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# Feeding Ecology of *Leporinus friderici* (Teleostei; Anostomidae) in the Upper Tocantins River, Central Brazil, before and after Installation of a Hydroelectric Plant

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## Abstract

The feeding ecology of *Leporinus friderici* Bloch, 1794 was investigated in the upper Tocantins River, before and after its impoundment by the Serra da Mesa Hydroelectric Dam. *Leporinus friderici* was classified as an euryphagic, omnivorous species. Allochtonous food items formed a high proportion of its diet in all periods analysed, except in the later stages of reservoir formation. Its diet did not vary significantly between high-water and low-water seasons in the riverine environment, although it differed qualitatively. *Leporinus friderici* was very opportunistic, rapidly changing its diet to profit from the abundant terrestrial food sources when the reservoir started to flood the surrounding land, and shifting again when terrestrial food items became exhausted.

## Resumo

A ecologia alimentar de *Leporinus friderici* Bloch, 1794 foi investigada no alto rio Tocantins antes e após seu represamento pelo AHE Serra da Mesa. A espécie foi classificada como onívora e eurifágica. Um consumo maior de itens alóctones foi observado em todos os períodos analisados, exceto em estágios posteriores de formação do reservatório. A dieta não variou significativamente entre as estações de águas altas e águas baixas no ambiente de rio, embora a composição qualitativa tenha sido diferente. *Leporinus friderici* demonstrou um comportamento claramente oportunista, mudando sua dieta rapidamente para aproveitar a abundância de itens de origem terrestre quando o reservatório começou a inundar as margens, e depois alterando novamente conforme esses itens foram se tornando escassos.

**Keywords:** Anostomidae, diet, omnivory, reservoir, Tocantins River, Brazil.

## Introduction

The family Anostomidae is a distinctive group of some ten genera endemic to South America, with representatives in all the Brazilian hydrographic basins (Géry, 1977). Many genera are monotypic, but the genus *Leporinus* contains more than 70 nominal species (Vari, 1983). *Leporinus friderici* seems to be the most widespread species of this genus, occurring in all the main South American river basins except the São Francisco (Garavello, pers. communication). This species is exploited by commercial and subsistence fisheries throughout its range; and is of interest because of its potential for farming, a growing economic activity in Brazil. Several studies have investigated aspects of its biology, e.g., reproduction (Godoy, 1975; Barbieri & Santos, 1988) and feeding ecology (Knöppel, 1972; Goulding, 1980; Barbieri & Garavello, 1981; Santos, 1982; Andrian et al., 1994). These studies have established that *L. friderici* is omnivorous, but the composition of its diet varies with region and type of environment.

*Leporinus friderici* was one of 14 anostomids recorded for the upper Tocantins River in the stretch impounded by the Serra da Mesa Hydroelectric Dam (Figueiredo et al., in press). The region has a well-defined hydrological regime: high water from November through April and low water from May through October. The river diversion tunnels were closed in October 1996, and filling of the reservoir continued until June 1998, when the power plant began operat-

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ing. *Leporinus friderici* was the second most important species, in terms of frequency and biomass, during the reservoir filling stage (Caramaschi et al., in press).

One major impact of reservoirs is their reduction of the natural periodicity of rivers. The biota in the new, lentic environment becomes subject to non-cyclic disturbances related to dam operations. A common response at the community level is the gradual reduction of species diversity (Agostinho et al., 1999). Some fish respond quickly to impoundment, whereas others respond only after years or decades, according to their trophic nature (Agostinho et al., op. cit.).

Because diet and feeding plasticity seem to be primary factors influencing the distribution and differential survival of species after damming (Hahn et al., 1997), the study of their feeding and interaction with the environment supplies crucial information. The nature of long-term changes in the fish fauna is less predictable for tropical than for temperate reservoirs (Hahn et al., 1997). These changes may depend on the autecology of many species, their generalised feeding plasticity, and the endemic features of each system. However, few consistent, long-term studies have examined the natural environment prior to the impact caused by damming (Hahn et al., 1997). According to Agostinho et al. (1999), the effects of damming on structural and functional characteristics of lotic ecosystems can be established by monitoring studies done before and after intervention, considering that the dam is an abrupt and permanent intervention.

