

## Feeding ecology of stream-dwelling Characidae (Osteichthyes: Characiformes) from the upper Tocantins River, Brazil

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**ABSTRACT.** In this contribution we studied the trophic ecology of four Characidae species from the Cavalo Stream, upper Tocantins River, considering diet overlap and trophic niche breadth. The diet of the four species was composed of adult and immature insects, both autochthonous and allochthonous in origin. Autochthonous items dominated the diet of *Moenkhausia dichroua* (Kner, 1858), *Bryconamericus* sp., and *Creagrutus atrisignum* Myers, 1917. By contrast, allochthonous items were dominant in the diet of *Astyanax bimaculatus* (Linnaeus, 1758). Trophic niche breadth varied among species, with the highest value recorded for *M. dichroua* (0.48), followed by *Bryconamericus* sp. (0.39), *A. bimaculatus* (0.33) and *C. atrisignum* (0.29). Similarity analysis revealed two groups with different patterns of food preference. The first group was composed of insectivorous and the second by omnivorous species. The overlap in food items consumed by the four species studied was high. We suggest that resources are not limited in this stream and that competition might not be regulating these populations. This is one more case corroborating the general pattern registered for Tropical environments, where resource partitioning and specialization are responsible by the organization of fish communities.

**KEY WORDS.** Allochthonous; autochthonous; niche; resource; stream.

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Fish communities are excellent models to test theoretical concepts about resource partitioning (ARANHA *et al.* 1998, 2000, MOTTA & UIEDA 2004), niche breadth (CASATI 2002) and niche overlap (DOUGLAS & MATTHEWS 1992, DOUGLAS *et al.* 1994, NOVAKOWSKI *et al.* 2008). Although stream-dwelling fish species consume a variety of food items available in their surroundings, competition does not seem to take place among them. It has been suggested that trophic specialization (VOJTECH *et al.* 2002, DYER *et al.* 2010) or resource partitioning (HYNES 1970, SCHOENER 1974, ROSS 1986, DYER *et al.* 2010) are responsible for this lack of competition. Several studies carried out in tropical aquatic systems have demonstrated that one food resource can be consumed by many different fish species in a community. It may also happen that many species will explore different resources (e.g., POUILLY *et al.* 2003, 2004, 2006, NOVAKOWSKI *et al.* 2008).

The coexistence of species in highly diverse communities has been explained by two main theories (GRAVEL *et al.* 2006). The first one, called “the niche theory”, considers that a niche is composed of different elements that supply the demands of a species and absorb the impacts of that species on the environment (CHASE & LEIBOLD 2003, NOBIS & WOHLGEMUTH 2004, MIKKELSON 2005). In this context, niche differences among species are fundamental to explain the maintenance of biodiversity in different scales (LEIBOLD & MCPHEEK 2006). The

second theory, called “the neutral theory”, claims that species diversity in a given area is the result of stochastic ecological and evolutionary factors that interact on both local and regional scales. The neutral theory renders the niche theory unnecessary for understanding patterns of species coexistence (HUBBELL 2001).

Studies conducted in different streams indicate that both theories can be used to explain the patterns of organization of many Neotropical stream-dwelling fish communities. The soaring trophic plasticity of these communities allows them to coexist while exploring variable food supplies (BALASSA *et al.* 2004). Resource partitioning and exploratory tactics to minimize feeding overlap, which represent alternatives to competition, are made possible by the great diversity of food items available, the great diversity of morphological adaptations, and the exploration of different microhabitats and periods of activity of species (HURLBERT 1978, CHASE & LEIBOLD 2003).

Species of Characidae are largely widespread and morphologically diversified (BRITSKI *et al.* 1999). The family is composed of many species (NELSON 1994), and many cases of trophic resource partitioning have been documented for them (UIEDA *et al.* 1997). The ictiofauna of the Cavalo stream, located at the upper Tocantins River, has 36 fish species. Of these, 10 (~28%) are Characiformes and four belong to the Characidae. The

population densities of the following species, which are found throughout the stream, are the highest among Characidae – *Astyanax bimaculatus* (Linnaeus, 1758), *Bryconamericus* sp., *Creagrutus atrisignum* Myers, 1927, and *Moenkhausia dichroua* (Kner, 1858) – (MIRANDA & MAZZONI 2003). The species selected for the present study were the most abundant and widespread in the studied stream.

