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Food-resource partitioning among fish species from a first-order stream in northwestern Paraná, Brazil

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This study addressed the feeding ecology of fish fauna from a first-order stream located in a rural area. The purposes were to evaluate the influence of interspecific, seasonal and spatial factors on the diet, examine the dietary overlap, and determine the predominant food sources. Sampling was conducted in December 2007, September 2008, and March 2009, in three 50-m stretches of Itiz stream (upstream, intermediate, and downstream), through electrofishing. A total of 1,102 stomach contents were analyzed from 14 species, by the volumetric method. In general, allochthonous resources were predominant in the diets. *Astyanax* aff. *fasciatus, Astyanax* aff. *paranae*, *Astyanax bockmanni,* and *Bryconamericus* aff. *iheringi* consumed a higher proportion of plant remains, and *Bryconamericus stramineus* consumed predominantly Hymenoptera. The diets of *Cetopsorhamdia iheringi*, *Characidium* aff. *zebra*, *Imparfinis schubarti*, and *Trichomycterus* sp. consisted of aquatic insects, especially immature forms of Trichoptera, Ephemeroptera, Plecoptera, and Diptera. *Hypostomus ancistroides*, *Hisonotus* sp., *Poecilia reticulata*, and *Rineloricaria* aff. *pentamaculata* exploited mainly detritus, while *Rhamdia quelen* used a variety of items, predominantly terrestrial insects. Detrended Correspondence Analysis (DCA) showed a clear distinction among the species, with different morphology and feeding tactics. The Multi-Response Permutation Procedure (MRPP) supported this differentiation, and also indicated significant spatial and temporal variations in the dietary composition; the Indicator Value Method (IndVal) indicated the main items that contributed to these differences. The diet overlap among species was low (< 0.4) to around 78% of pairs, and the mean value did not vary significantly among the sites or between hydrological periods within each site. According to the null model of Pianka's index, the values for dietary overlap were significantly higher than expected at random, showing evidence of resource sharing. This was related to the availability of allochthonous resources, highlighting the importance of riparian vegetation as a source of these resources for maintaining the fish fauna of the stream.

Este estudo abordou a ecologia alimentar da ictiofauna de um riacho de primeira ordem situado em área rural. Os objetivos foram verificar a influência dos fatores interespecíficos, sazonais e espaciais sobre a dieta, avaliar a sobreposição alimentar, além de determinar os recursos alimentares predominantes. As amostragens foram realizadas em dezembro/2007, setembro/2008 e março/2009, em três pontos do riacho Itiz (montante, intermediário e foz) com extensões de 50 m, através de pesca elétrica. Foram analisados 1102 conteúdos estomacais referentes a 14 espécies de acordo com o método volumétrico. De forma geral observou-se que a maior contribuição na dieta das espécies foi de recursos alóctones. *Astyanax* aff. *fasciatus, Astyanax* aff. *paranae, Astyanax bockmanni*, *Bryconamericus* aff. *iheringi*, consumiram maior proporção de vegetal e *Bryconamericus stramineus* predominantemente Hymenoptera. *Cetopsorhamdia iheringi*, *Characidium* aff. *zebra, Imparfinis schubarti* e *Trichomycterus* sp. tiveram sua dieta baseada em insetos aquáticos, especialmente formas imaturas de Trichoptera, Ephemeroptera, Plecoptera e Diptera. *Hypostomus ancistroides*, *Hisonotus* sp., *Poecilia reticulata* e *Rineloricaria* aff. *pentamaculata* exploraram principalmente detrito, enquanto *Rhamdia quelen* usou uma variedade de itens, com predomínio de insetos terrestres. A análise de Correspondência com Remoção do Efeito do Arco (DCA) demonstrou uma segregação evidente entre as espécies com morfologia e táticas alimentares distintas. O Procedimento Permutacional de Multiresposta (MRPP) além de corroborar essa diferenciação, também mostrou variações espaciais e temporais significativas na composição da dieta das espécies, e o Método de Valor Indicador (IndVal) apontou os principais itens que contribuíram para essas diferenças. A sobreposição alimentar entre as espécies foi baixa (< 0.4) para cerca de 78% dos pares e a média não variou significativamente entre os locais, assim como entre os períodos hidrológicos dentro de cada ponto. De acordo com o modelo

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nulo do índice de Pianka**,** os valores de sobreposição alimentar foram significativamente maiores do que o esperado ao acaso, apresentando evidência de partição de recursos. Isto se deve à disponibilidade de itens alóctones, evidenciando a importância da mata ciliar como fonte desses recursos para a manutenção da ictiofauna do riacho estudado.

Key words: Allochthonous resources, Diet, Fish fauna, Trophic segregation, Riparian vegetation.

Introduction

Studies on trophic ecology have revealed a dietary pattern for fish from Neotropical streams, where the diet is mainly based on allochthonous food resources (Casatti, 2002; Mazzoni *et al*., 2010a; Tófoli *et al*., 2010), with the maximum use of environmental resources (Brandão-Gonçalves *et al*., 2010; Rezende *et al*., 2011) and high trophic plasticity of the species (Lowe-McConnell, 1999; Abelha *et al*., 2001).

However, some mechanisms are still little understood by ecologists, such as resource partitioning and other factors that allow the species to coexist (Esteves & Galetti, 1994; Gerking, 1994; Higgins & Strauss, 2008). Therefore, dietary analysis may reveal important information about trophic dynamics and resource partitioning among fish species (Ross, 1986), especially with regard to environments that are subject to sudden changes, such as streams (Johnson & Arunachalam, 2012).

