Trophic structure of a fish community in Bananal stream subbasin in Brasília National Park, Cerrado biome (Brazilian Savanna), DF

Mariana Schneider1, Pedro De Podestà Uchôa de Aquino1, Maria Júlia Martins Silva1 and Claudia Padovesi Fonseca2

The aim of this study was to determine the trophic structure of the fish community in the Bananal stream subbasin, which belongs to a well-preserved Cerrado area (Brazilian Savanna) in Brasília National Park, Brazil. We also evaluated the influence of environmental variations in the diet of fish species. Four samples were taken in each 30 m long established transect, two in the rainy season and two in the dry season. A total of 1,050 stomachs of the 13 most abundant species were analyzed. A total of 36 food items were consumed, where 24 were autochthonous, 8 allochthonous, and 4 of undetermined origin. Non-metric multidimensional scaling (NMDS) analysis, in addition to the results of frequency of occurrence and abundance charts, was used to determine four groups of feeding guilds: detritivores, omnivores (tending toward herbivory and invertivory), invertivores and piscivores. Around 69% of the volume of resources consumed was allochthonous, which proves the importance of the resources provided by riparian vegetation. The contribution of autochthonous and allochthonous items in the diet differed due to seasonality for Aspidoras fuscoguttatus, Astyanax sp., Characidium xantheropterum, Hyphessobrycon balbus, Kolpotocheirodon theloura, Moenkhausia sp., Phalloceros harpagos, and Rivulus pictus. Despite the Cerrado climate characteristics, there was no significant influence of season on the fish diet. The absence of seasonal variation and the predominance of allochthonous items in the fish diet are probably associated with the presence of riparian vegetation, which acts as a transition area in the Cerrado biome and provides resources for the aquatic fauna. This work shows the importance of studies in non-disturbed areas considered here as a source of information concerning the biology of fish species and as a guide for direct conservation policies on the management of aquatic resources, recovery of damaged areas and determination of priority areas for conservation.

Key words: Feeding guilds, Seasonal variation, Stream fish, Trophic ecology.

1Laboratório de Bentos, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, Campus Darcy Ribeiro, ICC norte, Asa Norte. 70.910-900 Brasília, DF, Brazil. marischneider224@gmail.com; pedropua@unb.br; mjsilva@unb.br
2Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília, Campus Darcy Ribeiro, ICC norte, Asa Norte. 70.910-900 Brasília, DF, Brazil. padovesi@unb.br
Introduction

The occurrence of fish species following patterns along environmental gradients as a result of the availability of resources may be determined starting with studies that focus on knowledge of fish feeding habits. Such studies provide a fair basis for understanding the ecological dynamics of fish populations and other aquatic organisms, besides the chance of making inferences on habitat usage, resources availability and behavioral characteristics (Hahn et al., 2004). In addition, knowledge of feeding habits also allows us to identify factors that affect the distribution and abundance of fish species (Deus & Petere-Junior, 2003).

Stream fish live together with temporal and spatial variation in their food availability (Matthews, 1998). Lowe-McConnell (1987) states that the ichthyofauna of tropical streams is affected by seasonal changes due to the expansion and contraction of their habitat. Because of local changes in water speed, bottom type, depth and vegetation, these environments assume mosaic-like patterns, greatly increasing the availability of habitats (Luiz et al., 1998). According to Melo et al. (2003), seasonal rainfall variations create and/or eliminate micro-habitats. Heavy rains cause an increase in water flow, greatly augmenting a stream’s discharge, carrying organic and inorganic materials and leading to changes in the stream’s bed configuration and in the washing out of the biota (Luiz et al., 1998).

Stream bed configuration is preserved by adjacent vegetation, which is denser in the stream head region (Ribeiro & Walter, 1998). This vegetation partially blocks light penetration, hindering autotrophic production, contributing to plant and particulate organic matter (Vannote et al., 1980). As the stream grows, the bed-derived material becomes less important, significantly magnifying autochthonous primary production (Vannote et al., 1980).

These changes along the water course are important for determining the community’s functional organization. At the stream heads, fish primarily depend on allochthonous material which derives from the surrounding vegetation (Lowe-McConnell, 1987). This material (such as leaves, branches and trunks) also affect autochthonous resources (which comes from inside the stream) creating microhabitats that bear young insect forms and other organisms as constituents of the basic autochthonous fish feeding resources (Russo et al., 2002).

Fish feeding habits represent an integration between feeding preferences and food availability and accessibility (Angermeier & Karr, 1984). Existing information on fish feeding preferences in tropical streams indicates that there is a lack of specialization or that specialization is rare and reversible (Lowe-McConnell, 1987).

The Cerrado biome (Brazilian Savanna) is home to the country’s headwaters of the main hydrological regions, such as the upper Paraná, where knowledge of the ichthyofauna of its small rivers and streams is increasing (Ferrante et al., 2001; Novaes-Pinto, 1993; Langeani et al., 2007; Langeani et al., 2009). In the last decade, intense environmental degradation of this biome, due to the introduction of exotic species, has affected the biotic and abiotic characteristics of the region’s rivers and streams (Novaes-Pinto, 1993).

The upper Paraná hydrographic region is completely within Brazilian territory, including the states of Paraná, São Paulo, Mato Grosso do Sul, Goiás, and Distrito Federal. One of the headwater regions of the upper Paraná basin is located in Brasília National Park, a subbasin of the Bananal stream. This subbasin is completely within the Park, and is a preserved area representative of a Cerrado biome.

