ORIGINAL ARTICLE

Do local environmental factors structure the trophic niche of the splash tetra, *Copella arnoldi*? A test in an Amazonian stream system

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ABSTRACT

Environmental variation affects the availability of spatial and trophic resources in Amazonian streams and may be important factors structuring the diet of fishes. We analyzed the diet composition and trophic niche breadth of the lebiasinid splash tetra, *Copella arnoldi,* aiming to evaluate how environmental variation in Amazonian streams affects the species' trophic niche. Fish were captured and environmental factors were recorded in 20 streams in the Caxiuanã National Forest, in the eastern Amazon, in November 2010. We made a semi-quantitative analysis of stomach contents of 200 individuals. *Copella arnoldi* exhibited an omnivorous diet composed mainly by detritus and allochthonous invertebrates. Environmental variation (stream width, stream depth, canopy cover and flow) did not affect the diet composition or trophic niche breadth of the species, possibly due to the regional integrity of the forest within the boundaries of the protected area. Riparian cover probably minimizes the effect of the small-scale variations in food resources, thus leading to a locally homogeneous diet composition in the splash tetra *C. arnoldi*.

KEYWORDS: environmental variation, Lebiasinidae, niche breadth, trophic ecology, Brazilian Amazon

Fatores ambientais influenciam o nicho trófico do tetra *Copella arnoldi*? Um teste em um sistema lótico amazônico

RESUMO

Variações ambientais afetam a disponibilidade de recursos espaciais e tróficos em igarapés amazônicos e podem ser fatores importantes estruturando a dieta de peixes. Analisamos a composição da dieta e a amplitude de nicho trófico do lebiasinídeo *Copella arnoldi*, tendo como objetivo avaliar como a variação ambiental em igarapés amazônicos afeta o nicho trófico da espécie. Indivíduos foram capturados e fatores ambientais foram medidos em 20 igarapés da Floresta Nacional de Caxiuanã, na Amazônia Oriental, em Novembro de 2010. Fizemos uma análise semi-quantitativa do conteúdo estomacal de 200 indivíduos. *Copella arnoldi* apresentou uma dieta onívora composta predominantemente por detritos e invertebrados alóctones. A variação ambiental (largura e profundidade do igarapé, cobertura de dossel e correnteza) não afetaram a composição da dieta ou a amplitude de nicho trófico da espécie, possivelmente devido à integridade regional da floresta na área protegida. A cobertura ripária provavelmente minimiza os efeitos da variação ambiental nos recursos tróficos, levando, assim, a uma dieta localmente homogênea de *C. arnoldi*.

PALAVRAS-CHAVE: amplitude de nicho, ecologia trófica, Lebiasinidae, variação ambiental, Amazônia brasileira

INTRODUCTION

The use of trophic resources by fish is greatly affected by temporal and spatial variation in food resources (Abelha *et al.* 2001; Silva *et al.* 2014; Peterson *et al.* 2017). Major examples are seasonal reproductive flights of winged ants and mayflies, or the fruitification of plants in marginal vegetation, which module the consumption of prey by numerous fish species (Netto-Ferreira *et al.* 2007; Correa and Winemiller 2014; Barbosa *et al.* 2015). Spatial variation in limnological factors and the physical structure of the stream and surrounding vegetation may affect the fitness of the consumer or the availability of prey (Pusey and Arthington 2003), thus affecting the diet of fishes.

Spatially structured environments are quite common in freshwater systems. Environmental variations from smaller (1st to 3rd order) to larger (4th to 5th order) streams decrease the relative importance of allochthonous input to aquatic systems, according to the River Continuum Concept (Vannote *et al.* 1980). In small streams, this input is important to local communities, as it affects not only the diet of a singular species, but also the size of the food web and the number of trophic guilds (Vannote *et al.* 1980; Nakano *et al.* 1999; Recalde *et al.* 2016). There is also evidence that spatially related variation in environmental conditions and the physical structure of streams affect food resources and the diet of fishes at smaller scales (Ceneviva-Bastos *et al.* 2010; Zeni and Casatti 2014).