The high trophic plasticity allows Neotropical fishes to adjust their feeding habits to fluctuations in food supply (Balassa *et al*., 2004). Both stochastic processes and the abundance of some foods may reduce intraspecific competition, facilitating the species' coexistence (Dias & Fialho, 2011; Uieda & Pinto, 2011). Other factors such as trophic morphology, use of different microhabitats, periods of activity, and tactics of capture can minimize overlap effects (Casatti, 2002; Brazil-Sousa *et al*., 2009; Cetra *et al*., 2011).

The trophic opportunism observed for Neotropical fish fauna is influenced by the great variety of foods and is also related to the considerable temporal and spatial variations in the streams (Power, 1983; Winemiller & Winemiller, 2003; Esteves *et al.,* 2008; Johnson & Arunachalam, 2012). In these environments, seasonal variations in the diet of fish species are common, with a wider niche breadth during the rainy season; in the dry season, these species become more specialized in a subset of resources (Winemiller *et al*., 2008). Nevertheless, in some environments these differences may not exist because the food resources remain available throughout the year in sufficient amounts (Mazzoni *et al*., 2010a; Schneider *et al*., 2011).

Streams are highly variable environments (Higgins, 2009; Winemiller *et al*., 2008) and have great habitat heterogeneity, with rocky rapids, pools, and small backwaters, which influence the composition of the fish fauna (Esteves & Aranha, 1999; Casatti *et al*., 2001; Casatti, 2002). These different characteristics along the stream, as well as the characteristics of the surroundings, also determine the availability of food resources in the ecosystem.

Tropical landscapes have undergone widespread and continuing deforestation (Achard *et al*., 2002; Lambin *et al*., 2003), and are increasingly dominated by agriculture, a very common situation in northwestern Paraná State and the vicinity of the Ivaí River basin (Parolin *et al*., 2010). The small rivers in this basin are quite heterogeneous, with distinct geomorphological and hydrological features (Leli *et al*., 2010; Parolin *et al*., 2010; Araújo *et al*., 2011). This heterogeneity contributes to the presence of a peculiar and endemic fish fauna (Maier *et al*., 2008), as in the Itiz stream, a rural stream that supports a high abundance of native species (Araújo *et al*., 2011).

Clearing of forests surrounding tropical streams is a critical threat to biodiversity, and may negatively impact the aquatic biota through habitat degradation and changes in the available food for the organisms (Lorion & Kennedy, 2009; Casatti, 2010). These changes influence the contribution of allochthonous resources from the terrestrial environment, which are essential for stream fish (Alvim & Peret, 2004; Rezende & Mazzoni, 2005; Winemiller *et al*., 2008; Tófoli *et al*., 2010). Riparian vegetation is of paramount importance in sustaining these ecosystems, by influencing the transfer of solar energy to the environment, intercepting sediments that enter streams, and providing food and shelter for the fish fauna (Pusey & Arthington, 2003; Abilhoa *et al*., 2008).

In the present study, the fish fauna from a first-order stream with different proportions of riparian vegetation was used to evaluate the hypothesis that the heterogeneity of the channel and surrounding environment will favor partitioning of food resources. The purposes of this study were to: (i) describe the feeding habits of the species; (ii) test the influence of interspecific, seasonal and spatial factors on the diet; (iii) examine the level of diet overlap among fish species; and (iv) determine the sources of the predominant resources in the species' diet.

Material and Methods

Study area. The study was performed in Itiz stream, a first-order stream (Strahler, 1957), located in Marialva Municipality, State of Paraná. This stream flows into other tributaries of Pinguim stream, which flows into the Ivaí River. The Ivaí River watershed has an area of 36,899 km² and a total course of 675 km, and is the second-largest basin and the second-longest river in Paraná (Suderhsa, 2009).

Itiz stream is situated in a rural area (Fig. 1) where the main economic activity is the cultivation of soybeans, wheat, corn, sugarcane and grapes (Ipardes, 2007). The main physical characteristics and geographical coordinates of the three sampling stations along the stream are listed in Table 1 and Fig. 1.