The study of the characteristics of fish communities in well-preserved regions (streams, for example) is essential to determine the natural conditions to which each species is submitted, with the least possible anthropic interference, besides the important role such knowledge plays in the conservation of its biodiversity, management of aquatic resources, recovery of degraded areas and the determination of conservation priority areas (Agostinho et al., 2005).

Taking into account the lack of information on fish feeding habits in Cerrado streams and the influence of this biome’s peculiar environmental variations on the fish community, the present study aimed at investigating the fish trophic structure in the Bananal stream subbasin by studying their feeding habits.

Material and Methods

Study area

Distrito Federal is located in the Central Brazilian Plateau, in the center of the Cerrado biome. Its high altitude and relief characteristics favor surface water drainage, giving home to the headwaters of three main Brazilian hydrographic regions: Tocantins-Araguaia, São Francisco, and Paraná (Novaes-Pinto, 1993; Ferrante et al., 2001).

This research was conducted in the Bananal stream subbasin belonging to the upper Paraná hydrographic region and fully encompassed by Brasilia National Park (BNP). BNP embraces the Cerrado biome and corresponds to the Distrito Federal Integral Protection Conservation Unit (created by Law Act No. 241, passed on September 11, 1961, enhanced by Law No. 11,285, passed on August 3, 2006).

The Cerrado is characterized by dry winters and rainy summers (Ribeiro & Walter, 1998). In the Distrito Federal, there is greater rainfall during the summer (December to April), with some changes over the years (Nimer, 1989).

Sampling design

Fish were collected every three months at seven sites distributed along the Bananal stream subbasin, totaling four collections at each site during ten months (from October 2006 to July 2007). Rainfall corresponding to the sampling period indicates that the months of October 2006 (526.4 mm) and January 2007 (261.5 mm) had the most precipitation (rainy season), while the months of April (50.1 mm) and July (0 mm) 2007 the least precipitation (dry season).
At each site, 30 m long stretches were sampled along the headwaters and principal course of the stream. Sampling sites localization was performed according to the Strahler's hierarchical system (1957) (Table 1 and Figs. 1-2), aiming at including the whole Bananal stream subbasin. Field campaigns were sought for evaluating streams in the two seasons, with collections performed during the rainy (October 2006 and January 2007) and dry (April and July 2007) seasons.

At each sampling site, the stream’s width, depth, current speed and vegetation cover upstream, in the middle and downstream, were measured. The width and depth were measured with a tape measure (30 m) and the current speed using flow meter for liquids. The canopy cover was measured with a spherical densiometer. More details can be found in Aquino et al. (2009).

**Fish collection**

Fish collection was performed in the daytime (from 8:00 am to 18:00 pm) by applying four methods: drag net, sieve, gill net, and fish hook. The combination of different fishing techniques was necessary due to the different habitat characteristics at each site sampled. Thus, we attempted to obtain representative samples of the total ichthyofauna present at each site. Sampling methods were all used until the number of individuals at each site tended toward zero (Malabarba & Reis, 1987).

Collected fish were preserved in the field in 10% formalin solution, and after 48 h were transferred in containers with 70% alcohol (Uieda & Castro, 1999). Each sample was identified, measured and weighed.

Species identification was done using keys for specific groups, aided by specialists in each group. Voucher material was sent to the Coleção Ictiológica da Universidade de Brasília (CIUnB). Some samples were addressed to the Coleção de Peixes do Departamento de Zoologia e Botânica da Universidade Estadual Paulista, São José do Rio Preto (DZSJRP), to confirm identification.

**Diet analysis**

In the laboratory, the stomach of each sampled fish was removed and preserved in 70% ethanol. Only species with more than five full stomachs were analyzed and their contents identified by means of a stereomicroscope.

To study the diet, the stomach contents were analyzed using the volumetric method proposed by Hyslop (1980). Stomach contents were separated into food item groups, and were identified with the aid of identification keys for aquatic insect groups (Merritt & Cummins, 1996) and terrestrial invertebrates (Borror & Delong, 1969). Each separated group was evenly compressed until reaching a height between 0.5 and 1 mm, and the volume was estimated according to the height and the area occupied on a strip of millimeter paper.

**Statistical analysis**

Only the species that showed more than five individuals in total were used for statistical analysis. Comparison of the fish species with respect to diet was made using the technique known as non-metric multidimensional scaling (NMDS) analysis, based on the Bray-Curtis similarity matrix (Krebs, 1998), using the values of percentage composition of food items of all sampled individuals of each species (Hyslop, 1980). Percentage composition was based on the items’ abundance values measured in volume (cm³). For matrix calculation, data were transformed into log(x+1) as to reduce the importance of more abundant items (Field et al. 1982). NMDS acts directly on the matrix ranking the similarity measurements between the species pairs, which are considered directly proportional to the distance in metric analysis. This analysis result does not assume linear relations (Clarke, 1993). Feeding preferences of the species found in the Bananal stream subbasin were determined using Costello’s chart method (1990), modified by Amundsen et al. (1996).

To check whether or not there was variation in the species’ diet according to food origin over the seasons, recorded food items were classified into autochthonous (coming from the stream itself) and allochthonous (coming from outside the stream). The relative participation of autochthonous and allochthonous items with respect to the seasons was calculated for each fish species. Analysis was performed with a χ² test with a 2 x 2 contingency table (Zar, 1999).

