

TROPHIC ECOLOGY OF THE FISH IN THE RIO DOS VEADOS (UPPER PARANAPANEMA RIVER, SP) DURING THE DRY AND RAINY SEASONS

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ABSTRACT - The aim of this study was to evaluate the trophic ecology of the principal species of fish (*Astyanax altiparanae*, *A. fasciatus*, *Bryconamericus stramineus*, *B. iheringii*, *Cheirodon stenodon*, *Characidium fasciatum*, *Geophagus brasiliensis*, *Hyphessobrycon anisitsi*, *Piabina argentea* and *Steindachnerina insculpta*) captured in the littoral region of the Rio dos Veados (23°16'80''S/48°38'67''W), an affluent of the Rio Paranapanema, SP. The collections were conducted monthly with a seine-type trawling net with a 5.0mm mesh size, taking place between August, 1996 and December, 1997. This collection time was subdivided into the dry (April to September) and rainy (October to March) seasons. The food contents were analyzed by a volumetric method, and the food overlap determined by the Morisita-Horn index. The ten species of fish consumed different food resources, which varied in abundance (volume percentage): detritus/sediment (30.0%), aquatic insects (23.4%), microcrustaceans (17.6%), terrestrial insects (13.9%), higher plants (6.2%), algae (5.6%), fish (1.8%), and macroinvertebrates and microinvertebrates grouped together (1.5%). Patterns of similarity among the species were constructed utilizing Detrended Correspondence Analysis (DCA) with removal of the arch effect and tested by analysis of variance (unifactorial ANOVA), showing that there was no significant variation in the composition of food resources utilized by the species during the dry and rainy seasons. The main resources consumed by the ten species were classified into three trophic categories: omnivores, detritivores and insectivores. Interspecies food overlap revealed indices of 0.059 to 0.961, showing it to be independent of the period studied, since the resources utilized were similar, both in qualitative and quantitative terms. Intraspecies food overlap in the different periods was minimal for *A. altiparanae* (0.662) and maximal for *S. insculpta* (1.0). The species studied showed little variation in relative length of intestine, with the exception of *S. insculpta* which had an elevated intestinal index. The variations in food resources utilized between the periods were of little relevance, indicating that the temporal factor did not influence the resources utilized by the species studied. Of the ten species studied, nine could be viewed as generalists, considering the food resources utilized during the two periods, and only *S. insculpta* behaved as a specialist.

Key words: Freshwater Fishes, feeding habits, food overlap.

ECOLOGIA TRÓFICA DE PEIXES DO RIO DOS VEADOS (ALTO RIO PARANAPANEMA, SP) DURANTE AS ESTAÇÕES SECA E CHUVOSA

RESUMO: Este estudo teve por objetivo avaliar a ecologia trófica das principais espécies de peixes (*Astyanax altiparanae*, *A. fasciatus*, *Bryconamericus stramineus*, *B. iheringii*, *Cheirodon stenodon*, *Characidium fasciatum*, *Geophagus brasiliensis*, *Hyphessobrycon anisitsi*, *Piabina argentea* e *Steindachnerina insculpta*) capturadas na região litorânea do rio dos Veados (23°16'80''S/48°38'67''W), afluente do rio Paranapanema, SP. As coletas foram realizadas mensalmente com uma rede de arrasto do tipo "pícaré" de 5,0mm de malha, entre agosto de 1996 e dezembro de 1997, sendo o período subdividido em dois; seco (abril/setembro) e chuvoso (outubro/março). Os conteúdos alimentares foram analisados através do método volumétrico e a sobreposição alimentar determinada pelo índice de Morisita-Horn. As dez espécies de peixes consumiram diferentes fontes alimentares, destacando-se em abundância (percentual do volume) os recursos detrito/sedimento (30,0%), insetos aquáticos (23,4%), microcrustáceos (17,6%), insetos terrestres (13,9%), vegetais superiores (6,2%), algas (5,6%), peixes (1,8%), macroinvertebrados e microinvertebrados agrupados (1,5%). Os padrões de similaridade entre as espécies foram sintetizados utilizando a análise de correspondência com remoção do efeito do arco (DCA) e testados através da análise de variância (ANOVA unifatorial), verificando-se que não houve variação significativa na composição dos recursos alimentares utilizados pelas espécies durante os períodos seco e chuvoso. Os principais recursos consumidos pelas dez espécies permitiram a organização destas em três categorias tróficas: onívoras, detritívoras e insetívoras. A sobreposição alimentar interespecífica revelou índices que variaram de 0,059 a 0,961, mostrando-se independente dos períodos, pois os recursos utilizados foram semelhantes, em termos quali-quantitativos. A sobreposição alimentar intraespecífica, nos diferentes períodos, foi mínima para *A. altiparanae* (0,662) e máxima para *S. insculpta* (1,0). As espécies analisadas mostraram pequenas variações no comprimento

relativo do intestino, com exceção de *S. insculpta* que apresentou um elevado índice intestinal. As variações nos recursos alimentares utilizados, entre os períodos, foram pouco relevantes, indicando que o fator temporal não influenciou nos recursos utilizados pelas espécies estudadas. Das dez espécies de peixes estudadas nove puderam ser enquadradas como generalistas, considerando os recursos alimentares utilizados durante todo o período e apenas *S. insculpta* se comportou como especialista.

Palavras-chave: Peixes de água doce, hábito alimentar, sobreposição alimentar.