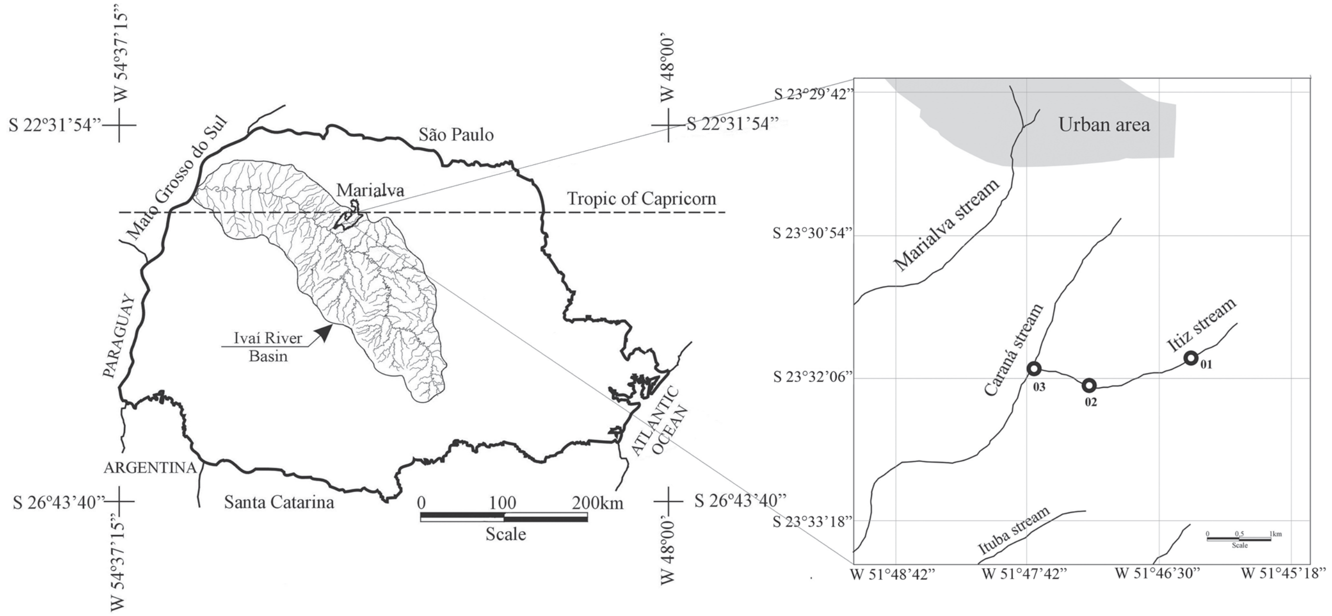

Fig. 1. Location of Itiz stream in the Ivaí River basin, state of Paraná, Brazil, indicating sampling sites (1, 2 and 3).

Fish collections. Fish were collected at three sampling stations located in the upstream, intermediate and downstream regions, with an approximate distance of 1.2 km between each station, during December 2007, September 2008 and March 2009 (Fig. 1). For the sampling, we used electrofishing with three passes of 30 min each, in stretches of 50 m per sampling station. The electrofishing equipment was powered by a portable generator (Honda, 2.5 kW, 220 V, 3--4 A) connected to a DC transformer, with two electrified net rings (anode and cathode). Output voltage varied from 400 to 600 V. For the sampling we installed blocking nets (mesh size 0.5 mm) at the ends of each stretch to prevent any fish from escaping. After sampling, fish were anesthetized with benzocaine (250 mg/L) and fixed in 10% formalin. Fish were collected under license from the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA; Process number 11253-1/2007).

Specimens were identified according to Graça & Pavanelli (2007), and then preserved in 70% ethanol. Each specimen captured was weighed on an analytical balance (standard and total lengths, in cm), and then eviscerated. Voucher specimens were deposited in the fish collection of Nupélia

Table 1. Physical characteristics of the sampling sites in Itiz stream, Ivaí River basin, Marialva Municipality, Paraná State, Brazil.

Sites	Coordinates	Width (m)	Depth (m)	Predominant substrate	Riparian vegetation	Channel physiography	Observations
1	23°31'49.9"S 51°46'26.9"W	1.5- 3.0	0.10- 0.50	Gravel, pebble, sand, silt and litter	Range of trees and shrubs at or higher than 30 m on the banks	Rapids with mean depth of 0.20 m, and pools up to 0.60 m deep	There is a disabled weir next to the sampling station, and water is pumped from the middle of the sampling stretch to irrigate nearby fields. Surrounding vegetation provides about 80% shade
2	23°32'11.2"S 51°46'59"W	1.5- 4.5	0.10-0.20	Rock, gravel, pebble; some backwaters with sand and mud	Range of trees and shrubs at or higher than 30 m on the banks, with little aquatic vegetation	Pools 5 m wide and up to 1.20 m deep; stretches with rapids 0.10 to 0.20 m deep; few backwater areas	1.5-m high waterfall upstream. Stretch with better-conserved riparian vegetation, with 90% shade
3	23°32'02.6"S 51°46'26.3"W	2.0-4.0	0.30-0.50	Rock, pebble, litter and sand	Range of trees lower than 10 m and invasive grasses	Stretches composed of rapids and sand	1.5-m high waterfall downstream; stretch with the lowest proportion of riparian vegetation, and walking trails along the banks. About 50% shade

(Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura), of the State University of Maringá, Brazil (Table 2).

Diet analysis. Gastric contents of 14 species based on all stomachs with food (fullness equal to or greater than 20%) were identified under optical and stereoscopic microscopes to the lowest taxonomic level possible. For species with an undifferentiated stomach, the contents of the anterior third of the digestive tube were examined. For the analysis of stomach contents, we used only species for which we had a total of five or more samples. Food items were identified using the identification keys of Bicudo & Bicudo (1970) for algae and of Mugnai *et al*. (2010) for invertebrates, and quantified according to the volumetric method; *i.e.*, the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents (Hyslop, 1980), using graduated test tubes and a glass counting plate (Hellawell & Abel, 1971).

Statistical analysis. A multivariate ordination technique (Detrended Correspondence Analysis, DCA; Hill & Gauch, 1980) was used to ordinate and summarize data for the species diet (Sheldon & Meffe, 1993). The input matrix for the DCA contained the value for the volume of each food item. Because some food items showed high values, we conducted a square-root transformation to minimize their effect on the ordination. In addition, we opted to run the DCA algorithm giving less weight to rare food items, also to remove their effect on the ordination. The first two DCA axes were retained for interpretation, because they showed eigenvalues greater than 0.20 (as recommended by Matthews, 1998).

The Multi-Response Permutation Procedure (MRPP) (McCune & Grace, 2002) was used to test the significance of differences in dietary composition among the 14 species, sites (1, 2, 3) and hydrological period (rainy - December 2007 and March 2009; and dry - September 2008), which were established through rainfall data obtained from the Weather Station of the State University of Maringá. MRPP is a non-parametric procedure for testing the null hypothesis of no difference between two or more groups of entities defined a priori. MRPP provides a test statistic (T) that describes the separation between the groups (the more negative the T value, the stronger the separation); a measure of "effect size" (A) is presented as a measure of the degree of within-group homogeneity, compared to random expectation where (Amax = 1 is when all items are identical within groups), and a *p*-value is useful for evaluating the likelihood that an observed difference is due to chance (the significance level used was < 0.05) (McCune & Grace, 2002). As the input distance matrix, we selected the Sørensen (Bray-Curtis) distance, with n/sum(n) as the weighting factor.