In order to evaluate how small-scale variations in the physical structure of streams (stream width, stream depth and canopy cover) and in limnological conditions (flow) affect the diet of fish species, we studied the diet of the splash tetra *Copella arnoldi* (Regan 1912) in streams of the National Forest of Caxiuanã, in the eastern Amazon. *Copella arnoldi* (Characiformes: Lebiasinidae) has a high commercial importance as ornamental fish and is the most abundant species in the streams of Caxiuanã (Montag *et al.* 2008; Benone 2012; Freitas *et al.* 2018). Lebiasinids are omnivorous and opportunistic species, and most studies found that they feed mainly on allochthonous arthropods (Román-Valencia 2004; Kemenes and Forsberg 2014), although Silva *et al.* (2016) reported allochthonous plant material (e.g. leaves, fruits and stems) as their main food source.

Aiming to evaluate the spatial variation in the diet of *C. arnoldi* in the streams of Caxiuanã, we analyzed: (i) the diet composition and general feeding strategies; and (ii) how environmental factors explained the variation in the diet composition and populational niche breadth of the species. We provide information about how small-scale natural variations may affect the diet of fishes, which may be useful in the current scenario of fast changes in the structure of the aquatic environments in Amazonia.

MATERIAL AND METHODS

Sampling sites

Twenty streams (1st to 3rd order) were sampled in the Caxiuanã National Forest, a protected area located in the region of the Lower Anapu River, Pará State, Brazil (Figure 1). Distances among sampled streams vary, but are large in average (mean = 35.23 km; range = 1.3 – 71.08 km). The Caxiuanã National Forest is covered predominantly by dense lowland t*erra-firme* rainforest (85% of its total area) (Lisboa 2002). 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). The mean air temperature is 26.7 ºC, ranging from a minimum of 23 ºC to a maximum of 32.7 ºC. Mean annual precipitation is around 2000 mm, reaching a mean
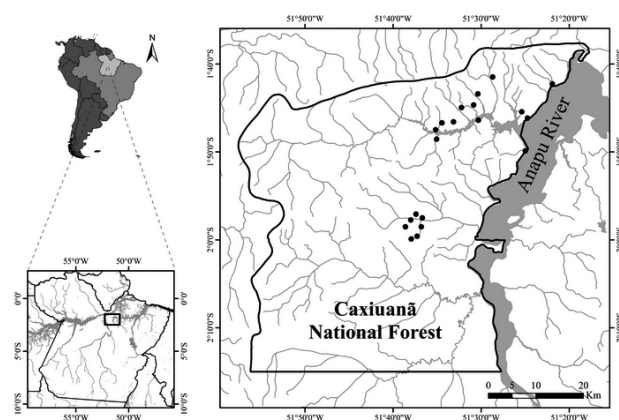

Figure 1. Location of the Caxiuanã National Forest within the lower Anapu River basin, Brazil. Circles represent the 20 stream sites where the specimens of *Copella arnoldi* were sampled.

monthly maximum of 379 mm in March and a minimum of 50 mm in October (Lisboa 2002). The lower Anapu River reaches its highest mean water level in April and May (180 cm), dropping to a minimum of 120 cm in November and December (Lisboa 2002).

Caxiuanã streams have acidic water (pH ≈ 5.5), streambeds densely covered by leaf litter and trunks, shallow depth (< 30 cm) and a main channel associated with permanent floodplains (Montag *et al.* 2009). The Caxiuanã hydrographic system is characterized as a ria lake, derived from the drowning of the valleys of the Anapu River during the Holocene (Behling and da Costa, 2000). In this type of system, the river system resembles a lake, with enlarged cross-sections near the mouth, very reduced flows, and an accumulation of fine sediments (Irion *et al.* 2009; Montag *et al.* 2009).

