Plasticity in the diet of *Astyanax taeniatus* in a coastal stream from south-east Brazil

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Abstract

In this work we aimed to characterise the diet of *Astyanax taeniatus* (Jenyns 1842) (Characiformes, Characidae) along the Mato Grosso stream and we hypothesised that the diet of this species would vary according to spatial, seasonal and ontogenetic differences. Specimens were collected every second month at three sites with different physical attributes. The feeding habits of 651 specimens were analysed using the Alimentary Index (IA_i). Analysis of the diet showed an effect of spatial, temporal and ontogenetic factors. Vegetal allochthonous items were more important in the diet of *Astyanax taeniatus* in upstream sites while animal autochthonous items were more important downstream. Ontogenetic differences in the diet were significant only in upstream sites, where adults consumed a greater amount of vegetal matter than juveniles. These results reinforce the idea that *Astyanax* species are opportunistic and show trophic plasticity.

Keywords: feeding, opportunism, stream fish.

Plasticidade trófica em Astyanax taeniatus de um riacho costeiro do Sudeste do Brasil

Resumo

Neste trabalho, objetivou-se caracterizar a dieta de *Astyanax taeniatus* (Jenyns 1842) (Characiformes, Characidae) ao longo do Rio Mato Grosso, com a hipótese de que a espécie apresente variações espaciais, sazonais e ontogenéticas. Os exemplares foram coletados bimestralmente em três localidades, que diferiram pelas variáveis físicas. As preferências alimentares foram analisadas a partir de 651 exemplares, utilizando-se o Índice Alimentar (IA_i). Foram avaliadas diferenças espaciais, sazonais e ontogenéticas a partir dos dados de dieta. Os itens de origem vegetal e alóctone foram mais importantes na dieta da espécie para as localidades com maior altitude, enquanto os itens animais e autóctones, na localidade baixa. Na dieta de jovens e adultos, houve diferença significativa na contribuição de itens de origem vegetal e animal somente na localidade mais alta, onde os adultos consumiram maior quantidade de matéria vegetal. Os resultados reforçam a ideia de que as espécies de *Astyanax* possuem hábito alimentar onívoro e oportunista, evidenciando sua alta plasticidade alimentar ao longo do riacho.

Palavras-chave: alimentação, oportunismo, peixe de riacho.

1. Introduction

An important aspect of stream fish ecology is to understand the coexistence and trophic adaptability of fishes in relation to the diversity, density and availability of resources in stream environments (Lowe-McConnell, 1999; Abelha et al., 2001; Rezende et al., 2011). The availability of resources can be influenced by spatial and temporal physical variables (Lawlor, 1980) and the presence or absence of vegetation cover which can affect the density of resources (Pinto and Uieda, 2007). Some studies have demonstrated that fish select food resources based on their availability in the environment (e.g. Russo et al., 2002; Rezende and Mazzoni, 2006; Pinto and Uieda, 2007; Rezende, 2009). According to Barrella et al. (2000), fish use comparatively more allochthonous resources (animal or vegetal) in smaller rivers in the Atlantic forest environment, highlighting the importance of riparian vegetation in the diets of species inhabiting these small streams (Cassemiro et al., 2002; Gomiero and Braga, 2003; Rezende and Mazzoni, 2006; Borba et al., 2008).

Fish are able to exploit various food items, and differential consumption is used to classify species into different trophic groups (Goulding et al., 1988; Luz-Agostinho et al., 2001). The ability to consume different food items is common in stream fish and may be influenced by the availability of resources, physical (e.g. seasonal) and/or ontogenetic changes (Wooton, 1990; Deus and Petrere-Junior, 2003). Furthermore, feeding strategies can change over the life span of a fish (Gerking, 1994).