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INTRODUCTION

Qualitative and quantitative alterations in the availability of food for aquatic organisms are caused principally by the hydrologic regimen (Junk 1980; Lolis & Andrian 1996). Therefore, changes in the environment tend to modify considerably the diet of fish (Silva, 2002). The diets of some species could vary seasonally in continental aquatic environments. Various authors have demonstrated the importance of seasonal differences in the diet of freshwater fish, including Esteves & Galetti (1995), Castillo-Rivera & Kobelkowsky (1996), Fugi (1998), Gaspar da Luz & Okada (1999), Aranha *et al.* (2000), Hahn *et al.* (2000), Hörppila *et al.* (2000), and Esteves & Pinto Lobo (2001).

Alterations in the physical-chemical and biological attributes of bodies of water, derived from dams, cause numerous modifications in biotic interactions in the aquatic ecosystem (Agostinho & Zalewski 1995; Araújo-Lima *et al.* 1995). In altered environments, some species of fish find favorable conditions for proliferation, while others tend to become locally extinct (Hahn *et al.*, 1998).

The consumption of a specific type of food for some species of specialist fish is a known fact, but changes could occur in tropical environments (Lowe-McConnell, 1999). These variations in diet can be associated with growth, age and morphology of the species, and therefore in most cases changes are accompanied by ontogenetic changes in the digestive tract (Nikolsky, 1963; Godoy, 1975; Zaret, 1980; Fugi *et al.*, 1996). For example, the size of the intestine is strictly related to the nature of the food ingested, where it is shorter in omnivores and carnivores and longer in herbivores and detritivores (Lagler *et al.*, 1977; Odum 1988).

Food relationships among species vary greatly from one place to another, due not only to lack of specialization, but also to the large diversity of environmental conditions (Larkin, 1956). Therefore, in studies covering the trophic relationships of fish communities, it is important to take into account the characteristics of the environment, which can influence availability of food resources (Uieda, 1995).

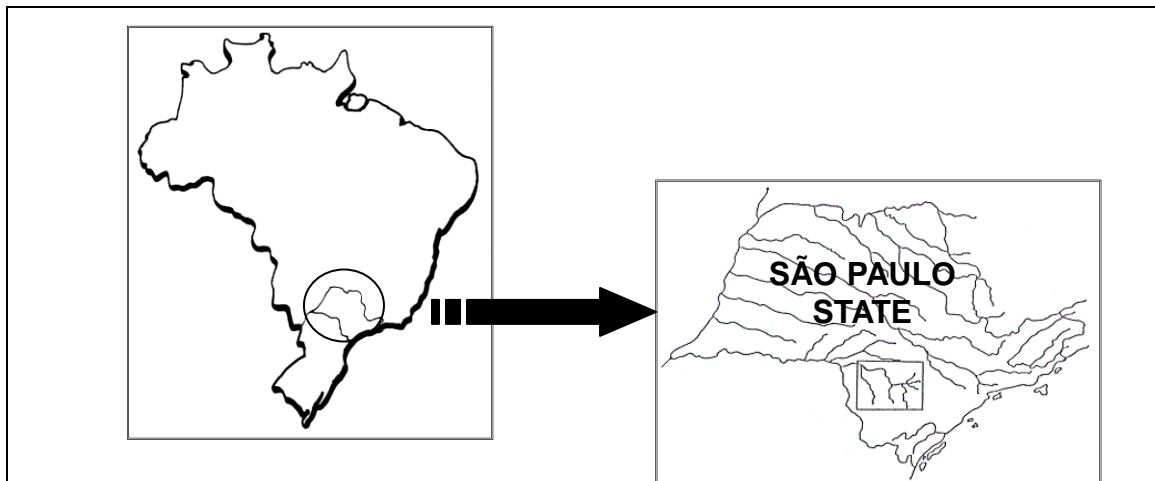
The Rio dos Veados, characterized as a semi-lotic environment created by the damming of the Rio Paranapanema, has been studied by Castro *et al.* (2003) who registered the presence of 27 species. Nevertheless, few species were shown to be abundant, whereby the large majority were found to be in small numbers, such as those we proposed to study to understand as part of the trophic ecology of the Rio dos Veados.

This study, characterizing the littoral zone of the Rio dos Veados, was conducted as a proposal to investigate the possible variations in the utilization of food resources by the main species of fish during two periods (dry and rainy) and to determine whether or not sympatric species of fish utilize the same food resources.

MATERIAL AND METHODS

Area of Stud

Collections of fish were performed in a stretch of mouth of the Rio dos Veados ($23^{\circ}16'80''\text{S}/48^{\circ}38'67''\text{W}$), part of the Rio Paranapanema (Figure 1), the principal tributary of the Jurumirim Reservoir (Upper Rio Paranapanema, SP), in the locality known as “Recanto dos Cambarás” (municipality of Itatinga/SP). According to Caramaschi (1986), the region is formed by heterogeneous relief with elevated points and encircles a sandy-basalt slope which divides the waters between the Rio Tietê and Rio Paranapanema. The river studied is born in the formation of the “Cuesta” of Botucatu inside the Environmental Protection Area of Botucatu, SP (APA - Botucatu).