The four Characidae mentioned above had been previously classified into different feeding guilds, depending on the study site and the composition of the community where they had been found. The objective of this study was to evaluate the trophic ecology of these species at the Cavalo stream. We considered interspecific variations in diet composition, diet overlap, and trophic niche breadth.

## MATERIAL AND METHODS

The Cavalo Stream (14°26'12"S, 48°34'53"W) is a 3<sup>rd</sup> order tributary of the Traíras River in the upper Tocantins Basin (14°40'S, 49°00'W and 13°10'S, 48°00'W). Samples were collected on a 150 m long stretch of the Cavalo Stream, at a site formed by rocky substrata of riffle and rapid zones interspersed by sandy-mud pools. The marginal vegetation was sparse and the canopy covered approximately 90% of the study site (MIRANDA & MAZZONI 2003).

The hydrological regimen of the upper Tocantins River Basin is well defined (CARAMASCHI *et al.* 2012), with the high tide season extending from October to April and the low season from May to September. Sampling was carried out at each first fortnight of April, June (low-water-level season) and December (high-water-level season) of 1996 and January (high-water-level season) of 1997. Samples were collected by electrofishing (Honda EX 1000 generator, 220V, 2-3A, CA) according to the sample design presented by MAZZONI *et al.* (2000). During each sampling, we tried to collect enough specimens to obtain a robust analysis. Unfortunately, however, when the water was high, the speed of the rapids hampered our sampling efforts.

After capture, fish were immediately fixed (formalin 10%) and transported to the laboratory for identification and processing. Two-hundred-thirty-one individuals were analyzed, of which 55 were *C. atrisignum*, 57 were *A. bimaculatus*, 61 were *Bryconamericus* sp. and 58 were *M. dichroua* (Table I). Voucher specimens of each species are available in the ichthyological collection of Museu Nacional do Rio de Janeiro (MNRJ –36169 to 36172). For each sampled specimen we first registered standard length (Sl, cm) and total weight (Wt, gr). We then removed its stomach after performing an abdominal incision. Stomach content analysis was performed under a stereomicroscope through the volumetric (Vo) and frequency of occur-

Table I. Number of analyzed stomachs (N), fish length interval (Sl) and Alimentary Importance Index (IAi) of each food item, considering allochthonous and autochthonous items, consumed by *M. dichroua*, *C. atrisignum*, *A. bimaculatus*, and *Bryconamericus* sp. from Cavalo stream at each sampling month. (Apr) April of 1996, (Jun) June of 1996, (Dec) December of 1996, (Jan) January of 1997. April, June, and January correspond to the high water season whereas June correspond to the low water season.

Species	<i>Moenkhausia dichroua</i>				<i>Creagrutus atrisignum</i>				<i>Astyanax bimaculatus</i>				<i>Bryconamericus</i> sp.			
	Apr	Jun	Dec	Jan	Apr	Jun	Dec	Jan	Apr	Jun	Dec	Jan	Apr	Jun	Dec	Jan
N	10	28	10	10	7	25	18	5	12	27	12	6	11	31	9	10
Sl (cm)	4.7–5.2				5.6–6.3				5.1–7.1				6.3–7.4			
Allochthonous Items (IA)																
Terrestrial Insects Pupae	6.5	5.9	4.1	5.5	–	–	–	–	–	–	–	–	–	–	–	–
Hymenoptera	8.2	8.9	7.0	8.5	–	–	–	–	69.9	68.7	68.1	67.2	14.9	15.4	16.3	15.7
Coleoptera	–	–	1.1	–	–	–	–	–	5.8	6.3	6.1	7.2	–	–	–	–
Hemiptera	0.4	0.9	1.0	1.1	–	–	–	–	–	–	–	–	22.3	21.7	20.4	21.5
Autochthonous Items (IA)																
Coleoptera Larvae	–	–	–	–	–	–	–	–	–	–	–	–	5.0	3.1	2.7	3.3
Ephemeroptera Nymph	49.7	48.7	50.2	49.1	15.9	16.7	12.1	16.2	0.3	0.6	1.0	0.5	6.1	6.3	6.1	6.8
Odonata Nymph	5.1	3.6	4.5	3.8	–	–	0.2	–	–	–	–	0.2	0.8	–	–	–
Chironomidae Larvae	10.1	9.5	7.1	9.1	54.0	50.0	52.2	49.8	–	–	–	–	–	–	–	–
Simuliidae Larvae	–	–	–	–	–	–	–	–	0.8	0.6	1.1	0.4	0.8	1.1	1.3	1.1
Trichoptera Larvae	20.0	22.5	25.0	22.9	30.1	33.3	35.5	34.0	0.1	–	–	0.2	50.1	52.4	53.2	51.6
Non identified Larvae	–	–	–	–	–	–	–	–	8.2	8.8	8.9	8.5	–	–	–	–
Vegetal Matter	–	–	–	–	–	–	–	–	8.9	8.4	8.0	8.8	–	–	–	–
Scales	–	–	–	–	–	–	–	–	6.0	6.6	6.8	7.0	–	–	–	–
% Allochthonous	15.1	15.7	13.2	15.1	–	–	–	–	75.7	75.0	74.2	74.4	37.2	37.1	36.7	37.2
% Autochthonous	84.9	84.3	86.8	84.9	100.0	100.0	100.0	100.0	24.3	25.0	25.8	25.6	62.8	62.9	63.3	62.8