The Indicator Value Method (IndVal), based on relative abundance and relative frequency, was used to detect how strongly each food item differed among sites and hydrological periods, according to the formula (Dufrêne & Legendre, 1997):

$$\text{IndVal}_{ij} = A_{ij} \text{ x } B_{ij} \text{ x } 100$$

where: IndVal_{ij} is the indicator value for species i in group j, A_{ij} is the relative abundance of species i in group j and B_{ij} is the relative frequency of species i in group j.

The indicator value of a food item varies from 0 to 100, and attains its maximum value when all items occur at all sites and hydrological periods within a single group. We tested the significance of the indicator value for each item with a Monte Carlo randomization procedure with 10,000 permutations (the level of significance was < 0.05). All statistical analyses and ordinations were performed in PC-ORD version 5.0 (McCune & Mefford, 1999).

Feeding overlap. For this analysis we used the 32 items found in the analysis of food types. Feeding overlap was measured for each site in both hydrological periods, using the Pianka index (1973), according to the formula:

$$O_{jk=}\sum P_{ij}\,P_{ik}/ \sqrt{}\,(\sum P_{ij} \sum P_{ik})$$

where: O_{jk} = Pianka's measure of niche overlap index between species *j* and *k*; p_{ij} = proportion of resource *i* of the total resources used by species *j*; p_{ik} = proportion of resource *i* of the total resources used by species *k*; and n = total number of resource states.

Overlap values were set at the following levels: high (> 0.6), intermediate (0.4-0.6) or low (< 0.4) (Grossman, 1986; Novakowski *et al*., 2008; Dias & Fialho, 2011). This index assumes that prey are equally available to all predators (Reinthal, 1990). To test differences in niche overlap for each site and hydrological period within each site, we used the non-parametric Kruskal-Wallis test in the software Statistica 7.1 (StatSoft, 2005).

We used a null model to evaluate the significance of Pianka's index (Juliano & Lawton, 1990; Winemiller & Pianka, 1990; Tokeshi, 1999). In this null model, the observed percentage of food-category values were randomized 10,000 times within each site in both hydrological periods, and for each randomization the Pianka's index was calculated. The *p*-value for the observed index was estimated as the proportion of the randomized index that was greater than the observed value. The null model analysis and feeding overlap were computed using EcoSim 7.0 (Gotelli & Entsminger, 2001).

Food resources. The items identified were grouped for graphical observation of the main food resources consumed by the species at the three sampling sites and in each hydrological period. The groupings were: aquatic invertebrates (Testate Amoebae, Gastropoda, Acarina, Amphipoda, Decapoda, Cladocera, Conchostraca, Copepoda, Ostracoda, Ephemeroptera, Odonata nymph, Plecoptera, immature Coleoptera, Trichoptera, immature Diptera, immature Lepidoptera, and aquatic insect remains), terrestrial invertebrates (Oligochaeta, Diplopoda, Araneae, Hemiptera, Hymenoptera, Coleoptera, adult Diptera, Orthoptera, and terrestrial insect remains), detritus, terrestrial plants (plant remains and seeds), algae, and fish (fish and scales).

Results

Diet composition. The composition of the diet of 1,102 individuals belonging to 14 species was analyzed (Table 2). We recorded 32 food items, where *Astyanax* aff. *fasciatus, Astyanax* aff. *paranae*, and *Astyanax bockmanni* consumed a high proportion of plant remains, followed by terrestrial insects. *Bryconamericus* aff. *iheringi* consumed similar amounts of plant remains, seeds, Hymenoptera and immature Lepidoptera, while *Bryconamericus stramineus* consumed mainly Hymenoptera. The diets of *Cetopsorhamdia iheringi*, *Characidium* aff. *zebra* and *Trichomycterus* sp. were based on aquatic insects, especially immature Trichoptera, Ephemeroptera, Plecoptera and Diptera. The species with high intake of detritus were *Hypostomus ancistroides*, *Hisonotus* sp., *Poecilia reticulata*, and *Rineloricaria* aff. *pentamaculata. Imparfinis schubarti* primarily consumed aquatic insect remains and Amphipoda. *Rhamdia quelen* showed a distinctive diet, consuming Diplopoda, terrestrial insect remains, and Orthoptera (Table 3).

In order to interpret the diet data through the DCA, axes 1 and 2 were retained (eigenvalues 0.77 and 0.47, respectively) (Fig. 2 a-b). Axis 1 explained most of the data variability, where the species that consumed predominantly plant remains and terrestrial insects had lower scores, and the species that consumed detritus, algae and other benthic organisms had higher scores. The species that fed on aquatic insects, especially immature Ephemeroptera, Plecoptera, and Trichoptera, showed intermediate scores.

The differences found in the dietary composition among species were corroborated by the MRPP analysis (T = -19.3; A = 0.06; $p < 0.05$), which also indicated significant differences in relation to sampling sites (T = -24.4; A = 0.02; $p < 0.05$). The food items that contributed to this differentiation were Gastropoda and seeds at site 1; Hymenoptera, aquatic insect remains and plant remains at site 2; and immature Lepidoptera and algae at site 3. The same analysis indicated a significant difference between hydrological periods (T = -191.8; A = 0.12; $p < 0.05$). In the rainy period, Testate amoebae, Hymenoptera, Gastropoda, detritus, and Cladocera were the items that accounted for these differences; while during the dry period, the indicator items were immature Diptera and Coleoptera, algae, seeds, and plant remains (Table 4).