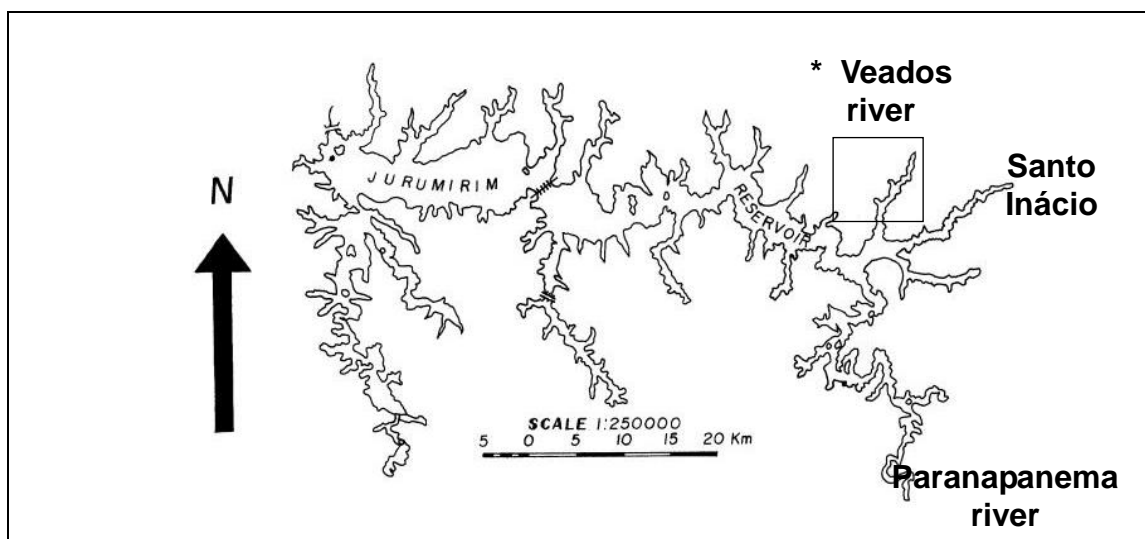


FIGURE 1. Location of the Veados river (*Stretch indicated).

The littoral area of the Rio dos Veados has a gradually sloping shoreline and a depth varying up to 1.5 m. The sediment is sandy or muddy, and in some locations mixed. The vegetation along the banks is comprised of various plant species. Some are typical of forest enclaves and flooded regions, such as the families Cyperaceae (*Fimbrisytilis diphylla*), Poaceae and Xyridaceae (*Xyris* sp). Others are plants completely submersed such as of the family Haloraceae (*Myriophyllum brasiliense* Camb.), and large number of grasses are found often totally or partially covered by water (Castro *et al.*, 2003).

Collection of biological material

Collections were performed monthly in the Rio dos Veados from August, 1996 to December, 1997, whereby this time interval was subdivided into the dry season, from April to September, and the rainy season, from October to March, following the criteria of determination proposed by Nimer (1979). The fish were captured utilizing a seine trawling net, which was 10m in length with a height of 1.5 m and had a mesh size of 5.0 mm. It was operated in the littoral region of the river using two consecutive trawlings. The material collected was duly identified with respect to number of sample, location and date of collection. After this procedure, all the material was fixed in 10% formalin buffered with CaCO_3 and kept in 70% ethanol.

Handling of biological material

To identify the food resources utilized by the ten main species of fish (those which were in greatest abundance in terms of number of individuals, totaling 91.16% of all specimens captured). The species examined were, *Astyanax altiparanae* Garutti & Britski, 2000, *Astyanax fasciatus* (Cuvier, 1819), *Bryconamericus stramineus* Eigenmann, 1908, *Bryconamericus iheringi* (Boulenger, 1887), *Cheirodon stenodon* Eigenmann, 1915, *Characidium fasciatum* Reinhardt, 1866, *Geophagus brasiliensis* (Quoy & Gaimard, 1824), *Hyphessobrycon anisitsi* (Eigenmann, 1907), *Piabina argentea* Reinhardt, 1867, *Steindachnerina insculpta* (Fernández-Yépez, 1948).

The specimens of fish were opened by evisceration and the stomach was removed. The relation between intestine length and diet for the species was determined for each individual. The length of the intestine was measured from the entrance to the small intestine (pylorus) to the anus, after removing all of the mesentery and then extending it to eliminate the curves. The intestinal index (Ii) was calculated according to the expression $Ii = ctd/Cp$, where ctd is the intestine length and Cp is the length of the animal.

The food content was placed in a Petri dish and examined under a stereomicroscope or light microscope.

Analysis of Data

The content of each stomach was analyzed, obtaining the volume of each food item by compressing the material with a glass slide on a millimeter-ruled plate to an established height (1.0 mm), whereby the result was converted to milliliters.

The food items were grouped into broad categories, designated as food resources. Basically, these consisted of: algae (filamentous and unicellular of different groups); microcrustaceans (copepods, cladocera, ostracods, etc.); aquatic insects (juvenile phases of diptera, ephemeroptera, tricoptera, odonata, plecoptera, hemiptera, etc.); terrestrial insects (hymenoptera, diptera, coleoptera, orthoptera, homoptera, unidentified fragments of adult insects, etc.); higher plants (fruits, seeds and leaves of higher terrestrial plants); macroinvertebrates (arachnids, nematodes, ticks, etc.); microinvertebrates (rotifers, rhizopoda, etc.); fish (scales, parts of the muscles and fin rays); detritus/sediment (amorphous, particular organic material in different stages of decomposition and with

mineral particles).

The species were classified into trophic categories according to the predominant food resource, considering the values equal to or greater than 50% in the food spectrum of each species.

The pattern of food overlap based on the composition of the resources utilized by the species was analyzed employing the index described by Morisita (1959) (modified by Horn, 1966). The coefficient varied from 0, when the food categories are completely distinct, to 1, when the diets showed the same composition proportional to their items. Based on the criteria adopted by Zaret & Rand (1971) and Esteves & Galetti (1995), only a value greater than 0.60 was considered a significant indicator of an elevated degree of overlap among diets of the species.

