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Feeding ecology of *Leporinus taeniofasciatus* (Characiformes: Anostomidae) before and after installation of a hydroelectric plant in the upper rio Tocantins, Brazil

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The feeding ecology of *Leporinus taeniofasciatus* in the upper rio Tocantins was characterized before (river phase) and after (reservoir phase) its impoundment by the Serra da Mesa Hydroelectric Dam. The importance of each food item was given by the Alimentary Index (IAi), which combines the frequency of occurrence and volumetric methods. A significant difference in the diet of *L. taeniofasciatus* between seasons in the river phase, detected by a multivariate analysis of variance, was not kept when the reservoir was formed. Its feeding activity, verified through the percentage of stomachs with different degrees of fullness, was not affected by the impoundment. *Leporinus taeniofasciatus* was able to incorporate terrestrial food items to its diet when they became abundantly available at the beginning of reservoir formation. Despite this plasticity, secondary factors such as predation and competition might have affected its adaptation in the new, more homogeneous environment. Its diet was not significantly different in the lotic sites between the distinct phases, suggesting that the remaining upstream lotic environments still provide favorable conditions for this species, reinforcing the need to preserve those habitats, as *L. taeniofasciatus*, which is apparently endemic to the Tocantins basin, may be threatened.

A ecologia alimentar de *Leporinus taeniofasciatus* no alto rio Tocantins foi caracterizada antes (fase rio) e após (fase reservatório) seu represamento pela Usina Hidrelétrica Serra da Mesa. A importância de cada item alimentar foi dada pelo Índice Alimentar (IAi), que combina os métodos de freqüência de ocorrência e volumétrico. Uma diferença sazonal significativa na dieta de *L. taeniofasciatus* durante a fase rio, que não foi mantida durante a formação do reservatório, foi detectada através de uma análise de variância multivariada. A atividade alimentar, verificada pela porcentagem de estômagos com diferentes graus de repleção, não foi afetada pelo represamento. *L. taeniofasciatus* foi capaz de incorporar itens alimentares terrestres a sua dieta quando estes se tornaram abundantes no começo da formação do reservatório. Apesar desta plasticidade, fatores secundários tais como predação ou competição podem ter afetado sua adaptação no ambiente novo e mais homogêneo. Sua dieta não foi significativamente diferente nas localidades lóticas entre as fases distintas, sugerindo que os ambientes lóticos remanescentes à montante ainda provêem condições favoráveis para esta espécie. Este fato reforça a necessidade de preservar estes ambientes, uma vez que *L. taeniofasciatus*, aparentemente endêmica à bacia do Tocantins, pode estar ameaçada.

Key words: diet, fish, Neotropical, reservoir.

Introduction

The construction of large dams remains a prevailing practice in Brazil to supply the increasing demand of energy, despite the numerous negative effects of such projects (*e.g.* Mérona *et al.*, 1987; Agostinho *et al.*, 1992; Agostinho *et al.*, 1999). The rio Tocantins had its upper stretch impounded by the Serra da Mesa Hydroelectric Dam in October 1996.

Current data estimate a total of approximately 200 fish species for this track (Figueiredo *et al.*, in press). The family Anostomidae, endemic to South America, consists of about 10 genera and 100 species (Géry, 1977), and is represented by 14 species in the studied area. *Leporinus taeniofasciatus* was recently described by Britski (1997), and no information about its biology had yet been made available. According to current data, this species is restricted to the Tocantins basin. It was recorded as one of the ten most important species in frequency and biomass in the affected region of the reservoir prior to the impoundment. However, from October 1997 on, it has been encountered only in the remaining upstream lotic sites (Pellegrini-Caramaschi *et al.*, in press).

A major impact of reservoirs is to reduce the natural

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periodicity of rivers, and a common response at the community level is the gradual reduction of species diversity. Some fish respond very quickly to impoundment whereas others respond gradually over years or decades, according to their trophic nature (Agostinho *et al.*, 1999).

