 60° 6’ 21.72”W), a second-order stream of Urubu River, which flows into the left margin of Amazon River, municipality of Presidente Figueiredo (Amazonas, Brazil). Marupiará stream is characterized by long rapids with stony bed, low depth (3 – 70 cm), narrow width (4.8 m on average), clear and acidic waters with high levels of oxygen, and surrounded by partially intact old-growth forest (Figure 2).

Data collection

Specimens of *Characidium* aff. *declivirostre* and *Leptocharacidium omospilus* were collected between June and December of 2009, and also in March of 2011 during the daytime, using small dip nets (1 mm mesh). The collected specimens were anaesthetized with Eugenol and fixed in 10% formaldehyde. Voucher specimens were deposited in the fish collection of the Instituto Nacional de Pesquisas da Amazônia (INPA33926, 33927, 33928, 33929), Brazil.

Data analysis

Stomach content of 20 adult individuals of *Characidium* aff. *declivirostre* (40.3 – 73.0 mm in standard length SL) and 23 of *Leptocharacidium omospilus* (40.0 – 68.5 mm SL) were analyzed using a stereoscopic microscope. Food items were identified to the lowest possible taxonomic level with the aid of specialised literature. Moreover, the degree of repletion was visually estimated (as the amount of food by stomach expressed in percentage) (adapted from Goulding et al. 1988).

Stomach contents were analyzed according to the methods of Frequency of Occurrence (FO%) (Hyslop 1980) and Relative Volume (Vol % = volume of a given food item/ volume of the stomach). To correct values with distinct amount of aliment, the relative volume was multiplied by the respective degree of stomach repletion (Soares 1979). Finally, the Feeding Index (IAi) was computed using the results previously provided from the determination of the frequency of occurrence as well as the percentage of volume (Kawakami & Vazzoler 1980). The Feeding Index determines the effective importance of each item found in species feeding and contributes to the analysis of the species feeding overlap (Kawakami & Vazzoler 1980).

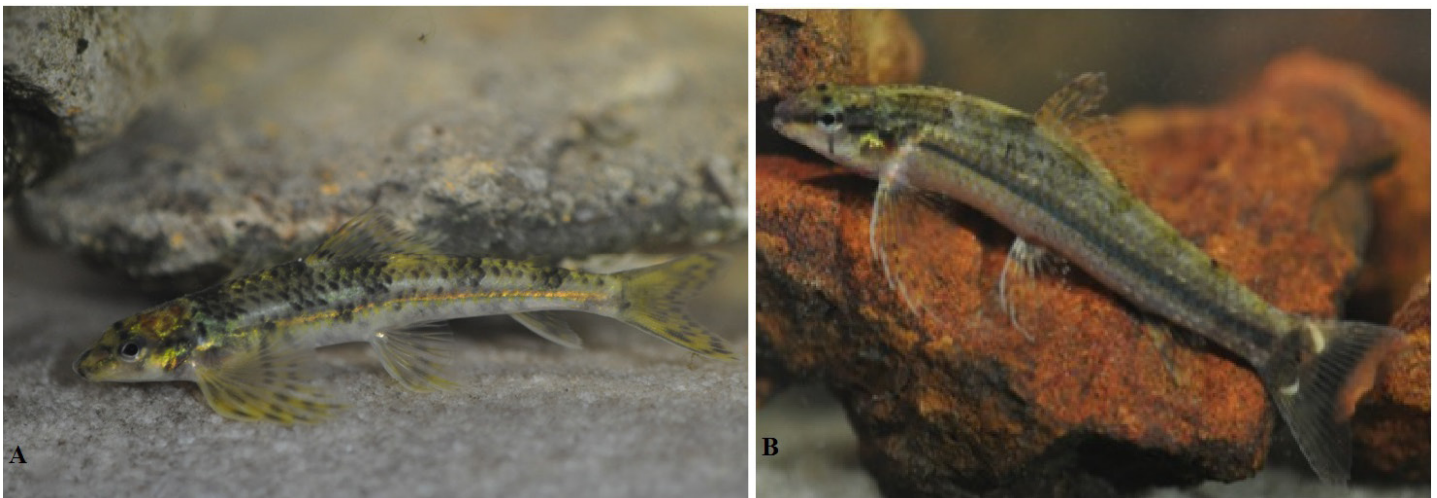


Figure 1: *Characidium* aff. *declivirostre* (A) and *Leptocharacidium omospilus* (B) specimens caught in Marupiará rocky stream, Presidente Figueiredo – Amazonas, Brazil. Photos taken in aquaria by R. P. Leitão.

