Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Original Article
Acta Limnologica Brasiliensia, 2022, vol. 34, e31
https://doi.org/10.1590/S2179-975X5621
ISSN 2179-975X on-line version

The effects of season and ontogeny in the diet of *Piabarchus stramineus* (Eigenmann 1908) (Characidae: Stevardiinae) from southern Brazil

Efeitos sazonais e ontogenéticos na dieta de *Piabarchus stramineus* (Eigenmann 1908) (Characidae: Stevardiinae) do sul do Brasil

Vinicius Renner Lampert[1]*, Tatiana Schmidt Dias[1], Karina Keyla Tondato-Carvalho[2] and Clarice Bernhardt Fialho[1]

[1]Laboratório de Ictiologia, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul – UFRGS, Avenida Bento Gonçalves, 9500, bloco IV, prédio 43435, CEP 91501-970, Porto Alegre, RS, Brasil

[2]Setor de Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva s/n, Bairro Universitário, Cidade Universitária, CEP 79070-900, Campo Grande, MS, Brasil

*e-mail: vinilampert@gmail.com

Cite as: Lampert, V.R., et al. The effects of season and ontogeny in the diet of *Piabarchus stramineus* (Eigenmann 1908) (Characidae: Stevardiinae) from southern Brazil. *Acta Limnologica Brasiliensia*, 2022, vol. 34, e31.

Abstract: Aim: In the present work we describe and analyze the diet of a small characin species, *Piabarchus stramineus*, from the Ibicuí River, Uruguay River Basin, southern Brazil. **Methods:** Samples were collected monthly from April 2001 to March 2002 with seine net. All fish were measured, weighed, and had its stomach extruded for gut content analysis. Months were grouped in seasons and fish were classified within three standard length classes (SLC). We tested for possible alimentary differences between the different seasons of the year and standard length classes. **Results:** The analysis of the content in 301 stomachs identified 27 food items and low to intermediary niche breadth. The main food item/category was allochthonous insects, regardless of the seasons, and *P. stramineus* can be classified as an insectivorous species. We observed no food overlap between smaller and larger fish (SLC1 and SLC3). On the other hand, we observed food overlap between small and intermediary fish (SLC1 and SLC2) and between intermediary and large fish (SLC2 and SLC3), evidencing a transition in food consumption along size classes. A temporal variation in diet composition was also observed among size classes. Thus, different sized fish differed in their diets, with smaller fish feeding mainly on cladocerans (SLC1 and SLC2) and larger fish (SLC3) feeding mainly on allochthonous Diptera and Hymenoptera. **Conclusions:** The species diet varies in time (seasons) and such variation is different in each size class. Allochthonous food items were important in the diet of the species in the different developmental phases, especially for larger fish, with autochthonous items also important, especially for smaller fish. The allochthonous food items are strongly related to the ciliary forest; thus, we emphasize the importance of the conservation of such environments.

Keywords: allochthonous insects; size classes; feeding; niche breadth; food overlap.

Resumo: Objetivo: No presente estudo, descrevemos e analisamos a dieta de *Piabarchus stramineus*, um pequeno lambari do rio Ibicuí, bacia do rio Uruguai, no sul do Brasil. **Métodos:** Amostragens foram feitas mensalmente de abril de 2001 a março de 2002 com rede de arrasto de praia. Todos os exemplares foram medidos, pesados e tiveram o estômago retirado para análise de seu conteúdo. Os meses foram agrupados em estações e os peixes classificados em três classes de comprimento padrão (CCP). Foram testadas possíveis diferenças entre as diferentes estações do ano e as diferentes classes de comprimento padrão. **Resultados:** O conteúdo de 301 estômagos foi analisado e identificou 27 itens alimentares e uma amplitude de nicho baixa a intermediária. O principal item/categoria alimentar foi insetos alóctones independentemente das estações do ano e *P. stramineus* pode ser classificada como uma espécie insetívora. Nós não observamos sobreposição alimentar entre os exemplares menores e maiores (CCP1 e CCP3). Por outro lado, observamos sobreposição alimentar entre exemplares pequenos e intermediários (CCP1 e CCP2) e entre exemplares intermediários e maiores (CCP2 e CCP3), evidenciando uma transição no consumo de alimento entre as classes de tamanho. Também foi evidenciado uma variação temporal na composição da dieta com interação entre as classes de comprimento. Desta forma, peixes de diferentes tamanhos tiveram dietas diferentes, com peixes menores se alimentando principalmente de cladóceros (CCP 1 e CCP2) enquanto peixes maiores (CCP3) se alimentaram principalmente de dípteros e himenópteros alóctones. **Conclusões:** Ocorre variação temporal na dieta, mas essa variação é diferente em cada classe de comprimento. Itens alóctones tiveram grande importância na dieta da espécie nas diferentes fases de desenvolvimento, especialmente para exemplares maiores, com itens autóctones importantes especialmente para peixes menores. Os itens alóctones são fortemente relacionados à mata ciliar, motivo pelo qual enfatizamos a importância da conservação destes ambientes.

Palavras-chave: insetos alóctones; classes de tamanho; alimentação; amplitude de nicho; sobreposição alimentar.

1. Introduction

Fish developed diversified foraging tactics and strategies, allowing them to use a wide range of food resources available in their environments and its surroundings (Brandão-Gonçalves et al., 2009), i.e., autochthonous and allochthonous resources. They can occupy all trophic levels in the food web (Wootton, 1992), so knowing about the diet of a species may allow recognizing different trophic guilds, make inferences on its structure, importance of the different trophic levels and interrelationships amongst its components. Knowing the diet range of fish through the stomach content analysis may also help the interpretation of its dynamics and habitat occupation.

Shifts in the diet of fish may be a result of temporal and/or seasonal resource availability (Abelha et al., 2006; Wolff et al., 2009), but also of natural changes in foraging areas due to flood and drought cycles (Wootton, 1999). Also, shifts in the diet of fish might be related to ontogenetic variations, which have been the object of broad discussion in the literature (Machado-Allison & Garcia, 1986; Winemiller, 1989; Hahn et al., 2000). In tropical environments, most fish species show broad flexibility in feeding habits (Lowe-McConnell, 1999), which may change during development according to morphological and behavioral changes (Villares-Junior, 2009; Baldasso et al., 2019).

Most species can change their diet following changes in resource availability, driven by space-temporal environmental changes. Distinct diets within a species are frequently found along different individual development stages, due to differences in energetic demand and morphological limitations, which imply in differentiated diets along development. Many studies on fish feeding habits also demonstrate the importance of riparian forests alongside the water bodies in supplying food items for fish (Graciolli et al., 2003; Barreto & Aranha, 2006; Ferreira et al., 2012).