Environmental variables

Environmental variables were measured prior to the collection of fish specimens. At each stream site, we measured the abiotic variables three times, one at each of three equidistant points (25 m between each pair) along the stream, and then averaged the three measures to represent the stream site. The following environmental variables were measured: (i) stream depth (m); (ii) stream width (m); (iii) flow velocity (m s⁻¹); and (iv) canopy opening (%). These variables are considered some of the most relevant for the study of fish assemblages in t*erra-firme* streams (Allan and Castillo 2007). We did not measure substrate type, frequently considered as one of the most important variables affecting fish assemblages, because of the very low variability in drowned streams (Montag *et al.* 2009). We found a large amount of leaf litter and wood debris accumulated on the bottom of most streams, which reached up to 1 m in depth.

Stream depth and width were measured using a surveyor's tape. Flow velocity was estimated by recording the time it took

a floating object to cover a predetermined distance. Canopy opening was analyzed using digital photographs taken with a camera located 1 m above the water surface. We used the same camera with the same parameters at all sampling points. Photographs were converted into black and white to calculate the percentage of white pixels, considered as canopy opening, in the image (Teresa *et al.* 2016).

Fish sampling

Fish specimens were collected in November 2010, during the dry period. The dry period is ideal to test spatial variation in biological attributes, since it maximizes differences among streams, and it is when local factors show the strongest association with aquatic fauna (Thomaz *et al.* 2007; Benone *et al.* 2018). A 50-meter reach was defined at each stream site, and fish sampling was conducted using hand nets with 2-mm mesh during a six-hour period, by three or four collectors. Fishes were killed with lethal doses of clove oil (Civil House, Federal Law no 11.794 of October 8, 2008), fixed in 10% formalin, and then conserved in 70% alcohol. Voucher specimens of *C. arnoldi* were deposited in the ichthyological collection of the Museu Paraense Emílio Goeldi, voucher number MPEG23411.

Data analysis

Stomach contents of 10 individuals of *C. arnoldi* per stream were analyzed under a stereoscopic microscope. Empty stomachs were not considered for further analyses. Food items were identified and quantified by frequency of occurrence (FO%) and a semi-quantitative assessment of the dominance of the item (D%) based on the feeding preference degree (FPD; Braga 1999). FPD may be used to quantitatively describe stomach contents when items are too small or fragmented to allow volumetric or gravimetric measurements. FPD scores items in each stomach content from 1 (low dominance) to 4 (total dominance, *i.e.* only this item was consumed). Then, D% was calculated as the ratio of the sum of the scores of each item to the total assigned scores. The relative importance of the food items for the species and for each stream was calculated by the alimentary Index (IAi; Kawakami and Vazzoler 1980): IAi = FOi% * Di%/($\sum$FOi% *Di) * 100, where i = 1, 2, ... *n* food items; FOi = frequency of occurrence of item *i*; and Di = dominance of the item *i*. As D% evaluates the proportion of the food items in each stomach content, it can be used in the alimentary index equation.

The feeding strategy was analyzed by the graphical method of Amundsen *et al.* (1996), based on the frequency of occurrence and prey-specific abundances (using D%) of food items. Food items are plotted in Amundsen's diagram and their position in the bivariate space indicate feeding strategy, importance of each food item for the population, and importance of the individuals niche breadth and niche overlap to the population's niche breadth. The higher the value in the horizontal axis, the higher the number of individuals in the population that consumed the food item, reaching 1 when all individuals consumed the given item. The higher the value in the vertical axis, the higher the specialization in the food item. The niche breadth of the population is determined by the diet breadth and overlap of the individuals. A generalist population with high niche breadth, for example, may be composed by generalist individuals with high niche overlap (high within-phenotype component and high values in the horizontal axis) or by specialist individuals with low niche overlap (high between-phenotype component and high values in the vertical axis and low values in the horizontal axis).

We estimated the niche breadth by Levins' index: BA = 1/$\sum$Pi², where BA = Levins' index, Pi is the proportion of the diet consisting of the item *i*. BA ranges from 1 (specialist) to *n* (generalist), where *n* is the total number of food items. All indices were calculated in the R environment (see supporting information below).

