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Spatial and temporal variation of the diet of the flag tetra *Hyphessobrycon heterorhabdus* (Characiformes: Characidae) in streams of the Eastern Amazon

Correspondence:
Naraiana Loureiro Benone
nbenone@gmail.com

Naraiana Loureiro Benone[1], Cleonice Maria Cardoso Lobato[2], Bruno Eleres Soares[3] and Luciano Fogaça de Assis Montag[2]

Spatial and temporal variations in streams promote large fluctuations of resource availability, thus affecting the diet of fishes. We evaluated the effects of hydrological periods and stream order within periods on the diet of the flag tetra *Hyphessobrycon heterorhabdus*. We analyzed 160 stomachs in eight streams ranging from 1st to 3rd order between dry and flood period. Sampled streams belonged to a well-preserved area in the Eastern Amazon. The flag tetra is omnivorous, with a tendency towards insectivory. During the dry period, the species exhibited a higher amount of autochthonous than allochthonous items. Fish consumed more allochthonous items in 1st and 2nd order streams in the dry period and in 1st and 3rd order streams in the flood period. These results reflect the interactions between temporal and longitudinal factors on resource availability and its influence on fish diet. This pattern is probably dependent on the extensive riparian vegetation as a direct and indirect source of food for stream fish.

Keywords: Feeding, Floodplain, Hydrological period, Riparian vegetation, Stream order.

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1 Universidade do Estado de Minas Gerais (UEMG), Unidade Passos, Av. Juca Stockler, 1130, Belo Horizonte, 37900-106 Passos, MG, Brazil. nbenone@gmail.com.

2 Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará (UFPA), Rua Augusto Corrêa, 01, Guamá, 66075-110 Belém, PA, Brazil. (CMCL) lobatocmc@gmail.com, (LFAM) lfamontag@gmail.com.

3 Laboratório de Limnologia, Universidade Federal do Rio de Janeiro (UFRJ), Av. Carlos Chagas Filho, 373, Ilha do Fundão, 21941-902 Rio de Janeiro, RJ, Brazil. soares.e.bruno@gmail.com.

Variações espaciais e temporais em habitats de riachos promovem grandes flutuações na disponibilidade de recursos, afetando assim a dieta dos peixes. Avaliamos os efeitos dos períodos hidrológicos e da ordem do riacho em cada período na dieta do tetra *Hyphessobrycon heterorhabdus*. Analisamos 160 estômagos em oito riachos variando de 1ª a 3ª ordem entre o período de seca e cheia. Todos os riachos foram amostrados em uma área bem preservada na Amazônia Oriental. O tetra é onívoro com tendência à insetivoria. Durante o período seco, a espécie exibiu maior quantidade de itens autóctones do que itens alóctones. Os peixes consumiram mais itens alóctones nos riachos de 1ª e 2ª ordem no período de seca e nos riachos de 1ª e 3ª ordem no período de cheia. Esses resultados refletem as interações entre fatores temporais e longitudinais na disponibilidade de recursos e sua influência na dieta de peixes. Este padrão é provavelmente dependente da extensa vegetação ripária como fonte direta e indireta de alimento para peixes de riachos.

Palavras-chave: Alimentação, Ordem dos riachos, Período hidrológico, Planície de inundação, Vegetação ripária

INTRODUCTION

Fish play an essential role in nutrient cycling by linking aquatic and terrestrial ecosystems (Milardi *et al*., 2016). They prey on terrestrial plants and invertebrates that fall on streams, incorporating terrestrial carbon in streams (Brejão *et al*., 2013; Milardi *et al*., 2016). On the other hand, fish also prey on the early stages of aquatic invertebrates (Pinto, Uieda, 2007), impairing the amount of aquatic carbon transferred to terrestrial ecosystems in the form of winged adults. Since headwater stream fish are mainly dependent on terrestrial subsidies, studying their diet and how it changes in time and space is vital to understand the food web connecting both systems (Deus, Petrere-Junior, 2003; Wesner, 2013; Wolff *et al*., 2013).

Spatial and temporal variations in the conditions of rivers and streams account for large fluctuations of resource availability (Thomaz *et al*., 2006; Lisboa *et al*., 2015). Lotic systems are highly heterogeneous due to their open nature and their interactions with their surrounding landscape (Ward, 1989). The variations on the longitudinal and temporal dimensions have profound effects on the diet of fishes (Deus, Petrere-Junior, 2003; Wolff *et al*., 2013).

In the longitudinal dimension, changes in the channel morphology and riparian cover can alter the type and variability of food items, with the increasing importance of autochthonous items downstream (Vannote *et al*., 1980; Wolff *et al*., 2013). Small forested streams are typically oligotrophic because of the extensive shading by the riparian vegetation. Given this, the aquatic fauna of headwaters relies on allochthonous input to sustain the trophic network. Fishes usually feed on terrestrial insects or larvae of aquatic insects that, by its turn, depend on allochthonous organic matter (Kemenes, Forsberg, 2014; Montag *et al*., 2019). However, reduced riparian cover in larger streams allows increased light input to the aquatic environment. This light stimulates primary production, allowing consumers to survive on autochthonous resources and enhancing the variety of food items to the fish fauna (Pouilly *et al*., 2006).