As diet and plasticity seem to be primary factors influencing distribution and differential survival of species after the damming of rivers (Hahn *et al.*, 1997), the study of their feeding and interaction with the environment supplies crucial information on the fish community in reservoirs. In comparison to temperate ecosystems, long-term alterations are less predictable for tropical reservoirs. Hahn *et al.* (1997) pointed out some associated problems, such as the lack of knowledge about the autoecology of many species, their generalized diet plasticity, the endemic features of each system, and the lack of consistent, long-term studies on the natural environment prior to the impact caused by the impoundment. According to Agostinho *et al.* (1999), the effects of damming can be monitored through studies on the before-after intervention type, and the management of reservoirs should aim not only to increase fisheries production but also to maintain species diversity.

Our data, combined with that obtained for other species, will allow the proposal of management strategies for the area impacted by the dam. In this paper we characterize the feeding ecology of *L. taeniofasciatus* in the upper rio Tocantins and relate it to environmental changes, both natural (hydrological regime) and anthropogenic (impoundment). The reduced occurrence of *L. taeniofasciatus* in the area under the influence of the impoundment leads us to hypothesize that its feeding ecology was affected by dam construction.

Material and Methods

The study area is located in the upper rio Tocantins, Brazil (48°06'/ 49°06'W and 13°34'/ 14°44'S) (Fig. 1), which was impounded in 1996 by the Serra da Mesa Hydroelectric plant. The reservoir filled until reaching its current size of 1724 km^2 in April 1998, when the dam started operating to generate energy. Before the impoundment, the affected portion of the river was a succession of waterfalls, riffles and pools within constrained reaches, surrounded by cerrado vegetation, a type of wet seasonal savanna occurring mostly in central Brazil (Felfili & Silva Jr., 1993). This region has a well-defined hydrological regime: high waters, from November to April, and low waters, from May to October.

Fish were captured bimonthly with a standardized set of gill nets left for 24 hrs and monitored every 8 hrs in 14 selected sites on the upper rio Tocantins, Brazil (Fig. 1), from February 1996 to April 1998. This period comprises the river phase (February 1996 to October 1996), corresponding to the natural river condition prior to damming, and reservoir phase (December 1996 to April 1998), corresponding to the filling stage, when sampling sites already presented lentic characteristics. Some remaining lotic sites were also sampled after the impoundment. In order to detect changes related to seasons, reservoir formation, or a combination of both, these phases were subdivided in river/flood, river/drought, reservoir/ flood and reservoir/drought, each of them encompassing a six-month period. The captured specimens were measured, weighed and their digestive tract removed and fixed in 5% formaldehyde.

Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo: MZUSP 51073 (holotype) and 51074, 51212-51219 (paratypes), and also at the Museu Nacional do Rio de Janeiro: MNRJ 15210.

The gut contents of 183 specimens of *L. taeniofasciatus* with standard length between 8.1 cm and 15.8 cm (mean = 11.2 cm) were analyzed. Food items were separated to categories and their volume was measured in a 1 mm high square-shaped transparent dish with a scale in millimeters underneath so that the area corresponded to the volume. Food items were identified to the lowest suitable taxonomic category and listed. Nevertheless, for graphical representation and statistical purposes the data was grouped in 22 categories, as shown in the results.

The frequency of occurrence (Hynes, 1950; Hyslop, 1980) and volumetric (quantitative) measurements were combined in the Alimentary Index (IAi) proposed by Kawakami & Vazzoler (1980) to characterize the diet.

In order to assess feeding activity, the degree of fullness of each stomach was recorded as follows: 1 (<25%); 2 (25-50%); 3 (50-75%) and 4 (75-100%). The percentage of half-full (1; 2) and totally full stomachs (3; 4) was verified for river and reservoir environments.