Here, we present data on the feeding ecology of *Leporinus friderici* in the upper Tocantins River, and relate it to environmental changes caused by the hydrological regime and by the impoundment. The extraordinary increase in catches of *L. friderici* during the filling stage (Mazzoni & Petito, in press) led us to hypothesise that this species profited from the reservoir formation because of its feeding behaviour. In the long term, we intend to use our data, combined with data for other species, to propose management strategies for the stretch of the river impacted by the dam.

## Materials and methods

### Sampling of fish

Fish were captured bimonthly with a standardised set of 15 to 150 mm-mesh gill nets, set out for 24 h and monitored every 8 h at 14 selected sites on the upper Tocantins River (14°44′S, 49°06′W; 13°34′S, 48°06′W) from February 1996 through April 1998. This period comprised the *river phase* (February 1996 through December 1996), corresponding to the natural stream environment prior to damming, and the *reservoir phase* (February 1997 through April 1998), corresponding to the filling stage, when sampling sites already showed lentic characteristics. Some remaining lotic sites were also sampled after the reservoir was formed. In order to detect temporal patterns related to season of the year, reservoir formation, or a combination of both, these phases were subdivided into six-month periods of *river/flood*, *river/drought*, *reservoir/flood 1*, *reservoir/drought* and *reservoir/flood 2*. The specimens captured were measured and weighed, and their digestive tract excised and fixed in 5% formaldehyde.

### Analysis of gut contents

The gut contents of 386 specimens of *L. friderici* with standard length varying from 8.5 cm to 23.5 cm (mean = 17.7 cm) were analysed. Food items were separated into categories, and their volume was measured in a 1 mm-high square transparent dish with a scale in millimetres underneath, so that the area corresponded to the volume. Food items were identified to the lowest suitable taxonomic category, and listed. For graphical representation and statistical purposes, these data were grouped into 22 categories.

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

### Analysis of feeding activity

In order to assess the feeding activity, the degree of repletion of each stomach was recorded as follows: 1 (<25%); 2 (25–50%); 3 (50–75%) and 4 (75–100%), and thereafter the percentage of partly full (repletion 1 + 2) and totally full (3 + 4) stomachs was determined for river and reservoir environments.

### Statistical analyses

A multivariate analysis of variance was performed using the MULTIV software (Pillar, 1999) to test significant differences in the diet of *L. friderici* related to environmental changes, such as season of the year and reservoir formation. In this method, each individual (stomach) is treated as a sampling unit and each prey as a variable, the value of which is given by its relative volume (VO%) in relation to the total volume of stomach content. A randomisation 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* and *flow/phase* (*river/lotic*, *reservoir/lotic* and *reservoir/lentic*). Because this analysis is akin to a conventional analysis of variance, differing only in the way that probabilities are obtained, the results are interpreted similarly. For details see Pillar and Orlóci (1996).

## Results

### Spectrum of food items and characterisation of diet

Twenty-two food categories were found in the stomach contents of *L. friderici* in the *reservoir phase*. Food of 15 categories was found in the *river phase*, during both high water and low water, although the absent items were not the same in the two seasons. The main food items varied according to period. In the river phase, the diet of *L. friderici* consisted mainly of vegetal material (plant debris, seeds and fruits) and organic matter (OM). Immediately following the impoundment, the importance of terrestrial arthropods (mainly isopterans and other insects) increased (Table 1). Figure 1 is a graphical representation of the IAi values of the main food items, except organic matter (OM), in the river and reservoir environments.

### Feeding activity

Stomachs with different degrees of repletion had nearly the same percentage of occurrence (Fig. 2). This indicated that feeding activity was similar in the river and the reservoir.

### Temporal variations in diet regarding season and damming

*Leporinus friderici* consumed more allochthonous than autochtonous food items in all periods analysed (Fig. 3). This difference was highest in the first six months of the filling phase. During the entire 1 1/2-year filling phase, the percentage of autochthonous resources reached about 50%.