Temporal changes markedly shape large rivers (Flood Pulse Concept, Junk *et al*., 1989), but are deemed less important in small streams since local stochastic rainfall events affect stream dynamics (Saito, Mazão, 2012). However, due to sea-level changes during the Holocene, the lower courses of several clear- and blackwater rivers in the Amazon are lake-like ("ria lake", "river-lake" or "drowned streams", Sioli, 1967). Their tributaries have slow flows and large widths permanently associated with broad floodplains (Behling, Costa, 2000; Benone *et al*., 2018). In the Anapu river basin (Eastern Amazon), Benone *et al.* (2018) showed that the width of such streams and their floodplains widely differed between the dry and the flood period, offering an opportunity for fish to explore several new environments and find more resources during the flood period.

To investigate the spatial and temporal variations in the diet of fishes in drowned streams, we chose the flag tetra *Hyphessobrycon heterorhabdus* (Ulrey, 1894) (Characiformes: Characidae), a common species in the lower Amazon river basin, as a model study. This gregarious species is nektonic and inhabits the backwaters predominantly, picking food particles in the upper layer of the water column (Brejão *et al*., 2013). We hypothesized that: 1) the smaller shading in downstream direction may allow increasing importance of autochthonous items to the food webs; thus, the diet of *H. heterorhabdus* would change from 1st to 3rd order streams, and 2) streams will be much broader during the flood period than during the dry period, increasing the availability of allochthonous items in the floodplain and their relative importance to the species' diet during this period.

MATERIAL AND METHODS

Study area. We sampled fish in streams within the Caxiuanã National Forest, a federal protected area located in Portel and Melgaço, State of Pará, Brazil, in the lower Anapu region, Eastern Amazon (Fig. 1). The Caxiuanã National Forest is covered predominantly by a dense lowland *Terra-Firme* rainforest (85% of its total area). The mean air temperature is 26.7°C, ranging from a minimum of 23°C to a maximum of 32.7°C (Lisboa, 2002). The local climate is tropical hot and humid, corresponding to Köppen's Am type, with a well-defined seasonality and a short dry period (Peel *et al*., 2007), with a dry season from July to November and a rainy season between December and June (Oliveira *et al*., 2008). The lower Anapu River reaches its highest water level in April and May (180 cm), dropping to a minimum of 120 cm in November and December. Due to the drowning of local valleys in the Holocene, the lower Anapu is impounded and gained lacustrine features (*i.e*., ria lakes) (Behling, Costa, 2000). It resulted in slow-flowing streams with acidic water and a dense amount of leaf packs and trunks covering the streambed. Their main channels are associated with broad floodplains that can reach > 100 m during the flood period (Benone *et al*., 2018).

Fish sampling. We selected eight streams, three of 1st order, two of 2nd order, and three of 3rd order. Each stream was sampled twice, one during the dry period (November 2010) and one in the flood period (April 2011). We sampled fish specimens with hand

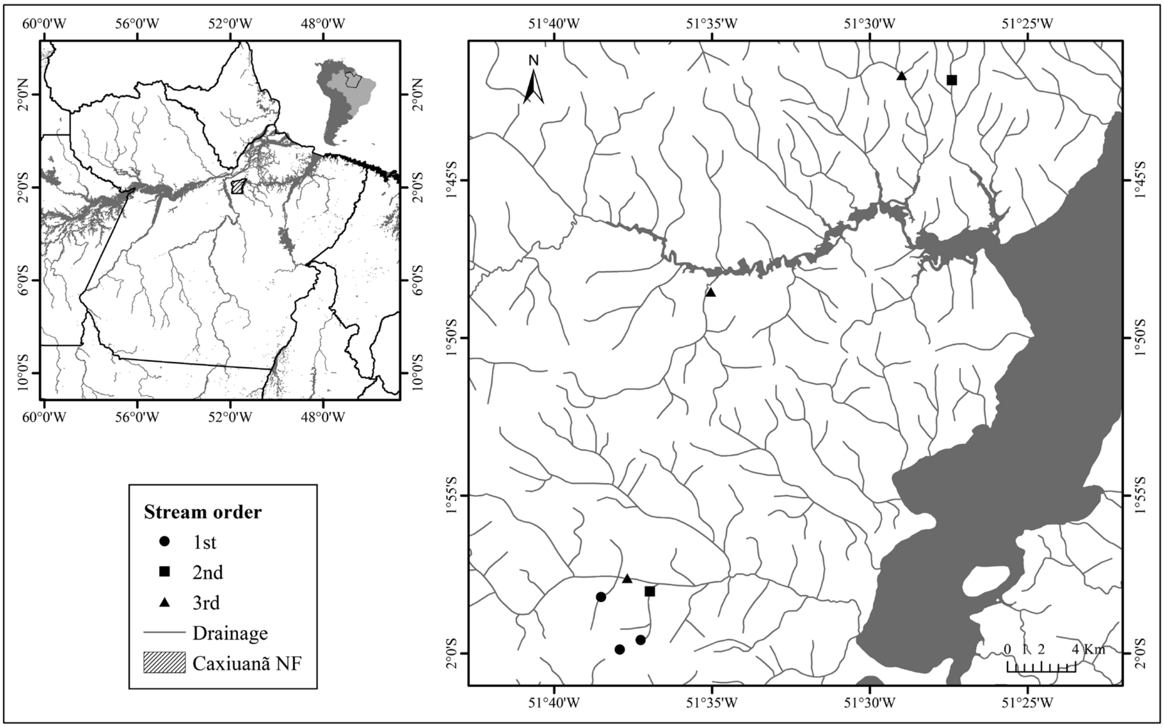

FIGURE 1 | Streams sampled during the dry period of 2010 and the flood period of 2011 in the Caxiuanã National Forest, Eastern Amazon, State of Pará, Brazil.

