

Ontogenetic and seasonal shifts in the diet of *Bryconamericus iheringii* (Characidae, Stevardiinae) from southern Brazil

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Abstract: The diet of *Bryconamericus iheringii*, a small characid, is described and analyzed aiming to test for possible differences among standard length classes (SLCs) and seasons. Fish were sampled monthly from April 2001 to March 2002 with seine net in the Vacacaí river, Laguna dos Patos system, southern Brazil. Results revealed a diet composed of 24 alimentary items and a narrow niche breadth. Significant differences in diet were found between seasons and SLCs. High consumption of detritus/sediment, vegetal matter and autochthonous insects was observed in all seasons and SLCs. Nevertheless, larger fish fed upon larger prey, which set them apart from smaller fish. High food overlap was observed among the different SLCs, possibly due to the consumption of detritus/sediment and vegetal matter, small items that can be consumed by all fish sizes. The species is detritivorous and our results support the idea of marginal forests as an important source of food for aquatic systems.

Key words: feeding, detritivory, niche breadth, food overlap, Neotropical.

Mudanças ontogenéticas e sazonais na dieta de *Bryconamericus iheringii* (Characidae, Stevardiinae) do sul do Brasil. Resumo: O presente estudo descreve e analisa a dieta de *Bryconamericus iheringii*, com o objetivo de testar possíveis diferenças entre classes de comprimento padrão (CCP) e estações do ano. Amostras mensais foram conduzidas de abril de 2001 a março de 2002 no rio Vacacaí, Sistema da Laguna dos Patos, sul do Brasil. Os resultados mostram uma dieta composta por 24 itens alimentares e foi identificada uma baixa amplitude de nicho. Diferenças significantes na dieta foram encontradas entre estações e entre CCP. Foi observado um elevado consumo de detrito/sedimento, matéria vegetal e insetos autóctones em todas as estações do ano e CCP. No entanto, peixes maiores se alimentaram de presas maiores, diferenciando-os dos peixes menores. Uma elevada sobreposição alimentar foi observada entre as diferentes CCP, possivelmente devido ao consumo de detritos/sedimento e matéria vegetal, itens pequenos que podem ser consumidos por peixes de todos os tamanhos. A espécie é detritívora e nossos resultados corroboram a importância das florestas marginais como fonte de alimento para sistemas aquáticos.

Palavras-chave: alimentação, detritivoria, amplitude de nicho, sobreposição alimentar, Neotropical.

Introduction

Characiformes is one of the most diverse orders of fish in the Neotropics, with a huge diversity of forms and adaptations (Vazzoler & Menezes 1992, Toledo-Piza *et al.* 2024), of which Characidae is the largest family with a broad distribution in Neotropical epicontinental waters (Thomaz *et al.* 2015). The characid genus *Bryconamericus* Eigenmann 1907 can be found in a broad variety of freshwater ecosystems of Central and South Americas, from Costa Rica to Western Argentina and on both sides of the Andean cordillera (Vari & Siebert 1990). The genus contains 49 valid species (*sensu* Toledo-Piza *et al.* 2024) all of which are small sized (< 10 cm), mainly omnivorous and active swimmers (Britski *et al.* 1988), and represent an important source of food for other fishes (Almeida *et al.* 1997). Around 24 species of *Bryconamericus* can be found in southern and southeastern Brazil (Fricke *et al.* 2024). The species *B. iheringii* occurs in the Laguna dos Patos lagoon system, Uruguay and Paraguay river drainages (Fricke *et al.* 2024).

Stream fishes commonly show the ability to feed on different items (i.e. trophic plasticity), usually influenced by resources availability, seasonal and/or ontogenetic changes (Wootton 1999, Deus & Petrere-Junior 2003). The wide trophic adaptability of fish fauna in tropical streams is reflected by the predominance of generalist and opportunistic species (Abelha *et al.* 2001). Characins show diverse feeding habits (Teixeira 1989, Sabino & Castro 1990), that can vary with seasons (Gracioli *et al.* 2003) and ontogeny (Mazzoni *et al.* 2010a, Dala-Corte *et al.* 2016b). Studies suggests that characin species are usually omnivores and generalistic, using similar dietary niches (e.g. Bonato *et al.* 2017).

Many studies of the diets of characid fish have contributed to understanding the diversity of their feeding strategies, their role in trophic chains, and resource partitioning in their habitats. Temporal and/or seasonal resource availability (Abelha *et al.* 2006, Wolff *et al.* 2009), and also natural changes in foraging areas due to flood and drought cycles (Wootton 1999) may drive shifts in the diet of fish. Besides biotic factors such as body size, environmental factors such as vegetal cover, stream flow, and conductivity may drive resource use of omnivore species (Fernando & Suárez 2020). Most fish species in tropical environments have highly flexible feeding habits (Lowe-McConnell 1999), which seems to be related to morphological (e.g., mouth gap) and behavioral (e.g., locomotion ability)

changes during development (Wootton 1999). Distinct diets are frequently found among different individual development stages of the same species due to differences in energetic demand and morphological limitations, which imply differentiated diets throughout development (Abelha *et al.* 2001).