Trophic plasticity is an important strategy that allows the use of abundant and available food resources in the environment (Abelha et al., 2001; Luz-Agostinho et al., 2006). The wide trophic adaptability of fish fauna in tropical streams is reflected by the predominance of generalist and opportunistic species (Abelha et al., 2001). According to Knöppel (1970), opportunistic species have high trophic plasticity due to their ability to use several resources in adverse environments, unlike less tolerant species. As a consequence, the high trophic plasticity found in freshwater fish (Lowe-McConnell, 1999; Abelha et al., 2001) may be related to the maintenance and renewal of food resources (Angermeier and Karr, 1983; Rezende and Mazzoni, 2006; Pinto and Uieda, 2007; Rezende et al., 2011).

The fish genus *Astyanax* has omnivorous feeding habits and is highly adaptable to changes in the physical environment (Menezes et al., 2007). They are generalist species that show high trophic plasticity in response to environmental changes and resource availability (Lobón-Cerviá and Bennemann, 2000) and have an increased chance of surviving extreme changes in their habitat (Menezes et al., 2007).

Astyanax species have omnivorous diets, which are composed of animal and vegetal items, both autochthonous and allochthonous in origin (Esteves, 1996; Andrian et al., 2001; Vilella et al., 2002; Cassemiro et al., 2002; Gomiero and Braga, 2003; Bennemann et al., 2005; Mazzoni and Costa, 2007). However, some studies report that

Astyanax has omnivorous/herbivorous (e.g. Esteves and Galetti, 1995; Aranha et al., 1998; Alvim and Peret, 2004; Lizama and Ambrosio, 2004; Loureiro-Crippa and Hahn, 2006; Ibañez et al., 2007), detritivorous/herbivorous (e.g. Abelha et al., 2006) or insectivorous feeding habits (e.g. Lizama and Ambrosio, 2004; Peretti and Andrian, 2008). These classifications into different trophic guilds are probably related to differences in the physical environment and resource availability (Luiz et al., 1998; Lobón-Cerviá and Bennemann, 2000). Furthermore, some of the literature on Astyanax reports feeding changes (e.g. Bennemann et al., 2005) which may be related to spatial changes in habitat (Schlosser, 1982).

Therefore the objective of this study was to compare the diet of *Astyanax taeniatus* (Jenyns 1842) at three different sites along an Atlantic rainforest stream. Considering the generalist feeding habits and trophic adaptability of *Astyanax* species, we hypothesised that the diet would change along the stream according to spatial, seasonal and ontogenetic factors.

2. Material and Methods

2.1. Study area

The Mato Grosso fluvial system is located in the northeast of the state of Rio de Janeiro and drains the north-west area of Saquarema city. The Mato Grosso (22° 52' S; 42° 40' W and 22° 53' S, 42° 34' W) is a third order stream with its headwaters 500 m above sea level. The stream is 11 km long and discharges into the Saquarema lagoon (Figure 1). It is a typical coastal stream with water levels regulated only by rainfall (~1500 mm.yr⁻¹) and run-off. Abundant summer rains (from November to March) accentuate the water fluctuations, however tropical storms (>120 mm/day) are very common throughout the year.

The study area comprised of three sites along the stream; site F1 (22° 53' 13,7" S and 42° 39' 44,4" W), site F2 (22° 53' 26,1" S and 42° 39' 19,7" W) and site A (22° 52' 24,7" S and 42° 39' 06,4" W). The three sites differ in: (i) altitude; (ii) the presence of different mesohabitats (riffles, rapids and pools); (iii) substrate; (iv) degree of vegetation cover; and (v) turbidity.