Characidae is the largest family within Characiformes with a wide distribution in Neotropical freshwaters (Thomaz et al., 2015). Within Characidae, *Piabarchus* Myers 1928 has only three species including *P. stramineus* (Eigenmann, 1908), whose distribution is restricted to La Plata and São Francisco basins (Eschmeyer et al., 2021). These fish usually do not exceed 10 cm of length, live in diversified environments, being mostly omnivorous and active (Britski et al., 1988), also serving as food for other fish (*P. stramineus*, Almeida et al., 1997). It is important to highlight that *Piabarchus stramineus* was, until recently, assigned to the genus *Bryconamericus* Eigenmann 1907. Once they are only distantly related to the type species *B. exodon* Eigenmann 1907, Thomaz et al. (2015) reallocated it within *Piabarchus*. Thus, most of the literature on this species regard it as *B. stramineus*. When referring to it in the present work, we use the current name, following Thomaz et al. (2015).

Many studies of the diets of characid fish have demonstrated the importance of allochthonous items (mostly insects) as a food resource for fish and that such resources are strongly related to the presence of marginal riparian forests (Costa, 1987; Sabino & Castro, 1990; Graciolli et al., 2003; Lampert et al., 2003). Thus, the present work aims to describe and analyze the diet of *P. stramineus* from the Ibicuí River in southern Brazil, identifying 1) the origin of food resources (if allochthonous or autochthonous); 2) the diet composition, niche breadth and food overlap; 3) possible differences in the diet amongst the different seasons of the year and amongst different size classes (ontogeny). Also, a discussion on the importance of ciliary forest in the diet of this species and other fish is provided.

2. Material and Methods

2.1. Data collection

Monthly samplings were conducted from April 2001 to February 2002 in the Ibicuí River (29° 50'14" S; 54° 47'53" W), Uruguay River Basin, in the city of Cacequi, RS, Brazil (Figure 1). The Ibicuí River is a large river with brown water due to high concentration of suspended sediment. Marginal riparian forest forms a narrow line on the left margin, while in the right margin the vegetation is composed essentially by grass and only a few bushes and trees. This vegetation is described as a savannah and a steppe savannah whose arboreal components' distribution follows the drainage system (Teixeira et al., 1986). Depth close to the left margin can reach over 2 m deep, while in the right margin there are shallows due to sandbanks, especially during the low water season. The surrounding areas are covered by pasture and agriculture.

Sampling was performed using seine net (three hauls; 10x2 m net size; 5 mm mesh size), close to the margins. The specimens were anesthetized with Eugenol (clove oil; 70 mg/L) and then euthanized and fixed in 10% formalin solution. In the laboratory, fish were transferred to 70% ethanol and identified to the species level. Voucher specimens were cataloged in the ichthyological collection of Universidade Federal do Rio Grande do Sul (UFRGS 6693).

Specimens were measured (standard length - SL; mm), weighed (total weight; g), and dissected for stomach extrusion and weighing.

Comparative analysis of *P. stramineus*'s diet, according to standard length classes (SLC), was carried out 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 SLC, as follows: SLC1 (n = 113) less than 28 mm, SLC2 (n = 136) 28.01-37 mm, SLC3 (n = 81) larger than 37 mm.

2.2. Data analysis

For diet composition analysis, stomach content was identified under a stereomicroscope to the lowest possible taxonomic level, following McCafferty (1981), Ribeiro-Costa & Rocha (2006), and Mugnai et al. (2010). Food items were grouped into broad categories as follows: crustacea (Cru), autochthonous insects (AUI), allochthonous insects (ALI); collembola (Col); aracnida (Arac); fish (Fis); fish scales (Sca); vegetal matter (VM); sediment (Sed). Sediment includes predominantly sand and mineral inorganic particles.

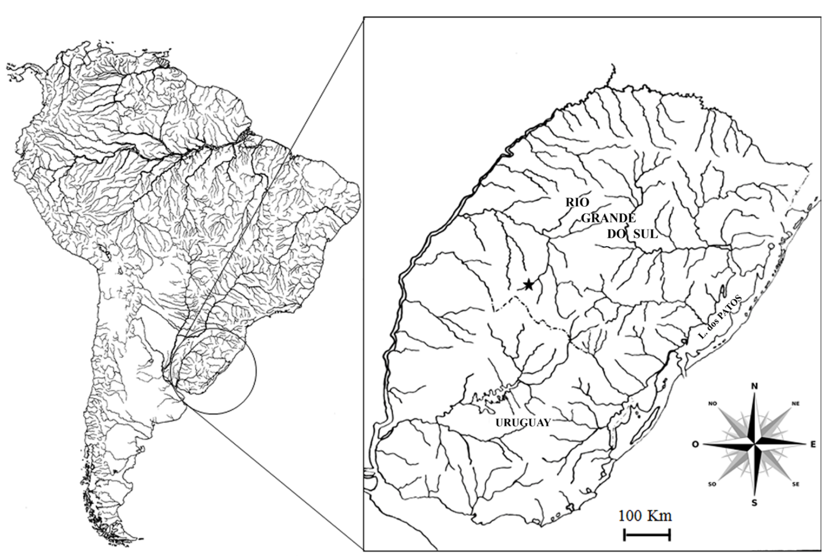

Figure 1. Sampling site location (star) in the Ibicuí River, city of Cacequi, Rio Grande do Sul state, southern Brazil.

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), December 2001, January and February 2002 (Summer/01). The seasons correspond to those in the southern hemisphere.

Stomach content analysis were conducted through the methods of 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, 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).

The importance of each food category was defined through the alimentary index (IAi) (Kawakami & Vazzoler, 1980), calculated according to the formula: $IAi = [(Fo_i \times Vo_i) / \Sigma(Fo_i \times Vo_i)] \times 100$, where i = food item; Fo = frequency of occurrence; and Vo = volumetric frequency.

The degree of diet specialization between the different SLCs was determined by calculating Levin's index (Krebs, 1989) for trophic niche breadth using Vo values. To standardize the measurement of trophic niche, Hurlbert's formula (Hurlbert, 1978) was calculated, which can range from 0 to 1, as: $Ba_i = \{[1 / (n - 1)] / [(1 - S_j p_{ij}^2) - 1]\}$, where: Ba_i = standardized Levin's index for predator i; p_{ij} = proportion of predator i diet that consists of prey j; and n = total number of alimentary items. Trophic niche breadths were then classified as high (> 0.61), intermediary (0.41 to 0.6), or low (< 0.4) (Novakowski et al., 2008).

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.

To assess the proportion of food items in the diet, Fo and Vo methods were combined in the graphical analysis proposed by Costello (1990) with Amundsen et al. (1996) modifications. This method consists of a two-dimensional representation of prey abundance values in the y axis, and frequency of occurrence in the x axis. Dots around 100% Fo and Vo indicates dominant items. Dots around 100% Fo and 1% Vo indicates a small consumption of different types of prey, being classified as a generalist. The opposite, with dots around 1% Fo and 100% Vo indicates a specialization towards a given item (Corrêa & Silva, 2010).