Studies have shown that the partition of resources among coexisting species are influenced by ontogeny (Borcherding *et al.* 2012). Also, there is a direct relationship between prey size and fish size; the larger the prey, the larger the fish (Scharf *et al.* 2000, Sanchez-Hernandez & Cobo 2012), and the types of prey may also change with the ontogenetic development due to shifts in foraging abilities or habitat use (Lukoschek & McCormick 2001, Nunn *et al.* 2012). Studies on Neotropical characins showed that the populations undergo ontogenetic shifts in their diets from terrestrial insects to fruits and leaves (e.g. Abelha *et al.* 2001, Drewe *et al.* 2004) or increasing vegetal matter consumption along growth (Dala-Corte *et al.* 2016a). Differences in diet throughout ontogeny may lead to deep ecological consequences for fish by, for instance, increasing individual growth and lifetime reproductive production or diminish the mortality risk (Sanchez-Hernandez *et al.* 2019). Nevertheless, the prevalence of ontogenetic shifts in natural characid populations and how these shifts connect to resource partitioning are still not well understood.

Rivers commonly show a gradient of complexity in their physical structure and biodiversity which increases upstream-downstream and determine a continuum of abiotic and biotic variation, patterns of transport, utilization and storage of organic matter along its length and are the basis of the River Continuum Concept (Vannote *et al.* 1980). Light penetration through the forest cover is limited, affecting primary production and the community of aquatic invertebrates. Besides, forest cover provides terrestrial invertebrates with fruits and seeds (Ferreira *et al.* 2012). The diet of neotropical fishes is largely based on allochthonous material (mainly terrestrial insects and terrestrial plant material) in upstream sites and on autochthonous material in downstream sites (Lowe-McConnell, 1999). Some studies have demonstrated the importance of allochthonous items (mostly insects) as a food resource for fish (Lowe-McConnell 1975, Soares 1979, Fernando & Suárez 2020), while others highlight the importance of autochthonous items (algae and aquatic invertebrates) (Costa 1987, Medeiros & Arthington

2011, Moraes et al. 2013). The study of the feeding habits of fish provides fundamental information about a species autecology (Fugi *et al.* 2007). Knowledge of natural feeding based on stomach content analysis has been used to understand the ecological role played by species (Windell & Bowen 1978).

Thus, considering the importance of understanding the diet and trophic organization of fish, this work analyzes the diet of a common tetra species, *B. iheringii*, of the Vacacaí river in southern Brazil. We hypothesize that the species diet will change according to fish size and season, following the natural changes in morphology (i.e. fish size) and resource availability. Thus, its niche breadth, diet composition and food overlap are evaluated and compared among different size classes (ontogeny) and seasons. The consumption of sediment is discussed.

Materials and Methods

Fish were sampled monthly from April 2001 to March 2002 in the Vacacaí river (30°21'34" S, 54°18'48" W) in the Jacuí river basin of the Laguna dos Patos lagoon system, near the city of São Gabriel, in the state of Rio Grande do Sul (RS), Brazil (Fig. 1). The Vacacaí river is large and its

water is brown due to the high concentration of suspended sediment and well-preserved marginal riparian forest on both margins. Its depth can reach over 2 m, with lower depth only along a narrow stretch close to the margin. The substrate is composed of fine sand and mud, with occasional rocks and trunks.

Sampling was performed using three hauls of a seine net (10x2 m, 5 mm mesh size) close to the margins. Collected specimens were anesthetized with eugenol (clove oil; 70 mg/L) and then euthanized and fixed in 10% formalin solution. In the laboratory, the specimens were transferred to 70% ethanol and identified to species level (according to Silva 1998). Voucher specimens were catalogued in the ichthyological collection of the Universidade Federal do Rio Grande do Sul (UFRGS 6692).

Specimens were measured for standard length (SL; mm), weighed (total weight; g), and dissected for stomach extrusion and weighing. The diet of *B. iheringii* was analyzed comparatively among standard length classes (SLC) to determine the influence of body size on feeding habits. The SLC were defined through the Sturges method (Vieira 1991), with the specimens being divided into three