rence (Fo) methods according to HYSLOP (1980) and BOWEN (1992). Food items were classified to the lowest taxonomic categories following PÉREZ (1988). The relative importance of each food item was assessed using the percentage values of the Alimentary Index ( $AI_i$  – KAWAKAMI & VAZZOLER 1980) as follows:  $AI_i = [Fo_i \times Vo_i / \sum (Fo_i \times Vo_i)] \times 100$ , where  $i = 1, 2, \dots, n$  food items;  $Fo_i$  = frequency of occurrence (%) of a given item;  $Vo_i$  = volume (%) of a given item.

Differences in dietary patterns occurring during the two hydrological seasons (four months) were tested for each species using the Spearman test (Statistica 11 – www.statsoft.com). When no differences were registered among the four sampling months, the data set was grouped for further analysis. Patterns of diet similarity, based on the AIi matrix of the four studied species, were assessed by a Bray Curtis cluster analysis (UPGMA distances) (McCUNE & MEFFORD 1997).

Diet breadth was assessed by the Levin's niche breadth index (B), where  $B = 1/\sum p_j^2$ ,  $p_j$  is the proportion of individuals using the resource  $j$  (KREBS 1989). The Levin's index varies from 0 (diet specialized in few prays) to 1 (generalist diet). Diet overlap was calculated using the Horn index ( $R_o$ ) as follows:  $R_o = (\sum (p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \sum p_{ij} \log p_{ij} - \sum p_{ik} \log p_{ik}) / 2 \log 2$  (KREBS 1989), where  $p_{ij}$  is the proportion of resource  $i$  compared to all resources used by species  $j$  and  $p_{ik}$  is the proportion of resource  $i$  compared to all resources used by species  $k$ . Following ZARET & RAND (1971) and JOHNSON & ARUNACHALAM (2012), overlap values that were higher than 0.6 were considered significant.

## RESULTS

The four studied species were abundant in the study area and occurred in both hydrological seasons (high and low-tide seasons) and provided enough stomach-content data (at least five individuals/species) to conduct the analyses. There were no significant differences in the general feeding pattern of all species between the hydrological seasons – Spearman rank correlation coefficients " $r_s$ " ZAR (1999) were always higher than 0.9 for  $p < 0.05$  (Table I). As a consequence, we grouped all data for the subsequent analyses (Table II).

The diet of *M. dichroua* was composed mainly of Diptera larvae (49.4%), followed by Trichoptera larvae (22.0%). The main components of the diet of *C. atrisignum* were Chironomidae larvae (51.5%) and Trichoptera (33.2%), whereas *A. bimaculatus* consumed mainly Hymenoptera (68.2%). The diet of *Bryconamericus* sp. was mostly based on Trichoptera larvae (51.3%) and Hemiptera (21.5%). Autochthonous items dominated the diet of *M. dichroua* (84.6%) and *Bryconamericus* sp. (63.0%), and composed 100% of the diet of *C. atrisignum*. Allochthonous items dominated the diet of *A. bimaculatus* (74.6%) (Table II).

Trophic niche breadth (Fig. 1) varied among species. The greatest values were registered for *M. dichroua* (0.48) followed by *Bryconamericus* sp. (0.39), *A. bimaculatus* (0.33) and *C. atrisignum* (0.29).