2.2. Sampling and data analysis

Samples were collected from March 2006 to February 2007 by electric fishing in sites F1 and F2 (CA – 1600 W, 220 V, 2-4 A – Mazzoni et al., 2000), and using dragnets (mesh size 5 mm) in site A due to difficult access and high water turbidity. Each study site was characterised by collecting the following data: (i) stream width; (ii) stream depth; (iii) current velocity; (iv) river bed substrate; (v) water turbidity; (vi) vegetation cover; and (vii) type of mesohabitats present. Measurements were taken across transects from one shore to the other at 5 m interval at each site. Substrate, turbidity and mesohabitat were visually evaluated by the proportions of each variable within the transect. Proportion of vegetation cover was estimated by taking digital photographs which were later analysed

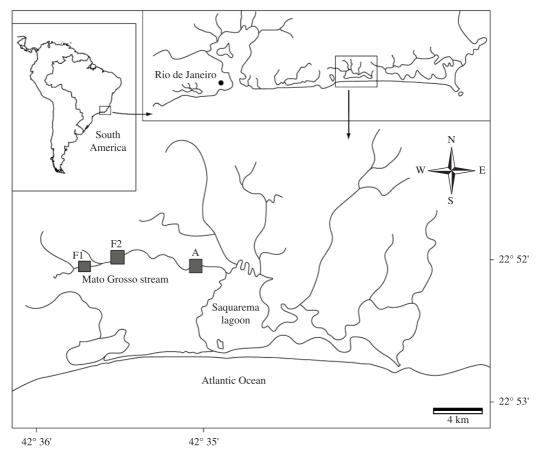


Figure 1. The Mato Grosso fluvial system with the study sites indicated (grey squares), adapted from Mazzoni et al. (2010b).

using Adobe Photoshop 8.0 to identify the proportion of pixels occupied by vegetation in relation to total pixels in the image. The width of the stream was measured from shore to shore using a measuring tape and the depth was measured using a ruler positioned perpendicular to the ground. Current velocity was measured using a digital flowmeter (Global Water FP 1010). Principal component analysis (PCA) was used to rank the sites according to physical variables.

Collected *Astyanax taeniatus* samples were stored in ice for transportation and then processed to determine standard length (SL, cm) and total weight (WT, g). Next they were dissected and the intestine length (cm) and stomach weight (g) were recorded. The stomachs were fixed in formalin (10%) and kept in alcohol solution (70° GL) for subsequent analysis. Stomach content was analysed under stereo microscope and quantified using the Volumetric (V_o) and Frequency of Occurrence (F_o) methods (Hyslop, 1980). Diet items were identified according to the literature (Salles et al., 2004; Triplehorn and Johnson, 2005; Passos et al., 2007; Mugnai et al., 2010) to the lowest feasible taxonomic level. The V_o and F_o values were used to calculate the Alimentary Index (IA $_i$) proposed by Kawakami and Vazzoler (1980) and

adapted by Hahn et al. (1997), according to the equation: $IA_i = (F_i^* V_i)/\Sigma F_i^* V_i)^*100$, where $i=1,2,\ldots n$ food items; $F_i =$ frequency of occurrence of a given food item; $V_i =$ volume of a given food item. Food items were grouped according to type (animal and vegetal) and origin (autochthonous and allochthonous). To test the hypothesis that the consumption of animal and vegetal items was proportionally equal we used a 2×2 contingency test (χ^2) (Zar, 1999). The same calculation was used to compare the proportions of autochthonous and allochthonous items. Non-metric multidimensional scaling analysis (NMDS) was used to examine the spatial-temporal variation of the diet using the total volume values of each item.

Using the formula: $Q_i = C_i/C_p$, where $C_i = length$ of the intestine and $C_p = standard$ body length, we calculated the intestinal quotient proposed by Angelescu and Gneri (1949) and Barbieri et al. (1994). The intestinal quotient was used to provide complementary information on the possible differences in feeding habits between juveniles and adults (Barbieri et al., 1994). The classification of juveniles and adults was based on research conducted in the Mato Grosso stream by Costa (2010) who found that the size (standard body length) of *Astyanax taeniatus* at first maturity was between 3,0-4,0 cm in males and

between 5,0-6,0 cm in females. The t test was used to test for differences in intestinal quotient between adults and juveniles at each site. The Kolmogorov-Smirnov test of normality and Levene's homoscedasticity of variances test were applied to the data to determine whether parametric ANOVA or non-parametric Kruskal-Wallis were used to test for differences in Qi of juveniles or adults among sites. Data that was not normally distributed and did not show homoscedasticity was log 10 transformed. Voucher specimens were deposited at the National Museum of Rio de Janeiro (*Museu Nacional do Rio de Janeiro*; MNRJ 29949; MNRJ 29950; MNRJ 29951).