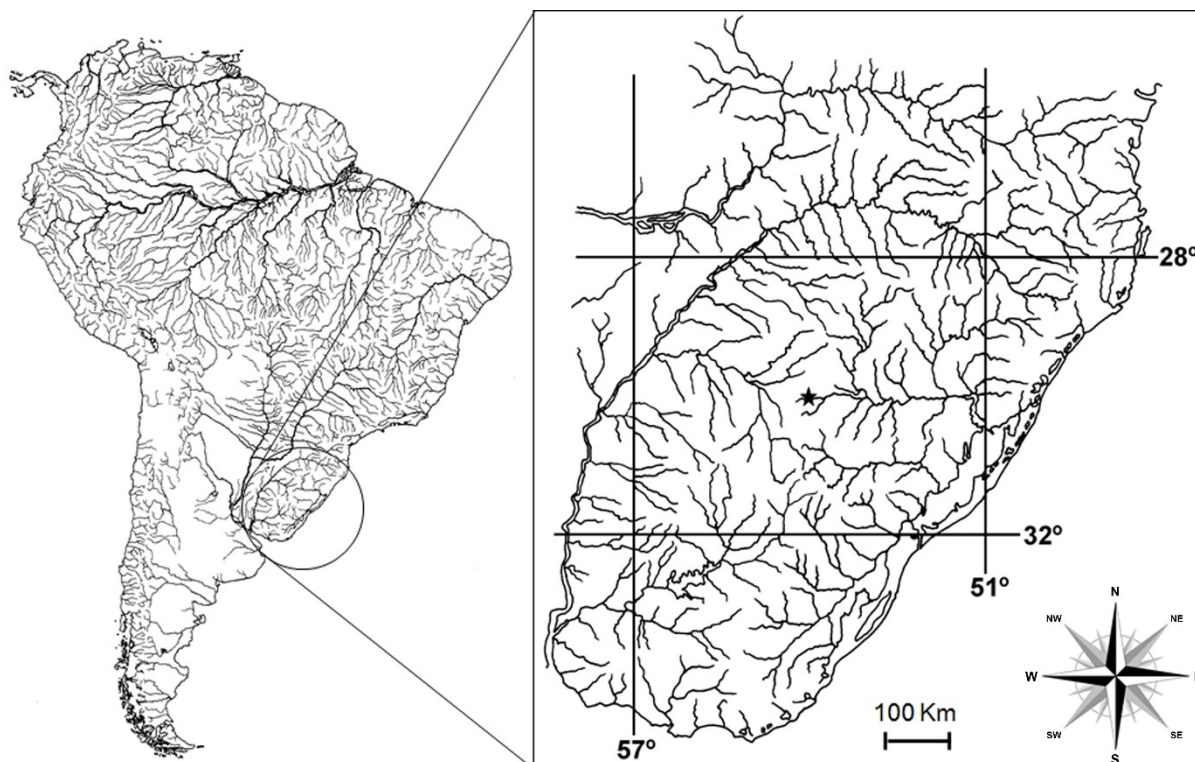


Figure 1. Sampling site location (star) in Rio Vacacaí, near the city of São Gabriel, in the state of Rio Grande do Sul, southern Brazil.

SLC, as follows: SLC1 ($n = 92$) < 31 mm, SLC2 ($n = 167$) 31-40 mm, SLC3 ($n = 114$) > 40 mm. Gonadal development and/or secondary sexual characteristics (according to Lampert *et al.* 2004) were used to classify specimens according to developmental phase. Individuals of SLC1 represent juveniles in the early and intermediate developmental phases, while those of SLC2 and SLC3 are young and mature adults in advanced developmental phases.

For diet analysis, stomach content was identified under a stereomicroscope to the lowest taxonomic level possible, following Needham & Needham (1978), McCafferty (1981), Ribeiro-Costa & Rocha (2006), and Mugnai *et al.* (2010). Food items were grouped into the following broad categories: Aracnida (Arac), autochthonous insects (AUI), allochthonous insects (ALI), Collembola (Col), Crustacea (Cru), Mollusca (Mol), fish (Fis), fish scales (Sca), vegetal matter (VM), detritus and/or sediment (Detr/Sed). Detritus is defined basically as highly particulate and clustered organic matter, while sediment includes predominantly sand and mineral particles.

Months were grouped into seasons as follows: March, April, and May (Autumn/01); June, July, and August (Winter/01); September, October, and November (Spring/01); and December 2001, January and February 2002 (Summer/01). Seasons correspond to those of southern hemisphere which follow astronomic events of solstices and equinoxes (same used in Lampert *et al.* 2004).

Stomach content was analyzed by frequency of occurrence (Fo, the number of stomachs with a particular food category in relation to the total number of stomachs) (Hynes 1950) and volumetric frequency (Vo in mm², estimated according to the quantitative contribution of each item as determined by the number of squares occupied by each item on a scaled paper in relation to the total number of squares occupied by all items) (Hyslop 1980, Dias *et al.* 2017).

In order to provide a general view of the species' diet, the methods of Fo and Vo were combined in the graphical analysis proposed by Costello (1990) with modifications by Amundsen *et al.* (1996). This method consists of a two-dimensional representation of prey abundance values on the y-axis, and frequency of occurrence on the x-axis. Prey-specific abundance is given by the following formula: $\%Pi = (\Sigma Si / \Sigma Sti) \times 100$, where Si = number of stomachs which contain exclusively prey i; Sti = total number of stomachs with prey i.

Dots around 100% Fo and 100% Vo indicate dominant items in the diet. Dots around 100% Fo and 1% Vo indicate a small consumption of different types of prey and are classified as generalist. The opposite, with dots around 1% Fo and 100% Vo indicate specialization towards a given item (Corrêa & Cândido da Silva 2010).

Diet overlap among SLCs was determined through pairwise-comparisons using the Morisita Index (Krebs 1989), which can range from 0 to 1, with 0 indicating a lack of diet overlap and 1 indicating complete overlap. According to Amundsen *et al.* (2003), values equal to or higher than 0.6 indicate a significant diet overlap.

Differences in the diet composition among different SLCs and seasons were tested through Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations (Anderson 2001, Anderson *et al.* 2008) based on a Bray-Curtis dissimilarity matrix (Legendre & Legendre, 2012). This analysis was based on the Vo values of food items and performed with the vegan package (Oksanen *et al.* 2019) in R software (R Core Team 2019).

A non-metric multidimensional scaling (NMDS) (Borcard *et al.* 2011) was also performed to reduce the diet composition multidimensionality of all fish and visualize the dispersion between seasons. The NMDS was performed using the Bray-Curtis dissimilarity distance indices (Legendre & Legendre, 2012), through the metaMDS function with the vegan package (Oksanen *et al.* 2019).

Results

A total of 373 specimens of *B. iheringii* were analyzed, ranging 17.9–51.47 mm in SL. The specimens fed mainly on detritus/sediment (Vo = 92.9%), and so the species is considered detritivorous.

The items with the highest values in the diet of individuals of all SLCs regardless of the analysis were detritus/sediment and vegetal matter, followed by Diptera larvae/autochthonous insects, especially for SLC1. SLC3 also showed high values for autochthonous and allochthonous insects and crustacea (see Table 1 for details). Niche breadth considering food items ($n = 24$) was low for all three size classes (SLC1 Ba = 0.2096; SLC2 Ba = 0.2152; SLC3 Ba = 0.2975).