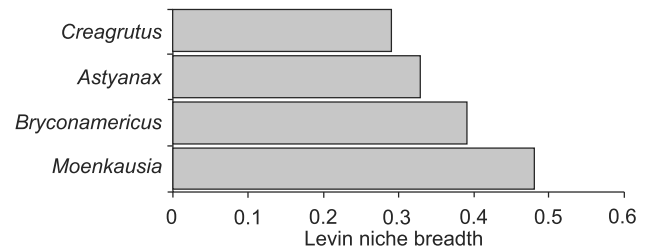


Figure 1. Niche breadth of *Moenkhausia dichroua*, *Creagrutus atrisignum*, *Astyanax bimaculatus* and *Bryconamericus* sp. from Cavalo stream.

Table II. Number of analyzed stomachs (N) and Alimentary Importance Index ( $IA_i$ ) of each food item from allochthonous and autochthonous origin, consumed by *M. dichroua* (MD), *C. atrisignum* (CA), *A. bimaculatus* (AB) and *Bryconamericus* sp. (BSP) from Cavalo stream. Pooled data for all sampled month.

Species	MD	CA	AB	BSP
N	58	55	57	61
Allochthonous Items ( $IA_i$ )				
Terrestrial Insects Pupae	5.4	–	–	–
Hymenoptera	8.0	–	68.2	15.5
Coleoptera	1.1	–	6.4	–
Hemiptera	0.9	–	–	21.5
Autochthonous Items ( $IA_i$ )				
Coleoptera Larvae	–	–	–	3.5
Ephemeroptera Nymph	49.4	15.1	0.6	6.3
Odonata Nymph	4.3	0.2	0.2	0.8
Chironomidae Larvae	9.0	51.5	–	–
Simuliidae Larvae	–	–	0.7	1.1
Trichoptera Larvae	22.0	33.2	0.2	51.3
Non identified Larvae	–	–	8.6	–
Vegetal Matter	–	–	8.5	–
Scales	–	–	6.6	–
% Allochthonous	15.4	–	74.6	37.0
% Autochthonous	84.6	100.0	25.4	63.0

Similarity analysis revealed two groups with different patterns of food preference. The first group was formed exclusively by invertivorous species and included *M. dichroua*, *Bryconamericus* sp., and *C. atrisignum*. The second group was composed of a single omnivorous species (*A. bimaculatus*). Nonetheless, group 1 was further subdivided into two subgroups. The diet of the species in the first group (*M. dichroua* and *Bryconamericus* sp.) contained both autochthonous and allochthonous items. By contrast, the second subgroup contained species that eat exclusively autochthonous items (*C. atrisignum*) (Fig. 2). We detected significant (overlap > 0.6 according to ZARET & RAND 1971) feeding overlap in three (75%) of the four pairs of species analyzed (Table III).

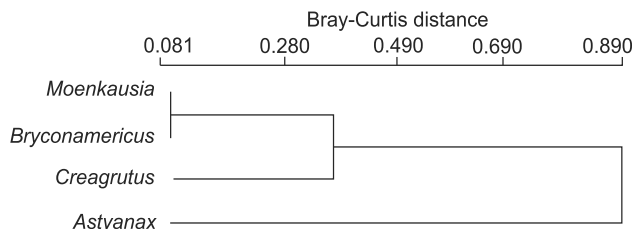


Figure 2. Similarity dendrogram based on diet composition of four species of fish analyzed in Cavalo stream.

Table III. Horn Index values (diet overlap) among the four Characidae species: *M. dichrourea* (MD), *C. atrisignum* (CA), *A. bimaculatus* (AB), and *Bryconamericus* sp. (BSP) from Cavalo stream. \* Values > 0.60 represent significant overlap according to ZARET & RAND (1971) and JOHNSON & ARUNACHALAM (2012).

	CA	AB	BSP
AB	0.29	–	–
BSP	0.74*	0.31	–
MD	0.69*	0.36	0.73*

## DISCUSSION

Species of Characidae, such as those studied in the present paper, are largely widespread through the Neotropics and Central America (REIS *et al.* 2003, BUCKUP *et al.* 2007, LIMA *et al.* 2007) and have been classified into different feeding guilds, for instance insectivorous (e.g., CASATTI *et al.* 2003, SANTOS *et al.* 2009, BONATO *et al.* 2012), herbivorous (e.g., MESCHIATTI 1995, CASSEMIRO *et al.* 2002) and omnivorous (e.g., CASSEMIRO *et al.* 2002, BRANDÃO-GONÇALVES *et al.* 2009, RONDINELLI *et al.* 2011), changing feeding habits according to the environment in which they occur. Our results showed that the diet of the four species studied is largely insectivorous, based both on autochthonous and allochthonous items, and that there are no seasonal differences related to the hydrological regimen. Other studies conducted in Neotropical streams also showed that small Characidae species frequently feed on invertebrates, and include both autochthonous and allochthonous items in their diets (TANK *et al.* 2010, ORTAZ *et al.* 2011, RONDINELLI *et al.* 2011, XIMENES *et al.* 2011, BONATO *et al.* 2012, MANNA *et al.* 2012).