The Feeding Index is determined by the equation: $IAi = Fi \times Vi \sum (Fi \times Vi)$. Where, F_i = Frequency of occurrence (%) of item i ; V_i = relative volume (%) of item i .

To assess the degree of diet overlap between the fish species, we used the Morisita-Horn Index (C_H ; Horn 1966, Krebs 1998), determined by the equation: $C_H = 2 \sum_i^n p_{ij} \times p_{ik} / \sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2$. Where, p_{ij} = proportion of item i relative to the total resources used by species j ; p_{ik} = proportion of item i relative to the total resources used by species k ; n = total number of resource items. C_H ranges from 0 (no food items shared) to 1.0 (complete overlap), with values > 0.6 indicating significant overlap (Richard & Wallace 1981). This analysis was based on the taxonomic levels of family and genus for the consumed items.

Results

Of the 43 individuals whose stomachs were examined, 13 had empty stomachs (three *Characidium* aff. *declivirostre* and 10 *Leptocharacidium omspilus*). We have registered 21 food items that were grouped into 12 taxonomic categories: larvae and pupae of Diptera (Chironomidae, Simuliidae, Empidae, Tipulidae and Ceratopogonidae), larvae of Trichoptera (Hydropsychidae, Odontoceridae and Hydroptilidae), larvae and adults of Coleoptera (Elmidae), larvae of Lepidoptera (Pyrilidae), nymphs of Ephemeroptera (Baetidae, Leptohiphyidae, Leptophlebiidae and Caenidae), larvae of Megaloptera, nymphs of Odonata (Colopterygidae) and nymphs of Plecoptera (Perlidae), arachnids (aquatic mites), algae, organic debris (amorphous organic matter) and plant material (Table 1).



Figure 2: Marupiará rocky stream, Presidente Figueiredo – Amazonas, Brazil. The samples were collected along stretch between less turbulent waters with dominance of released stones (left) and more turbulent waters with slabs of rock (right).

Table 1: Values of Frequency of occurrence (FO %), Relative volume (Vol %) and Feeding Index (IAi) for each of the food items consumed by *Characidium* aff. *declivirostre* and *Leptocharacidium omspilus*. l = larvae, p = pupae, n = nymph, a = adult

Items	Origin	<i>Characidium</i> aff. <i>declivirostre</i> (n=17)			<i>Leptocharacidium omspilus</i> (n = 13)		
		FO%	Vol%	IAi*100	FO%	Vol%	IAi*100
Chironomidae (l+p)		100.00	33.68	49.03	69.23	2.40	3.80
Simuliidae (l)		17.65	3.55	0.91	15.38	1.65	0.58
Empidae (l)		23.53	0.95	0.33	-	-	-
Tipulidae (l)		5.88	1.78	0.15	-	-	-
Ceratopogonidae (l)		5.88	0.57	0.05	7.69	0.24	0.04
Hydropsychidae (l)		17.65	2.44	0.63	38.46	28.57	25.14
Odontoceridae (l)		-	-	-	7.69	0.65	0.11
Hydroptilidae (l)		88.24	15.62	20.05	61.54	19.00	26.76
Elmidae (l+a)	autochthonous	17.65	0.95	0.24	23.08	2.29	1.21
Pyrilidae (l)		41.18	11.33	6.79	38.46	22.82	20.08
Baetidae (n)		52.94	22.8	17.57	30.77	6.92	4.87
Leptohiphyidae (n)		5.88	0.04	0.00	-	-	-
Leptophlebiidae(n)		-	-	-	15.38	0.90	0.32
Caenidae (n)		-	-	-	7.69	1.29	0.23
Megaloptera (l)		-	-	-	7.69	0.32	0.06
Colopterygidae (n)		-	-	-	7.69	0.39	0.07
Perlidae (n)		5.88	0.14	0.01	-	-	-
Algae		5.88	0.38	0.03	-	-	-
Plant material	alloctone	23.53	0.41	0.14	7.69	0.48	0.09
Acari		35.29	0.24	0.12	23.08	0.38	0.20
Organic debris	unidentified	52.94	5.12	3.94	61.54	11.68	16.45