The graphic method of Costello done for each SLC shows that detritus/sediment was the main food category for all size classes. Autochthonous insects and vegetal matter were the second and third

Table I. Frequency of occurrence (Fo%) and volumetric frequency (Vo%) of the food items and categories found in the diet of different size classes (SLC) of *Bryconamericus iheringii* from Vacacaí river, southern Brazil, between April 2001 and February 2002. A = adult; L = larvae; N = nymph. White and grey areas group food items into food categories.

Food categories	Food items	SLC1		SLC2		SLC3	
		Fo	Vo	Fo	Vo	Fo	Vo
Mollusca	Gastropoda					0.9	0.02
Crustacea	Decapoda					0.9	0.02
	Microcrustacean	8.7	1.3	10.2	0.3	19.3	0.3
Allochthonous insects	Coleoptera A	3.3	0.5	3.6	0.4	11.4	1.1
	Diptera A	3.3	0.4	4.8	0.3	10.5	1.9
	Heteroptera A			1.2	0.2	0.9	0.03
	Hymenoptera A	4.3	0.3	15	1	28.1	3
	Orthoptera A					1.7	0.4
	Thysanoptera A			0.6	0.02	0.9	0.02
Autochthonous insects	Coleoptera L	3.3	0.2	2.4	0.06	6.1	1.5
	Diptera L	30.4	2.1	31.7	1.3	43	2.1
	Diptera N	3.3	0.2	3.59	0.13	3.51	0.24
	Ephemeroptera L	15.2	1.4	13.2	0.7	37.7	3
	Heteroptera L			0.6	0.02	1.7	0.07
	Odonata L	1.1	0.05	12	0.9	21	2.9
	Plecoptera L	1.1	0.03	0.6	0.05	0.9	0.1
	Trichoptera L	4.3	0.46	3.59	0.12	4.4	0.2
Collembola	Collembola			1.8	0.04	3.5	0.1
Arachnida	Acarina	1.1	0.05	4.2	0.1	7	0.1
	Aranae	1.1	0.02	0.6	0.1	2.6	0.5
Fish	Fish			0.6	0.1	0.9	0.1
	Fish scales	3.3	0.4	10.2	1.2	14	1.1
Vegetal matter	Vegetal matter	34.8	2.45	56.9	5.3	73.7	17.9
Detritus/sediment	Detritus/sediment	88	90	93.4	87.6	88.6	53.7

categories, respectively, for SLC1, but far below detritus/sediment (Fig. 2a). Consumption of vegetal matter increases and of autochthonous insects decreases from SLC1 to SLC3. Consumption of all other categories by *B. iheringii* was low (Figs. 2b-2c). These results allow *B. iheringii* to be characterized as a detritivorous species, since detritus/sediment is highly frequent and abundant in its diet regardless fish size and season, while other items, such as vegetal matter and autochthonous insects, are only frequent.

Diet overlap was observed among all size classes considering Vo values (SLC1 x SLC2 = 0.9989; SLC1 x SLC3 = 0.8543; SLC2 x SLC3 = 0.8691). Detritus/sediment had high values for all analyses (Fo, Vo) regardless of season. Vegetal matter also had high values in all analyses in Autumn/01 and Spring/01 and high Fo values in Winter/01 and Summer/01, especially for SLC2 and SLC3. Autochthonous insects had high values in Winter/01 and Summer/01 for Fo and Vo analyses when food categories were considered. Other important food items (besides detritus/sediment and vegetal matter) were larvae of Diptera,

Ephemeroptera and Coleoptera in Winter/01 and Summer/01 (see Table 2).

The two-way PERMANOVA identified significant temporal variation in diet composition among seasons ($F = 11.2$; $p = 0.001$) and SLCs ($F = 7.2$; $p < 0.001$), but no interaction between seasons and SLC's ($F = 1.53$; $p = 0.059$). The NMDS show the two axes extracted after 20 interactions with a stress of 0.16 and a linear fit of $R^2 = 0.97$, summarizing the variation of the diet composition between the individual fish (Figure 3a-3b). Ordination showed that the predominance of detritus/sediment in all seasons has low influence in diet variation through time and ontogeny (Figure 3a-3b). However, ordination showed variation for all other food categories. In the summer, all other food categories are consumed by fish regardless their size, with autochthonous insects and vegetal matter, respectively, as the most consumed. In autumn the same food categories are highly consumed, but vegetal matter comes first, then autochthonous and allochthonous insects. In winter, crustacea, autochthonous insects and Collembola are highly consumed, resulting a different pattern when