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 Euclidean dissimilarity (Legendre & Legendre, 1998). 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 Euclidean distance coefficient (Legendre & Legendre, 1998), through the metaMDS function with the vegan package (Oksanen et al., 2019).

3. Results

We analyzed 301 specimens of *P. stramineus* ranging from 16.96 to 50.42 mm SL who fed mainly on allochthonous (IAi = 41,5%) and autochthonous (IAi = 16,4%) insects, therefore being classified as insectivores (Table 1). Smaller fish (SLC1) fed more on microcrustacean and autochthonous insects than larger ones, while larger fish (especially SLC3) fed more on allochthonous insects (Table 2).

High values for allochthonous insects were observed in both Autumn/01 and Winter/01 in all analyzes (FO, Vo, IAi). In Spring/01 and Summer/01, high values for microcrustaceans, vegetal matter, and autochthonous items were more often observed. These results are shown in the Table 2.

Niche breadth among the different size classes was low (n = 27) (SLC1 Ba = 0.3161; SLC2 Ba = 0.3388; SLC3 Ba = 0.3983).

The graphic method of Costello calculated for each SLC showed that Crustacea and autochthonous insects were the main food category for fish from SLC1, followed closely by allochthonous insects (Figure 2a). An increase in the importance of allochthonous insects can be observed from SLC2 to SLC3. Autochthonous insects and vegetal matter were important categories for both SLCs, while a decrease in the importance of Crustacea can be observed from SLC2 to SLC3 (Figure 2b-2c).

Diet overlap was observed among all size classes when Vo values were considered (SLC1 x SLC2 = 0.9629; SLC1 x SLC3 = 0.6444; SLC2 x SLC3 = 0.7834). Diet overlap was lower among SLC1 and SLC3 and among SLC2 and SLC3, respectively.

Table 1. Frequency of occurrence (Fo%), Volumetric frequency (Vo%), Alimentary index (Iai%), of the food items and categories found in the diet of *Piabarchus stramineus* from the Ibicuí River, southern Brazil, between April 2001 and February 2002. A = adult; L = larvae; N = nymph; Allo Ins = Allochthonous insect; Au Ins = Autochthonous insect; VM = vegetal matter. Values of 50% and over are highlighted (bold).

Alimentary categories	Alimentary items	FO	Vo	IAi
Crustacea	Decapoda	0.61	0.09	0.002
	Microcrustacea	43.94	19.04	25.6
Allochthonous insects	Allo Ins remains	3.94	0.44	0.05
	Coleptera A	7.27	1.74	0.39
	Diptera A	47.27	19.1	27.63
	Heteroptera A	1.82	0.22	0.01
	Homoptera A	3.33	1.98	0.2
	Hymenoptera A	28.48	15.06	13.12
	Odonata adulto	2.12	1.21	0.08
	Plecoptera A	0.3	0.04	0.001
	Thysanoptera A	2.73	0.25	0.02
Autochthonous insects	Au Ins remains	1.82	0.33	0.02
	Coleoptera L	5.15	1.61	0.25
	Diptera L	41.21	5.45	6.87
	Diptera N	9.7	1.83	0.54
	Ephemeroptera L	24.55	11.34	8.52
	Heteroptera L	2.73	0.42	0.04
	Odonata L	3.03	0.77	0.07
	Plecoptera L	0.91	0.2	0.006
	Trichoptera L	5.45	0.64	0.11
Collembola	Collembola	5.45	0.57	0.1
Arachnida	Acarina	0.91	0.04	0.001
	Aranae	4.85	1.29	0.19
Fish	Fish	0.61	0.77	0.01
	Fish Scales	1.82	0.53	0.03
Vegetal Matter	Vegetal Matter	37.27	13.62	15.53
Sediment	Sediment	13.94	1.42	0.61
n/sum/sum		301	100	100

The two-way Permanova identified a significant variation ($F = 3.7$; $p = 0.001$) in diet composition when the interaction between seasons and SLCs was analyzed. Thus, the temporal variation in the diet is not the same in the different SLCs.

In addition, the NMDS showed that the two axes (extracted after 20 interactions with a stress of 0.14 and a linear fit of $R^2 = 0.97$) summarized the variation of the diet composition between the individual fish. The ordination evidenced distinct diets among seasons, with autumn and winter positioned in the extreme ends of the ordination space, followed by spring (Figure 3).

4. Discussion

The results of the present study allowed the classification of the studied population of *P. stramineus* as insectivorous, which feed on insects from both allochthonous and autochthonous origins, but also including microcrustacea and vegetal matter. Different sized fish showed slight differences in their diets as evidenced by the low niche breadth and low food overlap when comparing smaller and larger individuals.

According to Casatti & Castro (1998), *P. stramineus* is a diurnal, nektonic species which occupy marginal riffle areas during the day, swimming in the middle water and surface (Uieda, 1984), and preying on drifting items in the water surface [*drift-feeding*, cf. Grant & Noakes (1987)], including terrestrial insects [*surface picking*, cf. Sazima (1986)]. Casatti & Castro (1998) defined *P. stramineus* as an omnivorous species in the headwater riffles of São Francisco River, due to the consumption of autochthonous and allochthonous insects, vegetal matter, algae, and microcrustaceans. Luiz et al. (1998) has also classified this species as an omnivore in two streams of Paraná River Basin, feeding on Chironomidae, vegetal remains and detritus in similar proportions. In Corumbá Reservoir, Goiás, Brazil, *P. stramineus* was also classified as omnivore, consuming autochthonous

Table 2. Frequency of occurrence (Fo%), Volumetric frequency (Vo%), Alimentary index (IAi%), by seasons of the food items and categories found in the diet of different size classes (SLC) of *Piabarchus stramineus* from the Ibicuí River, southern Brazil, between April 2001 and March 2002. Aut = autumn; Win = winter; Spr = spring; Sum = summer; A = adult; L = larvae; N = nymph; Allo Ins = Allochthonous insect; Au Ins = Autochthonous insect; VM = vegetal matter. Values of 50% and over are highlighted (bold).