Similarity analysis (ANOSIM) was carried out to check for significant variations in fish diet between the dry and rainy seasons using the same NMDS similarity matrix. The ANOSIM is a multivariate randomization procedure analogous to variance analysis (ANOVA) of a factor (Chapman & Underwood, 1999).

Similarity analysis (ANOSIM) was performed aided by the statistical program R (R Development Core Team, 2007) using the vegan packs (Oksanen et al., 2007). The ordination (NMDS) was aided by the statistical program PC-ORD (McCune & Mefford, 1999). The significance level for all analyses was 0.05.

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**Table 1.** Localization, altitude and streams order at the sampling sites (scale 1: 10.000) at the Bananal stream subbasin, Paranoá Lake basin, DF.

| Site    | Stream name          | Geographical Coordinates | Order | Altitude (m) |
|---------|----------------------|---------------------------|-------|--------------|
| 1       | Poço d’Água stream   | 15°43’58.70’S, 48°05’40.80’W | 2     | 1102         |
| 2       | Bananal stream       | 15°43’6.80’S, 48°04’9.80’W  | 2     | 1082         |
| 3       | Capão Comprido stream| 15°42’49.94’S, 47°53’6.04’W | 1     | 1089         |
| 4       | Rego stream          | 15°43’31.69’S, 47°56’24.17’W | 1     | 1052         |
| 5       | Acampamento stream   | 15°45’17.90’S, 47°58’26.07’W | 2     | 1080         |
| 6       | Acampamento stream   | 15°44’44.86’S, 47°57’1.20’W  | 3     | 1057         |
| 7       | Bananal stream       | 15°43’42.70’S, 47°54’39.44’W | 4     | 1011         |
Results

For characterization of the sites, the environmental variables were collected at each study site and are shown in Table 2. Data refer to values obtained upstream, in the middle and downstream of each site for each variable. Measurements are presented with average ± pattern deviation/shift.

In general, all sites are narrow, well fitted with high vegetation cover and with little depth and width (Fig. 2 and Table 2). Exceptions to this pattern were site 2, which is the deepest one, and site 7, which is wider and deeper since it is of the fourth order. Vegetation cover of site 6 is low, with its surrounding vegetation composed of mid- and small-sized trees and shrubs.

Concerning seasons, the rainy season and the transition from rainy to dry weather showed the highest values in width and depth. Contrarily, the transition from dry to rainy season showed lower values for the same variables. Vegetation cover remained practically unchanged over the seasons at all sites (Table 2).

The highest current speed was found in the dry season, in which the smaller water volume increases current speed in the rapids. Nevertheless, as it can be observed in Table 2 that the standard deviation was high because in this season there were sites where the water flow was practically zero, forming pools along the stream course.

Feeding guilds

A thousand and fifty stomachs were analyzed, pertaining to the 20 species found in the Bananal stream subbasin. The species number and the number of analyzed stomachs, according to each species and season, are described in Table 3. Of the 20 recorded species, only 13 had stomach content studies, because they each had more than 5 stomachs available for analysis.

In accordance with the stomach analysis of the species found in the Bananal stream subbasin, 36 types of food were consumed, of which 24 were autochthonous, 8 were allochthonous, and 4 were of unknown origin (Table 4).

The non-metric multidimensional scaling analysis of the species’ diet, irrespective of the season, showed a separation into four large groups (Fig. 3). The first two axes accounted for 86% of the data ($R^2 = 0.86$). These groups reflect similarity in species’ diet according to the dominant food items in the diet. The closer they are in the ordination, the greater the similarity is among species. Thus, the ordination revealed the
separation of the species into four trophic guilds: detritivorous, omnivorous, invertivorous and piscivorous. The omnivorous could be separated into two groups: one with greater plant matter consumption (omnivorous tending toward herbivory), and the other with greater consumption of animal fragments (omnivorous tending toward invertivory).

The gap found in the ordination is supported by the results of the food preference charts (Figs. 4-5), where group A represents the omnivorous species tending toward herbivory and the species in group B are the omnivorous tending toward invertivory.

The third guild identified was invertivorous that ate mainly invertebrates, especially aquatic ones. *Aspidoras fucoguttatus*, *Heptapterus* sp., *Kolpotocheirodon theloura*, *Rhamdia quelen*, and *Rivulus pictus* belong to this guild. *Aspidoras fucoguttatus*, even though having detritus as the most frequent and abundant food item, displayed a high frequency of Chironomidae. *Heptapterus* sp. consumed large amounts of Diptera pupae and aquatic invertebrate larvae. *Kolpotocheirodon theloura* consumed a large variety of low frequency prey. Large amounts of Chironomidae larvae and other aquatic insects were consumed by *Rivulus pictus*, a fact that qualifies this species as quasi specialist on aquatic invertebrates.