Diet overlap. In general, the diet overlap among species was low (< 0.4) for about 78% of pairs of species. Medium and high overlap values were recorded for all sites in both hydrological periods, but with frequencies lower than 15% (Fig. 3), and these values were related to the congeneric species of Characidae and individuals of Loricariidae that showed extensive overlap in the foods consumed. The means of diet overlap, evaluated through the Kruskal-Wallis test, did not indicate significant differences among the three sampling sites (H = 5.48; $p = 0.06$), or between the hydrological periods at each site (Site 1: H = 2.52, $p = 0.11$; Site 2: H = 2.35, $p = 0.12$; Site 3: H = 0.10, $p = 0.74$). According to the null model of Pianka's index, the values of diet overlap within each site in both hydrological periods were significantly higher than expected by chance (null communities) ($p < 0.05$), suggesting that these values are not random, *i.e.*, showing evidence of resource sharing.

Food resources. When the food items were grouped into broader categories and compared by sites and hydrological

Table 2. Number of stomachs analyzed, for each fish species from Itiz stream, Ivaí River basin, Paraná State, Brazil.

Order/Family/Species	Species Code	Voucher specimens	N analyzed stomachs Rainy	Dry	Largest and smallest standard length (cm)
CHARACIFORMES					
Crenuchidae					
Characidium aff. *zebra* Eigenmann, 1909	Cze	NUP 11817	25	23	3.00-5.70
Characidae					
Astyanax aff. *fasciatus* (Cuvier, 1819)	Afa	NUP 11797	36	43	2.70-10.92
Astyanax aff. *paranae* Eigenmann, 1914	Apa	NUP 11794	107	69	2.10-11.59
Astyanax bockmanni Vari & Castro, 2007	Abo	NUP 11793	11	41	3.52-8.29
Bryconamericus aff. *iheringi* (Boulenger, 1887)	Bih	NUP 11791	28	35	3.30-5.80
Bryconamericus stramineus Eigenmann, 1908	Bst	NUP 11818	16		4.90-6.40
SILURIFORMES					
Trichomycteridae					
Trichomycterus sp.	Tri	NUP 11800/11811	112	74	2.20-7.76
Loricariidae					
Hisonotus sp.	His	NUP 11808	15	13	2.50-4.00
Rineloricaria aff. *pentamaculata* Langeani & de Araújo, 1994	Rpe	NUP 11815	58	23	1.70-9.80
Hypostomus ancistroides (Ihering, 1911)	Han	-	44	22	1.40-7.80
Heptapteridae					
Cetopsorhamdia iheringi Schubart & Gomes, 1959	Cih	NUP 11816	6		1.80-7.20
Imparfinis schubarti (Gomes, 1956)	Ish	NUP 11799	4	4	2.30-6.20
Rhamdia quelen (Quoy & Gaimard, 1824)	Rqu	NUP 11805	14	10	7.00-17.20
CYPRINODONTIFORMES					
Poeciliidae					
Poecilia reticulata Peters, 1859	Pre	NUP 11807	169	100	1.20-3.63
Total number			1102		

Table 3. Food items consumed by the fish fauna in Itiz stream, Ivaí River basin, Paraná State, Brazil. Values based on data for volume percentage of the food item. Asterisk indicates values less than 0.1%. See Table 2 from names of fish species.

Food items/ fish fauna	Afa	Apa	Abo	Bih	Bst	Cze	Cih	Han	His	Isc	Pre	Rpe	Rqu	Tri
AUTOCHTHONOUS														
Testate Amoebae	*	*	*	1.1		0.2		*		*	8.7	0.8	*	*
Gastropoda						0.5					1.3		0.1	
Acarina			*			0.3					*			*
Amphipoda		*		1.4	0.3	2.8				36.3	0.1	0.2	2.9	10.3
Decapoda													7.3	
Cladocera		*									*			
Conchostraca						*					0.3	0.3		
Copepoda											*			
Ostracoda		*	*	0.1	*	1.9					0.1	1.1	*	*
Ephemeroptera	0.5	0.4	0.2	2.7	1.1	31.7	54.3			3.1	2.4	6.7		17.5
Odonata nymph		0.3		2.1							0.1			2.2
Plecoptera	0.2	0.4	0.1	1.1		2					0.5			15.4
Immature Coleoptera	1	2.2	2.6	2.3	0.6	3.2					0.2	0.1	0.4	0.9
Trichoptera	1.4	3	0.3	6.1	0.6	35.3	0.7			12.6	3.7	17.9	0.1	26.4
Immature Diptera	3.6	1.2	1.9	8	0.4	13.6	8.3	*		*	10.4	10.7	0.8	8.6
Immature Lepidoptera	2.7	2.8	6.7	10.6	0.2						0.3			2.2
Aquatic insect remains	0.1	0.8	0.2	8.5	0.1	0.1	27.7			45.7	0.5	*	0.7	3.3
Scales	*			0.1									*	
Fish		0.8	2.8										5.7	
Algae								*	1.5		1.4	0.3		*
ALLOCHTHONOUS														
Oligochaeta				1.9		2.3					*		0.3	3
Diplopoda													34.6	
Araneae	0.2	0.6	0.3	0.8	0.8								2.3	
Hemiptera		0.3	0.1	0.5	0.1								2.7	0.1
Hymenoptera	6.6	13.3	14.4	9.5	94.5								2.2	0.4
Coleoptera	5.9	7	4.6	4.2	0.5	1.3					0.7		5.8	0.4
Adult Diptera	1.7	0.4	0.1	0.2		0.6					0.9	*		
Orthoptera		0.5		0.7									11.8	
Terrestrial insect remains	24.1	4.6	7.8	6.8							0.1		13.7	1.4
Seeds	4.6	5.9	3.4	11.4	0.4						*		0.1	1.2
Plant remains	46.5	55.2	54.5	13.6	0.4	0.7	0.7			2.3	0.6	0.8	6.5	2.2
UNDETERMINED														
Detritus	0.8	0.2	*	6.4		3.6	8.2	99.9	98.5		67.7	61.2	1.9	4.3