The diet of *Characidium* aff. *declivirostre* was composed of 16 food items, and the most representative (i.e., with the highest IAI values) were: larvae and pupae of Chironomidae (49.02%), shelters and larvae of Hydroptilidae (20.05%), and nymphs of Baetidae (17.56%) (Table 1 and Figure 3). Moreover, *Leptocharacidium omspilus* also consumed 16 food items, and the most relevant items were: larvae of Hydroptilidae (26.75%), larvae of Hydropsychidae (25.13%), larvae of Pyralidae (20.07%) and organic debris (16.44%) (Table 1 and Figure 3). Overall, food items were more equally distributed in *L. omspilus* than in *C. aff. declivirostre*, as a clear predominance of one food category was observed for *C. aff. declivirostre* (Figure 3).

Based on the Morisita-Horn Index applied to the taxonomic level of family of the consumed items, a moderate degree of diet overlap was detected between the two syntopic species ($C_H = 0.4$). However, given the great importance of Hydroptilidae for the diet of both fish species, we conducted a more thorough analysis by identifying and quantifying the different genera of this family. This analysis revealed a clear difference between the proportions of each item consumed by the crenuchids. For example, the genus *Anchitrichia* composed almost half of Hydroptilidae (Vol = 47%) found in *C. aff. declivirostre* diet, but it was not observed in the

diet of *L. omspilus* (Figure 4). On the other hand, the genus *Neotrichia* represented more than 70% of Hydroptilidae consumed by *L. omspilus*, but only 6% of Hydroptilidae consumed by *C. aff. declivirostre* (Figure 4).

Discussion

The diet of *Characidium* aff. *declivirostre* and *Leptocharacidium omspilus* is mainly composed of aquatic or terrestrial insects in its aquatic phase. Therefore, we may categorize both species as autochthonous insectivores. Similar results have been found by other diet studies developed with species of the same sub-family such as, *Characidium* sp., *C. lanei*, *C. pterostictum* and *C. vidali* (in streams of Atlantic Forest: Sabino & Castro 1990, Aranha et al. 2000, Rezende et al. 2013), *C. pteroides* and *Characidium* sp. (in Amazonian streams: Anjos 2005, Carvalho 2008).

The great variety of preys ingested by both species suggests that they are generalist feeders. However, given the high proportion of a single family of insects (Chironomidae: 49.02%) in its diet, *C. aff. declivirostre* has also shown some tendency to specialization. This may be due to ecological causes associated with the Optimal Foraging Theory as many generalist populations could be composed by individuals with tendency to