Alimentary categories	Alimentary items	SLC1											
		Aut/01			Win/01			Spr/01			Sum/01		
		FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi
Crustacea	Decapoda												
	Microcrustacea	**62.5**	12.5	18.3	11.8	1.2	0.3	**57.6**	21.0	28.3	**96.9**	**81.1**	**95.5**
Allochthonous insects	Allo ins remains												
	Coleoptera A	4.2	1.2	0.1				9.1	2.2	0.5			
	Diptera A	**50**	27	31.6	**52.9**	24	30.8	48.5	7.2	8.2	25	3.6	1.1
	Heteroptera A	4.2	1.8	0.2									
	Homoptera A	16.7	2.6	1.0									
	Hymenoptera A	29.2	22.9	15.6	29.4	16.8	12	9.1	0.6	0.1	18.7	7.4	1.7
	Odonata A				5.9	0.8	0.1				3.1	0.7	0.03
	Plecoptera A												
	Thysanoptera A	16.7	2.0	0.8									
Autochthonous insects	Au ins remains				5.9	1.6	0.2						
	Coleoptera L												
	Diptera L	**70.8**	17.2	28.5	23.5	7.0	4.0	48.5	8.5	9.6	31.2	3.9	1.5
	Diptera N	16.7	2.9	1.1				6.06	1	0.1	6.2	1.0	0.08
	Ephemeroptera L	4.2	0.6	0.1	**52.9**	39.4	**50.6**	45.4	34.3	36.5	3.1	0.3	0.01
	Heteroptera L							9.1	0.7	0.2			
	Odonata L				5.9	1.6	0.2	9.1	3	0.6			
	Plecoptera L												
	Trichoptera L	4.2	0.3	0.03	5.9	0.4	0.06	3.0	0.2	0.02	3.1	0.3	0.01
Collembola	Collembola							6.1	0.6	0.1	3.1	0.3	0.01
Arachnida	Acarina				11.76	1.2	0.3						
	Aranae	8.3	3.5	0.7	5.9	2.4	0.3	6.1	0.7	0.1			
Fish	Fish												
	Fish scales	4.2	2.3	0.2									
Vegetal Matter	VM	25	2.9	1.7	11.8	2.8	0.8	36.4	16.8	14.3	6.2	0.9	0.07
Sediment	Sediment	4.2	0.3	0.03	5.9	0.8	0.1	18.2	2.9	1.2	6.2	0.5	0.04
n			24			17			33			32	

Alimentary categories	Alimentary items	SLC2											
		Aut/01			Win/01			Spr/01			Sum/01		
		FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi
Crustacea	Decapoda							2.2	0.2	0.01			
	Microcrustacea	40	1.6	1.1	23.8	2.2	1.2	**51.1**	33.4	37.8	**72.3**	45.5	**71.1**
Allochthonous insects	Allo ins remains				4.8	0.5	0.06	4.4	0.2	0.02	4.2	0.3	0.03
	Coleoptera A	20	4.4	1.4	9.5	1.6	0.4	4.4	0.7	0.07	4.2	0.9	0.1
	Diptera A	**80**	33	42.5	**52.4**	28.7	36.4	40	6.1	5.4	36.2	21.5	17
	Heteroptera A	20	0.5	0.2				4.4	0.3	0.04			
	Homoptera A	40	4.4	2.8									
	Hymenoptera A	**60**	49.4	47.8	23.8	8.1	4.7	6.7	0.8	0.1	19.1	11	4.5
	Odonata A												
	Plecoptera A												
	Thysanoptera A	40	3.3	2.1									
Autochthonous insects	Au ins remains										2.1	1.1	0.05
	Coleoptera L				4.8	0.5	0.06	6.7	0.9	0.1	8.5	6.6	1.2
	Diptera L	40	3.3	2.1	**61.9**	6.0	9.0	48.9	6.7	7.3	34.0	4.7	3.4
	Diptera N				4.8	1.1	0.1	13.3	1.7	0.5	8.5	1.7	0.3
	Ephemeroptera L				33.3	12.7	10.3	**53.3**	21.1	25	6.4	1.7	0.2
	Heteroptera L							6.7	0.6	0.1			
	Odonata L				4.8	0.5	0.06	6.7	0.9	0.1			
	Plecoptera L							6.7	1.1	0.2			
	Trichoptera L				14.3	3.2	1.1	2.2	0.2	0.01	2.1	0.1	<0.01
Collembola	Collembola							20	1.6	0.7	2.1	0.2	<0.01
Arachnida	Acarina				4.8	0.2	0.02						
	Aranae				9.5	8.7	2.0						
Fish	Fish												
	Fish scales							2.2	0.1	<0.01			
Vegetal Matter	VM				**57.1**	24.9	34.5	44.4	22.7	22.4	19.1	2.3	1.0
Sediment	Sediment				4.7	0.8	0.1	13.3	0.6	0.2	23.4	2.3	1.1
n			5			21			45			47	

Table 2. Continued...

Alimentary categories	Alimentary items	SLC3											
		Aut/01			Win/01			Spr/01			Sum/01		
		FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi	FO	Vo	IAi
Crustacea	Decapoda							3.7	0.4	0.05			
	Microcrustacea				10.7	0.6	0.2	29.6	7.5	6.0	10	1.9	0.6
Allochthonous insects	Allo ins remains				17.9	2.3	1.0	3.7	0.2	0.02	10	1.9	0.6
	Coleoptera A	16.7	0.5	0.1	7.1	1.3	0.2	11.1	1.7	0.5	30	16.1	13.9
	Diptera A	**100**	31	39.4	53.6	23.4	29.4	44.4	14.2	16.9	**50**	13.5	19.5
	Heteroptera A				3.6	0.5	0.04	3.7	0.4	0.05			
	Homoptera A	33.3	8.1	3.4									
	Hymenoptera A	**91.7**	43.4	**50.6**	**53.6**	13.5	17.0	40.7	11.3	12.3	20	9.6	5.6
	Odonata A				7.1	3.4	0.6				10	6.4	1.9
	Plecoptera A				3.6	0.5	0.04						
	Thysanoptera A	25	0.7	0.2									
Autochthonous insects	Au ins remains				10.7	1.8	0.5	3.7	0.2	0.02			
	Coleoptera L	8.3	0.1	<0.01	14.3	1.3	0.4	3.7	0.2	0.02	20	18.0	10.4
	Diptera L	8.3	0.1	0.01	39.3	3.9	3.6	44.4	10.1	12.0	**60**	3.9	6.7
	Diptera N	8.3	0.7	0.08	10.7	3.4	0.8	14.8	4.3	1.7	30	4.5	3.9
	Ephemeroptera L				21.4	6.5	3.3	40.74	21.1	23.1	10	0.6	0.2
	Heteroptera L							7.4	1.1	0.2			
	Odonata L							7.4	2.8	0.6			
	Plecoptera L												
	Trichoptera L	8.3	0.1	<0.01	7.1	1.3	0.2	7.4	1.2	0.2	10	1.9	0.6
Collembola	Collembola	16.7	0.7	0.1	7.1	0.8	0.1	3.7	0.2	0.02			
Arachnida	Acarina												
	Aranae	25	0.7	0.2	10.7	6	1.5	11.11	0.6	0.2			
Fish	Fish	8.3	4.2	0.4									
	Fish scales	25	2.1	0.7									
Vegetal Matter	VM	**50**	7.1	4.5	**64.3**	26.6	40.0	48.1	18.8	24.4	**60**	20.9	36.2
Sediment	Sediment	25	0.3	0.1	17.9	2.9	1.2	18.5	3.5	1.7	10	0.6	0.2
n			12			28			27			10	

(67%) and allochthonous (28%) insects, and small amounts of vegetal matter (Luz-Agostinho et al., 2006). Such studies corroborate at least in part the findings of the present study and differences may be associated to the lower proportion of microcrustacea and vegetal matter found for *P. stramineus* from the Ibicuí River. In the Upper Paraná River floodplains, this species was considered as insectivorous, feeding mainly on Chironomidae (Luz et al., 2001). Casatti et al. (2003) recorded a predominance of autochthonous insects (54.2%), represented mainly by larvae of Diptera; allochthonous items (43.2%) were also present in the diet of the species, being adult Diptera the most frequent. These results are in accordance with the present study, especially in respect to the predominance of Diptera (allochthonous and autochthonous) in the diet of the species.