Patterns in the use of food resources by the species studied were identified from the volume of food resources consumed by each species, weighing the resources of low abundance (Sheldon & Meffe, 1993), by Detrended Correspondence Analysis (DCA), with the removal of the arch effect (Hill & Gauch 1980; Gauch, 1986; Jongman *et al.*, 1995). This analysis was performed using the PC-ORD program (McCune & Mefford, 1999). The hypothesis that the dry and rainy periods produce an effect on trophic patterns was tested by analysis of variance (unifactorial ANOVA) applied to the scores of the two primary axes of the DCA, with the dry season and rainy season as independent factors.

RESULTS

Twenty-six species of fish were registered, and found to belong to five orders, nine families and 20 genera. The ten species most abundant represented 91.16% of the total number collected (Castro *et al.*, 2003). These species were arranged in decreasing order of numerical abundance; *Bryconamericus stramineus* (20.92%), *Cheirodon stenodon* (16.31%), *Hyphessobrycon anisitsi* (15.84%), *B. iheringii* (9.29%), *Piabina argentea* (7.52%), *Geophagus brasiliensis* (6.50%), *Characidium fasciatum* (4.19%), *Astyanax altiparanae* (3.81%), *Steindachnerina insculpta* (3.65%), and *A. fasciatus* (3.13%).

Composition of Food Resources Utilized by the Ten Species

A total of 577 specimens of fish were studied, whereby the stomachs of 556

specimens (96.36%) contained food. There was a larger percentage of individuals (2.08%) with empty stomachs during the rainy season than during the dry season (1.56%).

An analysis of the abundance of resources utilized by the ten species of fish, during the two periods, revealed that the most widely consumed was detritus/sediment (30.0% of the total volume). Other less consumed items included aquatic insects (23.4%; comprised mainly of immature stages of ephemeroptera, diptera and tricoptera), microcrustaceans (17.6%), terrestrial insects (13.9%; hymenoptera, coleoptera and diptera), higher plants (6.2%), algae (5.6%), fish items (1.8%; including scales, parts of tissues and rays), and other items comprising 1.5% of the total volume consumed (Figure 2).

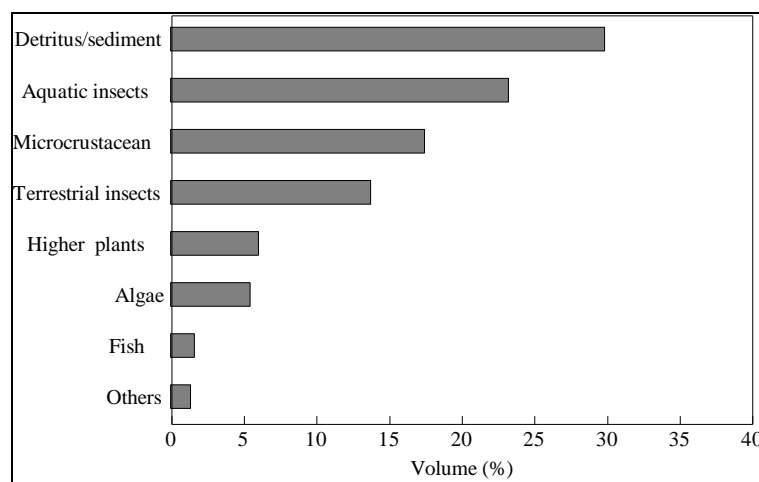


FIGURE 2. Total abundance (% volume) of the food items consumed by ten species of fish captured in the Rio dos Veados, during the period of August, 1996 to December, 1997.

The findings on the temporal variation (dry season and rainy season) of the food resources consumed by the ten species are summarized in Table 1.

TABLE 1. Percentage of abundance (volume) of food resources exploited by 10 species of fish in the Rio dos Veados. Abbreviations: Acr – acronym; Ds – dry season; Rs – rainy season; N - number de stomachs analyzed; Al – algae; Mc – microcrustaceans; Ai – aquatic insects; Ti – terrestrial insects; Hp – higher plants; Ma – macroinvertebrates; Mi – microinvertebrates; Fi – fish and Ds – detritus/sediment.

Species	Acr	CP(mm)	N		Al		Mc		Ai		Ti		Hp		Ma		Mi		Fi		Ds	
			Min-max	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds	Rs	Ds
<i>Astyanax altiparanae</i>	Aal	19,0-55,0	15	23	0,4	14,8	-	8,6	23,8	32,5	57,1	18,1	5,9	5,1	0,4	0,5	-	-	9,5	7,2	2,9	13,2
<i>Astyanax fasciatus</i>	Afa	19,5-50,0	20	29	0,3	1,8	13,1	4,1	27,5	7,6	51,8	40,8	2,0	39,3	0,3	0,2	-	-	0,3	0,5	4,6	5,8
<i>Bryconamericus iheringii</i>	Bih	25,5-48,0	36	42	0,8	6,0	9,2	15,0	6,4	11,2	6,6	7,2	2,4	4,8	1,2	0,1	-	-	-	4,9	73,5	50,9
<i>Bryconamericus stramineus</i>	Bst	22,0-59,5	22	37	3,1	0,4	54,3	51,8	14,8	13,5	21,8	26,3	3,6	2,2	-	0,1	-	-	-	1,7	2,3	3,9
<i>Characidium fasciatum</i>	Cfa	24,0-60,0	30	24	0,3	0,5	1,8	1,6	79,6	83,3	3,3	5,3	4,9	0,9	1,8	1,4	-	-	1,2	0,5	7,0	6,6
<i>Cheirodon stenodon</i>	Cst	16,0-38,0	29	43	21,6	18,3	32,7	32,6	7,9	16,3	2,3	5,5	5,0	5,5	3,2	3,2	1,3	1,1	0,3	-	25,8	17,5
<i>Geophagus brasiliensis</i>	Gbr	16,0-88,0	25	33	0,2	0,1	3,5	1,0	49,0	65,8	23,1	4,3	6,7	3,0	1,7	4,1	0,2	2,4	1,2	1,0	14,2	18,2
<i>Hyphessobrycon anisitsi</i>	Han	36,0-48,0	41	26	6,1	8,2	30,6	25,4	17,8	9,6	10,8	12,8	4,6	8,5	0,3	-	-	-	-	0,4	29,9	35,3
<i>Piabina argentea</i>	Par	25,0-39,0	22	20	1,2	5,3	24,8	24,3	21,1	16,6	13,6	13,2	13,0	6,2	0,3	0,2	0,3	-	1,5	7,3	24,1	26,9
<i>Steindachnerina insculpta</i>	Sin	25,0-74,0	26	13	1,2	1,6	-	-	0,3	0,3	-	-	0,2	-	-	0,3	-	-	-	-	98,3	97,7