We used a redundancy analysis (RDA) to evaluate how spatial differences in environmental factors (stream width, stream depth, canopy cover and flow as independent factors) explained the variation in the diet composition of the species (dependent factor). We used the Hellinger transformation on the chi-squared proportional dominance of prey items consumed by each specimen and environmental data were standardized before analysis. A multiple regression was used to test how environmental factors explained variation in the niche breadth. Analyses were performed in the *vegan* package in the R environment.

We provide supporting information, R scripts and datasets (dietary information of each individual, as well as alimentary indices and measured environmental conditions for each stream) in the Figshare digital repository: 10.6084/m9.figshare.8866055.

RESULTS

We analyzed 200 individuals with standard length ranging from 18.8 mm to 39.9 mm (mean ± SD: 27.5 ± 4.2). Thirty-nine individuals had empty stomachs (19.5%). *Copella arnoldi* consumed 15 food items in the streams of the National Forest of Caxiuanã and exhibited an omnivorous diet predominantly composed by detritus (Table 1). Besides sediment/detritus (IA% = 66.1%), stomach contents of *C. arnoldi* were composed mainly by Formicidae (16.4%) and insect remains (14.6%), a food item composed by fragmented parts of insects from which taxon and source (allochthonous or autochthonous) could not be identified.

Stream width ranged from 2.5 to 31.3 m (9.09 ± 8.51), stream depth ranged from 0.3 to 1.4 m (0.9 ± 0.4), canopy opening ranged from 16.6 to 37.4% (27.6 ± 5.3) and stream flow ranged from 0 to 0.14 m/s (0.08 ± 0.04). Neither one of these environmental factors affected the diet composition of *C. arnoldi*

Table 1. Frequency of occurrence (FO%), dominance (D%) and alimentary index (IA%) calculated for food items consumed by **Copella arnoldi** in 20 streams of the National Forest of Caxiuanã, Pará, Brazil.

Items	FO%	D%	IA%
Allochthonous arthropods			
Aranae	4.3	1.9	0.2
Blattodea	1.2	0.8	0.0
Coleoptera	3.1	1.5	0.1
Diptera	6.2	0.0	0.0
Formicidae	36.0	21.6	16.4
Isoptera	6.2	2.7	0.4
Hemiptera	6.2	0.3	0.0
Other insects	6.2	2.9	0.4
Autochthonous arthropods			
Crustacea	0.6	0.2	0.0
Diptera larvae	4.3	0.6	0.1
Hydracarina	1.2	0.0	0.0
Insect remains			
Insect remains	42.2	16.4	14.6
Vegetal matter			
Algae	13.0	5.9	1.6
Vegetal remains	3.7	1.6	0.1
Sediment/debris			
Sediment/debris	72.0	43.5	66.1

Figure 2. Feeding strategy of **Copella arnoldi** in 20 streams of the National Forest of Caxiuanã, Pará, Brazil revealed by the Amundsen diagram. Codes: 1 – sediment/debris; 2 – insect remains; 3 – algae; 4 – plant remains; 5 – Formicidae; 6 – Diptera larvae; 7 – other insects; 8 – Diptera; 9 – Coleoptera; 10 – Crustacea; 11 – Aranae; 12 – Isoptera; 13 – Hydracarina; 14 – Blattodea; 15 – Hemiptera.

DISCUSSION

Copella arnoldi consumed mainly sediment/debris and allochthonous arthropods, and can be classified as an omnivorous species with a tendency for a detritivorous habit. Despite the environmental variation in the streams of the National Forest of Caxiuanã, *C. arnoldi* exhibited a similar diet composition in all sites, showing no evidence for diet shifts mediated by local-scale changes in the habitat.