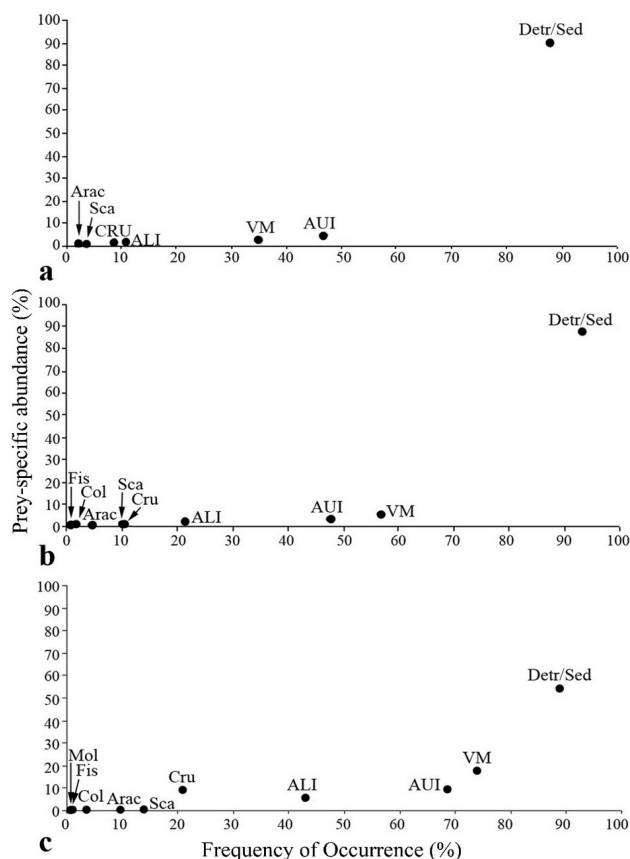


Figure 2. Graphic representations following the method proposed by Costello (1990, with modifications by Amundsen *et al.* 1996) showing the proportion of food categories found in the diet of three standard length classes (SLC) of *Bryconamericus iheringii* from Vacacáí river, southern Brazil, between April 2001 and February 2002. a = SLC1; b = SLC2; c = SLC3. Ali = allochthonous insects; Aui = autochthonous insects; VM = vegetal matter; Detr/Sed = detritus/sediments; Cru = Crustacea; Sca = fish scales; Fis = Fish; Arac = Arachnida; Col = Collembola; Mol = Mollusca.

compared to autumn. Finally, the diet composition in spring is similar to that of autumn, with more of allochthonous insects and fish, especially for smaller individuals (Figure 3b). Regarding the ontogenetic variation in the diet, in addition to detritus/sediment predominance, ordination showed the use of all secondary categories except autochthonous insects which decrease along development. Smaller fish (SLC1) feed especially on autochthonous insects, crustacea and allochthonous insects while larger fish feed on all categories in similar proportions. Food consumption in intermediary fish (SLC2) has high autochthonous and allochthonous insects, similar to that of SLC1, except for crustacea (Figure 3a).

Discussion

The present work provides information on the diet of *B. iheringii* in a floodplain river of southern Brazil, characterizing the species as a detritivore. A thorough review of studies on the diet of this species in diverse watersheds revealed that the present results enlarge the body of work who classify it as a detritivorous species. The feeding habits of *B. iheringii* are well-studied and many studies report the consumption of detritus/sediment, although its trophic characterization ranges from omnivorous (Oliveira & Bennemann 2005, Oricolli & Bennemann 2006, Dala-Corte *et al.* 2016a, Kokubun *et al.* 2018) to insectivorous (Escalante 1987, Oricolli 2002, Russo *et al.* 2004, Rosso 2006) or even detritivorous (Castro 2003, Oricolli & Bennemann 2006) and planktophagous (phytoplankton) (Destefanis & Freire 1972, Escalante 1983, Grosman *et al.* 2000, Borges *et al.* 2006, Rosso 2006). The presence of detritus/sediment in the diet of *B. iheringii* is discussed and linked to its morphology, foraging behavior and the environment.

Detritivorous species eventually show other items in their diet, often showing variation among them indicating a tendency towards another trophic characterization. Castro (2003) considered *B. iheringii* in the Rio dos Veados, a tributary of the Paranapanema river, Brazil, to be a detritivorous species with a tendency towards omnivory during the rainy season. Also, Oricolli & Bennemann (2006), studied the diet of *B. iheringii* in streams of the Rio Tibagi basin, within the same watershed as the previous author, and identified 20 food items defining the species as omnivorous, including algae, detritus and vegetal and insect remains. In one stream, Ribeirão Taquari, the species was considered a detritus specialist. According to Rosso (2006), the diet of *B. iheringii* differs according to the environment that a given population inhabits and its trophic charge. The diet of fish from small streams has a strong component of allochthonous material due to the low productivity in these systems, while in environments with higher primary productivity, such as lakes, algae and microcrustacean are the most common food items (Rosso 2006). Oricolli & Benneman (2006), found that *B. iheringii* feeds in all strata of the water column: at the surface it catches seeds and terrestrial insects; in midwater it feeds on filamentous algae; and on the bottom it feeds on detritus and Chironomidae, while ingesting large amounts of sediment.

Table II. Frequency of occurrence (Fo%) and Volumetric frequency (Vo%) by season of the ingested items and categories found in the diet of different size classes (SLC) of *Bryconamericus iheringii* from Vacacaí river, southern Brazil, between April 2001 and March 2002. A = adult; L = larvae; N = nymph; Aut = autumn; Win = winter; Spr = spring; Sum = summer. White and grey areas group food items into food categories.

Food Categories	Food items	SLC1							
		Aut/01		Win/01		Spr/01		Sum/01	
		Fo	Vo	Fo	Vo	Fo	Vo	Fo	Vo
Mollusca	Gastropoda								
Crustacea	Decapoda								
	Microcrustacea	16.7	1.6	21	4.8	4.2	1.9		
	Coleoptera A					8.3	1.9	8.3	0.7
	Diptera A			15.8	2.9				
Allochthonous insects	Heteroptera A								
	Hymenoptera A	11.1	1.5	5.3	0.3	4.2	0.5		
	Orthoptera A								
	Thysanoptera A								
	Coleoptera L	5.6	0.1	5.3	0.3			8.3	0.7
	Diptera L	22.2	1.3	31.6	2.2	25	1.3	50	3.2
	Diptera N			5.3	0.7			8.3	0.2
Autochthonous insects	Ephemeroptera L	33.3	3.6	26.3	3.8	8.3	2.1	8.3	0.2
	Heteroptera L								
	Odonata L							8.3	0.3
	Plecoptera L	5.6	0.2						
	Trichoptera L	11.1	2.1	5.3	1	4.2	0.2		
Collembola	Collembola								
Arachnida	Acarina			5.3	0.3				
	Aranae			5.3	0.1				
Fish	Fish								
	Fish scales					8.3	1.5	8.3	0.7
Vegetal matter	Vegetal matter	55.6	10	21.0	2	33.3	1.8	41.7	1.9
Detritus/sediment	Detritus/sediment	83.3	79.4	78.9	81.4	83.3	88.7	100	92.1
n		18		19		24		12	