A. altiparanae consumed terrestrial (57.1%) and aquatic (23.8%) insects, which represented 80.9% of the food volume during the dry season. On the contrary, in the rainy season, there was decrease in the consumption of terrestrial insects (18.1%) and an increase in the amount of aquatic insects (32.5%), and these items were important because they represented 50.6% of the total volume. In addition, the algal item was shown to be considerably increased between the dry and rainy periods, with values changing from 0.4% to 14.8%, respectively.

Astyanax fasciatus had a diet composed of terrestrial and aquatic insects, totaling 79% of the volume in the dry season. During the rainy season, there was slight drop in the consumption of terrestrial insects, while the contribution of higher plants showed in general a marked elevation (40.8%).

Bryconamericus iheringii utilized detritus/sediment during both dry and rainy periods, at 73.5% and 50.9%, respectively. Besides this item, microcrustaceans (9.2%), aquatic insects (6.4%) and terrestrial insects (6.6%) were also consumed in the dry season. Microcrustaceans and aquatic insects together represented 26.2% of the total volume consumed by this species in the rainy season.

The microcrustacean item was the main one for *B. stramineus* during both periods, with values greater than 50.0%. This item was also important for *C. stenodon*, representing 32.7% and 32.6% in the dry and rainy periods, respectively. This species also consumed high volumes of algae and detritus/sediment in the dry season, making a total of 47.7%.

Piabina argentea utilized microcrustaceans in a manner similar to that of *B. stramineus*, but consumed greater proportions of detritus/sediment, 24.1% in the dry season and 26.9% in the rainy season. The detritus/sediment item was important for the species *H. anisitsi* in the rainy season. However, in the dry season, the item that predominated was microcrustaceans, with 30.6% of the volume consumed by this species.

Characidium fasciatum and *Geophagus brasiliensis*, during the dry and rainy periods consumed primarily aquatic insects, at 79.6% and 49.0%, respectively. In the dry season, terrestrial insects were also very important for *G. brasiliensis*, corresponding to 23.1% of the total volume.

The stomachs of *S. insculpta* contained an elevated abundance of detritus/sediment during both periods, with values of 98.3% (dry) and 97.7% (rainy). The other items were of limited importance in the diet of this species.

The resources utilized by *H. anisitsi* constituted mainly microcrustaceans (30.6%) and detritus/sediment (29.9%) in the dry season, with an increased consumption of the latter item (35.3%) during the rainy season and a slight diminution of microcrustacean consumption (25.4%).

Food overlap

The values calculated for interspecies food overlap were in general elevated (>0.60 according to Morisita-Horn) between the two periods (Table 2).

In the dry season, the food items responsible for the greater overlap among the species were aquatic and terrestrial insects (*A. altiparanae/A. fasciatus*), detritus/sediment (*B. iheringii/S. insculpta*), and microcrustaceans (*C. stenodon/H. anisitsi*). Elevated indices of food overlap during the rainy season were shown between the species *G. brasiliensis* and *C. fasciatum* (0.961), which both consumed aquatic insects at the same time in large quantities. In comparing *P. argentea* and *H. anisitsi*, the index was 0.957, and 0.921 for *H. anisitsi* and *B. iheringii*, with all of these species consuming mainly detritus/sediment in the rainy period (Table 2).

TABLE 2. Index of interspecies feed overlapping (Morisita-Horn) calculated from the volume of food resources obtained in the dry and rainy seasons. The values >0.60 (bold) were considered significant. The acronyms are found in Table 1.

	Aal	Afa	Bih	Bst	Cfa	Cst	Gbr	Han	Par	Sin
D R Y ↓	Aal	0,506	0,576	0,523	0,652	0,725	0,750	0,661	0,789	0,230
	Afa	0,958		0,292	0,434	0,179	0,311	0,224	0,446	0,452
	Bih	0,159	0,213		0,402	0,266	0,680	0,444	0,921	0,852
	Bst	0,427	0,621	0,199		0,259	0,762	0,273	0,662	0,719
	Cfa	0,413	0,483	0,179	0,274		0,347	0,961	0,247	0,377
	Cst	0,138	0,303	0,582	0,699	0,209		0,439	0,864	0,886
	Gbr	0,721	0,782	0,355	0,430	0,856	0,350		0,394	0,512
	Han	0,367	0,536	0,679	0,756	0,398	0,904	0,610		0,956
	Par	0,483	0,620	0,596	0,727	0,475	0,801	0,718	0,957	
	Sin	0,044	0,069	0,949	0,036	0,089	0,428	0,220	0,493	0,409

RAINY →

The intraspecies overlap of diet was increased for all the species between the periods. The lowest index (0.662) was shown in *A. altiparanae*, while the highest (1.0) was obtained for *S. insculpta* (Figure 3).