sieves of 55 cm and 3 mm mesh in a 50 m stretch for 6h divided among three or four collectors. Specimens were fixed in 10% formalin and preserved in 70% ethanol under voucher number MPEG 23389 (Ichthyological Collection, Museu Paraense Emílio Goeldi, Belém, PA, Brazil).

Diet description. To assess diet composition of *H. heterorhabdus*, we selected ten individuals in each stream, with 160 specimens divided into 80 per hydrological period. We analyzed their stomach contents under a stereoscopic microscope. We identified food items using the literature (Mugnai *et al*., 2010; Hamada *et al*., 2014) and with the input from specialists. To obtain the percentage composition of each food item, we placed the stomach contents in a dish over a graph paper and then counted the grid cells covered by each food item. Dataset is available in the Figshare digital repository (10.6084/m9.figshare.12967901). We converted counts into percentages by comparing then to the total grid cells covered by all items in each stomach (Hynes, 1950). Dominance is the percentage that an item occupied most of the content of each stomach related to the total number of stomachs, while the frequency of occurrence is the percentage of the number of stomachs in which an item occurs over the total number of stomachs (Hyslop, 1980). We combined these indices to calculate the Alimentary index (Ai%, Kawakami, Vazzoler, 1980) for hydrological periods and orders. Ai% estimates the relative importance of each food item to the species' diet.

We analyzed the feeding strategy of *H. heterorhabdus* using the graphical method of Amundsen *et al.* (1996) based on the frequency of occurrence and prey-specific abundance of food items, which is calculated using their dominance. We plotted food items in a bivariate space to analyze the species' feeding strategy, and the contribution of individual niche breadth and niche overlap among individuals to the niche breadth of the population. Higher values in the horizontal axis indicate common use of the food item by the population. Higher values in the vertical axis indicate specialization in the food item. The importance of individuals' strategies to the niche breadth of the population may be assessed from a diagonal axis, starting in the minimum value in the horizontal axis and maximum value in the vertical axis. The high between-phenotype component indicates a population composed of specialist individuals, and a high within-phenotype component shows a population consisting of generalist individuals.

Statistical analysis. We used the square-rooted percentage composition of each specimen to build a dissimilarity matrix based on the Bray-Curtis index (Legendre, Legendre, 2012). To evaluate if the diet of *H. heterorhabdus* varied between hydrologic periods and stream orders, we used a permutational multivariate analysis of variance (PERMANOVA, Anderson *et al*., 2008). To assess differences in diet heterogeneity within factors (hydrologic periods and stream orders), we used a permutational analysis of multivariate dispersions (PERMDISP, Anderson *et al*., 2008). For both analyses, we considered stream orders nested within periods and applied pairwise *posthoc* tests. P-values were obtained through Monte-Carlo procedures. We performed a similarity percentage breakdown (SIMPER) to evaluate the contribution of each food item to the dietary dissimilarities between periods and stream orders (nested within periods). Data variation was visualized by running a principal coordinate analysis (PCoA, Legendre, Legendre, 2012). We ran all analyses using 999 permutations in the R environment (R Core Team, 2016), using the vegan package (Oksanen *et al*., 2016) and codes provided by Soares *et al.* (2020).

RESULTS

From the 160 stomachs, one was empty, so we used 159 stomachs for further analysis. The species diet was composed of 18 items, ten allochthonous, seven autochthonous, and one of unknown origin (Tab. 1). The diet of *H. heterorhabdus* is mainly composed of exoskeleton fragments and by a variety of insect groups, such as Odonata, Hemiptera, and Trichoptera, followed by allochthonous vegetal fragments. The species consumed higher amounts of autochthonous items than allochthonous ones in the dry period (Ai%: 33.30 *vs.* 29.09), but the inverse occurred in the flood period (Ai%: 42.60 *vs.* 49.56). Fish consumed more allochthonous items in 1^{st} and 2^{nd} order streams in the dry period and in 1^{st} and 3^{rd} order streams in the flood period (Tab. 1).

In the Amundsen graph (Fig. 2), most items were positioned in the lower and upper left, indicating that this species has a generalist diet based mostly on rarely consumed food items (frequency of occurrence % < 50%) and some specialized individuals. The predominance of food items with a low frequency of occurrence supports the importance of the between-phenotype component for the niche breadth of the population. This pattern was similar in both hydrological periods and stream orders.