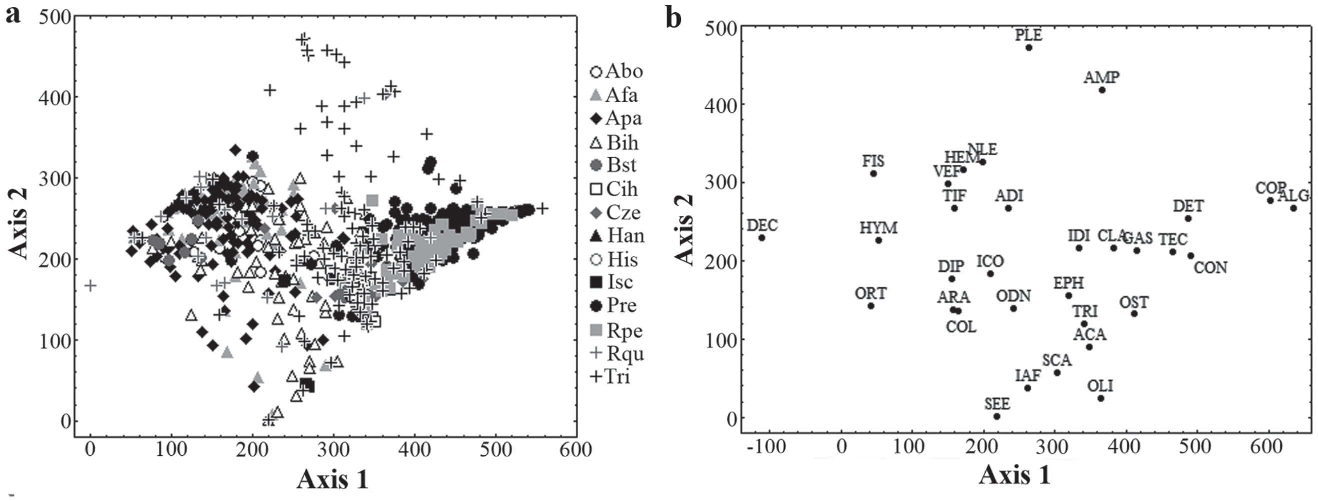

Fig. 2. Ordination of species (**a**) and food items (**b**) in Itiz stream, Ivaí River basin, Paraná State, Brazil, along the axis derived from Detrended Correspondence Analysis (DCA). See Table 2 for names of fish species. ACA = Acarina; ADI = Adult Diptera; ALG = Algae; AMP = Amphipoda; ARA = Araneae; CLA = Cladocera; COL = Coleoptera; CON = Conchostraca; COP = Copepoda; DEC = Decapoda; DET = Detritus; DIP = Diplopoda; EPH = Ephemeroptera; FAI = Aquatic insect remains; FIS = Fish; FTI = Terrestrial insect remains; GAS = Gastropoda; HEM = Hemiptera; HYM = Hymenoptera; ICO = Immature Coleoptera; IDI = Immature Diptera; ILE = Immature Lepidoptera; ODN = Odonata nymph; OLI = Oligochaeta; ORT = Orthoptera; OST = Ostracoda; PLA = Plant remains; PLE = Plecoptera; SCA = Scales; SEE = Seeds; TEA = Testate amoebae; TRI = Trichoptera.

Table 4. Relative abundance (RA), relative frequency (RF) and Indicator value (Indval) of food items consumed by the fish community, discriminated among sites and hydrological period in Itiz stream, Ivaí River basin, Paraná State, Brazil. Only items with signicant values, $p < 0.05$, Monte Carlo permutation test are listed.

Factor	Group	Food items	RA %	RF %	Indval	*p*
Sites	Site 1	Gastropoda	95	4	4	0.000
		Seeds	73	7	5	0.012
	Site 2	Aquatic insect remains	51	17	8	0.043
		Hymenoptera	64	11	7	0.002
		Plant remains	49	37	18	0.005
	Site 3	Immature Lepidoptera	55	6	4	0.029
		Algae	51	19	10	0.008
Hydrological periods	Rainy	Testate amoebae	71	21	15	0.012
		Hymenoptera	73	17	12	0.000
		Gastropoda	94	3	3	0.005
		Detritus	57	51	29	0.034
		Cladocera	100	1	1	0.046
	Dry	Immature Diptera	64	50	32	0.002
		Immature Coleoptera	59	12	7	0.046
		Algae	65	16	11	0.023
		Seeds	72	6	5	0.050
		Plant remains	64	43	27	0.000

periods, at the three sampling sites, terrestrial invertebrates proved to be the resource that was most consumed by the fish fauna during the rainy period (values higher than 40%). In the dry period, the main resource varied among the sites: at sites 1 and 2, terrestrial plants were the most consumed item (45.1% and 56.7%, respectively), and at site 3, terrestrial invertebrates and terrestrial plants were most consumed (29.4% and 25.8%, respectively) (Figs. 4-5-6).

Discussion

The fish fauna used a range of food items, especially insects (terrestrial and aquatic), plants and detritus, corroborating the general dietary pattern described in the literature for tropical streams (Casatti, 2002; Borba *et al*., 2008; Brandão-Gonçalves *et al*., 2010; Mazzoni *et al*., 2010b; Tófoli *et al*., 2010; Schneider *et al*., 2011).