Food Categories	Food items	SLC2							
		Aut/01		Win/01		Spr/01		Sum/01	
		Fo	Vo	Fo	Vo	Fo	Vo	Fo	Vo
Mollusca	Gastropoda								
Crustacea	Decapoda								
	Microcrustacea	3.2	0.05	20.5	1.2	20	1	2.5	0.03
	Coleoptera A	3.2	0.3	7.7	1.9	5.7	0.6		
	Diptera A			12.8	1.7	8.6	0.4		
Allochthonous insects	Heteroptera A			2.6	0.8	2.9	0.1		
	Hymenoptera A	9.7	0.6	28.2	3.2	8.6	1	15	0.6
	Orthoptera A								
	Thysanoptera A			2.6	0.1				
	Coleoptera L	3.2	0.1	5.1	0.2			2.5	0.03
	Diptera L	25.8	0.5	51.3	4.1	20	0.8	32.5	1
	Diptera N			10.3	0.6	2.9	0.1	2.5	0.1
Autochthonous insects	Ephemeroptera L	12.9	0.4	25.6	1.7	11.4	2	2.5	0.2
	Heteroptera L	3.2	0.1						
	Odonata L	12.9	0.6	15.4	1.3	8.6	1.5	17.5	1.4
	Plecoptera L			2.6	0.3				
	Trichoptera L	3.3	0.1	2.6	0.05	11.4	0.7		
Collembola	Collembola			7.7	0.3				
Arachnida	Acarina	3.2	0.05	10.3	0.3	5.7	0.1		
	Aranae			2.6	0.8				
Fish	Fish							2.5	0.2
	Fish scales	6.4	0.2	10.3	1.1	14.3	3.3	10	1.5

Vegetal matter	Vegetal matter	71	11.3	56.4	5.6	51.43	9	60	2.8
Detritus/sediment	Detritus/sediment	90.3	85.6	94.9	74.6	88.6	79.3	97.5	92.1
n		31		39		35		40	

Food Categories	Food items	SLC3							
		Aut/01		Win/01		Spr/01		Sum/01	
		Fo	Vo	Fo	Vo	Fo	Vo	Fo	Vo
Mollusca	Gastropoda			2	0.05				
Crustacea	Decapoda			2	0.05		1.1		
	Microcrustacea	6.2	0.1	40	21.7		0.3		
Allochthonous insects	Coleoptera A	12.5	1.6	14	1.3	10.7	1.1	14.3	1.8
	Diptera A	6.2	0.3	14	1	14.3	5.7		
	Heteroptera A			2	0.1				
	Hymenoptera A	6.2	0.8	46	3.9	25	4.8		
	Orthoptera A			4	0.9				
	Thysanoptera A					3.6	0.09		
	Coleoptera L			4	0.3	10.7	1.6	14.3	14.7
Autochthonous insects	Diptera L	31.2	1.2	64	3.8	32.1	1.2	28.6	1.1
	Diptera N			6	0.5	3.6	0.1		
	Ephemeroptera L	31.2	3	46	4	32.1	3.6	28.6	0.7
	Heteroptera L			4	0.2				
	Odonata L	12.5	1.1	22	2.2	32.1	6.9	14.3	1.1
	Plecoptera L			2	0.2				
	Trichoptera L	6.2	0.8	4	0.2	7.1	0.3		
Collembola	Collembola			8	0.3				
Arachnida	Acarina			10	0.1	3.6	0.03	14.3	0.1
	Aranae			4	0.5	3.6	1.0		
Fish	Fish							14.3	1.1
	Fish scales	25	1.8	8	0.6	17.9	1.8	28.6	1.1
Vegetal matter	Vegetal matter	75	28.1	70	10.1	78.6	37.8	85.7	5.5
Detritus/sediment	Detritus/sediment	81.2	61.1	94	47.9	85.7	32.3	100	72.6
n		16		50		28		7	

Many studies indicate the great importance of algae and aquatic invertebrates in the diet of fish (Teixeira 1989, Henderson & Walker 1990, Sabino & Castro 1990). Thus, the relative importance of autochthonous and allochthonous food items to fish assemblages might depend on the typical environmental conditions of each river or stream, such as the presence of marginal forests and water transparency and velocity (Luz-Agostinho *et al.* 2006), as well as other factors, such as species-specific preferences for certain types of food. Other studies (Moyle & Senanayake 1984, Costa 1987, Uieda *et al.* 1997, Casatti 2002) have found that autochthonous items are also dependent on organic matter nutrients from riparian vegetation, the basis of the trophic chain of stream ecosystems (Gregory *et al.* 1991). Such results increase the importance of conserving riparian areas for aquatic communities (Angermeier & Karr 1984). Terrestrial and aquatic systems are related in many ways (Barrella *et al.* 2000) and the removal of ciliary forests is one of the most harmful alterations affecting these

relationships. Changes in riparian forests can ultimately cause changes not only in the supply of allochthonous material, but also in the nutrients of organic matter derived from this allochthonous material, which may also affect the food chain.