TABLE 1 | Alimentary index (Ai%) per hydrological period and stream order for *Hyphessobrycon heterorhabdus*. Bold values indicate items with a strong contribution to diet (≥ 20%).

Food item	Hydrological period		Total	Stream order					
				Dry			Flood		
	Dry	Flood		1st order	2nd order	3rd order	1st order	2nd order	3rd order
Animal (autochthonous)									
Ephemeroptera (nymph)	9.26	5.66	7.77	6.45	-	17.45	-	15.38	7.89
Odonata (larvae)	9.92	17.76	14.15	7.74	12.99	4.55	2.29	**26.92**	1.32
Coleoptera (larvae)	-	1.22	0.33	-	-	-	3.86	-	-
Diptera (larvae)	2.32	-	1.33	5.16	3.9	-	-	-	-
Diptera (eggs)	6.17	2.42	4.45	-	-	**31.82**	-	-	11.84
Diptera (pupae)	0.99	0.2	0.44	2.59	1.3	-	0.48	-	-
Exoskeleton fragments	4.64	15.34	2	-	6.49	1.23	-	**46.15**	18.42
Animal (allochthonous)									
Isoptera (adult)	0.44	2.42	1.33	0.65	1.3	-	11.59	-	-
Formicidae (adult)	0.55	-	0.47	3.23	-	-	-	-	-
Trichoptera (adult)	2.32	17.26	8.66	2.59	6.49	-	**28.99**	2.88	7.89
Hemiptera (adult)	1.85	-	3.19	17.42	5.19	3.5	-	-	-
Ephemeroptera (adult)	-	1.51	0.67	-	-	-	-	0.96	5.26
Orthoptera (adult)	-	0.44	0.11	-	-	-	-	-	2.63
Coleoptera (adult)	3.53	1.98	2.5	-	-	18.18	-	-	1.32
Heteroptera (adult)	-	2.12	0.44	-	-	-	1.14	-	-
Exoskeleton fragments	7.28	1.2	4.27	2.65	7.79	-	3.86	-	-
Animal (unknown source)									
Exoskeleton fragments	**28.67**	9.82	18.98	**25.86**	**31.17**	13.64	15.94	-	3.95
Vegetal (allochthonous)									
Vegetal fragments	13.12	**22.63**	19.98	7.74	**23.38**	1.14	4.84	7.69	**39.47**

We found differences between periods (pseudo-F = 2.60, $p < 0.01$) and order (pseudo-F = 4.95, $p < 0.01$) for the diet of *H. heterorhabdus* (Figs. 3–4). Within dry period, diet varied between 1^{st} and 3^{rd} orders and 2^{nd} and 3^{rd} orders, while it varied among all pairs of orders within flood period (Tab. 2). The PERMDISP analysis showed no difference in diet heterogeneity for period (F = 1.63, p = 0.20) or for orders within the dry period (Dry: F = 0.17, p = 0.83). Orders within the flood period showed distinct levels of heterogeneity (Flood: F = 6.23, $p < 0.01$), resulting from 2^{nd} and 3^{rd} order streams difference (average distance to median: 1^{st} = 0.57, 2^{nd} = 0.51, 3^{rd} = 0.62) (Tab. 3).