The multivariate analysis detected no seasonal differences in the diet of *L. friderici* in the *river phase*. In contrast, *reservoir/flood 1* was significantly different from all the other cases. The second flood in the reservoir was not significantly different from the riverine environment. Independently of chronological subdivisions, lotic and lentic environments were significantly different, although the significance was not as high between lotic sites in the *river* and *reservoir phases*. *P* values are shown in Table 2.

## Discussion

### Spectrum of food items and characterisation of diet

*Leporinus friderici* is omnivorous with a tendency to herbivory; items from vegetal sources (plant debris, fruits and seeds, filamentous algae) accounted for more than 60% of its diet in the riverine environment. Organic matter (OM) and items from vegetal sources together composed more than 98% of its diet in the river. OM, a mixture of indistinguishable animal or vegetal matter, was always among the most important items; the amount of OM is probably related to the degree of digestion of the entire gut contents. OM is a complicating factor for analysis of diet, because the contribution of other, recognisable items becomes diluted because their importance is calculated from two relative measures (FO% and VO%).

Although the measured amount of inorganic matter, mainly sediment, is not very important, the consumption of other substrate-associated items, such as benthic filamentous algae (oedogoneaceans and zygnemaceans), benthic micro-crustaceans (conchostracans and ostracodes) and insect larvae, suggests that *L. friderici* feeds close to the bottom. Some items are predominantly found in association with submerged rotten wood (some ephemeropteran nymphs) or bottom sediment in shallow places (dipterans and molluscs), indicating that this fish probably feeds near the banks. This conclusion accords with that of Andrian et al. (1994), who reported fruits of *Polygonum* sp. and Poaceae, also demonstrating shore-associated habitats as the main components of the diet of *L. friderici* in the Paraná River floodplain. Goulding (1980) and Santos (1982) found that dipteran larvae and ephemeropteran nymphs and vegetal material, respectively, were the main food items of *L. friderici* in the Amazon Basin. This species is, however, also reported as occurring in the main channels of rivers (Tito de Morais et al., 1995).

The dietary composition of *L. friderici* suggests it is a particulate-feeder, i.e., feeds on small living food items, making use of visual cues to seek and capture its prey (Gerking, 1994). This is evidenced not only by the consumption of benthic prey, but also of zooplankton organisms such as cladocerans and cyclopoid copepods, which are relatively weak swimmers (Keenleyside, 1979). The searching behaviour of diurnally active fishes, which *L. friderici* is (pers. obs.), reinforces the importance of vision in this process. Zuanon (pers. communication) observed an active, diurnal foraging behaviour for all anostomid species in the Xingu River of the Amazon basin. Browsing and particulate feeding have been reported as foraging strategies for *L. friderici* in a wide variety of habitats in this river. Goulding (1980) reported that *L. friderici* had swallowed whole fish in some flooded Amazon forests. In the specimens examined for the present report, the fish remains found, consisting of pieces of flesh with spines, vertebrae, eyes and fin rays, suggested a scavenging habit. Sazima (1986) observed occasional scavenging as well as fin-biting and scale-eating behaviour for *L. lacustris*, and classified this species as a *nibbler*. The records of both cycloid and ctenoid scales of several sizes in the gut contents of *L. friderici,* independently and more frequently than other fish parts, strongly suggest that this anostomid may also be a nibbler. *Leporinus friderici*'s wide versatility in foraging strategies may explain its broad distributional range. Euryphagy is an important characteristic of ubiquitous species, and generalists have better chances than specialists of becoming widely distributed (Lowe-McConnel, 1987).

Although IAi, VO% and FO% are mean values, which might lead to biased results that neglect individual variations, assessment of these parameters is useful to detect changes at the population level. The feeding habits of fish are, in general, extremely plastic and flexible (Keenleyside, 1979). This flexibility can be observed through comparisons between individuals, as well as ontogenetic, seasonal and diel changes in the diet (Gerking, 1994).