A multivariate analysis of variance was performed in the MULTIV software (Pillar, 1999) to test significant differences in the diet of *L. taeniofasciatus* related to environmental changes, such as season and reservoir formation. In this method each individual (stomach) is treated as a sampling unit and each prey as a variable, whose value is given by its volume relative to the total volume of stomach content (VO%). A randomization test was performed with 1000 iterations in order to test comparisons between groups of sampling units. These units were defined by two factors, namely season/ phase (river/ flood, river/ drought, reservoir/ flood and reservoir/ drought), and flow/ phase (river/ lotic, reservoir/ lotic and reservoir/ lentic). As the aforementioned analysis is akin to a conventional analysis of variance, differing only in the way probabilities are obtained, results are interpreted similarly. For details see Pillar & Orlóci (1996).

Results

All 22 food categories were found in the stomach contents of *L. taeniofasciatus* in the river phase, and 18 were present in the reservoir phase, when seasonal differences are not accounted for. The frequency of occurrence (FO%), percentual volume (VO%) and IAi values for each item are shown in Table 1. The graphical representation of IAivalues of the main food items in the river and reservoir environments is shown in Fig. 2. Vegetal material (plant debris and seeds +

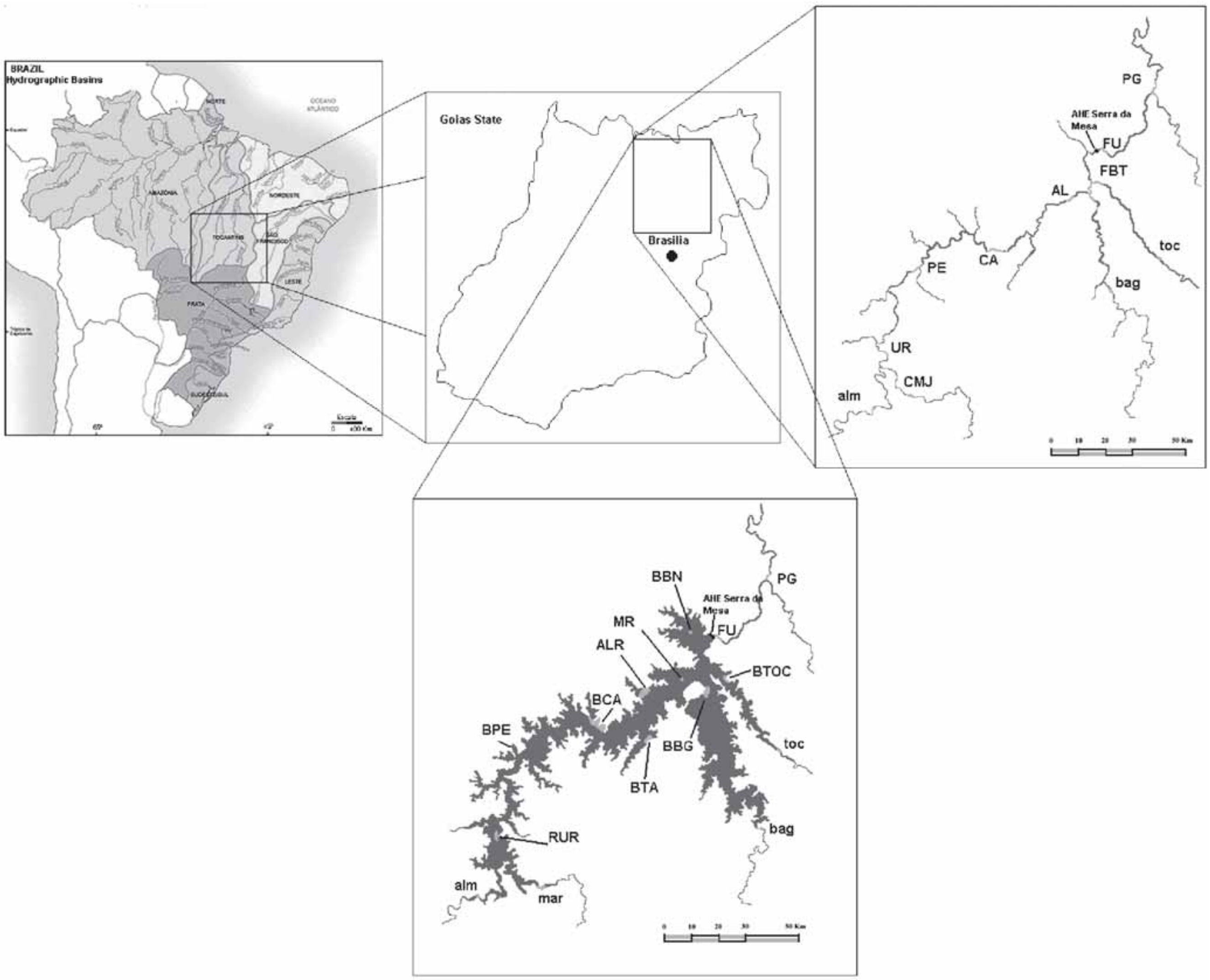

Fig. 1. Location of the upper rio Tocantins, showing the region where the Serra da Mesa hydroelectric plant was installed. Details show sampling sites during the river (top on the right) and reservoir phases.