Patterns of food segregation were observed among the species in the present study, and this demarcation can be explained by differences in the use of microhabitats, trophic morphology, and feeding tactics. For example, in the case of microhabitat use, the characids *Astyanax* and *Bryconamericus* were positioned in the water column where they collect food items carried by the current and available on the water surface, such as terrestrial insects and plants; whereas the heptapterid *Rhamdia quelen* showed a benthic habit, foraging on the bottom. The generalist feeding habit in streams, especially for small characids, has been reported previously, since these species are usually trophic opportunists and may change their diet according to spatial variations and interactions with other species (Casatti *et al.*, 2001; Bennemann *et al.*, 2005; Abilhoa *et al.*, 2008; Corrêa & Silva, 2010; Uieda & Pinto, 2011).

With regard to morphological adaptations for feeding and restricted to one type of food, a pattern was observed for the

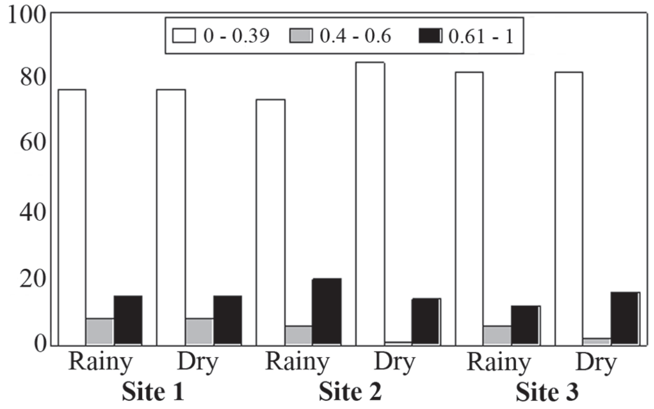

Fig. 3. Overlap values for the fish fauna of Itiz stream, Ivaí River basin, Paraná State, Brazil, using Pianka's index, for each sampling site in the rainy and dry hydrological periods. Diet overlap was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1).

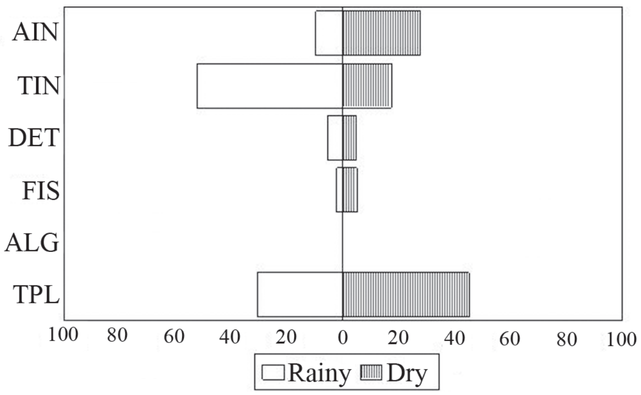

Fig. 4. Percentage composition of food resources consumed by fish species of Itiz stream, Ivaí River basin, Paraná State, Brazil, at site 1 in each hydrological period. AIN = aquatic invertebrates; TIN = terrestrial invertebrates; DET = detritus; FIS = fish; ALG = algae; TPL = terrestrial plants.

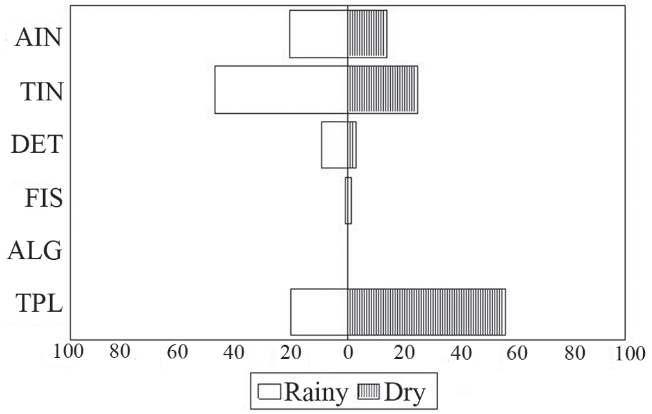

Fig. 5. Percentage composition of food resources consumed by fish species of Itiz stream, Ivaí River basin, Paraná State, Brazil, at site 2 in each hydrological period. AIN = aquatic invertebrates; TIN = terrestrial invertebrates; DET = detritus; FIS = fish; ALG = algae; TPL = terrestrial plants.

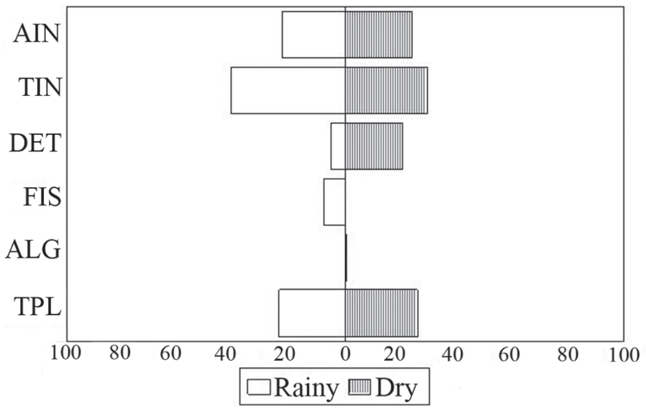

Fig. 6. Percentage composition of food resources consumed by fish species of Itiz stream, Ivaí River basin, Paraná State, Brazil, at site 3 in each hydrological period. AIN = aquatic invertebrates; TIN = terrestrial invertebrates; DET = detritus; FIS = fish; ALG = algae; TPL = terrestrial plants.

detritivorous species *Hypostomus ancistroides, Hisonotus* sp. and *Rineloricaria* aff. *pentamaculata,* as also observed in other tropical waters (Lowe-McConnell, 1999). These species have a feeding tactic of using predominantly benthic resources, where they collect algae, detritus, and other microorganisms (Oliveira & Bennemann, 2005; Dias & Fialho, 2011), aided by the ventral, sucker-shaped mouth (Delariva & Agostinho, 2001; Casatti, 2005; Adriaens *et al*., 2009).