Even though the multivariate test indicated a high degree of significance in comparisons between some groups, the

Table 1. Relative volume (VO%), frequency of occurrence (FO%) and Alimentary Index (IAi) of food items in the diet of *L. friderici* from the upper Tocantins River before and during the filling stage of the reservoir of the Serra da Mesa Hydroelectric Dam, central Brazil. Values presented for the reservoir phase correspond only to lentic sites.

| | *river/flood* | | | *river/drought* | | | *reservoir/flood 1* | | | *reservoir/drought* | | | *reservoir/flood 2* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Food items | VO% | FO% | IAi | VO% | FO% | IAi | VO% | FO% | IAi | VO% | FO% | IAi | VO% | FO% | IAi |
| Arthropoda (aquatic) | – | – | – | 0.008 | 8.7 | 0.0010 | 0.001 | 2.4 | 0.0000 | 0.004 | 2.7 | 0.0002 | 0.003 | 3.8 | 0.0002 |
| Chironomidae (larvae and pupae) | 0.271 | 20.8 | 0.0647 | 0.011 | 17.4 | 0.0029 | 0.385 | 44.6 | 0.2972 | 3.255 | 72.0 | 4.1033 | 2.638 | 68.3 | 2.5224 |
| Other Diptera (larvae and pupae) | 0.05 | 8.3 | 0.0005 | – | – | – | – | – | – | 0.005 | 1.3 | 0.0001 | 0.003 | 3.8 | 0.002 |
| Coleoptera (larvae) | 0.083 | 8.3 | 0.0079 | 0.037 | 13.0 | 0.0069 | 0.032 | 3.6 | 0.0020 | 0.046 | 5.3 | 0.0043 | 0.040 | 3.8 | 0.0021 |
| Lepidoptera (larvae) | 0.172 | 8.3 | 0.0164 | – | – | – | 0.221 | 3.6 | 0.0139 | 0.241 | 1.3 | 0.0056 | 0.176 | 1.9 | 0.0047 |
| Trichoptera (larvae and pupae) | – | – | – | 0.023 | 21.7 | 0.0072 | – | – | – | 6.307 | 10.7 | 1.1780 | 4.760 | 42.3 | 2.8204 |
| Ephemeroptera (nymphs) | 0.016 | 4.2 | 0.0008 | 0.206 | 17.4 | 0.0517 | 0.036 | 6.0 | 0.0037 | 0.336 | 9.3 | 0.0548 | 0.236 | 10.6 | 0.0350 |
| Odonata (nymphs) | – | – | – | – | – | – | 0.074 | 2.4 | 0.0031 | 0.842 | 22.7 | 0.3342 | 1.897 | 13.5 | 0.3576 |
| Arthropoda (terrestrial) | – | – | – | – | – | – | 3.162 | 30.1 | 1.6480 | 0.046 | 14.7 | 0.0119 | 0.167 | 11.5 | 0.0271 |