fruits) was among the main food items in all periods, whereas chironomids were more important during the dry periods, both in the river and reservoir phases. Isoptera was one of the main items during the period of six months after the impoundment (reservoir/ flood), when a substantial increase in consumption of rests of insects was also registered.

When items are assigned as either autochthonous or allochthonous, the former shows a greater importance in the diet of *L. taeniofasciatus* in all periods analyzed, except during the river/ flood, as shown in Fig. 3. The lowest and highest percentages were found during the high waters and the low waters in the river phase, respectively (Fig. 3). Stomachs with different degrees of fullness had nearly the same percentage of occurrence (Fig. 4), indicating a similar feeding activity both in the river and in the reservoir.

The statistical analysis showed highly significant differences in the diet of *L. taeniofasciatus* between high waters and low waters in the river phase, and between lotic and lentic sites (Table 2). Remaining lotic sites in the reservoir phase were not significantly different from the river phase. The six-month period right after the damming showed a significantly different diet composition for *L. taeniofasciatus* when compared to all the other periods (Table 2).

Discussion

The diet of *Leporinus taeniofasciatus* is comprised of both vegetal and animal resources, characterizing an omnivorous feeding habit. The substantial amounts of sediment and benthic organisms such as insect larvae and filamentous algae in the stomach contents indicate a bottom-associated feeding behavior. This evidence is also supported by its subterminal mouth (Albrecht *et al.*, 2001), although mouth position is not always a strict indication of feeding habit for anostomids (Santos & Rosa, 1998).