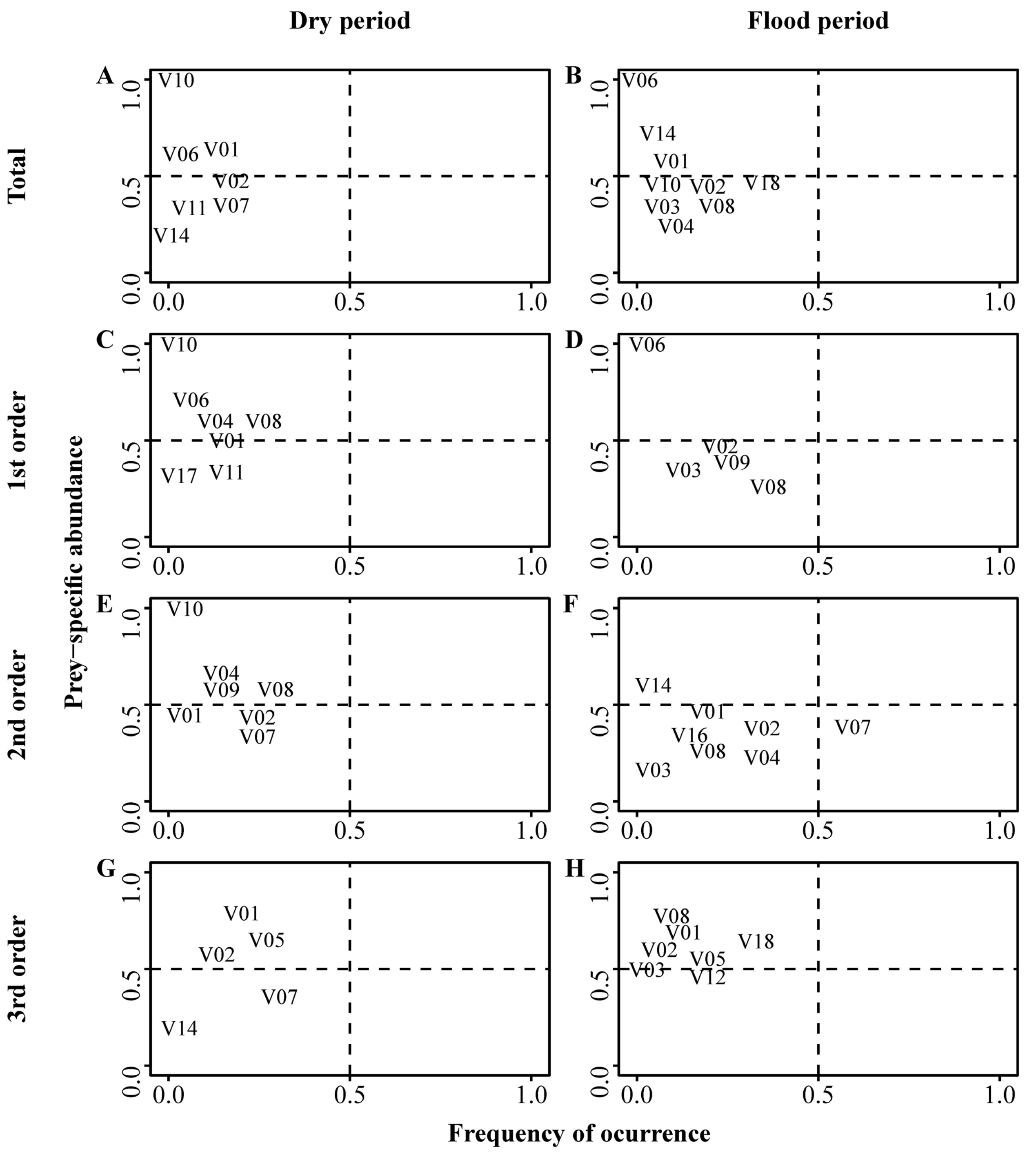

FIGURE 2 | Feeding strategy revealed by Amundsen diagram of *Hyphessobrycon heterorhabdus* sampled in eight streams of a protected area in the Eastern Amazon, Brazil. **A**, **C**, **E**, and **G** represent feeding during the dry period, while **B**, **D**, **F**, and **H** represent the flood period. **A** and **B** show the diet considering all streams, whilst **C** and **D** represent 1st order streams, **E** and **F** represent 2nd order streams, and **G** and **H** represent 3rd order streams. V01 = Ephemeroptera (nymph); V02 = Odonata (larvae); V03 = Coleoptera (larvae); V04 = Diptera (larvae); V05 = Diptera (eggs); V06 = Diptera (pupae); V07 = Exoskeleton fragments (autochthonous source); V08 = Exoskeleton fragments (unknown source); V09 = Exoskeleton fragments (allochthonous source); V10 = Isoptera; V11 = Formicidae; V12 = Trichoptera; V13 = Hemiptera; V14 = Ephemeroptera; V15 = Orthoptera; V16 = Coleoptera; V17 = Heteroptera; V18 = Vegetal fragments (allochthonous source).