| Isoptera | 0.825 | 12.5 | 0.1181 | – | – | – | 56.636 | 69.9 | 68.4857 | 4.568 | 22.7 | 1.8132 | 3.734 | 19.2 | 1.0059 |
| Rests of insects | 1.306 | 33.3 | 0.4986 | 3.383 | 43.5 | 2.1235 | 0.100 | 7.2 | 0.0126 | 0.240 | 13.3 | 0.0561 | 0.277 | 24.0 | 0.0934 |
| Cladocera + Copepoda | – | – | – | – | – | – | 0.0002 | 1.2 | 0.0000 | 0.001 | 16.0 | 0.0003 | 0.001 | 7.7 | 0.0001 |
| Conchostraca + Ostracoda | – | 4.2 | 0.0001 | – | – | – | 0.020 | 6.0 | 0.0021 | 2.816 | 50.7 | 2.4982 | 2.854 | 47.1 | 1.8833 |
| Mollusca (Gastropoda + Bivalvia) | 0.001 | 4.2 | 0.0001 | 0.002 | 4.3 | 0.0001 | 0.038 | 3.6 | 0.0024 | 0.041 | 4.0 | 0.0029 | 0.028 | 1.9 | 0.0008 |
| Invertebrate eggs | – | – | – | 0.006 | 4.3 | 0.0004 | 0.013 | 7.2 | 0.0017 | 0.066 | 22.7 | 0.0262 | 0.095 | 50.0 | 0.0666 |
| Rests of fish | – | – | – | 2.882 | 8.7 | 0.3618 | 9.981 | 13.3 | 2.2890 | 2.025 | 24.0 | 0.8510 | 2.366 | 15.4 | 0.5099 |
| Scales | 0.109 | 25.0 | 0.0311 | 2.611 | 30.4 | 1.1473 | 0.621 | 22.9 | 0.2461 | 0.919 | 45.3 | 0.7298 | 0.950 | 35.6 | 0.4736 |
| Plant debris | 53.155 | 91.7 | 55.8023 | 14.152 | 73.9 | 15.1028 | 6.658 | 65.1 | 7.4957 | 30.399 | 73.3 | 39.0364 | 31.306 | 93.3 | 40.8963 |
| Seeds and fruits | 15.857 | 66.7 | 12.1069 | 42.516 | 60.9 | 37.3648 | 2.961 | 15.7 | 0.8025 | 18.821 | 21.3 | 7.0309 | 19.205 | 50.0 | 13.4494 |
| Filamentous algae | 0.368 | 4.2 | 0.0175 | 2.633 | 13.0 | 0.4958 | – | – | – | 2.924 | 30.7 | 1.5701 | 2.426 | 6.7 | 0.2287 |
| Organic matter | 27.341 | 100.0 | 31.3116 | 31.371 | 95.7 | 43.3239 | 15.504 | 67.5 | 18.1012 | 25.541 | 90.7 | 40.5498 | 26.417 | 96.2 | 35.5771 |
| Inorganic matter | 0.490 | 4.2 | 0.0234 | 0.160 | 4.3 | 0.0100 | 3.556 | 9.6 | 0.5932 | 0.555 | 14.7 | 0.1426 | 0.420 | 7.7 | 0.0452 |
| ***n*** | | **24** | | | **22** | | | **78** | | | **150** | | | **112** | |