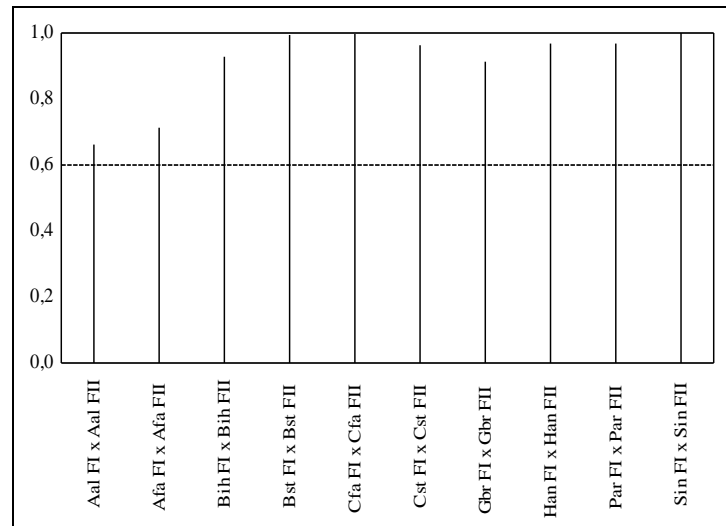


FIGURE 3. Index of interspecies feed overlapping (Morisita-Horn) between the dry season (F I) and the rainy season (F II). Aal – *A. altiparanae*, Afa – *A. fasciatus*, Bih – *B. iheringii*, Bst – *B. stramineus*, Cfa – *C. fasciatus*, Cst – *C. stenodon*, Gbr – *G. brasiliensis*, Han – *H. anisitsi*, Par – *P. argentea*, Sin – *S. insculpta*.

Intestinal index

The intestines of the all species studied showed similar indices, except for *S. insculpta*. In this species, the intestine was very long and thin, and occupied a large part of the abdominal cavity, arranged in circumvoluted manner. The mean intestinal index for *S. insculpta* was 11.8. In contrast, *C. fasciatus* exhibited the lowest intestinal index ($Ii = 0.45$) (Table 3).

TABLE 3. Mean values of the intestinal index, with the relationship between length of intestine (li) and the standard length (sl), number of individuals and trophic category of the species of fish studied.

Species	Acronyms	Number	li/sl	Trophic category
<i>Astyanax altiparanae</i>	Aal	38	0,70	Insectivores
<i>Astyanax fasciatus</i>	Afa	49	0,65	Insectivores
<i>Bryconamericus iheringii</i>	Bih	78	0,54	Detritivores
<i>Bryconamericus stramineus</i>	Bst	59	0,58	Omnivores
<i>Characidium fasciatus</i>	Cfa	54	0,45	Insectivores
<i>Cheirodon stenodon</i>	Cst	72	0,62	Omnivores
<i>Geophagus brasiliensis</i>	Gbr	58	0,78	Insectivores
<i>Hyphessobrycon anisitsi</i>	Han	67	0,70	Omnivores
<i>Piabina argentea</i>	Par	42	0,61	Omnivores
<i>Steindachnerina insculpta</i>	Sin	39	11,8	Detritivores

Trophic structure of species

The order of the species de fish, based on the food resources consumed along axis 1 of the DCA (eigenvalue 0.388), showed that the species with more specialized diets had

scores with extreme values. This resulted in a gradient among generalists, which had intermediate scores, and specialists (detritivores and insectivores) which were located respectively to the right and to the left in Fig. 4. Meanwhile, the variations in the positioning of the scores along the first axis of the DCA (Fig. 4b) were not significantly different when comparing the dry and rainy periods (unifactorial ANOVA; $F = 0.0264$, $p > 0.05$).

The findings shown in Figure 4 a-b allowed the identification of at least three trophic categories among the species: 1) detritivores, 2) insectivores and 3) omnivores.

The scores of food resources and the species, along the first axis of the DCA, shows that the highest correspond to the items detritus/sediment, algae and microcrustaceans. The species *S. inscupta* and *B. iheringii* tended to consume detritus/sediment, being essentially detritivores in both periods. On the other hand, the species *A. fasciatus*, *C. fasciatum* and *G. brasiliensis* (species with scores less than 40) consumed basically aquatic insects, terrestrial insects and higher plants, placing them in the trophic category of insectivores.

The species *B. stramineus*, *P. argentea*, *H. anisitsi* and *C. stenodon* exhibited intermediate scores for food resources, occupying a central region in Fig. 4a. These species consumed a variety of resources, including algae, microcrustaceans, micro- and macroinvertebrates, and fish, which would classify them as omnivores with a tendency toward being insectivores and detritivores. Significant changes were seen in the resources consumed by *A. altiparanae* and *B. iheringii* during the periods studied. *A. altiparanae*, in the dry season, consumed increased proportions of terrestrial insects, and were thus insectivores in this period. However, during the rainy season, this species resorted to other food resources as well, demonstrating a tendency toward being omnivores. *B. iheringii*, consumed in the dry season more detritus/sediment, and in the rainy season more algae and microcrustaceans, tending to be also omnivores, which could be reinforced by the distances observed for the species between the periods.