3. Results

The principal component analysis (PCA) confirmed that there was vegetation cover at the two highest sites (sites F1 and F2), and an absence of vegetation cover at the lower site (A). The first axis had an eigenvalue of 4.445

and the second axis had a value of 1.821. The percentage of variance explained by each axis was 26.150% and 10.712% respectively. Vegetation cover was the main variable influencing the separation of sites along the first axis (with an eigenvalue of 0.924), followed by turbidity (–0.934), sand substrate (–0.815) and width (–0.714) (Figure 2).

The diet of 651 Astyanax taeniatus individuals from three sites was analysed, and a total of 50 different food items were identified (Table 1). Vegetal items composed most of the diet at sites F1 ($\chi^2 = 93.74$; df = 1; p < 0.05) (IAi = 98.4%) and F2 ($\chi^2 = 10.20$; df = 1; p < 0.05) (IAi = 65,9%) while animal items made the largest contribution to the diet at site A ($\chi^2 = 94.51$; df = 1; p < 0.05) (IAi = 98.6%) (Figure 3a). The proportion of autochthonous and allochthonous items in the diet was also significantly different, with allochthonous items making a larger contribution at sites F1 ($\chi^2 = 39.79$; df = 1; p < 0.05) (IAi = 99.6%) and F2 ($\chi^2 = 98.60$; df = 1; p < 0.05) (IAi = 81.5%) and autochthonous items making

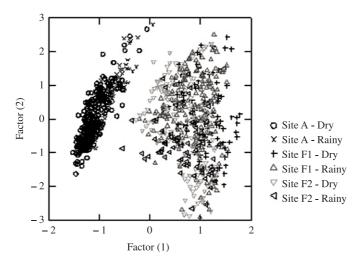


Figure 2. Principal components analysis using the physical variations of each site in the Mato Grosso stream, Saquarema, Rio de Janeiro.

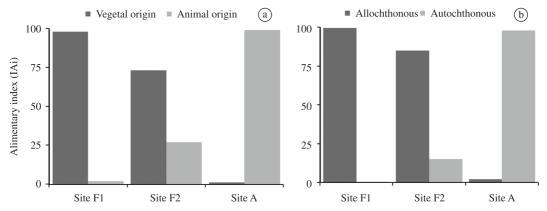


Figure 3. Alimentary Index (IA_1) of (a) vegetal and animal, (b) autochthonous and allochthonous items consumed by *Astyanax taeniatus* at three sites in the Mato Grosso stream, Saquarema, Rio de Janeiro.

Table 1. Percentage composition by volume (V_o) , occurrence (F_o) and Alimentary Index (IA_p) of each food item identified in the diet of $Astyanax\ taeniatus$ in three sites from the Mato Grosso stream, Saquarema, Rio de Janeiro. Allochthonous items are marked with *.