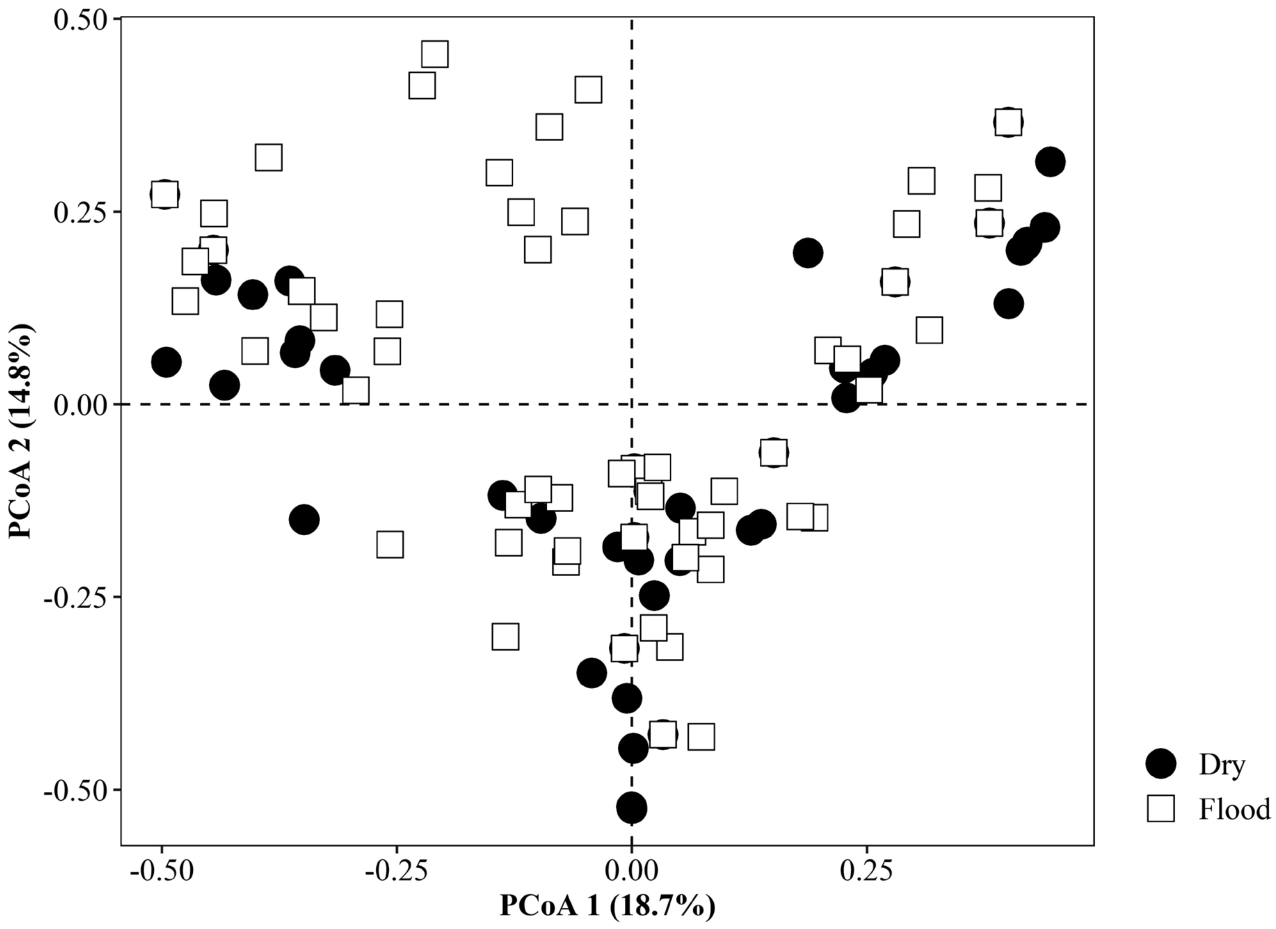

FIGURE 3 | Ordination of the diet of *Hyphessobrycon heterorhabdus* between hydrological periods in eight streams of a protected area in the Eastern Amazon, Brazil.

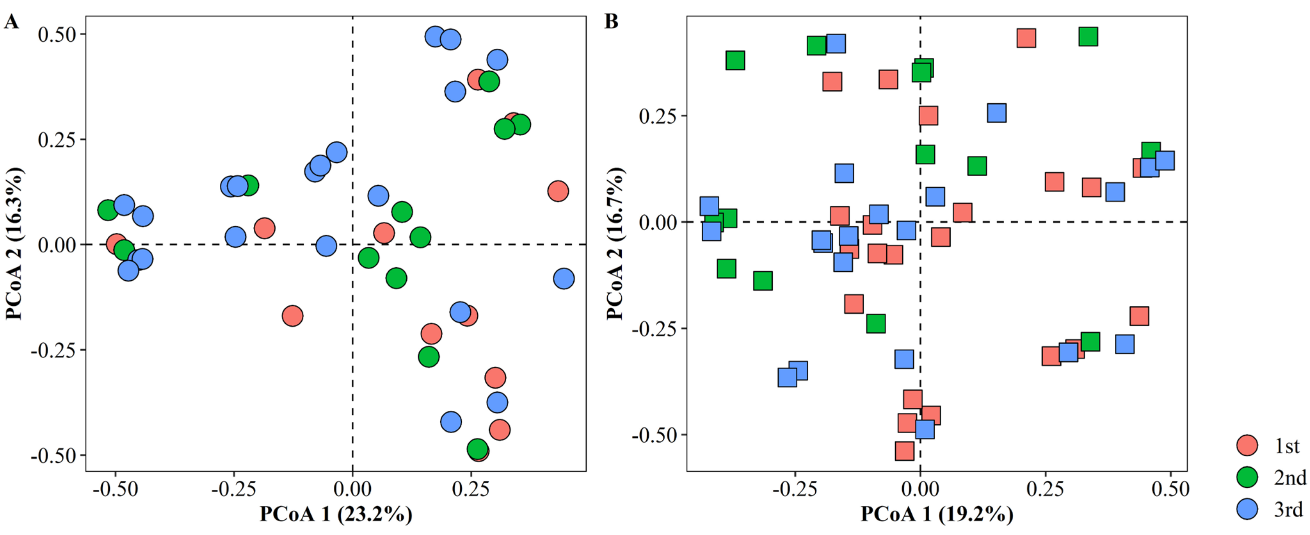

FIGURE 4 | Variation of the diet of *Hyphessobrycon heterorhabdus* among stream orders during **A**. dry and **B**. flood periods in eight streams of a protected area in the Eastern Amazon, Brazil.

TABLE 2 | Results of pairwise PERMANOVA for stream orders nested within periods. Data refers to the diet of *Hyphessobrycon heterorhabdus* sampled in eight streams in a protected area in the Eastern Amazon. *significant values at $\alpha < 0.05$.