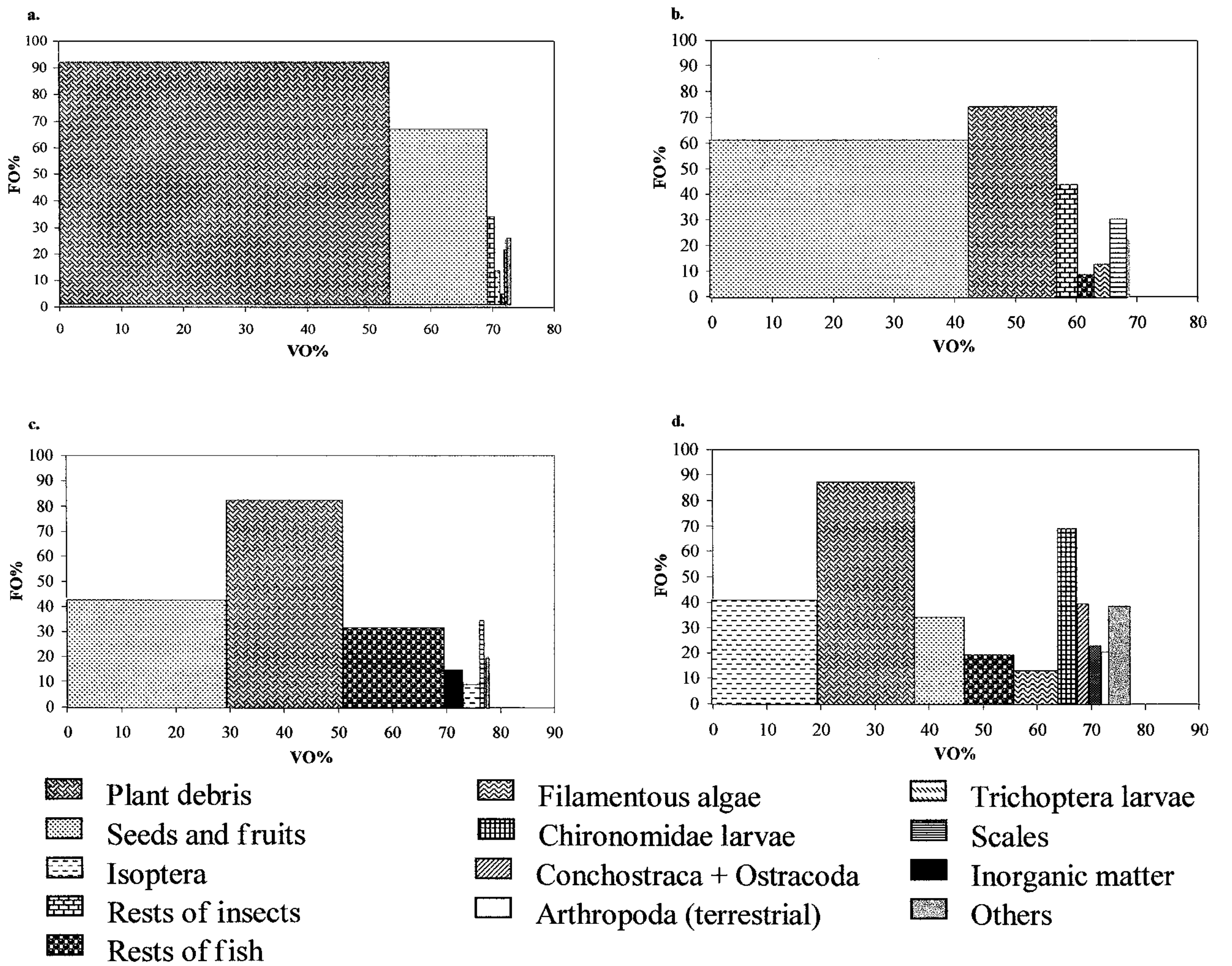


Fig. 1. Graphical representation of the main food items, except organic matter (OM), in the diet of *Leporinus friderici* in the upper Tocantins River, region of Serra da Mesa. (a) *River/flood*; (b) *river/drought*; (c) *reservoir/lotic*; (d) *reservoir/lentic*.

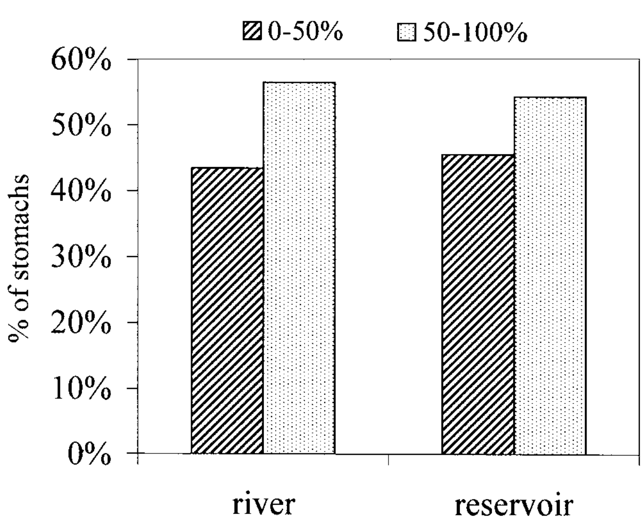


Fig. 2. Percentage of stomachs of *L. friderici* with different degrees of repletion.