Gerking (1994) utilized the term particulate feeders for

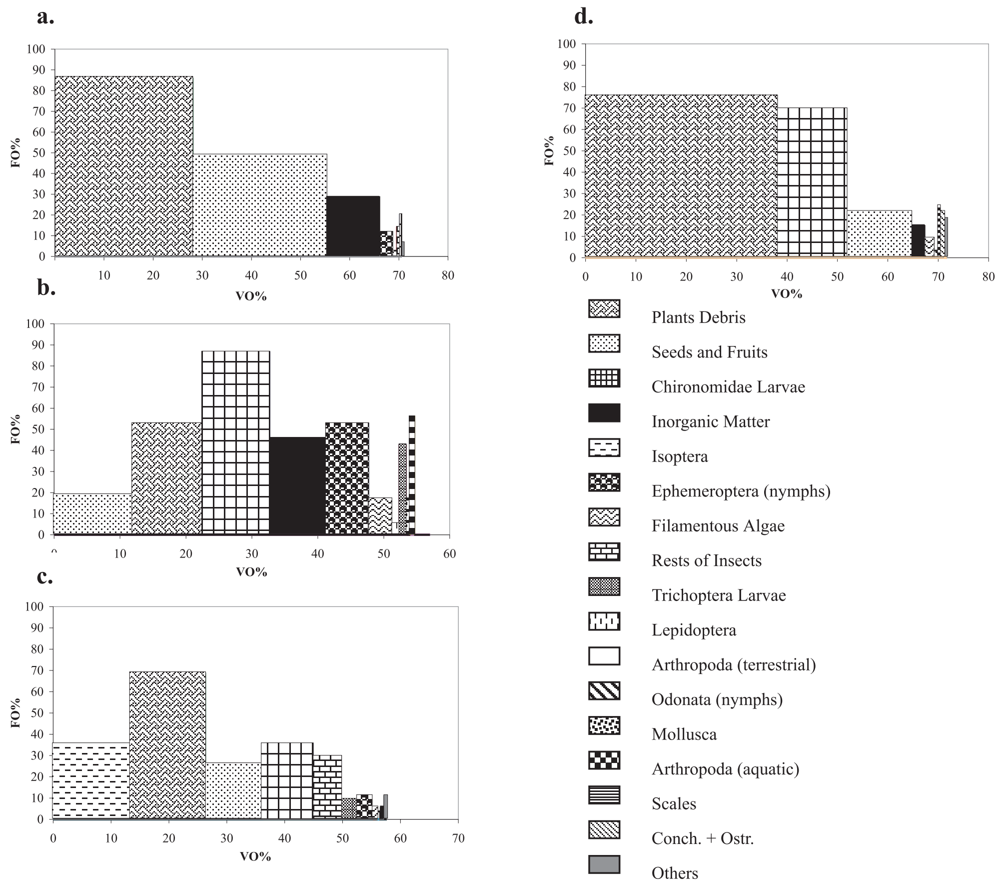

Fig. 2. Representation of the main food items, except organic matter (OM), in the diet of *Leporinus taeniofasciatus* in the upper rio Tocantins, region of Serra da Mesa. **a.** River/ flood; **b.** River/ drought; **c.** Reservoir/ flood; **d.** Reservoir/ drought.

species that use visual cues to search and capture small, living food items, which seems to be the case for *L. taeniofasciatus*. Keenleyside (1979) suggests that cladocerans and cyclopoid copepods, which are relatively weak swimmers, would thus be caught by particulate feeding. These were, in fact, the only zooplanktonic organisms found, albeit never in great amounts, in the stomach contents of *L. taeniofasciatus*. Their relative scarcity is probably a consequence of not being strained from the water by the gill raker apparatus (Albrecht *et al.*, 2001). Furthermore, the searching behavior of diurnally active fishes, as *L. taeniofasciatus* is (pers. obs.), shows the importance of vision in this feeding process.

Fishes are highly responsive to seasonal changes in food availability (Hart, 1986; Lowe-McConnel, 1987), a tendency clearly observed in the diet of *L. taeniofasciatus.* During the flood period, vegetal resources and organic matter, probably of allochthonous origin, were the most abundant items. It seems to be energetically more advantageous to catch drift items that fall into the water than to make the effort to sink and hold position for bottom feeding. Another interpretation is that washing out of invertebrates is one of the immediate effects of floods on stream ecosystems in general, thus affecting short-term feeding opportunities for fish (Matthews, 1998). Increased turbidity can also be regarded as a factor changing foraging regime of fish either directly by interfering with visual references to search for food, or indirectly by reducing primary production (Matthews, 1998). There is a great deal of literature reporting seasonal dietary shifts with a higher consumption of allochthonous items during the high water seasons (*e.g.* Goulding, 1980; Angermeier, 1982; Braga, 1990; Winemiller & Jepsen, 1998; Albrecht & Caramaschi, 2003).