One of the main factors favoring the occupation of different environments by different species of *Bryconamericus* is their trophic adaptability (Oriccoli & Benneman 2006). One of the factors that cause diet shifts in generalist species is the condition of the environment in which they live (Goldstein & Simon 1999). Generalist species, whose trophic flexibility is known, may change their diet according to the local and interactions with other species, being influenced by resource availability through time which evidences its opportunism (Oriccoli & Bennemann 2006). According to Gerking (1994), such behavior is more related to the sudden abundance of a particular food item in a particular period. Dala-Corte *et al.* (2016a) found that populations of *B. iheringii* in riparian-

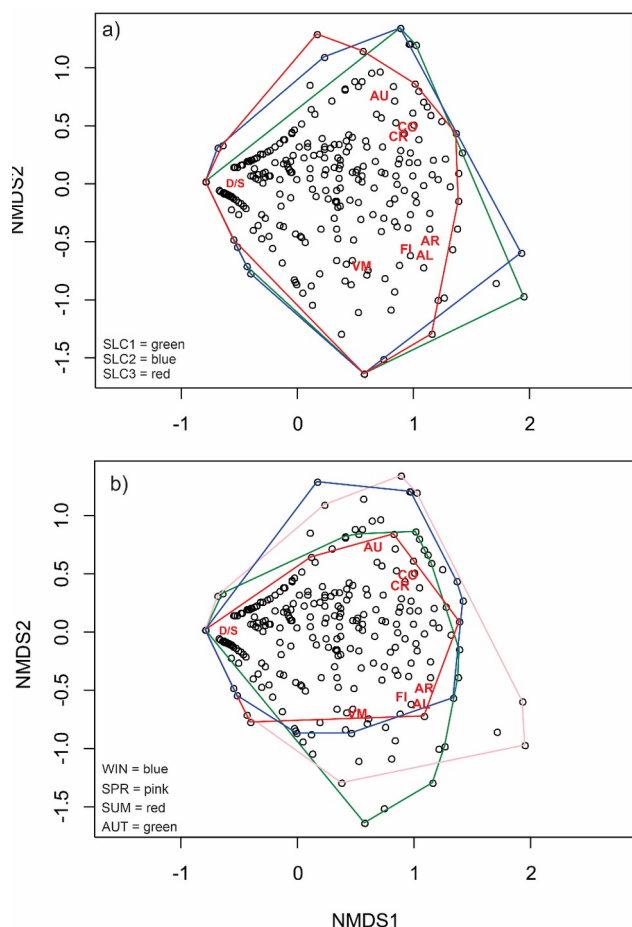


Figure 3. Graphical representation of the two first NMDS axis showing the diet (categories) organization of *Bryconamericus iheringii* from Vacacaí river, southern Brazil, between April 2001 and February 2002. SLC = standard length classes (SLC1 = green line; SLC2 = blue line; SLC3 = red line); Win = winter (blue line); Spr = spring (pink line); Sum = summer (red line); Aut = autumn (green line); D/S = detritus/sediment; VM = vegetal matter; FI = fish parts; AU = autochthonous insects; AL = allochthonous insects; AR = Arachnidae; CO = Collembola; CR = Crustacea.

degraded streams increased the consumption of detritus, filamentous algae and aquatic plants, and reduced the ingestion of aquatic and terrestrial invertebrates as well as terrestrial plant fragments. Although Oricolli & Benneman (2006) and Dala-Corte *et al.* (2016a) states that higher sediment consumption might be related to poor or degraded environmental conditions, this was not observed for the sampling site in the present study. The higher consumption of sediment in this case might be related to its high availability, as well as to the foraging behavior of the species, which picks up food items from the bottom, ingesting sediment with vegetal matter and insect larvae.

Detritivorous fish constitute a great proportion

of Neotropical freshwater fish biomass (Petrere Jr. 1978; Lowe-McConnell 1999), which is especially true for large rivers where there is high availability of detritus. According to Bowen (1983), the majority of detritivorous fish actually derive their nutrition from microorganisms and invertebrates associated with the substrate. Soares *et al.* (2017) explain that the dominance of detritus in the stomach contents of two species of Gymnotiformes that consumed high proportions of sediments/detritus may be due to its ingestion during the search for more nutritive prey. At least in part, a complementary hypothesis is that the consumed detritus might have been part of the protective tunnels that larvae of species of some chironomid clades construct (Trivino-Strixino 2014). Higher proportions of detritus in stomach content usually occur in environments with high amounts of organic matter (Qasim & Sankaranarayanan 1972). Detritus is used as food by a large variety of animals, being a link between organic production and animal nutrition, thus increasing energy exchange among trophic levels (Qasim & Sankaranarayanan 1972).