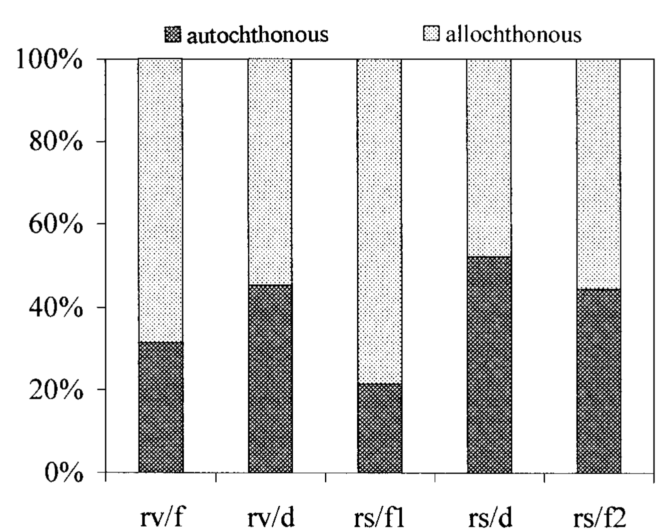


Fig. 3. Proportion of autochthonous and allochthonous items present in the stomach contents of *L. friderici* from the upper Tocantins River. (a) *River/flood* (rv/f); (b) *river/drought* (rv/d); (c) *reservoir/flood 1* (rs/f1); (d) *reservoir/drought* (rs/d); (e) *reservoir/flood 2* (rs/f2).

Table 2. Probabilities generated in the randomisation test of the independence of dietary composition of *L. friderici* 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, following this order: *river/flood* (rv/f), *river/drought* (rv/d), *reservoir/flood 1* (rv/fl), *reservoir/drought* (rs/d), and *reservoir/flood 2* (rs/f2) 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:*** | | | | | | |
| Between-groups contrasts: | | | | | 9.233 | 0.001 |
| **rv/f** | **rv/d** | **rs/$f_1$** | **rs/d** | **rs/$f_2$** | | |
| 1 | −1 | 0 | 0 | 0 | 0.42071 | 0.335 |
| 1 | 0 | −1 | 0 | 0 | 2.728 | 0.001 |
| 1 | 0 | 0 | −1 | 0 | 0.78962 | 0.059 |
| 1 | 0 | 0 | 0 | −1 | 0.30893 | 0.536 |
| 0 | 1 | −1 | 0 | 0 | 3.7007 | 0.001 |
| 0 | 1 | 0 | −1 | 0 | 1.4085 | 0.003 |
| 0 | 1 | 0 | 0 | −1 | 0.58952 | 0.17 |
| 0 | 0 | 1 | −1 | 0 | 4.896 | 0.001 |
| 0 | 0 | 1 | 0 | −1 | 5.2825 | 0.001 |
| 0 | 0 | 0 | 1 | −1 | 1.0342 | 0.017 |
| ***phase/flow:*** | | | | | | |
| Between-groups contrasts: | | | | | 4.6624 | 0.001 |
| **rv** | **rs/lt** | **rs/ln** | | | | |
| 1 | −1 | 0 | | | 0.83503 | 0.039 |
| 1 | 0 | −1 | | | 2.3497 | 0.001 |
| 0 | 1 | −1 | | | 2.8825 | 0.001 |
| ***phase/season x phase/flow*** | | | | | (−)0.78278 | 0.996 |
| Between groups | | | | | 13.113 | 0.001 |
| Within groups | | | | | 129.73 | |
| Total | | | | | 172.84 | |

variation in diet explained by phase, flow and season was very low compared to the total. This indicates that other factors besides those measured must have contributed to the observed differences. Some other factors, such as degree of repletion and sampling sites, were previously tested and the results showed similar patterns (data not provided), i.e., there was a high degree of significance between some cases, but simultaneously a high variation within groups. Therefore, we believe that this high variation may be attributable to individual differences in foraging.

## Temporal variations in diet and feeding activity

Fish are highly responsive to seasonal variations in food availability (Lowe-McConnel, 1987), with many examples from tropical environments (e.g., Prejs & Prejs, 1987; Winemiller & Jepsen, 1998). Knöppel (1972), on the contrary, found no substantial differences in food intake related to season, for *L. friderici* and other species. In our study, the multivariate test did not detect any significant difference in diet between flood and drought in the river phase. This test is little influenced by low values and zeros; thus the non-significant differences between flood and drought seasons, although the qualitative composition was distinct. During high water, the diet of *L. friderici* was composed mainly of plant debris and seeds + fruits, probably taken from drift, whereas filamentous algae, fish scales and some insects became more important in the low-water period. Most of the diet of *L. friderici* is allochthonous in origin, especially during the flood season. On the contrary, Horeau et al. (1998) found almost exclusively aquatic organisms in the stomachs of individuals of *L. friderici* living in rapids.