Lebiasinids are usually considered as allochthonous insectivores that feed mainly on insects and other arthropods that fall into the water from the riparian vegetation (Román-Valencia 2004; Kemenes and Forsberg 2014; Silva *et al.* 2016). This feeding behavior is favoured by occupying the surface of the water column, where the fish picks up food items that fall from surrounding vegetation (Sabino and Zuanon 1998; Brejão *et al.* 2013). Nonetheless, *Copella arnoldi* in our sample fed mainly on detritus/sediment in the streams of the Caxiuanã basin, while *Copella nigrofasciata* showed moderate detritus consumption in 1st order streams of the Trombetas River basin (Silva *et al.* 2016).

In addition of surface picking, lebiasinids exhibit grazing as an additional feeding strategy (Sabino and Zuanon 1998). Brejão *et al.* (2013), for example, observed numerous lebiasinids browsing periphyton-covered substrate in Amazonian stream impoundments. Waterflow velocity is usually high in headstreams (Vannote *et al.* 1980), but the low declivity of lowland streams allows debris to accumulate on the bottom of the stream. This is a particularly strong feature in the streams of Caxiuanã, as it is a drowned system with shallow and low flow waters (Benone *et al.* 2017; Benone *et al.* 2018). In these environments, debris is a food item that requires low

(RDA; p = 0.27). Variation in diet composition indicated higher within-stream variation than between streams (see supporting information in Material and Methods), but low sample size per stream did not allow us to address this in greater detail.

Niche breadth ranged from 1.02 to 5.26, and did not exhibit any response to the environmental factors (multiple regression; $R^2 = 0.2$; p > 0.7). *Copella arnoldi* exhibited a generalist feeding strategy due to the moderate frequency of consumption of sediment/debris, ants and insect remains associated with low to moderate levels of prey-specific abundance for most of the food items (Figure 2). Amundsen's diagram did not show any strong patterns of between-phenotype or within-phenotype importance to the niche breadth. Moderate to highly frequent items with moderate prey-specific abundance values indicated some importance of the within-phenotype component, while moderate values of prey-specific abundances of unfrequently consumed items indicated some importance of the between-phenotype component.
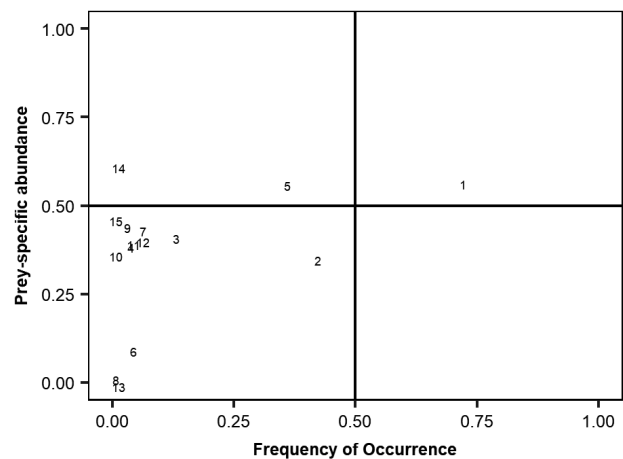
energetic investment for search and capture, and it is usually found in the diet of numerous fishes in headwater streams (Kemenes and Forsberg 2014). Given the high abundance of debris in this stream system and the grazing feeding tactics in slow-flow microhabitats, it would be expected for *C. arnoldi* to mainly consume debris/sediment.

Our findings of high detritus/sediment consumption by *C. arnoldi* contradict previous studies that characterize the diet of lebiasinids as insectivores with a tendency to omnivory. Similarly, *Pyrrhulina australis* Eigenmann & Kennedy, 1903 had a different trophic composition in lagoons of the middle Paraná River, based primarily on aquatic larvae of dipterans and cladocerans (Arias and Rossi 2005; Ibarra-Polesel and Poi 2016). Therefore, lebiasinids exhibit a larger variation in their trophic niche than usually assumed, varying from diets composed mainly by allochthonous prey to diets composed mainly by autochthonous prey.