	Site F1			Site F2			Site A		
	$\overline{V_o}$	F_o	$\overline{IA_I}$	$\overline{V_o}$	F_o	IA_I	$\overline{V_o}$	F_o	$\overline{IA_I}$
Vegetal origin	-								
Algae				0.27	5.31	0.02	2.68	16	0.62
Fruit*				0.14	5.31	0.01	0.91	4	0.05
Vegetal matter	87.93	90.41	98.32	61.97	84.07	75.31	1.22	8	0.14
(leaves and twigs)*									
Seeds*	1.50	4.70	0.09	0.38	7.08	0.04			
Animal origin									
Ephemeroptera									
Baetidae	0.35	12.03	0.05	0.06	2.65	0.002	0.30	4	0.02
Leptohyphidae	0.005	0.38	< 0.001						
Leptophlebiidae	0.002	0.19	< 0.001						
Ephemeroptera Ninphae				0.02	0.88	< 0.001			
Unidentified				0.09	0.88	0.001			
Odonata									
Anisoptera Libellulidae	0.01	0.38	< 0.001	0.006	0.88	< 0.001			
Odonata unidentified	0.04	0.75	< 0.001						
Plecoptera									
Gripopterygidae	0.07	0.75	0.001						
Perlidae	0.06	1.50	0.001						
Megaloptera									
Corydalidae	0.22	0.75	0.002						
Unidentified	0.005	0.19	< 0.001						
Trichoptera									
Philopotamidae	0.09	1.69	0.002	0.008	1.77	< 0.001			
Leptoceridae	0.02	1.69	< 0.001	0.05	2.65	0.002			
Hydropsychidae	0.45	3.76	0.02						
Hydroptilidae	0.03	0.75	< 0.001						
Unidentified larvae							0.18	4	0.01
Lepidoptera									
Pyralidae	0.23	1.13	0.003				0.61	8	0.07
Coleoptera									
Curculionidae				3.78	14.16	0.77	61.60	72	63.88
Elmidae	0.009	0.94	< 0.001	1.04	2.65	0.04			
Hydraenidae (fragment)				0.28	0.88	0.004			
Diptera									
Ceratopogonidae	0.006	0.56	< 0.001	0.03	1.77	0.001			
Chironomidae	0.04	5.64	0.003	0.02	2.65	0.001	0.12	4	0.007
Chironomidae pupae	0.07	1.32	0.001						
Simuliidae	0.93	18.05	0.21	0.07	4.42	0.005			
Simuliidae pupae	0.05	1.88	0.001						
Empididae	0.06	1.50	0.001						
Dixidae	0.002	0.19	< 0.001						
Diptera with cocoon	0.003	0.19	< 0.001						
Unidentified larvae				0.02	3.54	0.001	0.30	16	0.07
Hemiptera									
Gerridae	0.01	0.38	< 0.001						

Table 1. Continued...

	Site F1			Site F2			Site A		
	V_o	F_o	IA	$\overline{V_o}$	F_o	IA _I	$\overline{V_o}$	F_o	IA
Decapoda									
Macrobrachium	0.15	1.13	0.002						
Trichodactylus	0.22	0.75	0.002						
(fragment)									
Aquatic arthropod	0.12	0.38	0.001	1.28	19.47	0.36	0.49	8	0.06
fragment									
Crustacean fragment				0.06	2.65	0.002	0.36	8	0.04
Invertebrate unidentified	0.30	2.26	0.008	14.76	80.53	17.18	23.84	96	32.96
larvae									
Hymenoptera*									
Formicidae*	0.35	4.89	0.02	2.32	25.66	0.86	2.34	20	0.67
Unidentified adult*	1.29	7.71	0.12	1.34	3.54	0.07			
Hemiptera fragment*	0.10	1.13	0.001	0.09	0.88	0.001			
Coleoptera*	0.71	4.89	0.04	3.34	4.42	0.21			
Diptera*	0.05	1.69	0.001	0.23	1.77	0.006			
Araneae*	0.14	1.50	0.003						
Terrestrial arthropod				7.48	46.90	5.07	3.41	24	1.18
fragment*									
Insect fragment*	4.10	21.43	1.09	0.82	2.65	0.03	1.09	8	0.13
Others items									
Oligochaeta	0.08	0.38	< 0.001						
Fish parts	0.17	0.19	< 0.001						
Scale	0.001	0.38	< 0.001	0.05	2.65	0.002	0.55	12	0.09

a larger contribution at site A ($\chi^2 = 91.77$; df = 1; p < 0.05) (IAi = 97.8%) (Figure 3b).