**Table 2.** Characterization of sampling sites and seasons concerning width, depth, current speed and vegetal cover in the Bananal stream subbasin, Paranoá Lake basin, DF. Sites (1 to 7) and Seasons (S-C = transition from dry to rainy, C = rainy season, C-S = transition from rainy to dry, S = dry season).

| Site | Width (cm) | Depth (cm) | Current speed (m/s) | Vegetation cover (%) |
|------|------------|------------|---------------------|----------------------|
| 1    | 131.0 ± 63.6 | 49.4 ± 28.2 | 0.31 ± 0.15 | 94.8 ± 7.8 |
| 2    | 222.5 ± 101.1 | 109.3 ± 32.1 | 0.16 ± 0.05 | 87.8 ± 24.1 |
| 3    | 122.0 ± 54.0 | 31.4 ± 16.7 | 0.09 ± 0.03 | 97.6 ± 5.2 |
| 4    | 132.8 ± 70.0 | 19.4 ± 6.5 | 0.23 ± 0.15 | 92.0 ± 6.3 |
| 5    | 114.4 ± 32.6 | 20.2 ± 10.1 | 0.01 ± 0.03 | 99.7 ± 1.2 |
| 6    | 144.3 ± 52.2 | 32.1 ± 21.1 | 0.58 ± 0.49 | 39.6 ± 20.2 |
| 7    | 386.0 ± 184.3 | 102.9 ± 25.1 | 0.54 ± 0.25 | 67.7 ± 19.1 |

**Fig. 2.** General view of sites 1 to 7 sampled at the Bananal stream subbasin, Paranoá Lake basin, DF.
Table 3. Occurrence, abundance and number of analyzed stomachs (in parentheses) of the fish species found in the seven samples sites, in each season, at the Bananal stream basin, Paranoá Lake basin, DF.

|                   | Site 1 Dry | Site 1 Rain | Site 2 Dry | Site 2 Rain | Site 3 Dry | Site 3 Rain | Site 4 Dry | Site 4 Rain | Site 5 Dry | Site 5 Rain | Site 6 Dry | Site 6 Rain | Site 7 Dry | Site 7 Rain |
|-------------------|------------|-------------|------------|-------------|------------|-------------|------------|-------------|------------|-------------|------------|-------------|------------|-------------|
| Aspidoras fuscoguttatus | 25 (25)    | 34 (33)     | 77 (27)    | 200 (40)    | 20 (19)    | 12 (11)     | 41 (34)    | 70 (39)     | 20 (20)    | 26 (26)     | 10 (10)    | 9 (8)       | 5 (5)      | 1           |
| Astyanax sp.       |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Bryconamericus stramineus | 36 (36)    |             | 54 (54)    |             |            |             |            |             |            |             |            |             |            |
| Characium gomesi   |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Characium xanthopterus | 6 (6)      |             | 1 (1)      |             |            |             |            |             |            |             |            |             |            |
| Ctenobrycon sp.    |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Erythromystax sp.  |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Haxanesia sp.      |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Hyphessobrycon balbus | 6 (5)      |             | 13 (12)    |             | 12 (12)    | 115 (35)    | 154 (41)   | 133 (37)    | 5 (4)      | 85 (20)     | 80 (40)    | 42 (34)     | 7 (6)      | 9 (5)       |
| Hypostomus sp.1    |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Hypostomus sp.2    |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Heptapterus sp.     |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Knodus moenkhassii  |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Kolpotochirodon theroula | 10 (10)    |             | 1 (1)      |             |            |             |            |             |            |             |            |             |            |
| Mecynocephalus longicolla | 4 (4)     |             | 1 (1)      |             |            |             |            |             |            |             |            |             |            |
| Moenkhassia sp.    |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Phalloceros harpagos | 1 (1)      |             | 1 (1)      |             |            |             |            |             |            |             |            |             |            |
| Planaltina myersi  |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Poecilia reticulata |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Rhamdia quelen     |            |             |            |             |            |             |            |             |            |             |            |             |            |
| Rivulus pictus     |            |             |            |             |            |             |            |             |            |             |            |             |            |

The only species that displayed piscivorous habits was *Rhamdia quelen*; however, fragments of terrestrial insects and oligochaetes were also present in its diet, representing 39.16% of the consumed total, while fish accounted for 40.24% of the composition (Table 4). Due to the fish representativeness in its diet as a unique category, against the ensemble of terrestrial insect fragments and oligochaetes, this species was classified as piscivorous.

**Allochthonous and autochthonous contributions**

Taking the fish community as a whole and considering the abundance of items, 69% of all resources consumed by the species were allochthonous. The contribution of allochthonous and autochthonous prey to the samples’ diet, according to the season (Fig. 6), was significant for *Aspidoras fuscoguttatus* ($\chi^2 = 26.3, p < 0.001$), *Astyanax* sp. ($\chi^2 = 11.8, p < 0.001$), *Characium xanthopterus* ($\chi^2 = 16.9, p < 0.001$), *Hyphessobrycon balbus* ($\chi^2 = 17.9, p < 0.001$), *Moenkhassia* sp. ($\chi^2 = 13.3, p < 0.001$), *Phalloceros harpagos* ($\chi^2 = 6.9, p < 0.001$), *Rhamdia quelen* ($\chi^2 = 139.1$ and $p < 0.001$), and *Rivulus pictus* ($\chi^2 = 7.2, p = 0.007$). As expected, four of these species (*Aspidoras fuscoguttatus*, *Kolpotochirodon theroula*, *Moenkhassia* sp., and *Phalloceros harpagos*) did not show an increase in the consumption of allochthonous material in the rainy season.

**Temporal variation**

Variation in the consumption of food items between seasons was not significant (ANOSIM, $R = -0.043$, and $p = 0.717$). No significant variation was observed in between sites (ANOSIM, $R = 0.06$, and $p = 0.364$).

**Discussion**

**Feeding guilds**

The four guilds found did not occur at all sites, and they grew when getting away from the headwater region. According to Angermeier & Karr (1984), patterns explain that increases are correlated with the increase in food availability.