As can be observed from the different works previously presented here, the feeding habits of this small fish encompass allochthonous and autochthonous items, either from animal and vegetal origins, thus evidencing the plasticity found in the diet of the same species in different environments. Such plasticity sometimes makes difficult the definition of trophic groups. Feeding plasticity results from an interaction between the quality and quantity of available food in the environment (Luz et al., 2001). This is a remarkable feature in tropical freshwater fish fauna (Goulding, 1980; Lowe-McConnell, 1999) once species can change food consumption according to changes in food resource availability (Goulding, 1980). In tropical regions, despite some fish species can be classified as specialists in a particular food type, most species exhibit trophic plasticity in their diets (Lowe-McConnell, 1999), making the definition of trophic patterns difficult.

Differences in the diet were found in the present study, and such differences can be observed both among SLCs as well as among seasons and they indicate that food consumption change diversely over time for each size class. Hence, the temporal variation is not maintained throughout its ontogeny.

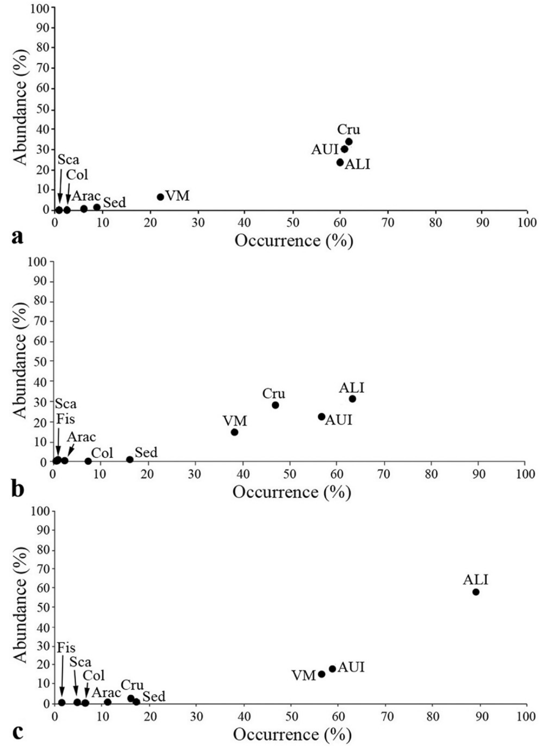

Figure 2. Graphical representations following the method proposed by Costello (1990) modified by Amundsen et al. (1996) showing the proportion of food categories found in the diet of three standard length classes (SLC) of *Piabarchus stramineus* from the Ibicuí River, southern Brazil, between April 2001 and February 2002. a = SLC1; b = SLC2; c = SLC3. ALI = allochthonous insects; AUI = autochthonous insects; VM = vegetal matter; Sed = sediment; Cru = Crustacea; Sca = fish scales; Fis = Fish; Arac = Arachnida; Col = Collembola.

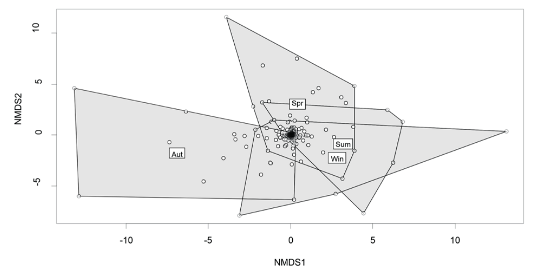

Figure 3. Graphical representation of the two first NMDS axis showing seasonal variation in the diet of *Piabarchus stramineus* in the Ibicuí River, southern Brazil, between April 2001 and February 2002. Aut = autumn; Win = winter; Spr = spring; Sum = summer.

Such finding suggests that each size class may have unique morphological and/or behavioral traits to minimize competition, which favor specific temporal changes for each class. Seasonal changes in the diet of fish may be attributed to food resource availability (Abelha et al., 2006; Wolff et al., 2009), and/or to natural changes in the habitat/foraging areas (Wootton, 1999). The feeding habits of *P. stramineus* was described in different streams of Guiraí River Sub-basin in Mato Grosso do Sul (Brandão-Gonçalves et al., 2009) and differed between seasons and sampling sites. However, in all sites the diet was basically composed by terrestrial insects.

Other authors recorded high consumption of allochthonous insects especially during the rainy season (Brandão-Gonçalves et al., 2009). According to these authors, the flood season is the main period of feeding, growth, and fat reserve accumulation. The flood invades the riverbanks and fertilizes the area, which becomes nutrient-rich due to organic decomposition, stimulating the growth of microorganisms and macroinvertebrates (insects, crustaceans, mollusks) used as food by fish (Lowe-McConnel, 1999).

Another study corroborates our findings regarding diet versus fish size. Suiberto et al. (2009) observed that small *P. stramineus* (larvae) fed mainly on microcrustaceans (Cladocera and Copepoda) while juvenile showed a transition to larger prey such as larvae of Diptera, suggesting a tendency towards invertivory. All main resources in the diet of larvae and juvenile *P. stramineus* were autochthonous, similar to the present study. This is in accordance with the pattern that in their early life stages, many fish species prey upon phytoplankton, zooplankton or small macroinvertebrates, but may switch to larger macroinvertebrates, fish, plants or detritus later in their development (Nunn et al., 2012; Huss et al., 2013).

As discussed above, depending on the study, the diet of adults may vary between autochthonous and allochthonous resources, often including both, but usually composed of terrestrial insects, with which our results agree. In many fish species, the prey size usually increases with fish size (Morinière et al., 2003; Sánchez-Hernández & Cobo, 2012), and different size classes typically consume different prey types as a result of, for example, differences in foraging abilities or habitat use (Mittelbach & Persson, 1998; Nunn et al., 2012). Fish undergo ontogenetic dietary shifts during their development (Blanco-Garrido et al., 2003; Fochetti et al., 2008). These shifts during life stage transitions may be accompanied by a marked reduction in intraspecific competition within the fish population, facilitating resource partitioning (Amundsen et al., 2003; Oscoz et al., 2006).