During the low water periods, *L. taeniofasciatus* seems to have been found closer to the bottom. This increases the likelihood of encounters with epibenthic prey and explains the increased consumption of non-drifting items such as chironomid and trichopteran larvae, and ephemeropteran nymphs. Chironomids are the most abundant and diversified components of benthic macroinvertebrate community (Strixino & Trivinho-Strixino, 1998), and play an important role in the diet of *L. taeniofasciatus*, mainly in the dry period. Likewise, benthic microcrustaceans (ostracods and conchostraceans) were more important during the dry season, when cladocerans and copepods were absent. Aquatic arthropods, primarily water mites, were much more frequently preyed upon within the flood period, but presented a low IAi value exactly due to the small

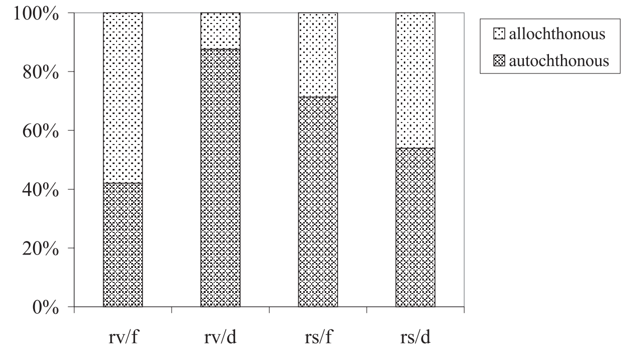

Fig. 3. Proportion of autochthonous and allochthonous items in the stomach contents of *L. taeniofasciatus* (based on IAi values) in the upper rio Tocantins before and during reservoir formation: River/ flood (rv/f); River/ drought (rv/d); Reservoir/ flood 1 (rs/f1); Reservoir/ drought (rs/d).

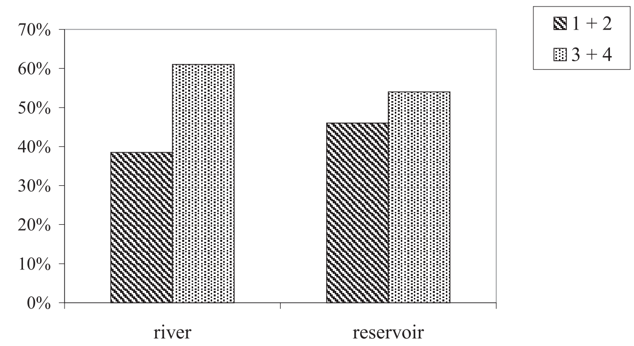

Fig. 4. Percentage of stomachs of *L. taeniofasciatus* with different degrees of fullness. 1 + 2 = half full, and 3 + 4 = totally full.

size of mites. Other aquatic arthropods like coleopterans or hemipterans were rarer. Although aquatic insects are widely distributed, they are not easily captured due to their fast and irregular swimming behavior (Andrian *et al.*, 1994).

Although IAi, VO% and FO% are average values, which might create biased results that neglect individual variations, their assessment is useful to detect changes at the population level. Indeed, individual variations proved to be very high within the groups, as the percentage explained by the analyzed factors is very low. However, unknown factors other than phase, flow and season could be also contributing to the feeding patterns. Fishes are very flexible as can be observed through comparisons between individuals, as well as ontogenetic, seasonal and diel changes in the diet (Gerking, 1994).

During the filling stage several islands were formed, thus providing several shores with abundant food sources. The differentiated seasonal dependence on autochthonous items was not maintained in the reservoir environment. Although the beginning of the filling stage coincides with a flood season, the percentage of allochthonous items was lower than in the river phase. This result, however, can be misleading, as organic matter, considered autochthonous, accounts for

Table 1. Relative volume (VO%), frequency of occurrence (FO%) and Alimentary Index (IAi) of food items in the diet of *L. taeniofasciatus* from the upper rio Tocantins before and during the filling stage of the reservoir of the Serra da Mesa Hydroelectric Dam, central Brazil. Reservoir/ lotic comprises both flood and drought seasons during the filling stage, whereas reservoir/ lentic was only sampled during the flood season (up to 6 months after the closure of detour tunnels).