Omnivorous species showed wider distributions, and those tending toward herbivory were present at all sites. Because this is the case of a well-preserved area, resources of plant origin are abundant everywhere. In this guild, a wide spectrum of food items was consumed, with low abundances and frequencies, making classification impossible in terms of the dominance of a unique food category. These characteristics indicate low selectivity and much feeding opportunism (Mazzoni & Rezende, 2003). According to Abelha et al. (2001), there are few tropical species with specialized feeding habits, the majority of which are generalists, with a certain degree of preference but using the resources available in the environment (Pereira et al., 2007).

Higher vegetation was consumed in considerable amounts, compared with other items consumed by omnivorous tending toward herbivory. Among them, the genus *Astyanax* includes some of the most common species, widely distributed and with less defined taxonomical limits (Abelha et al., 2006). In general, there is the consensus that this genus comprises generalists.
Table 4: Number of analyzed stomachs, standard length amplitude (SL), percentual composition (%) of consumed feeding items by the 11 species that presented n > 5 individuals, and number of feeding categories consumed by each species in the Bananal stream subbasin, Paranoá Lake basin, DF. Species abbreviations: Aspidoras fuscoguttatus (aspfus), Astyanax sp. (astsp), Characidium xanthopterum (chaxan), Hasemania sp. (hassp), Hyphessobrycon balbus (hypbal), Heptapterus sp. (hepsp), Knodus moenkhausii (knomoe), Kolpotocheirodon theloura (kolthe), Moenkhausia sp. (moesp), Phalloceros harpagos (phahar), Planaltina myersi (plamye), Rhamdia quelen (rhaque) and Rivulus pictus (rivpic).

with very variable diet (Zaret & Rand, 1971; Costa, 1987; Castro & Casatti, 1997; Luiz et al., 1998; Castro et al., 2003; Castro et al., 2004; Motta & Uieda, 2004; Bennemann et al., 2005; Oliveira & Bennemann, 2005; Ferreira & Casatti, 2006; Luz-Agostinho et al., 2006). The diet composition can vary according to the environmental characteristics, as well as food availability, which may be different from one region to another.
Aspidoras fuscoguttatus specifically invertivorous of the Bananal stream subbasin were possibly the most diverse (Goldstein & Simon, 1998). Species such as molluscs. They form the largest trophic guild and terrestrial and aquatic insects, as well as other invertebrates, both terrestrial and aquatic insects. classified as omnivorous, even tough, in general, they prefer of animal fragments. Thus, these species continue to be categories explains the high frequency and abundance values (2004). In the case of the Bananal stream species, the presence of aquatic invertebrates, Chironomidae larvae and detritus. **Rivulus pictus** consumes mainly aquatic invertebrates, as found by Melo et al. (2004). Shibatta & Bennemann (2003), when studying the feeding plasticity of the same species in a small lagoon in Distrito Federal, recorded omnivory as its feeding habit tending toward planktivory. The large plankton abundance in lacustrine environments favors this feeding preference, unlike in riverine environments, which have little particulate organic matter leading to scarce primary production (Russo et al., 2002).

According to the theory proposed by Vannote et al. (1980), the detritivore guild is expected to become more diverse when far away from the stream’s head, which is usually distant from the headwaters. In the case of the study area, detritivorous were present only at the sites very distant from the headwaters. When far from its headwaters, the decrease in current speed favors detritus deposition in the substrate, allowing the occurrence of detritivorous species (Vannote et al., 1980; Melo et al., 2004). Plant matter transport, originally from the riparian vegetation along the stream, restricts its use by detritivorous fish in the headwater area, since it has not yet transformed into detritus. The guild distribution pattern found in the Bananal stream follows the pattern proposed by Luiz et al. (1998) and Garutti (1988), who reported omnivores’ predominance in the headwater region and detritivorous near the mouth in streams of the high Paraná basin.

In the case of **Characidium xanthonpterum**, detritus was the main feeding item, followed by aquatic invertebrates. Studies on fish feeding habits of some species of the same genus (C. schubarti, C. lanei, C. zebra, C. gomesi, and C. pterostictum) in Brazilian streams demonstrated that their nurture is based almost exclusively on aquatic insect larvae (Uieda, 1984; Costa, 1987; Sabino & Castro, 1990; Castro & Casatti, 1997; Uieda et al., 1997; Aranha et al., 1998; Esteves & Lobón-Cerviá, 2001; Castro et al., 2003; Ferreira & Casatti, 2006), with sporadic high consumption of aquatic invertebrates (Melo et al., 2004).

![Fig. 3. Non-metric multidimensional scaling analysis for the 13 more abundant fish species’ diet found in the Bananal stream subbasin, Paranoá Lake basin, DF. Indication of four groups A, B, C and D. Species abbreviations: Aspidoras fuscoguttatus (asfus), Astyanax sp. (astsp), Characidium xanthonpterum (chaxan), Hasemania sp. (hassp), Hyphessobrycon balbus (hybal), Heptapterus sp. (hepsp), Knodus moenkhaußii (knomoe), Kolpotocheirodon theloura (kolthe), Moenkhausia sp. (moesp), Phalloceros harpagos (phahar), Planaltina myersi (plamye), Rhamdia quelen (rhaque) and Rivulus pictus (rivpic).](image)

it easier for the settling of insects in the substrate. Omnivorous species tending toward inverteivory showed a large variety of consumed items, where animal fragments were the most frequent and abundant in their diet. Animal fragments included remains of semi-digested insects and exoskeleton pieces of terrestrial and aquatic insects that could not be identified (Vilella et al., 2002; Melo et al., 2004). Catching this sort of food is considered an advantage because these remains maintain the insect’s nutritional value as a whole (Melo et al., 2004). In the case of the Bananal stream species, the presence and consumption of several terrestrial and aquatic invertebrate categories explains the high frequency and abundance values of animal fragments. Thus, these species continue to be classified as omnivorous, even tough, in general, they prefer both terrestrial and aquatic insects.