Coexistence among fish species can be better understood through studies on resource partitioning. Eventually, even when shared food resources are abundant, small differences in diet may facilitate species coexistence (Knickle & Rose, 2014). The same may occur to different life cycle phases within the same species, leading to profound ecological consequences for fish; for example, enhancing individual growth and reproductive output or reducing the risk of mortality (Sánchez-Hernández et al., 2019). Sometimes, even small variations in diet can facilitate coexistence among species (Hynes, 1970; Gatz Junior, 1979). Therefore, differences in item consumption found between the SLCs of *P. stramineus* are not sufficient to change their general diet pattern. On the other hand, they may represent a contribution in resource partitioning and species coexistence in their different life cycle phases.

Allochthonous food items are strongly related to marginal forests (Alvim & Peret, 2004), whose importance for fish feeding is well documented in the literature (Angermeier & Karr, 1983; Sabino & Castro, 1990; Sabino & Zuanon, 1998; Castro, 1999; Lowe-McConnell, 1999). The conservation of such environments may guarantee a broad variety of food items supply to the fish fauna (Lowe-McConnell, 1999). Despite some studies have found a higher contribution of autochthonous items in the diet of fish (Moyle & Senayake, 1984; Uieda et al., 1997; Casatti, 2002), these items are also dependent on organic matter and nutrients inputs from riparian vegetation, the basis of trophic chain in stream ecosystems (Gregory et al., 1991), which increase the importance of riparian areas and their conservation for aquatic communities (Angermeier & Karr, 1983).

Considering the results of our study together with data found in the literature, we believe that *P. stramineus* shows high plasticity of food item consumption allowing resource partitioning within the studied population, especially between the different size classes. The high frequencies of allochthonous resources identified in the stomach content analysis corroborates the importance of riparian vegetation as source of food items, as evidenced by many previous studies.

Acknowledgements

We are thankful to our colleagues at the Ichthyology Lab/UFRGS for field and laboratory work assistance. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a MSc scholarship along this study to the first author (process 464545/00-5 and 476821/2003-7). We also thank the anonymous reviewers whose comments greatly improved this manuscript.

References

Abelha, M.C.F., Goulart, E., Kashiwaqui, E.A.L., & Silva, M.R., 2006. *Astyanax paranae* Eigenmann, 1914 (Characiformes: Characidae) in the Alagados Reservoir, Paraná, Brazil: diet composition and variation. Neotrop. Ichthyol., 4(3), 349-356. http://dx.doi.org/10.1590/S1679-62252006000300006.

Almeida, V.L.L., Hahn, N.S., & Vazzoler, A.E.A.M., 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). Ecol. Freshwat. Fish., 6(3), 123-133. http://dx.doi.org/10.1111/j.1600-0633.1997.tb00154.x.

Alvim, M.C.C., & Peret, A.C., 2004. Food resources sustaining the fish fauna in a section of the upper São Francisco River in Três Marias, MG, Brazil. Braz. J. Biol., 64(2), 195-202. PMid:15462291. http://dx.doi.org/10.1590/S1519-69842004000200003.

Amundsen, P., Bohn, T., Popova, O.A., Staldvik, F.I., Reshetnikov, Y.S., Kashulin, N.A., & Lukin, A.A., 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. Hydrobiologia, 497(1-3), 109-119. http://dx.doi.org/10.1023/A:1025465705717.

Amundsen, P.-A., Gabler, H.-M., & Staldvik, F.J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data modification of the Costello (1990) method. J. Fish Biol., 48(4), 607-614. https://doi.org/10.1111/j.1095-8649.1996.tb01455.x.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol., 26, 32-46.

Anderson, M.J., Gorley, R.N., & Clarke, K.R., 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. Retrieved in 2022, February 5, from http://updates.primer-e.com/primer7/manuals/PERMANOVA+_manual.pdf

Angermeier, P.L., & Karr, J.R., 1983. Fish communities along environmental gradients in a system of tropical streams. Environ. Biol. Fishes, 9(2), 117-135. http://dx.doi.org/10.1007/BF00690857.

Baldasso, M.C., Wolff, L.L., Neves, M.P., & Delariva, R.L., 2019. Ecomorphological variations and food supply drive trophic relationships in the fish fauna of a pristine neotropical stream. Environ. Biol. Fishes, 102(5), 783-800. http://dx.doi.org/10.1007/s10641-019-00871-w.

Barreto, A.P., & Aranha, J.M.R., 2006. Alimentação de quatro espécies de Characiformes de um riacho da Floresta Atlântica, Guaraqueçaba, Paraná, Brasil.

Rev. Bras. Zool., 23(3), 779-788. http://dx.doi.org/10.1590/S0101-81752006000300023.

Blanco-Garrido, F., Sánchez-Polaina, F.J., & Prenda, J., 2003. Summer diet of the Iberian chub (*Squalius pyrenaicus*) in a Mediterranean stream in Sierra Morena (Yeguas Stream, Córdoba, Spain). Limnetica, 22(3-4), 99-106. http://dx.doi.org/10.23818/limn.22.23.

Borcard, D., Gillet, F., & Legendre, P., 2011. Numerical ecology with R. New York: Springer. http://dx.doi.org/10.1007/978-1-4419-7976-6.

Brandão-Gonçalves, L., Lima-Junior, S.E., & Suarez, Y.R., 2009. Hábitos alimentares de *Bryconamericus stramineus* Eigenmann, 1908 (Characidae), em diferentes riachos da sub-bacia do Rio Guiraí, Mato Grosso do Sul, Brasil. Biota Neotrop., 9(1), 135-143. http://dx.doi.org/10.1590/S1676-06032009000100016.

Britski, H.A., Sato, Y., & Rosa, A.B.S., 1988. Manual de identificação de peixes da região de Três Marias – com chave de identificação para os peixes da bacia do rio São Francisco. Brasília: Ministério da Irrigação/CODEVASF, 115 p.

Casatti, L., & Castro, R.M.C., 1998. A fish community of the São Francisco River headwaters riffles, southeastern Brazil. Ichthyol. Explor. Freshwat., 9(3), 229-242.

Casatti, L., 2002. Alimentação dos peixes em um riacho do Parque Estadual Morro do Diabo, bacia do Alto Rio Paraná, sudeste do Brasil. Biota Neotrop., 2(2), 1-14. http://dx.doi.org/10.1590/S1676-06032002000200012.

Casatti, L., Mendes, H.F., & Ferreira, K.M., 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, southeastern Brazil. Braz. J. Biol., 63(2), 213-222. PMid:14509843. http://dx.doi.org/10.1590/S1519-69842003000200006.