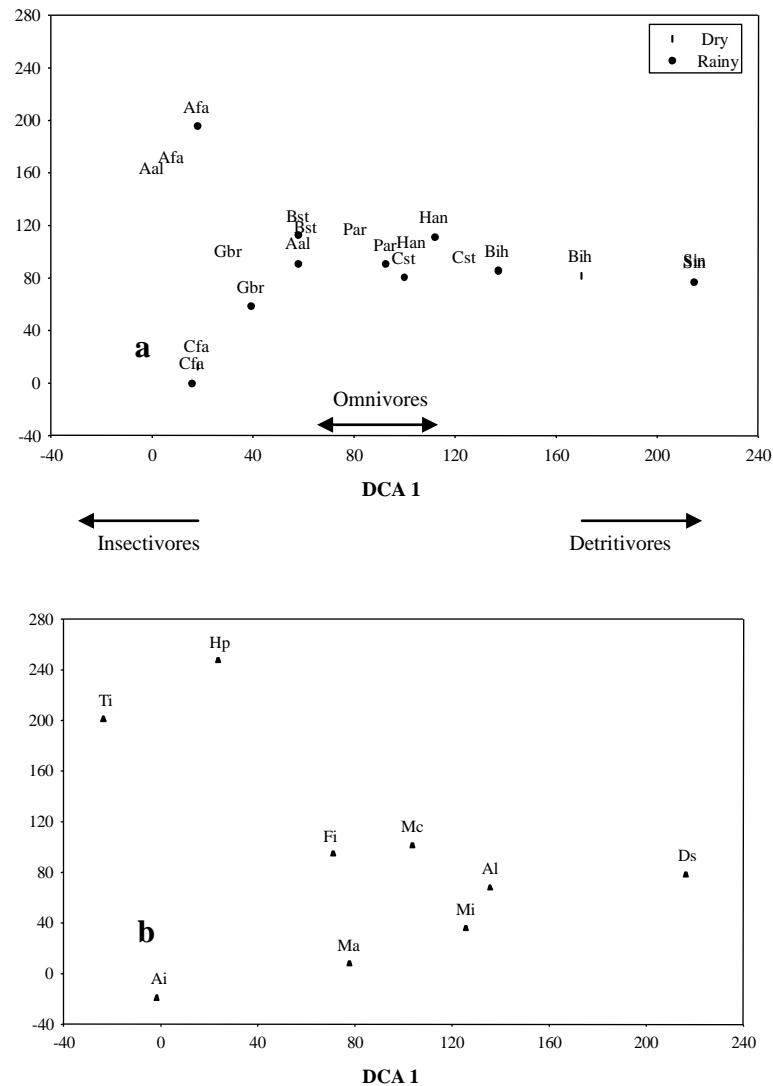


FIGURE 4. Scores derived from correspondence analysis, with removal of the arch effect (DCA), considering the species (A) and the food items (B), in the dry and rainy seasons. Abbreviations: Ti – terrestrial insects, Ai – insects aquatic, Hp – higher plants, Fi – fish, Mc – microcrustaceans, Ma – macroinvertebrates, Mi – microinvertebrates, Al – algae and Ds – detritus/sediment.

DISCUSSION

The species of fish studied were small in size, some typically found in streams (such as the species *P. argentea*, *C. fasciatus* and *C. stenodon*). Two species of the genus *Astyanax*, *A. altiparanae* and *A. fasciatus*, two of the genus *Bryconamericus*, *B. iheringii* and *B. stramineus*, and *G. brasiliensis*, *S. insculpta* and *H. anisitsi* are widely distributed in various types of environments (in streams, reservoirs, lakes and rivers), as demonstrated in the basin of the Rio Tibagi by Shibatta *et al.* (2002), and in other rivers, streams and lakes in the Rio Paraná basin by Agostinho *et al.* (1997). Pavanelii & Caramaschi (1997) registered seven of these species as common to two streams of the Rio Paranapanema basin.

According to Wellcome (1985), Lowe-McConnell (1999) and Fernando & Hölcík (1991), species adapted to the lacustral and preexisting conditions of the river are the ones that tend to make up the species of a reservoir. The Rio dos Veados, in the stretch studied, has become a transition area between the old river and the Jurumirim Reservoir, in which the main species present are those that probably lived in the area prior to changes caused by the reservoir. Agostinho (1992), Lowe-McConnell (1999) and Carvalho & Silva (1999) noted that in the formation of a reservoir, there is a proliferation of species of small size, which have a high reproductive potential, short life span and high food flexibility.

The increased abundance of the species of small-sized fish shown in the present study differs from that reported in reservoirs, because of the method of capture, which was with a trawling net. However, larger-sized species have been collected as shown by Castro *et al.* (2003), in which specimens were obtained of the species studied in the present work. In studies of the Rio Paranapanema at the Rosana Reservoir, Casatti *et al.* (2003) utilized strainers to capture fish from the shoreline associated with banks of macrophytes, and captured twenty species, of which the most abundant were small-sized species.

The main food resources utilized by these species were detritus/sediment and aquatic insects, representing more than 50.0% of the total volume. Despite the predominance of the two categories of food described above, the ten species demonstrated a large flexibility and broad spectrum of food categories, consuming from rotifers and small microcrustaceans up to higher plants and fish. The consumption of algae, aquatic insects and detritus/sediment by all of the species studied during the two periods, could have resulted from an elevated abundance of these items in the environment. Alternatively, the small size of these food items would have facilitated their capture by small-sized species, especially the detritus/sediment category, which represented a substantial volume of the total consumed for almost all the species. Another explanation for the presence of these food resources in fish content stomachs is that it is purely coincidental, or indirectly linked to the form of capture of other resources near the bottom with the sediment. Nonetheless, the curimatids and prochilodontids utilize these resources essentially as their main food (Hahn *et al.*, 1997). Bowen (1983) and Lowe-McConnell (1999) considered the species of these two groups as the most specialized in tropical environments, which utilize these food sources directly, while in temperate regions these sources are utilized indirectly by invertebrates. In fact, *S. insculpta*, belonging to the curimatids, was the only species with specialist behavior utilizing detritus/sediment among the ten species studied in the Rio dos Veados.