Ants and other allochthonous invertebrates are highly important in the diet of fishes in headstreams (Mendonça *et al.* 2012; Gonçalves *et al.* 2013; Silva *et al.* 2016; Cardoso and Couceiro 2017) mainly due to the low productivity within the streams, which makes these streams highly dependent on the invertebrate input from the riparian vegetation (Vannote *et al.* 1980). This input reflects on the predominance of ants in comparison with other allochthonous food items in the diet of *C. arnoldi* and several other Amazonian fishes (Mendonça *et al.* 2012; Gonçalves *et al.* 2013; Silva *et al.* 2016), since ants are highly dominant in the soil macrofauna of Amazonian forests (Fittkau and Klinge 1973). Beyond the high availability, terrestrial arthropods are also high-quality items due to their low C:N ratio (Baxter *et al.* 2005; Small *et al.* 2013).

The generalist feeding strategy recorded for *Copella arnoldi* explains the high variation in niche breadth observed among streams. This feeding strategy is common in tropical lotic systems (Silva *et al.* 2016) and in other lebiasinids (Arias and Rossi 2005; Silva *et al.* 2016), and is related to the unstable allochthonous input. This population of *C. arnoldi* is composed of generalist individuals that consume debris/sediment in high frequency and varies in the consumption of secondary items (numerous items with low frequency of occurrence and low to moderate levels of prey-specific abundances). Therefore, both the within-component and the between-component are important to the high niche breadth of the species.

Despite the great variation in the physical structure of the streams and canopy opening, we found no systematic variation in diet composition and niche breadth between streams. We believe this similarity is not caused by movements of individuals across streams. Distances between streams are large and lebiasinids have reduced swimming ability (Sabino and Zuanon 1998). A previous study in the region (Benone *et al.* 2018) suggested that fish can move between streams during the flood period, but the same was not observed during the dry period. Additionally, our data is a snapshot of the species' diet, reflecting patterns in a smaller temporal scale than movement across distant streams would take.

Land use has profound impacts on the ichthyofauna of Amazonian streams, both in local, catchment and regional scale (Leitão *et al.* 2017; Brejão *et al.* 2018). For example, fragmentation leads to functional homogenization of fish communities (Leitão *et al.* 2017), and local loss of riparian vegetation reduces trophic guilds based on allochthonous food resources (Bojsen 2005; Borba *et al.* 2008; Ferreira *et al.* 2012). The National Forest of Caxiuanã harbors a large and well-preserved forest (~ 200,000 ha) that allies human use, biodiversity conservation and scientific research. National forests are important pieces in the national planning for nature conservation as they comprise a large amount of the sustainable use areas (Rylands and Brandon 2005). The conservation status of our study sites provides an unfragmented riverscape with a continuous forest. These characteristics appear to minimize the effects of small-scale variations in food resources and on the diet of the splash tetra, *Copella arnoldi* during the dry season. During the wet season, drowned areas reach more than 100 m into the forest, which may provide a large amount of resources to aquatic fauna.

CONCLUSIONS

Lebiasinids are generally pictured as links between the terrestrial and aquatic environment as they feed primarily on allochthonous invertebrates. Nevertheless, *C. arnoldi* fed primarily on detritus in Caxiuanã streams, probably favored by the high accumulation of debris due to the hydromorphological features of these streams. Therefore, lebiasinids exhibit a broad trophic niche diversity and may have an important role in the autochthonous food chain. This importance may be regulated by environmental factors, but we did not find any evidence that the variation in the diet and niche breadth of *C. arnoldi* were related to canopy opening, stream width and depth, or water flow. Sampled streams are located within a protected area that effectively maintains natural conditions in river catchments and surrounding forest. The given local context may minimize small-scale variations in food resources and in the diet of subpopulations of *C. arnoldi*. Information on the natural history of fish species in the Amazon provides knowledge on the ecological processes of aquatic systems that are important for monitoring and management activities. Observed patterns may change temporally as the streamflow and precipitation change through the year. Therefore, further studies should consider the temporal variation in the diet of *C. arnoldi* and other small-bodied species to fully understand their role linking the terrestrial and aquatic systems and recycling detritus within the aquatic system.

ACKNOWLEDGMENTS

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