Period	Orders	F Model	R^2	Adjusted p-value
Dry	1st *vs.* 2nd	1.30	0.02	0.82
	1st *vs.* 3rd	4.41	0.07	< 0.01*
	2nd *vs.* 3rd	3.04	0.06	0.02*
Flood	1st *vs.* 2nd	5.49	0.10	< 0.01*
	1st *vs.* 3rd	4.41	0.07	< 0.01*
	2nd *vs.* 3rd	2.71	0.05	0.01*

TABLE 3 | Results of pairwise PERMDISP for stream orders during the flood period. Data refers to the diet of *Hyphessobrycon heterorhabdus* sampled in eight streams in a protected area in the Eastern Amazon. *significant values at $\alpha < 0.05$.

Pairs	Difference between medians	Lower limit	Upper limit	Adjusted p-value
1st - 2nd	-0.06	-0.14	0.01	0.13
1st - 3rd	0.05	-0.02	0.12	0.19
2nd - 3rd	0.11	0.04	0.19	0.00*

Differences in the diet composition of *H. heterorhabdus* between periods were related to the higher consumption of vegetal fragments and adult Trichoptera during the flood period and higher consumption of exoskeleton fragments of unknown origin and adult Hemiptera during the dry period (SIMPER; Tab. 4). This analysis confirmed the higher ingestion of autochthonous items during the dry period than in the flood period.

During the dry period, fish in the 1^{st} and 2^{nd} order streams consumed more allochthonous items than fish in 3^{rd} order streams. The most consumed items in lower orders were Hemiptera, exoskeleton fragments, and vegetal fragments. Coleoptera and Diptera (egg) were exclusively consumed in 3^{rd} orders streams. In the flood period, 1^{st} order eggs had five exclusive items, four of them of allochthonous origin. Fish in 2^{nd} order streams consumed large amounts of exoskeleton fragments (autochthonous source), whereas fish in 3^{rd} order streams largely ingested vegetal fragments and two exclusive items (eggs of Diptera and adults Ephemeroptera).

TABLE 4 | Results of SIMPER analysis. Values represent the contribution of food items for the diet of *Hyphessobrycon heterorhabdus* per hydrological periods and stream orders.

Items	Period		Dry			Flood		
	Dry	Flood	1st	2nd	3rd	1st	2nd	3rd
Animal (autochthonous)								
Ephemeroptera (nymph)	9.42	2.85	7.04	-	15.07	-	5.07	5.64
Odonata (larvae)	9.4	9.71	5.54	12.66	-	9.41	14.35	-
Coleoptera (larvae)	3.85	3.24	-	-	21.31	-	-	-
Diptera (eggs)	4.2	-	-	-	23.25	-	-	10.65
Diptera (larvae)	-	-	5.12	6.3	-	-	8.03	-
Exoskeleton fragments	7.06	14.4	-	9.08	16.59	-	43.7	18.47
Animal (allocthonous)								
Isoptera (adult)	-	-	-	-	-	5.98	-	-
Formicidae (adult)	-	4.04	-	-	-	13.32	-	-
Trichoptera (adult)	-	14.2	-	14.37	-	20.89	-	11.52
Hemiptera (adult)	11	-	25.58	-	-	-	-	-
Ephemeroptera (adult)	-	-	-	-	-	-	-	6.71
Heteroptera (adult)	-	-	-	-	-	7.03	-	-
Exoskeleton fragments	6.08	3.68	18.19	-	-	9.1	-	-
Animal (unknown source)								
Exoskeleton fragments	25	8.37	21.06	24.68	11.76	13.35	-	-
Vegetal (allochthonous)								
Vegetal fragments	17.3	30.6	11.91	27.2	5.78	14.8	19.55	40.93
Mean similarity	14	11.8	13.93	13.96	16.2	19.15	26.71	12.5

DISCUSSION

Our results show that *H. heterorhabdus* is omnivorous and tends towards insectivory, feeding both on autochthonous and allochthonous items. Regarding our hypotheses, we found that the fish diet differs between stream orders and hydrological periods. We believe these results reflect temporal and spatial changes in the resources' availability. However, since we evaluated temporal changes only within a single year, we recognize that our results must be taken with caution.

The generalist diet of *H. heterorhabdus* is similar to the reported to other congeneric species, which feed on a large variety of items. Although species of this genus are usually classified as invertivores (Casatti *et al*., 2003; Pelicice, Agostinho, 2006; Prado *et al*., 2016), previous reports detected omnivorous diets (Coutinho *et al*., 2000; Sánchez-Botero *et al*., 2007; Soneira *et al*., 2016), paralleling our results and confirming the high plasticity of characids (Abelha *et al*., 2001; Portella *et al*., 2016). Insects were the most important items in the stomachs of *H. heterorhabdus* in our study, a result commonly reported for the diet of tropical stream fish, either as falling items drifting on the surface (Silva *et al*., 2016) or as aquatic insects in multiple stages of development associated to the streambed

(Pinto, Uieda, 2007; Rolla *et al*., 2009). This finding shows the importance of the quality and amount of the riparian vegetation for the diet of stream-dwelling fish since aquatic invertebrates depend on allochthonous organic matter to thrive (Malmqvist, 2002).