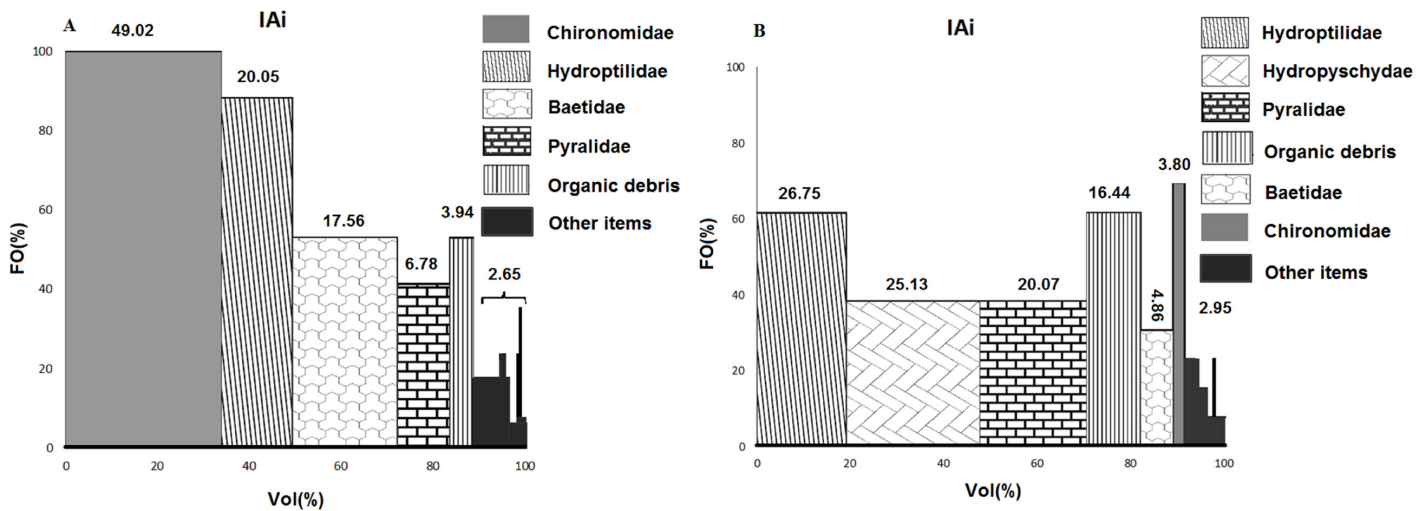


Figure 3: Frequency of occurrence (FO %) and Relative volume (Vol %), for the food items consumed by *Characidium* aff. *declivirostre* (A) and *Leptocharacidium omspilus* (B).

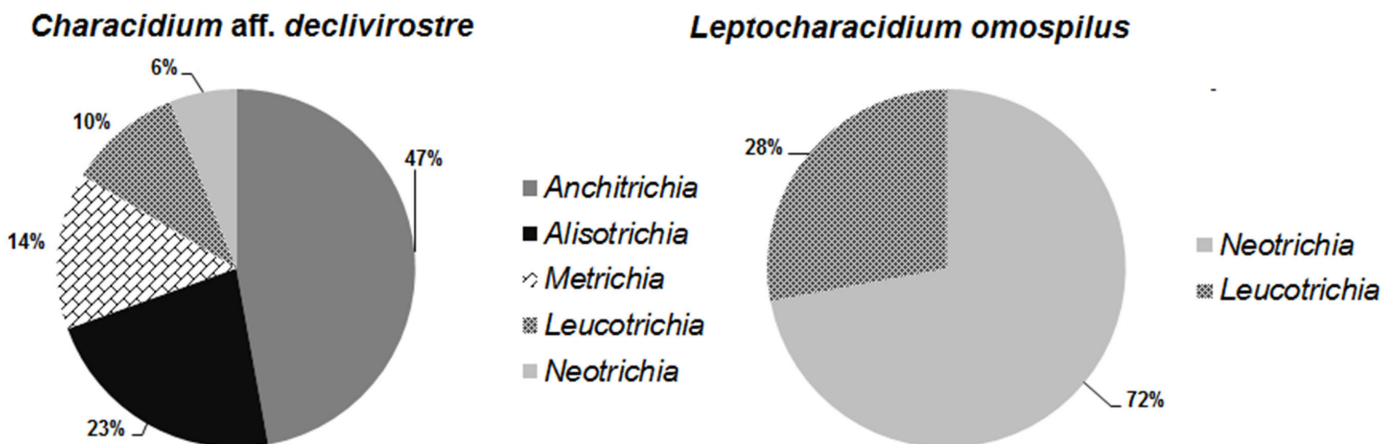


Figure 4: Family Hydroptilidae - Relative volume (%) of genera identified for *Characidium* aff. *declivirostre* and *Leptocharacidium omspilus*.