The feeding strategy of *B. iheringii* can also be explained through its morphology. Mouth position, shape, and size are closely related to feeding habits, especially the mode of food apprehension (Nikolsky 1963). The mouth of *B. iheringii* is positioned slightly downwards, which allows easier exploration of the bottom, where its main food items are located. The results presented here show the importance of detritus/sediment, vegetal matter, and insect larvae in the diet of this species. Bonato *et al.* (2017) show similar results, indicating that the ingestion of benthic items, such as detritus, aquatic insect larvae, organic matter, and algae, is related to the position of the mouth of *B. iheringii*. According to Kokubun *et al.* (2018), a subterminal mouth orientation might be due to a great consumption of items from the stream bottom, including allochthonous plants. Russo *et al.* (2004) found that *Bryconamericus* sp.1, with a sub-terminal mouth and thicker upper lip, fed mainly on aquatic insect larvae, while *Bryconamericus* sp.2, with terminal mouth and thin lips, fed mainly on terrestrial insects. The differences in morphology lead to different behaviors, which are reflected in the choice of food items and, in turn, play an important role in reducing interspecific competition and allowing coexistence (Russo *et al.* 2004).

On the other hand, the effect of this relationship between morphology and diet may be minimal (Kokubun *et al.* 2018). Such pattern may be

the result of the fact that feeding traits are labile so that they rapidly respond to changes in prey availability (Gerking 1994). Nevertheless, even if the species show a phenotypic plasticity which allows them to modify their phenotype according to environmental changes (Parsons *et al.* 2016), such physical traits still respond more slowly than behavior (like feeding).

Changes in feeding habits can occur due to the ontogenetic development of morphological structures, such as dentition, intestinal tract and mouth (size), and to improved locomotion (Wootton 1999, Hahn *et al.* 2000). Mouth gape may limit small individuals from ingesting large items (Wootton 1999, Abelha *et al.* 2001, Vitule *et al.* 2008). Thus, the larger mouth of larger *B. iheringii* may account for the differences found in diet among SLCs. The consumption of larger items by larger fish is an expected result, however, this must be taken with caution since there is a higher number of fish in the larger SLC. On the other hand, the high food overlap found among the different SLCs must be due to the consumption of detritus/sediment and vegetal matter, which are small items consumable by all mouth sizes.

Despite the predominance of detritus/sediment, there was a significant ontogenetic variation in the diet with smaller (SLC1) and intermediary (SLC2) fish feeding mainly on insects (autochthonous and allochthonous). Insects are a high-quality protein source, providing essential amino acids and fatty acids, that can enhance growth and health of smaller fish in various aquatic ecosystems (Nogales-Mérida *et al.* 2019). On the other hand, larger individuals (SLC3) fed on all categories in a more homogeneous way, including crustacea, exploring more broadly the resources. Our results suggests that a protein-rich diet may be crucial for fish growth. Besides, morphological characteristics unique to each size class, such as mouth size, swimming agility, in addition to behavioral changes to reduce competition, may determine specific ontogenetic changes for each class.

The results of the present study indicated that the resource diversity associated with the predominance of detritus/sediment determine a significant change in their feeding strategy throughout their development. This suggests three main possibilities regarding its cost-benefits: i) Food resource diversity in Vacacaí river may be low and a high energetic effort may be necessary to select for more nutritive items, especially for SLC1 and SLC2.

This is more evident when observing the separation of SLC3 regarding diet overlap, where larger fish consume different and larger items, such as fish, Decapoda, Gastropoda, and Orthoptera; ii) Based on the results of Soares *et al.* (2017), the search for more nutritious items may have led to an indirect ingestion of detritus/sediment in all SLCs because it is a small and highly available item; iii) Food items availability is constant through time, with high availability of detritus/sediment with enough variation (especially for all other – secondary – items) to demand changes in the feeding strategy to species survival throughout ontogeny.

The temporal variation was also significant for diet composition even with detritus/sediment predominance. Temporal and/or seasonal variation in the diet of fish species are often attributed to resource availability (Abelha *et al.* 2006, Wolff *et al.* 2009), but also to natural changes in the habitat, such as an increase and decrease of foraging areas in relation to floods and droughts (Wootton 1999). Food categories were uniformly consumed in the summer, especially autochthonous insects and vegetal matter. In winter, crustacea were frequently consumed. Thus, our results suggests that environmental factors such as temperature and precipitation might be influencing diet seasonality, with high crustacea availability in winter, where pluviosity is high and temperature is low (higher river flow, expanding habitats). On the other hand, vegetal matter is highly consumed in spring and summer, drier and warmer periods, when productivity tend to be higher. The greater ingestion of food during the winter found in the present study occurs prior to the reproductive period of this species, which takes place in spring and summer (September to January) (Lampert *et al.* 2004), which may be related to reserve gain.

Conclusions

The results of the present study indicate that *B. iheringii* of the Vacacaí river is a detritivorous species, complementing its diet with autochthonous insects and vegetal matter. Such results are in accordance with other studies for this same species in other watersheds. However, given the intraspecific feeding plasticity of *B. iheringii*, many studies classify these fishes as omnivorous, insectivorous or planktophagous. Besides, the present study also shows differences in the diet of fish among seasons and size classes. The results showed that fish feed more during winter, prior to the reproductive period of this species in spring and

summer, which may be related to reserve gain. In the summer, drier and warmer period when productivity tend to be higher, food categories were uniformly consumed, especially autochthonous insects and vegetal matter. In winter, crustacea were frequently consumed. Despite the predominance of detritus/sediment, there was a significant ontogenetic variation in the diet, with smaller (SLC1) and intermediary (SLC2) fish feeding mainly on insects (autochthonous and allochthonous). On the other hand, larger individuals (SLC3) fed on all categories in a more homogeneous way, including crustacea, exploring more broadly the resources. Also, larger individuals, with larger mouth, consuming different and larger items. On the other hand, there was also a high food overlap due to the consumption of detritus/sediment and vegetal matter, small items that can be ingested by all mouth sizes.

Ethical statement

All applicable institutional and/or national guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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