The formation of the reservoir represented a kind of intensified flood, with exceptional terrestrial input into the aquatic system. This period is normally regarded as the heterotrophic phase (Petrere & Ribeiro, 1994). *Leporinus friderici* rapidly changed its diet when it was offered a vast amount of easy prey, such as isopterans. This item, in the first six months after impoundment (*reservoir/flood 1*), exceeded all the others in importance, accounting for 68% of the total volume and occurring in nearly 70% of the specimens from the lentic sites analysed. Termites thus contributed most to the highly significant difference in diet compared to all the other periods. At the same time, other terrestrial arthropods, totally absent from the stomach contents in the river phase, became somewhat important, whereas the importance of vegetal resources decreased.

In recently formed reservoirs, euryphagy and flexible strategies become particularly important to profit from the food sources that suddenly become abundantly available. Petts (1984) argued that food supply is a determinant factor in the success and stabilisation of fish populations in impounded rivers. Moreover, Hahn et al. (1997) concluded that during the colonisation process, allochthonous food sources combined with environmental stress are primary factors affecting the differential survival of species. The feeding plasticity of many species facilitates this process, and becomes decisive when secondary selection takes place as a consequence of reproductive potential, longevity, size of first maturation and the interspecific interactions that occur during the first years (Hahn et al., 1997).

According to Araújo-Lima et al. (1995), fish communities in older reservoirs seem to be sustained mainly by autochthonous resources. Besides the increased nutrient input, the slower current speed also promotes the growth of filamentous algae in reservoirs (Matthews, 1998). In our study, further changes were reflected in the consumption of autochthonous resources, such as the increased importance of filamentous algae, chironomid larvae and microcrustaceans in the diet of *L. friderici* in the *reservoir/drought* and *reservoir/flood 2*.

The higher quantity and frequency of fish remains in the stomachs of *L. friderici* in the reservoir may reflect the action of other predators, such as piranhas (*Serrasalmus rhombeus*), which also increased their population in the new, lentic environment (Mazzoni & Petito, in press). Matthews (1998) pointed out that the action of this kind of mutilating piscivore, which makes available remains that attract other species, may have an important effect on the ecosystem and on trophic relationships in general.

The degree of repletion did not change significantly with formation of the reservoir. This contrasts to the situation reported for Corumbá Reservoir, where the fish generally showed a substantial increase in stomach weight during the filling stage (Agostinho et al., 1999). According to Lagler et al. (1997), however, the availability of food to a fish also influences the amounts consumed. *Leporinus friderici* fed on a wider range of items in the reservoir, but apparently it ate at the same rate as in the river. Species that feed in the littoral zone normally have a large food supply and feed often. Agostinho and Zalewski (1995) stressed the importance of riparian ecotones in reservoirs for spawning and feeding of fish.

According to Gerking (1994), the term ‘diet switching’ has acquired two meanings. One is that individuals offered food choices will feed disproportionately on the most abundant food item until it reaches some low threshold that makes them switch to an alternate choice; the other simply refers to an unpredictable switch when the cause is unknown. *Leporinus friderici* at first depended directly on terrestrial input (i.e., the terrestrial prey themselves, such as termites or other insects); but after the formation of the reservoir, increased their consumption of autochthonous resources, such as filamentous algae and zooplankton. Filamentous algae and zooplankton may have become more available as nutrients increased in the water. Because lentic environments have depositional characteristics, light penetration and hence primary production is increased, mainly in shallow places. This also facilitates the localisation of smaller prey, such as cladocerans and copepods. Although *L. friderici* is in general more dependent on allochthonous items, it is more influenced by primary and secondary production in the new lentic environment, showing a capability to switch its diet when terrestrial resources are exhausted.

Our results showed that *L. friderici* is opportunistic, rapidly varying its diet to capitalise on the sudden abundance of particular food items. This species profited from the new environment, as shown by its increases in numbers and biomass during the filling stage (Mazzoni & Petito, in press). The feeding ecology of *L. friderici* reflected the rapid decline of food supplies of terrestrial origin during the heterotrophic phase of reservoir formation, and its subsequent increased dependence on autochthonous resources.

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