specialization (Araújo et al. 2011). The generalist strategy here observed may be favored by the typical seasonality of prey availability found in Neotropical streams (Gerking 1994, Zuanon & Ferreira 2008). Indeed, many of the stream fishes have already been categorized as generalists, consuming the most abundant resources available in their habitats (Esteves & Aranha 1999). The results found in this study were not an exception, in fact, the vast abundance of larvae and pupa of Dipterans detected seem to support such information as they also use to be well represented in rapids (Carvalho 2008, Hamada et al. 2014). Great abundance and richness of aquatic insects such as larvae of Trichoptera (32 genera and 11 families) have also been recorded for the rocky streams of Presidente Figueiredo (Pes 2001). Therefore, and also according to the Optimal Foraging Theory, generalist strategy may be favored because the ingestion of the most available preys will represent a reduction in energy costs when searching and selecting them (Stephens & Krebs 1986).

Many aquatic insects found in the diet of both fish species (e.g., Simuliidae, Hydroptilidae and Baetidae) have morphological and physiological characteristics that allow them to remain in fast-flowing waters (Hamada et al. 2014). For example, larvae of Simuliidae have adhesive hooks that efficiently adhere to the substratum surface, and larvae of Hydroptilidae attach its shelters to large pieces of submerged wood (Hamada et al. 2014). Thus, here we show evidences that *C. aff. declivirostre* and *L. omspilus* are foraging in fast-flowing and turbulent rapids.

Based on the Morisita-Horn Index applied to the taxonomic level of family of the consumed items, a moderate degree of diet overlap was detected between the two syntopic species. This is probably explained by the similar overall composition of items, although the amount of each item is quite distinct between *C. aff. declivirostre* and *L. omspilus*. A more in-depth assessment of one of the most important prey families (the Hydroptilidae) has shown a very distinct contribution of genera between species diets. Therefore, despite *C. aff. declivirostre* and *L. omspilus* being phylogenetically related species, living in the same habitat, they seem to be, at least partly, segregating its niche dimension (i.e., diet).

Meanwhile, high feeding overlap has been extensively registered between closely related species, and the spatial segregation (e.g., meso or microhabitats) was considered as the most important partitioning mechanism (Schoener 1974, Aranha et al. 1998, Aranha et al. 2000, Mazzoni et al. 2012, Silva et al. 2012, Leitão et al. 2015, Barros et al. 2017). In Amazonian streams, high dietary overlap (60%) was registered between syntopic characids (*Bryconops inpai* and *B. giacopinii*), but they were occupying distinct positions in the water column (Barros et al. 2017). Furthermore, competition between species with similar dietary habits would also be reduced by the high amount of preys found in this same area (Knoppel 1970). However, the few studies developed in Amazonian streams were restricted to those streams with geomorphology typical of the region (i.e., low declivity and current velocity, sandy bottom with trunks and a dense layer of humus) (Santos 2005, Fernandes 2014, Barros et al. 2017). Streams with more homogenous and continuous rocky bottom (i.e., slab) with strong currents, as those of Presidente Figueiredo region, may offer less feeding opportunity and great difficulty of swimming and fish positioning along the water column. So, the co-existence of *C. aff. declivirostre* and *L. omspilus* may be favored by their partial partitioning of resources that probably is also reducing the competition between them (Pianka 1973, Schoener 1974). Notwithstanding, further studies on other niche dimensions, such as the use of microhabitats, are certainly desirable to a better elucidation of the mechanisms promoting their co-occurrence in these streams.

Fish feeding studies are crucial for several theoretical and practical aspects. Regardless of the vast biodiversity of Amazonia, such approach is still rare for stream systems. Particularly for rocky streams with rapids, this is the first study that aimed to investigate the fish diet and the importance of such niche dimension for explaining species co-existence,

being an important basis for the knowledge of the natural history of the Amazonian ichthyofauna.

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