Streams that run through dense forests have low light levels due to the closed canopy. Consequently, the input of allochthonous organic matter (ARAÚJO-LIMA *et al.* 1995) and terrestrial arthropods (REZENDE & MAZZONI 2003, MOULTON 2006) in these streams often outweighs the autochthonous algal production (VANNOTE *et al.* 1980, HENRY *et al.* 1994, THORP 2002, TANK *et al.* 2010), affecting fish diet, as well as the entire trophic web (DODDS 2007). Thus, the input of allochthonous matter (animal and vegetal) is an important determinant of the dynamics of a stream, because it provides food for both fish and

micro/macro-invertebrates, which in turn are food resources for many other stream-dwelling organisms. The importance of such allochthonous matter as an energy source flowing through the food chain was demonstrated for both Temperate (FISHER & LIKENS 1973, VANNOTE *et al.* 1980, MCINTIRE & FLECKER 2010) and Tropical (GONÇALVES *et al.* 2006, MOULTON 2006, SELVA *et al.* 2007) streams. In conclusion, the contribution of allochthonous material, as a direct or indirect source of food for fish, has been shown to be very important in streams, as the one studied in the present work (e.g., HENRY *et al.* 1994, UIEDA & KIRUCHI 1995, MAZZONI & REZENDE 2003, REZENDE & MAZZONI 2003).

We observed that among the four species studied, three feed mainly on autochthonous and one consumed mainly allochthonous items. These results indicate that both allo- and autochthonous processes are operating in the maintenance of the stream-dwelling fish community. Similar results had been previously documented for other tropical systems (e.g., ALVIM & PERET 2004) and could confirm the relative importance of different sources of energy to streams in Tropical areas. Nonetheless, based on dietary overlap and similarity analysis, we registered that 50% of the analysed species pairs used similar food resources. Among the four co-existing Characidae, three species used the same food resource (autochthonous matter).

Several reports on the feeding ecology of stream-dwelling fishes have shown that an overlap in resource use does not necessarily imply that there is competition among the species involved, since temporal and spatial segregation are strategies that minimize direct confrontation in the use of resources (CASATTI 2002, KOTLER & BROWN 2007). Three species in our study (*M. dichrourea*, *C. atrisignum* and *Bryconamericus* sp.) shifted among insect prey. They all preyed almost exclusively on autochthonous items and their diets overlapped in about 50% of the items. *Moenkausia dichrourea* preyed mainly on larvae of Ephemeroptera (48.75%), *C. atrisignum* preyed mainly on larvae of Chironomidae (50%) and *Bryconamericus* sp. preyed mainly on larvae of Trichoptera (52.4%). Such strategy could reflect the specific morphological adaptations of each species and/or their use of the microhabitat (CASATTI & CASTRO 2006, MAZZONI *et al.* 2010) and could explain the co-existence of these close related species. Although resource availability was not measured in the present study, we suppose that the available prey items were diverse enough to allow for the observed feeding patterns of these Characidae fish species.

Studies in Amazonian streams showed that the diet of almost all fish species that shared a food source consisted of allochthonous plants or allochthonous insects (LOWE-MCCONNELL 1999). These findings reveal that the similarity in the use of feeding resources may be a consequence of the wide availability of them and/or a consequence of their shared use. Several examples of studies in Amazonian and other river systems in the Neotropical region have shown that this alternative is valid and recurrent (e.g., SABINO & ZUANON 1998, CASATTI 2002, NOVAKOWSKI *et al.* 2008, ROLLA *et al.* 2009). Based on previ-

ous data on community persistence and the temporal maintenance of the densities of the four studied species in the Cavalo Stream (MIRANDA & MAZZONI 2009), we suggest that these species share unlimited resources, and that competition is not regulating their populations.

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