Only site F2 showed significant difference in diet composition between seasons ($\chi^2 = 12.08$; df = 1, p < 0.05), due to increased consumption of vegetal items during the dry season (V% = 80.25 and IAi = 81.04). Diet did not alter significantly between seasons at sites F1 and A, with vegetal items having higher values at site F1 $(\chi^2 = 0.76; df = 1; p > 0.05) (V\%_{dry} = 90.32, V\%_{rainy} = 88.46; IAi_{dry} = 95.03, IAi_{rainy} = 90.87) and animal items having$ higher values at site A in both seasons ($\chi^2 = 2.17$; df = 1; p > 0.05) (V% $_{\rm dry}$ = 97.13, V% $_{\rm rainy}$ = 95.06; IAi $_{\rm dry}$ = 99.51, IAi $_{\rm rainy}$ = 98.38). In the NMDS analysis, the sites with higher vegetation cover (F1 and F2) were grouped along the first axis due to similarity in diet composition, but the different diet composition at site A located it further away on this axis, with seasonal changes in diet at site A evident on the second axis (Figure 4). This result was observed because of the higher occurrence and volume (V% = 64.4and FO% = 78.9) of the food item Curculionidae at site A during the rainy season.

The Alimentary Index of vegetal and animal items showed a significant difference between the diets of juveniles and adults at site F1 ($\chi^2 = 20.27$; df = 1; p < 0.05), where adults consumed higher amounts of vegetal matter than juveniles (IAi _{adults} = 93.49 and IAi _{juveniles} = 67.20). At sites F1 and F2 a significant difference in intestinal quotient (Qi)

was observed between juveniles and adults, with average values of 0.68 for juveniles and 0.86 for adults at site F1 (t = 4.856; df = 598; sd = 0.18; p < 0.05) and 0.66 for juveniles and 1.02 for adults at site F2 (t = 3.039; df = 99; sd = 0.24; p < 0.05). At site A there was no significant difference in the average Qi between adults (0.93) and juveniles (0.73) (t = 1.942; df = 23; sd = 0.28; p > 0.05). The analysis of variance (ANOVA) of the average Qi for juveniles showed no significant difference among the three sites (F = 2.25; sd = 0.16; p > 0.05). However in adults, the Kruskal-Wallis test found the average Qi to be significantly different among the sites (χ^2 = 34.38; df = 2; sd = 0.18; p < 0.05).

4. Discussion

The diet of Astyanax taeniatus varied among the sites in the Mato Grosso stream with evidence of a relationship between diet and environmental characteristics, supporting our hypothesis. According to the river continuum concept proposed by Vannote et al. (1980), there is a gradient of physical conditions within a river that determines a continuum of abiotic variation and patterns of transport, utilization and storage of organic matter along is length. The diet of neotropical fishes is largely based on allochthonous material (mainly terrestrial insects and terrestrial plant

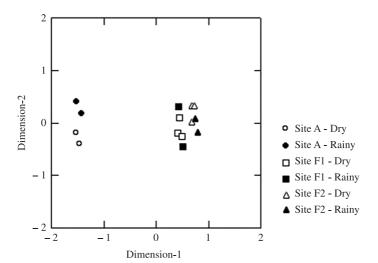


Figure 4. NMDS analysis of volumetric data of food items in the diet of *Astyanax taeniatus* at three sites in the Mato Grosso stream, Saquarema, Rio de Janeiro.

material) in upstream sites and on autochthonous material in downstream sites (Lowe-McConnel, 1999). In the Mato Grosso stream *Astyanax taeniatus* had a varied diet. Distinct feeding behaviour with high plasticity has been previously described for this genus (Costa, 1987; Cassemiro et al., 2002; Gomiero and Braga, 2003; Borba et al., 2008; Wolff et al., 2009). In this study, and in another by Bennemann et al. (2005), the diet of *Astyanax* species was found to consist primarily of allochthonous insects and terrestrial plant debris, and changes in the consumption of these resources were related to physical changes in the environment.