The invertivore guild comprises species that feed on both terrestrial and aquatic insects, as well as other invertebrates, such as molluscs. They form the largest trophic guild and possibly the most diverse (Goldstein & Simon, 1998). Species specifically invertivorous of the Bananal stream subbasin were Aspidoras fuscoguttatus, Heptapterus sp., Kolpotocheirodon theloura, and **Rivulus pictus**. The invertivorous feeding habit of **Aspidoras fuscoguttatus** is in agreement with that found in the literature, involving mostly aquatic insects (Melo et al., 2004; Ferreira & Casatti, 2006). Studies on the feeding habits of species the genus Heptapterus revealed that they were invertivorous (Sabino & Castro, 1990; Castro & Casatti, 1997; Uieda et al., 1997; Luiz et al., 1998; Esteves & Lobón-Cerviá, 2001; Castro et al., 2003; Ferreira & Casatti, 2006), with sporadic high consumption of aquatic invertebrates (Melo et al., 2004).

There are no studies on newer species concerning their biology and ecology. Little is known about the biology of Kolpotocheirodon theloura Malabarba & Weitzman, 2000, probably because it is a recently described species. The individuals sampled showed a diet composed of fragments of aquatic invertebrates, Chironomidae larvae and detritus. **Rivulus pictus** consumes mainly aquatic invertebrates, as found by Melo et al. (2004). Shibatta & Bennemann (2003), when studying the feeding plasticity of the same species in a small lagoon in Distrito Federal, recorded omnivory as its feeding habit tending toward planktivory. The large plankton abundance in lacustrine environments favors this feeding preference, unlike in riverine environments, which have little particulate organic matter leading to scarce primary production (Russo et al., 2002).

According to the theory proposed by Vannote et al. (1980), the detritivore guild is expected to become more diverse when far away from the stream’s head, which is usually distant from the headwaters. In the case of the study area, detritivorous were present only at the sites very distant from the headwaters. When far from its headwaters, the decrease in current speed favors detritus deposition in the substrate, allowing the occurrence of detritivorous species (Vannote et al., 1980; Melo et al., 2004). Plant matter transport, originally from the riparian vegetation along the stream, restricts its use by detritivorous fish in the headwater area, since it has not yet transformed into detritus. The guild distribution pattern found in the Bananal stream follows the pattern proposed by Luiz et al. (1998) and Garutti (1988), who reported omnivores’ predominance in the headwater region and detritivorous near the mouth in streams of the high Paraná basin.

In the case of Characidium xanthonpterum, detritus was the main feeding item, followed by aquatic invertebrates. Studies on fish feeding habits of some species of the same genus (C. schubarti, C. lanei, C. zebra, C. gomesi, and C. pterostictum) in Brazilian streams demonstrated that their nurture is based almost exclusively on aquatic insect larvae (Uieda, 1984; Costa, 1987; Sabino & Castro, 1990; Castro & Casatti, 1997; Uieda et al., 1997; Aranha et al., 1998; Esteves & Lobón-Cerviá, 2001; Castro et al., 2004; Motta & Uieda, 2004; Barreto & Aranha, 2006; Luz-Agostinho et al., 2006). This variation in the results obtained is related to the characteristics of the environment in which specimens were collected. All Characidium xanthonpterum samples belonging to the Bananal stream subbasin were collected at site 6, which had the smallest percentage of vegetation cover along with high current speed and turbidity. These characteristics can affect the abundance of aquatic insects barring their settling and permanence, because under such conditions they do not find substrate for attachment.
Fig. 4. Feeding items distributed according to the frequency of fish species occurrence (axis X) and relative abundance (axis Y), based upon the method proposed by Amundsen et al (1996): *Aspidoras fuscoguttatus*, *Astyanax* sp., *Characidium xanhopterum*, *Hasemania* sp., *Hyphessobrycon balbus*, *Heptapterus* sp., *Knodus moenkhausii* and *Kolpotocheiron don theloura*. The number of analyzed stomachs is shown in parentheses.
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Fig. 5. Feeding items distributed according to the frequency of fish species occurrence (axis X) and relative abundance (axis Y), based upon the method proposed by Amundsen et al (1996): Moenkhausia sp., Phalloceros harpagos, Planaltina myersi, Rhamdia quelen and Rivulus pictus. The number of analyzed stomachs is shown in parentheses.

(leaves and branches). The species’ feeding plasticity allows the exchange of preferential resources according to their abundance, taking detritus as an alternative food source as to ensure their survival at the site.