	river/ flood			**river/ drought**			**reservoir/ lotic**			**reservoir/ lentic**		
food items	**VO (%)**	**FO (%)**	**IAi*100**	**VO (%)**	**FO (%)**	**IAi*100**	**VO (%)**	**FO (%)**	**IAi*100**	**VO (%)**	**FO (%)**	**IAi*100**
Arthropoda (aquatic)	0.047	5.71	0.00422	0.575	55.93	0.50578	0.013	5.66	0.00116	0.006	2.94	0.00031
Chironomidae (pupae and larvae)	0.112	20.00	0.03497	9.939	86.44	13.51367	6.591	47.17	4.92896	14.645	50.00	11.93597
Other Diptera (larvae and pupae)	0.040	5.71	0.00352	0.256	55.93	0.22491	0.030	11.32	0.00543	0	0	0
Coleoptera (larvae)	0.028	5.71	0.00246	0.182	22.03	0.06301	0	0	0	0	0	0
Lepidoptera (larvae)	0	0	0	1.171	5.08	0.09368	0	0	0	0	0	0
Trichoptera (pupae and larvae)	0.002	2.86	0.00011	0.971	42.37	0.64746	3.453	7.55	0.41316	0.087	8.82	0.01251
Ephemeroptera (nymphs)	2.457	11.43	0.43694	6.251	52.54	5.16618	3.157	9.43	0.47215	0.106	5.88	0.01017
Odonata (nymphs)	0	0	0	0.490	3.39	0.02612	0	0	0	0.573	5.88	0.05492
Arthropoda (terrestrial)	0.002	2.86	0.00011	0.079	6.78	0.00841	0	0	0	1.167	5.88	0.11187
Isoptera	0.008	2.86	0.00035	0.018	3.39	0.00094	6.045	7.55	0.72337	16.244	44.12	11.68201
Rests of Insects	0.430	14.29	0.09551	0.328	15.25	0.07861	4.312	20.75	1.4188	3.055	26.47	1.31809
Cladocera + Copepoda	0.032	2.86	0.00141	0	0	0	0	0	0	0.006	2.94	0.00031
Conchostraca + Ostracoda	0.007	8.57	0.00095	0.290	15.25	0.06961	0.001	1.89	4.3E-05	0.212	5.88	0.02034
Mollusca (Gastropoda + Bivalvia)	0.316	8.57	0.04211	0.681	16.95	0.18143	0.310	9.43	0.04634	0	0	0
Invertebrate Eggs	0.002	2.86	0.00011	0.135	15.25	0.03233	0.130	13.21	0.02716	0.129	5.88	0.01241
Rests of Fish	0.047	2.86	0.00211	0.077	5.08	0.00612	0.072	1.89	0.00216	0.366	5.88	0.03509
Scales	0.007	8.57	0.00095	0.537	23.73	0.20043	0.180	20.75	0.05908	0.019	8.82	0.00275
Plant Debris	28.023	85.71	37.38185	10.640	52.54	8.79371	24.554	73.58	28.6464	10.711	67.65	11.81132
Seeds and Fruits	27.071	48.57	20.46328	12.075	18.64	3.54116	11.273	33.96	6.07033	9.758	8.82	1.40352
Filamentous Algae	1.029	2.86	0.04573	3.598	16.95	0.95930	1.214	7.55	0.14528	0.942	5.88	0.09031
Organic Matter	29.418	80.00	36.62635	43.006	88.14	59.62169	37.217	96.23	56.7802	41.337	91.18	61.43708
Inorganic Matter	10.923	28.57	4.85696	8.704	45.76	6.26543	1.448	11.32	0.25995	0.636	5.88	0.06102
n		**37**			**59**			**59**			**28**	

more than 60%. Isoptera, which was a rather chance item in the diet of *L. taeniofasciatus* in the natural environment, becomes one of the most important items during the filling stage. This importance is detectable mainly in the six first months after the dam closure, which also coincides with the seasonal flood period. As isopterans are also very rare during the natural high waters, and as it is present only in specimens from lentic sites, we can deduce that it became available as a consequence of reservoir formation, being readily incorporated into *L. taeniofasciatus* diet. Their amount, however, declined rapidly following the initial reservoir filling stage and became absent from stomach contents in the following six months. From this period on, alterations in the diet of *L. taeniofasciatus* in the reservoir were not verifiable, as the species became restricted to lotic sites.