Astyanax taeniatus in the Mato Grosso stream shows trophic opportunism, meaning that the feeding habits of the species change according to the physical conditions of the environment, in this case, a decrease in the amount of allochtonous resources (mainly plant debris) along the river continuum. According to Gerking (1994) opportunistic species are able to use food items that are different from their usual diet. Opportunism has been observed previously in the Astyanax genus and is exemplified by the change in feeding habits observed in Astyanax altiparanae following the impoundment of a reservoir (Cassemiro et al., 2005) and by a study of Astyanax fasciatus which fed mainly on zooplankton in a reservoir (Arcifa et al., 1991).

In contrast with other studies, which found the input of allochthonous material (e.g. plant debris) to be higher during the rainy season rather than the dry season (e.g. Costa, 1987; Afonso et al., 2000), this study found the consumption of vegetal allochthonous items to be higher during the dry season in upstream sites. This seasonal variation in diet may be related to the opportunistic habits of the species (Gerking, 1994), which seeks food according to its availability in different seasons (Andrian et al., 2001). Temporal changes in fish diet (e.g. Vilella et al., 2002; Mazzoni and Rezende, 2003; Pinto and Uieda, 2007) may be influenced by a seasonal variation in the availability of

food resources (Schlosser, 1982) affecting predator-prey interactions (Winemiller, 1989).

At the downstream site, *Astyanax taeniatus* exploited different items of the same (animal) origin at each season. Moraes (2010) previously studied a species of the Heptapteridae family at the same site in the Mato Grosso stream and found that during the rainy season Curculionidae was a highly significant diet item, an observation also made in the present study. Aquatic larvae of the Curculionidae family (Coleoptera) are herbivorous, and inhabit emerging aquatic plants and have an intimate relationship with the aquatic and semi-aquatic flora (Triplehorn and Johnson, 2005). At this site of the Mato Grosso stream, there is marginal vegetation (Costa, 1987; Miranda, 2009; Mazzoni et al., 2010b) and as a consequence, a high availability of these invertebrates, contributing to their presence as a diet item.

Adults of *Astyanax taeniatus* from the Mato Grosso stream consumed a higher proportion of vegetal items than the juveniles. This is also seen in other species of the Characidae family (e.g. Barreto and Aranha, 2006; Wolff et al., 2009; Mazzoni et al., 2010a), indicating that the relationship between intestine length and the standard length of a species varies during the growth of an individual (Mazzoni et al., 2010a). The intestinal quotient (Qi) can be a useful tool for evaluating ontogenetic variations in the diet of fish (Zavala-Camim, 1996), and an increase in the intestinal quotient of adults may be associated with high plasticity, the capacity for food spectrum expansion (Andrian et al., 2001) and the utilization of less digestible (e.g. vegetal) food items (Sabino and Castro, 1990; Zavala-Camim, 1996).

The differences in intestinal quotient (Qi) of adults at the three sites of the Mato Grosso stream may be associated with a higher contribution of vegetal allochthonous material, as seen in sites where there is an influence of riparian vegetation in the fish diet (Afonso et al., 2000; Cassemiro et al., 2002;

Gomiero and Braga, 2003; Borba et al., 2008). This agrees with the findings of Barbieri et al. (1994) that showed fish with herbivorous feeding habits have higher intestinal quotient than omnivores who tend to insectivorous diets.

The occurrence of the changes in diet observed in this study is consistent with the dynamics of each environment causing fluctuations in the availability of food resources (Abelha and Goulart, 2004). Additionally, the species composition, trophic groups and their ecology (e.g. trophic ecology) can change along the stream course due to abiotic factors (Vannote et al., 1980). The Mato Grosso stream is a third order system in which variations are found along its course, which allowed observations of dietary changes in Astyanax taeniatus to be made. Therefore, this species can be considered to be generalist and opportunistic, showing high trophic plasticity by using different types of resources (vegetal and animal) of different origin (alochthonous and autochthonous), in concordance with several other reports for species of the same genus (e.g. Andrian et al., 2001; Deus and Petrere-Junior, 2003; Bennemann et al., 2005; Pinto and Uieda, 2007).

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