The segregation can also be guided by the availability of resources in the aquatic environment (Gerking, 1994; Casatti *et al*., 2009; Rezende *et al*., 2011), where a type of food is widely and continually available, this can favor non-restrictive trophic specialization. This pattern was evident for *Poecilia reticulata* and for the insectivores *Trichomycterus* sp., *Characidium* aff. *zebra* and *Cetopsorhamdia* aff. *iheringi*, which capture benthic aquatic insects (Casatti, 2002; Abilhoa *et al*., 2008; Rezende *et al*., 2011). The high consumption of immature ephemeropterans, plecopterans and trichopterans was probably related to their high abundances in Itiz stream, as observed by Bagatini *et al.* (2012) in samples of macroinvertebrates collected simultaneously with this study.

The spatial variations observed in the dietary composition can be explained by the different microhabitats and characteristics of the surroundings of the sampling sites, which influence the supply of food resources. At site 1, water is pumped out for a cultivated area on the right bank, where papaya (*Carica papaya* L.) and other crops are grown. Different seeds from these plantations were abundant in the diets of several species, comprising a distinctive trophic feature for this site. At site 2, *Bryconamericus stramineus* was present in higher abundance and consumed predominantly hymenopterans. This site had the highest proportion of riparian vegetation, essential for the input of allochthonous items such as terrestrial insects and plants, which were more important in this stretch of the stream. At site 3, the indicator food items were related to the less-structured riparian vegetation, which allows more light into the aquatic environment and thus increases autochthonous primary production (algae).

The hydrological periods also markedly influenced the availability of food in this stream. During the rainy period, the most important items were hymenopterans carried in by the rainfall, along with sediment from the surrounding areas, which caused an increase of items from the bottom, such as detritus, testate amoebae, gastropods and cladocerans. In the dry period, the situation was different, since the leaves and seeds fall into the water and serve as food for fish, and as a refuge for aquatic insects that are consumed together with this material.

The low overlap values observed suggest resource partitioning between most pairs of species. According to Schoener (1974), resource partitioning involves any substantial difference in the use of food that mitigates the effects of niche overlap and allows the species to coexist. Ross (1986) stated that in fish, segregation through food is considered among the most important factors. For the species examined in this study, the small overlap was related to the spatial and temporal differentiation observed in the dietary composition, the supply of food resources, and the different foraging tactics and dietary preferences by the species.

Resource partitioning among fish species from Neotropical streams is well reported in the literature, where the wide variety of aquatic and terrestrial organisms available as potential prey items leads to a wide diversity of tactics and feeding habits (Casatti, 2002; Barreto & Aranha, 2006; Abilhoa *et al*., 2008; Brandão-Gonçalves *et al*., 2010; Alves *et al*., 2011; Cetra *et al*., 2011; Uieda & Pinto, 2011).

High overlap values were recorded only between congeneric species of Characidae and Loricariidae, which because of their kinship, similar morphology and co-occurrence, used the same food sources (Casatti, 2002; Mazzoni *et al*., 2010c; Alves *et al*., 2011; Dias & Fialho, 2011). However, this high overlap was probably associated with the high abundance of these resources (Bennemann *et al*., 2005; Dias & Fialho, 2009; Uieda & Pinto, 2011).

The mean dietary overlap did not vary for each sampling site or between hydrological periods at each site, revealing that the species did not significantly change their feeding habits; and the overlap occurred for the same pairs of species. Perusal of the literature reveals no discernible temporal pattern influencing the degree of diet overlap in rivers and streams. Studies suggest that during the dry season, the degree of overlap is higher, due to the scarcity of resources in this period (Deus & Petrere-Junior, 2003). Nevertheless, Zaret & Rand (1971), Tófoli *et al.* (2010) and Alves *et al.* (2011) recorded high values of overlap during the rainy season. In contrast, other studies have found no difference in the degree of overlap between the hydrological periods (Bastos, 2002; Dias & Fialho, 2009, 2011; Johnson & Arunachalam, 2012), similarly to our results.

Grouping the food items into broader categories revealed differences in resource intake among the seasons of the year, which may be explained by the effect of seasonality on the life cycles of the organisms used as food (Wootton, 1990). During the rainy period, which in this region coincides with the warmest period of the year, the higher consumption of terrestrial invertebrates was due to greater emergence of arthropods, mainly adult insects, which, along with the rainfall, favors the transport of these organisms into the aquatic environment (Angermeier & Karr, 1983; Rezende & Mazzoni, 2005; Tófoli *et al*., 2010). In the dry season, the high intake of allochthonous plant material is caused by the lower current flow and water volume, which allows leaves and tree trunks to accumulate along the stream banks, making them available for the community (Schneider *et al*., 2011). The greater senescence of leaves of the Seasonal Semideciduous Forest, typical of the region, also contributed to this availability.

Plant material from riparian vegetation forms the base of the trophic chain of many aquatic ecosystems (Melo *et al*., 2004). According to Casatti (2010), changes in the composition and structure of riparian vegetation may cause alterations in food availability and consequently in the feeding habits of fish. This pattern was observed in this study, since this stream featured headwater characteristics, with low primary productivity, making the organisms dependent on allochthonous food resources.

Thus, the characteristics of the surroundings, degree of integrity of the riparian vegetation, and physiography of the channel at each site increased the availability of food items in the stream. These characteristics contributed to the higher consumption of allochthonous resources by the fish community, and, together with the different feeding tactics, were essential for the segregation and low trophic overlap in the species' diets.

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