Castro, R.M.C. 1999. Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos causais. In: Caramaschi, E.P., Mazzoni, R., Bizerril, C.R.S.F. & Peres-Neto, P.R., eds. Ecologia de peixes de riachos: estado atual e perspectivas. Rio de Janeiro: Oecologia Brasiliensis VI, 139-155, 260 p. http://dx.doi.org/10.4257/oeco.1999.0601.04.

Corrêa, F., & Silva, G.C., 2010. Hábito alimentar de *Astyanax asuncionensis* (Géry, 1972) durante um período de seca e cheia, no Córrego do Onça, Coxim, Mato Grosso do Sul. Rev. Bras. Biocienc., 8(4), 368-372.

Costa, W.J.E.M., 1987. Feeding habits of a fish community in a tropical coastal stream, rio Mato Grosso, Brazil. Stud. Neotrop. Fauna Environ., 22(3), 145-153. http://dx.doi.org/10.1080/01650528709360728.

Costello, M.J., 1990. Predator feeding strategy and prey importance: a new graphical analysis. J. Fish Biol., 36(2), 261-263. http://dx.doi.org/10.1111/j.1095-8649.1990.tb05601.x.

Dias, T.S., Stein, R.J., & Fialho, C.B., 2017. Ontogenetic variations and feeding habits of a Neotropical annual fish from southern Brazil. Iheringia Ser. Zool., 107, e2017020. http://dx.doi.org/10.1590/1678-4766e2017020.

Eschmeyer, W.N., Fricke, R., & van der Laan, R., 2021. Catalog of fishes: genera, species, references [online]. San Francisco: California Academy of Sciences. Retrieved in 2021, January 16, from http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Ferreira, A., Gerhard, P., & Cyrino, J.E.P., 2012. Diet of *Astyanax paranae* (Characidae) in streams with different riparian land covers in the Passa-Cinco River basin, southeastern Brazil. Iheringia Ser. Zool., 102(1), 80-87. http://dx.doi.org/10.1590/S0073-47212012000100011.

Fochetti, R., Argano, R., & Figueroa, J.M.T., 2008. Feeding ecology of various age-classes of brown trout in River Nera, Central Italy. Belg. J. Zool. (Online), 138, 128-131. Retrieved in 2022, November 8, from https://core.ac.uk/download/pdf/41155912.pdf

Gatz Junior, A.J., 1979. Community organization in fishes as indicated by morphological features. Ecology, 60(4), 711-718. http://dx.doi.org/10.2307/1936608.

Goulding, M., 1980. The fishes and the forest: explorations in Amazonian natural history. Berkeley: University of California Press, 280 p. http://dx.doi.org/10.1525/9780520316133.

Graciolli, G., Azevedo, M.A., & Melo, F.A.G., 2003. Comparative study of the diet of Glandulocaudinae and Tetragonopterinae (Ostariophysi: Characidae) in a small stream in southern Brazil. Stud. Neotrop. Fauna Environ., 38(2), 95-103. http://dx.doi.org/10.1076/snfe.38.2.95.15932.

Grant, J.W.A., & Noakes, D.L.G., 1987. A simple model of optimal territory size for drift- feeding fishes. Can. J. Zool., 65(2), 270-276. http://dx.doi.org/10.1139/z87-042.

Gregory, S.V., Swanson, F.J., McKee, W.A., & Cummins, K.W., 1991. An ecosystem perspective of riparian zones. Bioscience, 41(8), 540-551. http://dx.doi.org/10.2307/1311607.

Hahn, N.S., Pavanelli, C.S., & Okada, E.K., 2000. Dental development and ontogenetic diet shifts of *Roeboides paranensis* Pignalberi (Osteichthyes, Characinae) in pools of the upper Rio Paraná. Rev. Bras. Biol., 60(1), 93-99. PMid:10838928. http://dx.doi.org/10.1590/S0034-71082000000100012.

Hurlbert, S.H., 1978. The measurement of niche overlap and some relatives. Ecology, 59(1), 67-77. http://dx.doi.org/10.2307/1936632.

Huss, M., Persson, L., Borcherding, J., & Heermann, L., 2013. Timing of the diet shift from zooplankton to macroinvertebrates and size at maturity determine whether normally piscivorous fish can persist in otherwise fishless lakes. Freshw. Biol., 58(7), 1416-1424. http://dx.doi.org/10.1111/fwb.12138.

Hynes, H.B.N., 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pigosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol., 19(1), 36-58. http://dx.doi.org/10.2307/1570.

Hynes, H.B.N., 1970. The ecology of running waters. Toronto: University of Toronto Press, 555 p.

Hyslop, E.J., 1980. Stomach contents analysis – a review of method and their application. J. Fish Biol., 17(4), 411-429. http://dx.doi.org/10.1111/j.1095-8649.1980.tb02775.x.

Kawakami, E., & Vazzoler, G., 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. Bol. Inst. Oceanogr., 29(2), 205-207. http://dx.doi.org/10.1590/S0373-55241980000200043.

Knickle, D.C., & Rose, G.A., 2014. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes. Environ. Biol. Fishes, 97(4), 343-355. http://dx.doi.org/10.1007/s10641-013-0156-0.

Krebs, C.J., 1989. Ecological methodology. New York: Harper Collins Publishers, 654 p.

Lampert, V.R., Azevedo, M.A., & Fialho, C.B., 2003. Hábito alimentar de *Mimagoniates microlepis* Steindachner, 1876 (Characidae: Glandulocaudinae) do canal de ligação entre as lagoas Emboaba e Emboabinha, Rio Grande do Sul, Brasil. Comun. Mus. Cienc. Tecnol. Pucrs. Ser. Zool., 16(1), 3-16.

Legendre, P., & Legendre, L., 1998. Numerical ecology (2nd ed.). NewYork: Elsevier, 853 p.

Lowe-McConnell, R.H., 1999. Estudos ecológicos de comunidades de peixes tropicais. São Paulo: Edusp, 536 p.

Luiz, E.A., Agostinho, A.A., Gomes, L.C., & Hahn, N.S., 1998. Ecologia trófica de peixes em dois riachos da bacia do rio Paraná. Rev. Bras. Biol. (Online), 58, 273-285. Retrieved in 2022, November 8, from http://repositorio.uem.br:8080/jspui/handle/1/5193

Luz, K.D.G., Abujanra, F., Agostinho, A.A., & Gomes, L.C., 2001. Caracterização trófica da ictiofauna de três lagoas da planície aluvial do alto rio Paraná, Brasil. Acta Sci. Biol. Sci. (Online), 23(2), 401-407. Retrieved in 2022, November 8, from http://repositorio.uem.br:8080/jspui/handle/1/5175

Luz-Agostinho, K.D.G., Bini, L.M., Fugi, R., Agostinho, A.A., & Júlio Júnior, H.F., 2006. Food spectrum and trophic structure of the ichthyofauna of Corumbá reservoir, Paraná river Basin, Brazil. Neotrop. Ichthyol., 4(1), 61-68. http://dx.doi.org/10.1590/S1679-62252006000100005.