Quirós & Boveri (1999) state that the change from a high flow to a low flow system tends to select a few riverine species previously adapted to floodplain habitats. Considering the degree of stomach fullness, the feeding activity of *L. taeniofasciatus* was not highly affected in the new lentic environment. Although the availability of food influences the amount consumed (Lagler *et al*., 1997), in the case of anostomids, feeding activity is also reported to be related to reproduction periods (Barbieri & Garavello, 1981; Santos, 1982). Lima (2000) showed that *L. taeniofasciatus* used the sampled area in the riverine environment as a spawning site and that its reproduction activity in the area was jeopardized by dam construction. Simultaneously, a rise in the condition factor (K) occurred in the reservoir (Lima, 2000). It can thus be interpreted that *L. taeniofasciatus* fed on highly energetic food sources during the filling stage but was not able to convert such gains into reproduction. Fish can change allocations of resources according to environmental conditions and population densities (Lowe-McConnel, 1987). The dam created a new, more homogeneous environment, where this species at first profited from the greater food supply. However, despite this plasticity, other factors may have subsequently affected the permanence of the species in the reservoir. The lack of lotic and heterogeneous microhabitats may have increased its vulnerability to other biotic factors such as predation and competition. Therefore, although indirectly, the diet of *L. taeniofasciatus* was affected by the reservoir formation.

This shift was accompanied by a sharp decrease in the capture of *L. taeniofasciatus* from the lentic environment, beginning in the ninth month after the start of the filling stage (Mazzoni & Petito, in press). Consequently, the feeding ecology of this species could no longer provide direct responses to questions about further environmental changes in the reservoir. Most of individuals representing the reservoir/ drought group originated from lotic sites. It could be thus expected that the periodicity was maintained, what was not observed, as the period corresponding to low waters in the reservoir differs from the drought period in the river, but not from the flood. In contrast, the fact that its diet did not vary significantly in lotic sites as a whole between the distinct periods (river and reservoir phases) indicates that the river environment still provides favorable conditions for this species.

Our results reinforce the need to preserve remaining upstream lotic environments, such as the rios Maranhão and Almas. *Leporinus taeniofasciatus*, which is by now believed to be endemic to the Tocantins basin, may be seriously threatened and such free flow habitats are critical to its survival.

Table 2. Probabilities generated in the randomization test of the independence of diet composition of *L. taeniofasciatus* from season and reservoir formation ($\alpha \leq 0.05$). Stomach contents are assigned to groups defined by the combination of (1) phase/ season, and (2) phase/ flow. Contrast coefficients specify which cases are compared, as follows: river/ flood (rv/f), river/ drought (rv/d), reservoir/ flood (rs/ f) and reservoir/ drought (rs/d) for group 1, and river/lotic (rv/lt), reservoir/lotic (rs/lt) and reservoir/ lentic (rs/ln) for group 2.

Source of variation				sum of squares	P
phase/season:				5.8848	0.001
Between groups					
Contrasts:					
rv/f	**rv/d**	**rs/f**	**rs/d**		
1	-1	0	0	3.931	0.001
1	0	-1	0	2.729	0.001
1	0	0	-1	0.62823	0.117
0	1	-1	0	1.0152	0.016
0	1	0	-1	1.9409	0.001
0	0	1	-1	1.2956	0.008
phase/flow:					
Between groups				1.5899	0.023
Contrasts:					
rv	**rs/lt**	**rs/ln**			
1	-1	0		0.63249	0.131
1	0	-1		0.90213	0.033
0	1	-1		0.93169	0.029
phase/season x phase/flow				-0.1269	0.655
Between groups				7.3478	0.001
Within groups				58.951	
Total				66.299	

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