The only species considered piscivorous was Rhamdia quelen, which had almost 40% of its diet composed of fish or parts of fish. This guild eats mostly fish and it is not strictly piscivorous (Goldstein & Simon, 1998). High abundance of oligochaetes and fragments of terrestrial insects indicate some bias towards inverteory, moderately resembling the feeding habits of Heptapterus sp., which belong to the same family. Luz-Agostinho et al. (2006) found that this species is piscivorous, but occasionally and to a lesser degree complements its diet with plants and other invertebrates. Loureiro-Crippa & Hahn (2006) endorse that it is piscivorous. The classification of Rhamdia quelen into trophic guilds varies in the literature, and it can be found as an insectivore, consuming terrestrial insects followed by aquatic insect larvae (Castro & Casatti, 1997; Casatti, 2002; Ferreira & Casatti, 2006), and as a generalist, tending to consume animal items (Deus & Petrere-Junior, 2003; Gomiero et al., 2007).

Allochthonous and autochthonous contributions

In the current study, considering the nine species that showed significant feeding variations between seasons, there was higher consumption of autochthonous items. Nevertheless, when taking into account the totality of individuals of all sampled species, allochthonous items were more important.
The higher representativeness of allochthonous items was due to the fact that the streams sampled showed headwater characteristics, with low primary productivity. Thus, there is more abundance of resources originating from riparian vegetation. Studies in a well-preserved stream belonging to the Mata Atlântica indicate that, despite that many species use autochthonous resources, when one considers its abundance, allochthonous resources grow in importance (Esteves & Aranha, 1999; Russo et al., 2002). In the case of the fish species found in the Bananal stream subbasin, the increase in the consumption of allochthonous material was observed in the rainy period. In the rainy season the current is usually stronger and is prone to carry the inner habitat structures downstream, hindering their accumulation in the deposition areas. The relative importance of allochthonous food increases with the increase of the stream’s size, while the vegetation cover diminishes (Angermeier & Karr, 1984). It is also worthwhile noting climatic effects, such as air turbulences which may be responsible for higher abundances of terrestrial organisms in open areas (Uieda & Kikuchi, 1995).

The season of the year affects the availability of autochthonous and allochthonous food resources. In the rainy season, the rain and the erosion wash out many terrestrial invertebrates toward the streams (Angermeier & Karr, 1984; Uieda & Kikuchi, 1995). In the case of the fish species found in the Bananal stream subbasin, the increase in the consumption of allochthonous material during the rainy period was observed only for five out of nine of the species that showed significant variations in the item’s origin and the year’s season (Esteves & Aranha, 1999; Russo et al., 2002).

The season of the year affects the availability of autochthonous and allochthonous food resources. In the rainy season, the rain and the erosion wash out many terrestrial invertebrates toward the streams (Angermeier & Karr, 1984; Uieda & Kikuchi, 1995). In the case of the fish species found in the Bananal stream subbasin, the increase in the consumption of allochthonous material during the rainy period was observed only for five out of nine of the species that showed significant variations in the item’s origin and the year’s season. (Aspidoras sp., Characidium xanhopterum, Hyphessobrycon balbus, Rhamdia quelen, and Rivulus pictus). Of these, Rivulus pictus occurred only at site 5, where the stream is relatively narrow and has a dense vegetation cover. Its main diet was composed of aquatic insects. Thus, during the rainy season, the increase in water volume and the wash out of benthic communities yielded higher consumption of allochthonous material brought by rains.

The four other species (Aspidoras fuscoguttatus, Kolpotocheirodon theloura, Moenkhausia sp. and Phalloceros harpagos) showed significant variation in the consumption of items of different origin; but, as expected, they did not ingest high amounts of allochthonous items during the rainy season. This is because the species occurred at sites 6 (Aspidoras fuscoguttatus) and 7 (Kolpotocheirodon theloura, Moenkhausia sp., and Phalloceros harpagos), where the vegetation cover is less dense and the stream is wider. Site 7 is of the fourth order and represents the widest site with the smallest vegetation cover. In the dry season, the higher consumption of allochthonous material is due to the slow current speed, which allows the gathering of leaves and branches at the stream’s banks, making them available for the fish community. In the rainy season the current is usually stronger and is prone to carry the inner habitat structures downstream, hindering their accumulation in the deposition areas. The relative importance of allochthonous food increases with the increase of the stream’s size, while the vegetation cover diminishes (Angermeier & Karr, 1984). It is also worthwhile noting climatic effects, such as air turbulences which may be responsible for higher abundances of terrestrial organisms in open areas (Uieda & Kikuchi, 1995).

When evaluating a fish community’s diet, the preferential use of allochthonous resources varies according to the environment characteristics and the trophic niche occupied by the species under study. Variations found by different authors may be related to the sampling methods used, the stream’s hydrological regime and the sampling period (Moyle & Senanayake, 1984).

**Temporal variation**

Despite the strong seasonality of the Cerrado biome, with one dry season and other rainy, the fish community in the Bananal stream subbasin did not show seasonal variation in its diet. This indicates that the hydrological variation over the year did not cause changes in prey availability along the year as to produce changes in the diet. Food items remained available throughout the year in sufficient amounts as not to induce variations in the feeding diet of the species inhabiting that environment. The literature shows that depending on the rain regime and on the characteristics of each study site, it is possible or not to detect diet variations according to seasonality (Esteves & Aranha, 1999). Esteves & Lobón-Cerviá (2001) found feeding regularity in the fish community of a Mata Atlântica stream over the year, with no significant differences between seasons. Seasonal variations on the fish diet are also found in the literature. Motta & Uieda (2004) determined those variations by studying the feeding habits of Astyanax scabripinnis and Characidium schubarti. The higher primary productivity and the greater abundance of Diptera larvae in the dry season assured its consumption in that year period. Mazzoni & Rezende (2003) found in the diet of Deuterodon sp. an alternation between items of plant and animal origin over the seasons. Diet differences between the seasons are due to changes in the proportions of the most important food items consumed by fish (Balcombe et al., 2005). Such changes can result in new feeding strategies, from generalist in the summer to specialists in the winter, according to the resources