The diet of *H. heterorhabdus* changed between the dry and flood period, which could be linked to the temporal fluctuations of the insect communities detected in other studies in the tropical region (Deus, Petrere-Junior, 2003; Peterson *et al*., 2017). Some studies did not observe variation in the diet between periods (Pinto, Uieda, 2007; Costa, Soares, 2015), which was associated with the wide availability of food items all year round, mainly insects (Rezende, Mazzoni, 2006). We believe that the temporal differences in our results are primarily caused by fluctuations of the water level that promote seasonal variability of stream physical conditions in the lower Anapu river (Benone *et al*., 2018; Montag *et al*., 2019), thus affecting the availability of insects and plant material.

Due to the natural impoundment in the Anapu river, the streams present wide floodplains covered by large extensions of primary forest (Benone *et al*., 2018), a prolific source of allochthonous material. The increased lateral connectivity between the stream channel and the floodplain during the flood period offers new areas for fish to explore and feed (Thomaz *et al*., 2006). This increased connectivity may explain the large proportion of terrestrial plant material ingested by *H. heterorhabdus*, especially in 3rd order streams during the flood period due to its increased accessibility in the forested floodplains (Thomaz *et al*., 2006; Junk *et al*., 2007) together with stronger winds and heavy rains (Pinto, Uieda, 2007). Although we did not measure the resource availability, we believe our points are valid since the studied area is highly preserved, and it shows large variations in stream width (Benone *et al*., 2018).

Diet composition changed between all orders within the flood period, being more heterogeneous in 3rd order streams. The increasing size of streams could encompass a growing variability of food items for fish because they are larger, have maximum habitat diversity, and contain more food sources (Cargnin-Ferreira, Forsberg, 2000; Wolff *et al*., 2013). Additionally, the floodplains should be more extensive in downstream water bodies, offering refugia to aquatic insects, and retaining falling terrestrial material (Braccia, Batzer, 2001).

Fish are expected to change their diet from allochthonous to autochthonous items in the downstream direction (Vannote *et al*., 1980; Angermeier, Karr, 1983; Pouilly *et al*., 2006; Wolff *et al*., 2013). We observed such a change for both periods, although not as evident in the flood. The smaller canopy provided by trees downstream limits the fall of terrestrial invertebrates (Pouilly *et al*., 2006). The autochthonous diet is favored by the large accumulation of organic material in these naturally impounded streams due to the low water flow. The richness and composition of aquatic insects are strongly associated with large woody debris and leaf litter since they provide cover and food (Smith *et al*., 1993; Braccia, Batzer, 2001; Montag *et al*., 2019). Individuals in 3rd order streams exhibited distinct diet composition, which could also be related to the longitudinal supply of food resources (Wolff *et al*., 2013).

The analysis of the feeding strategy showed generalist populations with specialized individuals, but our sampling design does not allow direct explanations for this pattern. Nevertheless, we raised some possibilities. First, resources may have clumped distributions (Bolnick *et al*., 2003), such as patterns of distribution of eggs and larvae from aquatic insects (Wesner, 2013). In this scenario, stomach contents would reflect punctual prey availability instead of long-term processes. Second, differential resource use might reflect individual variation in morphology, behavior, and physiology (Bolnick *et al*., 2003; 2011). Trade-offs regarding resource recognition, prey capture efficiency, or resource handling ability generate individuals with different degrees of specialization and could be a result of the diversifying effect of intraspecific competition (Bolnick *et al*., 2011). Moreover, the studied streams also contain several species of *Hemigrammus* Gill, 1858 and *Hyphessobrycon* Durbin, 1908 (Benone *et al*., 2018; Freitas *et al*., 2018). Both genera occupy similar niches (Brejão *et al*., 2013), indicating a role for interspecific competition. However, to elucidate the reasons behind individual specialization, it is necessary to conduct studies on a larger timescale to evaluate the temporal consistency of observed patterns.

In conclusion, our study evidenced the temporal and spatial changes in the diet of a regionally common characid species. Although these patterns are predicted in ecological theories such as the River Continuum Concept (Vannote *et al*., 1980), few studies have been conducted in small tropical streams. These temporal and spatial fluctuations can affect the natural history of individual species (Costa, Soares, 2015; Silva *et al*., 2016) and the trophic structure of fish assemblages (Pouilly *et al*., 2006; Peterson *et al*., 2017), and should be considered in future studies. Additionally, our study was conducted in a well-preserved area, offering an opportunity to observe natural patterns and contrast them with the alterations in fish diet promoted by human disturbances.

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AUTHOR'S CONTRIBUTION

Naraiana Loureiro Benone: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Visualization, Writing-original draft.
Cleonice Maria Cardoso Lobato: Conceptualization, Data curation, Investigation, Methodology, Validation, Writing-review and editing.
Bruno Eleres Soares: Formal analysis, Investigation, Methodology, Validation, Writing-review and editing.
Luciano Fogaça de Assis Montag: Funding acquisition, Project administration, Resources, Supervision, Validation, Writing-review and editing.

ETHICAL STATEMENT

We used lethal doses of anesthetic (eugenol, as required by Brazilian Civil Law 11,794/2008) to sacrifice the specimens. Samplings were approved by the UFPA Ethics Committee (CEUA #8293020418/2018) and Collection License SISBIO #25060-1.

COMPETING INTERESTS

The authors declare no competing interests.

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