Confirming the specialist behavior of *S. insculpta*, the intestinal index was much greater than for the other species studied. Ribble & Smith (1983) showed that the intestinal length is an adaptive factor in the food ecology of fish. Fugi *et al.* (1996) reported greater intestinal length values with food that was difficult to digest, including detritus, higher plants and organic material. Fryer & Iles (1972) noted that the degree of intestine development is related to the trophic status of the species.

The main foods (aquatic insects and detritus/sediment) utilized by the species studied represent abundant resource in environments of reservoirs and streams also. In regard to reservoirs, the trophic structure varies greatly when considering the number of individuals or biomass of the species that comprise these environments, mainly when they are included as the predominant species, because they represent the ichthyophagous species. In one of the principal studies conducted on Brazilian reservoirs, Araújo-Lima *et al.* (1995) noted detritus and insects as the main resources in shallow stretches of the river. Arcifa & Meschiatti (1993) showed that in environments with these characteristics these two resources predominate. However, in the littoral zone of the Rio Tibagi, considered an area of transition between the river and the Capivara Reservoir, Bennemann *et al.* (2000) also reported insects and detritus as being important resources for the diet of fish, although they were not the most abundant. The differences determined are probably due to species that were examined, which in the case of the Rio Tibagi, the majority was medium to large-sized and the fish category was shown to be of greatest abundance. In an environment similar to the one in this study, Casatti *et al.* (2003) found insects, algae and microcrustaceans among the main food consumed by the species of small size, which live along the banks of macrophytes along the edges of the Rosana Reservoir.

In tropical environments, the studies of food overlap vary greatly and are very heterogeneous, mainly with regard to the environment and which species are studied (Lowe-McConnell, 1991). The values for interspecies food overlap in the Rio dos Veados were elevated in both the dry and rainy seasons, where the highest index observed in the dry period occurred between *A. altiparanae* and *A. fasciatus*, and in the rainy period between *G. brasiliensis* and *C. fasciatum*. During the dry season, the foods responsible were terrestrial insects, and aquatic insects in the rainy period. The behavior of species of the genus *Astyanax* corresponds to what Gerking (1994) describes as the switching from one food source to another that is more advantageous, which occurs in opportunistic species in a given period of time. This could have been the case with terrestrial insects, which were possibly in abundance in that phase. The opportunistic behavior of species

included in the genus *Astyanax* is well known from studies reported in the literature, such as Arcifa *et al.* (1992), Esteves (1996), Vilella *et al.* (2002).

Another explanation for the high overlap values in the two periods is that the majority of the diet items during that time for the species studied, except for specialist *S. insculpta*, was of autochthonous origin, although each one utilized distinct proportions whereby the principal food was on or more of these items. This could be explained by the little variation in resources over time in this environment in the stretch of the Rio dos Veados studied, characterized by having limited areas with large quantities of submersed grassed and macrophytes, where insects, algae and microcrustaceans are in abundance. Still, food overlap could be minimized by spatial distribution, as demonstrated by Castro *et al.* (2003) with the same species in this study.

The results of intraspecies food overlap were high and independent of period, since the resources utilized were similar, in qualitative and quantitative terms. Despite that the conditions, specific and/or imposed by the environment, varied between the dry and rainy periods, the species did not change their trophic conditions seasonally, suggesting that the environment has a certain degree of stability with respect to available resources.

There have been reports of distinct tendencies of food overlap in other types of environments. Meschiatti (1995) observed greater overlap in the dry season, when analyzing 29 species of a marginal lake of the Rio Mogi Guaçu. Goulding (1980) noted that in rivers, as well known in Amazonia, there is greater food overlap during the rainy season, when there is a greater abundance of resources. Esteves & Galetti (1995) studied the fish of a lake in the Rio Paraná basin and found high overlap values among omnivorous species in the rainy period and among herbivores in the dry period.

Trophic structure appeared to be related to species adapting perfectly to lacustral conditions and having great flexibility in their food strategies. Among the ten species, nine were characterized as generalists, which reinforces the preceding idea that trophic structure is based on species adapted to lacustral life. In the littoral area studied in the Rio dos Veados, there is an area of transition between the river and the reservoir, where species characterized as small in size are established. These species of fish have advantages with regard to the utilization of types of food resources, which also appear to be well established and abundant, and associated with aquatic vegetation. Also related to the observed predominance of small-sized species is that among the specimens analyzed, there were very few without any contents in their digestive tract. This behavior is characteristic of small-sized species, because they eat all the time, as shown by Oricolli & Bennemann (in

preparation) and demonstrated in the results reported by Casatti *et al.* (2003). The generalist behavior of these species of fish supports the hypothesis of utilization of the same food resources. Some ecologic aspects were not determined, such as availability of food resources in the environment and the period of greatest activity of the species studied. However, it is suggested that species of small size have an advantage in seeking the same food and are successful in the transition environment because they are in some way abundant all the time, which minimizes the competition from large-sized species which live in large areas of reservoirs.

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