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**Table 5.** Trophic guilds of the 13 species of fish with n>5 recorded for the Bananal stream subbasin, Paranoá Lake Basin, DF.

| Species                    | Trophic Guilds                  |
|----------------------------|---------------------------------|
| Aspidoras fuscoguttatus    | Invertivorous                   |
| Astyanax sp.               | Omnivorous tending to herbivory  |
| Characidium xanhopterum    | Omnivorous tending to herbivory  |
| Rasemania sp.              | Omnivorous tending to inverteivory|
| Hyphessobrycon balbus      | Omnivorous tending to herbivory  |
| Heptapterus sp.            | Invertivorous                   |
| Kolpotocheirodon theloura   | Omnivorous tending to herbivory  |
| Knodus moenkhauasi         | Omnivorous tending to herbivory  |
| Moenkhausia sp.            | Omnivorous tending to inverteivory|
| Phalloceros harpagos       | Detritivorous                   |
| Planalbina myersi          | Omnivorous tending to inverteivory|
| Rhamdia quelen             | Piscivorous                     |
| Rivulus pictus             | Invertivorous                   |
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Fig. 6. Proportion of autochthonous feeding items (black) and allochthonous (gray) with respect to the rainy (C) and dry (S) seasons for the fish species that presented this significant variation. Species abbreviations: Aspidoras fuscoguttatus (asfus), Astyanax sp. (astsp), Characidium xanthopterum (chaxon), Hasemania sp. (hassp), Hyphessobrycon balbus (hyphbal), Heptapterus sp. (hepsp), Knodus moenkhausii (knomoe), Kolpotocheirodon theloura (kolthe), Moenkhausia sp. (moesp), Phalloceros harpagos (phahar), Planaltina myersi (plamye), Rhamdia quelen (rhaque) and Rivulus pichtus (rivpic).

Spatial and seasonal differences in the species’ diet are related to temporal alterations, peculiar to each environment (Barreto & Aranha, 2006). The sites sampled showed headwater availability, as reported by Deus & Petrere-Júnior (2003). Spatial and seasonal differences in the species’ diet are related to temporal alterations, peculiar to each environment (Barreto & Aranha, 2006). The sites sampled showed headwater availability, as reported by Deus & Petrere-Júnior (2003).

The ichthyofauna taxocenose of the Bananal stream subbasin is maintained by a great variety of resources where the ones originally from the riparian vegetation are essential for the maintenance of most of the fish biomass. The lack of seasonal variation and the predominance of allochthonous items in the diet are probably linked to the presence of riparian vegetation which acts as a buffer and resource supply zones for the aquatic biota. The preservation of the riparian vegetation guarantees the supply of resources for lotic environments, besides serving as a contention barrier for sudden environmental changes. Studies on preserved areas are essential for the identification of the natural conditions to which the communities are submitted. By doing so, it will be possible to evaluate anthropic actions on the fish communities and to formulate management plans aimed at the recovery of degraded areas.

**List of voucher specimens:** Voucher material of the 20 fish species collected in the Bananal stream subbasin, Paraná Lake Basin, DF, registered in the Coleção Ictiológica da Universidade de Brasília (CIUnB) and in the Coleção de Peixes do Departamento de Zoologia e Botânica da Universidade Estadual Paulista, São José do Rio Preto (DZSJR P): Aspidoras fuscoguttatus CIUnB 14, 16, 173, 180, 220, DZSJR 10813; Astyanax sp. CIUnB 1-3, 6, 7, 12, 50-52, 54, 55, 59, 60, 63, 161, 162, 165-168, 178, 183, 209-212, 218, 228, 312, 318, DZSJR 10824; Bryconamericus stramineus CIUnB 61; Characidium gomesi CIUnB 15, Characidium xanthopterum CIUnB 13, 221, DZSJR 10812; Ctenobrycon sp. CIUnB 64, Hasemania sp. CIUnB 22, 67, 93, 174, 185, 219, 223, 320, DZSJR 10801, 01829; Hyphessobrycon balbus CIUnB 5, 9, 23, 53, 58, 65, 65, 170, 215, 310, 311, 313, 316, 317, 319, 321, 326-330, 334-336, DZSJR 10825; Hypostomus sp.1 CIUnB 164; Hypostomus sp.2 CIUnB 230; Heptapterus sp. CIUnB 11, 57, 171, 213, DZSJR 10803, 10804, 01815; Knodus moenkhausii CIUnB 4, 20, 62, 68, 163, 177, 186, 187, 216, 222, DZSJR 01808, 01828, 01830; Kolpotocheirodon theloura CIUnB 18, 179, 226, DZSJR 10831; Microlepidogaster longicollis CIUnB 181, 229, DZSJR 10827; Moenkhausia sp. CIUnB 21, 66, 188, 225, DZSJR 10799, 10800, 10805; Phalloceros harpagos CIUnB 24, 182, 227, DZSJR 10826; Planaltina myersi CIUnB 19, 69, 175, 184, 224, DZSJR 10802; Pooecilia reticulata CIUnB 17; Rhamdia quelen CIUnB 8, 172, 217; Rivulus pichtus CIUnB 10, 56, 169, 214, DZSJR 10814.

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