Machado-Allison, A., & Garcia, C., 1986. Food habits and morphological changes during ontogeny in three serrasalmin fish species of the Venezuelan floodplains. Copeia, 1986(1), 193-195. http://dx.doi.org/10.2307/1444905.

McCafferty, W.P., 1981. Aquatic entomology: the fishermen's and ecologists. Illustrated guide to insects and their relatives. Boston: Jones and Bartlett Publishers.

Mittelbach, G.G., & Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci., 55(6), 1454-1465. http://dx.doi.org/10.1139/f98-041.

Morinière, E.C., Pollux, B.J.A., Nagelkerken, I., & van der Velde, G., 2003. Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations. Estuar. Coast. Shelf Sci., 57(5-6), 1079-1089. http://dx.doi.org/10.1016/S0272-7714(03)00011-8.

Moyle, P.B., & Senayake, F.R., 1984. Resource partitioning among the fishes of rainforest streams in Sri Lanka. J. Zool., 202(2), 195-223. http://dx.doi.org/10.1111/j.1469-7998.1984.tb05951.x.

Mugnai, R., Nessimian, J.L., & Baptista, D.F., 2010. Manual de identificação de macroinvertebrados aquáticos do estado do Rio de Janeiro. Rio de Janeiro: Technical Books.

Novakowski, G.C., Hahn, N.S., & Fugi, R., 2008. Diet seasonality and food overlap of the fish assemblage in a Pantanal pond. Neotrop. Ichthyol., 6(4), 567-576. http://dx.doi.org/10.1590/S1679-62252008000400004.

Nunn, A.D., Tewson, L.H., & Cowx, I.G., 2012. The foraging ecology of larval and juvenile fishes. Rev. Fish Biol. Fish., 22(2), 377-408. http://dx.doi.org/10.1007/s11160-011-9240-8.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H., 2019. Vegan: community ecology package. R package version 2.5-7 [online]. Retrieved in 2022, November 8, from https://CRAN.R-project.org/package=vegan

Oscoz, J., Leunda, P.M., Miranda, R., & Escala, M.C., 2006. Summer feeding relationships of the co-occurring *Phoxinus phoxinus* and *Gobio lozanoi* (Cyprinidae) in an Iberian river. Folia Zool. (Online), 55(4), 418-432. Retrieved in 2022, November 8, from https://www.ivb.cz/wp-content/uploads/55_418-432.pdf

R Core Team, 2019. R: A language and environment for statistical computing [online]. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, Novmber 8, from https://www.R-project.org/

Ribeiro-Costa, C.S., & Rocha, R.M., 2006. Invertebrados: manual de aulas práticas. Ribeirão Preto: Holos.

Sabino, J., & Castro, R.M.C., 1990. Alimentação, período de atividade e distribuição espacial dos peixes de um riacho da Floresta Atlântica (sudeste do Brasil). Rev. Bras. Biol., 50(1), 23-36.

Sabino, J., & Zuanon, J., 1998. A stream fish assemblage in Central Amazonia: distribution, activity patterns and feeding behavior. Ichthyol. Explor. Freshwat., 8(3), 201-210.

Sánchez-Hernández, J., & Cobo, F., 2012. Summer differences in behavioural feeding habits and use of feeding habitat among brown trout (Pisces) age classes in a temperate area. Ital. J. Zool., 79(3), 468-478. http://dx.doi.org/10.1080/11250003.2012.670274.

Sánchez-Hernández, J., Nunn, A.D., Adams, C.E., & Amundsen, P.-A., 2019. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. Biol. Rev. Camb. Philos. Soc., 94(2), 539-554. PMid:30251433. http://dx.doi.org/10.1111/brv.12468.

Sazima, I., 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. J. Fish Biol., 29(1), 53-65. http://dx.doi.org/10.1111/j.1095-8649.1986.tb04926.x.

Suiberto, M.R., Galuch, A.V., Bialetzki, A., & Nakatani, K., 2009. Ontogenetic shifts in the digestive tube and diet of *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae). Acta Limnol. Bras. (Online), 21(4), 465-472. Retrieved in 2022, November 8, from https://www.ablimno.org.br/acta/pdf/acta_v21n4_210411.pdf

Teixeira, M.B., Neto, A.B.C., Pastore, U., & Rangel-Filho, A.L.R., 1986. Vegetação – as regiões fitoecológicas, sua natureza e seus recursos econômicos. Estudo fitogeográfico, 545-600. In: Projeto RADAMBRASIL, org. Levantamento de recursos naturais, volume 33, folha SH 22 Porto Alegre e parte das folhas SH 21 Uruguaiana e SI 22 Lagoa Mirim. Rio de Janeiro: Instituto Brasileiro de Geografia e Estatística, 545-560.

Thomaz, A.T., Arcila, D., Ortí, G., & Malabarba, L.R., 2015. Molecular phylogeny of the subfamily Stevardiinae Gill, 1858 (Characiformes: Characidae) classification and the evolution of reproductive traits. BMC Evol. Biol., 15(1), 1-25.

Uieda, V.S., 1984. Ocorrência e distribuição dos peixes em um riacho de água doce. Rev. Bras. Biol., 44(2), 203-213.

Uieda, V.S., Buzzato, P., & Kikuchi, R.M., 1997. Partilha de recursos alimentares em peixes em um riacho de serra no sudeste do Brasil. An. Acad. Bras. Cienc. (Online), 69, 243-252. Retrieved in 2022, November 8, from http://hdl.handle.net/11449/65351

Vieira, S., 1991. Introdução à bioestatística. Rio de Janeiro: Editora do Campus.

Villares-Junior, G.A., 2009. Medindo a morfologia dos peixes. Bol. Soc. Bras. Ictiologia, 97, 7-9.

Winemiller, K.O., 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in Venezuelan Llanos. Environ. Biol. Fishes, 26(3), 177-199. http://dx.doi.org/10.1007/BF00004815.

Wolff, L.L., Abilhoa, V., Rios, F.S., & Doinatti, L., 2009. Spatial, seasonal and ontogenetic variation in the diet of *Astyanax* aff. *fasciatus* (Ostariophysi: Characidae) in an Atlantic Forest river, southern Brazil. Neotrop. Ichthyol., 7(2), 257-266. http://dx.doi.org/10.1590/S1679-62252009000200018.

Wootton, J.H., 1999. Ecology of teleost fish. Alphen aan den Rijn: Kluwer Academic Publishers, 386 p.

Wootton, R.J., 1992. Fish ecology. New York: Chapman & Hall. http://dx.doi.org/10.1007/978-94-011-3832-1.

Received: 18 August 2021
Accepted: 08 November 2022

Associate Editor: Fernando Mayer Pelicice.