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Spatial variation in the stable isotopes of ^{13}C and ^{15}N and trophic position of *Leporinus friderici* (Characiformes, Anostomidae) in Corumbá Reservoir, Brazil

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ABSTRACT

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used to describe sources of energy and trophic position for adult *Leporinus friderici* in the area of the Corumbá Reservoir, Brazil. Samples were collected from April 1999 to March 2000. Spatial variations were not identified in the isotopic composition. The maximum and minimum contribution of C_4 plants calculated integrating the variation of plants and fish were 47.7% and 2.4%, respectively. Among C_3 plants, periphyton presented closer isotopic values to those observed for fishes, corresponding to an important carbon source. The proportion of ingested plant item is larger in rivers upstream from the reservoir (42.7%), which justifies the smaller trophic level among there. However, in the reservoir, the ingestion of fish was 81.4%, while ingested plants contributed with 18.6%. Downstream from the dam, participation of plant item was even smaller (14.4%). Although the trophic position calculated with diet data was proportional to the one calculated with $\delta^{15}N$ values, the former elevated the trophic level of *L. friderici* in the food web, because estimated trophic positions were based on fish items belonging to the 2nd (a) and to the 3rd (b) trophic levels.

Key words: stable isotopes, reservoir, *Leporinus friderici*, food web.

INTRODUCTION

The use of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) has been intensified in the last years (Hobson and Wassenaar 1999). These isotopes are used to describe sources of energy and trophic relationships in food chains of terrestrial, marine and freshwater ecosystems (Peterson and Fry 1987). The $\delta^{13}C$ usually identifies pathways of carbon transference, starting from the primary producers, whereas the $\delta^{15}N$ characterizes the trophic position of the organisms in food chains (Vander Zanden et al. 1997). The amount of $\delta^{15}N$ in tissues of consumers is, usually, enriched in 3‰ in relation to their prey. However, $\delta^{13}C$ is slightly enriched (1‰) with the increase in trophic levels (Jennings et al. 1997). The application of such techniques has been useful in investigation of ecology (Martinelli et al. 1991, McArthur and Moorhead 1996, Keough et al. 1996, France 1997), as well as in analyzing effects of anthropogenic impacts (McClelland and Valiela 1998). In dammed areas, stable isotopes help to understand the processes determining dynamic changes imposed to the new environment and, consequently, supporting conservation and management decisions (Angradi 1994).

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Transformations of carbon (or energy) began with CO_2 fixation by plants. Plants C_3 and C_4 plants differ between themselves by their respective photosynthetic pathways, resulting in different values for carbon stable isotope (Farquhar et al. 1989). Due to selection for lighter isotope during fixation of carbon, C_3 plants are significantly more enriched in ^{12}C. These isotopic differences turn relatively easy to identify carbon of C_3 and C_4 plants (Forsberg et al. 1993).

Primary sources of energy in the area of influence of Corumbá Reservoir are C_4 grasses, C_3 plants (constituted by the riparian vegetation), phytoplankton and periphyton (Benedito-Cecilio et al. 2004). Aquatic macrophytes are scarce in the area of the Corumbá Reservoir (Luz-Agostinho et al. 2006). Studies have indicated that, in spite of the great quantity of biomass produced by C_4 plants, isotopic carbon signatures in fish are more related to algae based food web (Araújo-Lima et al. 1986, Forsberg et al. 1993).

Leporinus friderici is an abundant species in the Corumbá Reservoir (Agostinho et al. 1999). This species is economically important in other areas of the Paraná River basin, in spite of the environmental modifications imposed by impoundments (Agostinho et al. 1989, 1994). Ecological studies with *Leporinus friderici* were conducted in the Brazilian stretch of Paraná River without dams (Andrian et al. 1994, Vazzoler et al. 1997), in Itaipu Reservoir (Agostinho et al. 1992, Benedito-Cecilio et al. 1997) and in the dammed stretch of the basin (Lopes et al. 2000, Benedito-Cecilio et al. 2005). These studies generated valuable information to support management actions.

Studies using stable isotopes of carbon were firstly carried out in the Amazonian ecosystem in the 80's (Araújo-Lima et al. 1986, Martinelli et al. 1991, Forsberg et al. 1993). However, for the Paraná River, isotope ratios were not described so far for any biotic component. Concepts of energy that flows in food webs have only been based on diet analysis and stomach content of fish, which maybe limited due to difficulties in identifying food items, or, when they can be identified, it is not safe to affirm that such items would be assimilated and, therefore, they will contribute to production (Jennings et al. 1997). In the present work, isotopic ratios of carbon and nitrogen of muscles of adult *Leporinus friderici* individuals are compared with available information in the literature, concerning the isotopic ratios of C_3 and C_4 plants and also the diet of the species. Our hypothesis is that the variations of $\delta^{13}C$ and $\delta^{15}N$ are specific for each area of the reservoir and, therefore, equivalent to the composition of the food ingested by the species.

MATERIALS AND METHODS

Leporinus friderici (Bloch 1794) was collected monthly from April 1999 to March 2000 in nine sites distributed in the lower Corumbá River basin and its tributaries localized predominantly scrubland in the Cerrado Biome. The Corumbá River dammed in September 1996, forming the Corumbá Hydroelectric Reservoir. Corumbá Reservoir presents a surface area of 65 km^2, a total volume of 1500×106 m^3, an average depth of 23 m and a hydraulic retention time of 30 days (Luz-Agostinho et al. 2006). Sample sites were grouped in three characteristic biotopes defined considering the influence of Corumbá Reservoir: (1) streams lotic and semi-lotic characteristics upstream from the reservoir (COPE, MOIT, AREI and PFOZ); (2) stations inside the reservoir (LISA, JACU, CPIR and PIRA); and (3) river downstream from the dam (JUSA) (Figure 1).

Gillnets with different mesh sizes were used to capture fish. For each fish, standard length (Ls) and total weight (Wt) were obtained. A sample of the muscle close to the insertion of the dorsal fin was removed from each individual. Leaves of C_3 (riparian vegetation) and C_4 (grasses) plants were sampled on bank areas. No aquatic macrophytes were found. Periphyton samples were washed in distilled water, filtered and maintained in fiberglass filter. Filters (GF/C Whatman) were previously undergone combustion at 550°C for 4 hours. Filtered samples were rinsed in 1N HCl solution to remove carbonates. Particulate Organic Carbon (POC) and zooplankton samples were collected respectively with 25μm- and 75μm -mesh nets. These samples were also conditioned in fiberglass filters.

To determine the $\delta^{13}C$ of phytoplankton is problematic due to contamination by carbon from vascular plants. Considering the results presented in Fry and Sherr (1984) for food webs of aquatic communities, the isotopic composition of phytoplankton was established through zooplankton with 1‰ fractionation per trophic

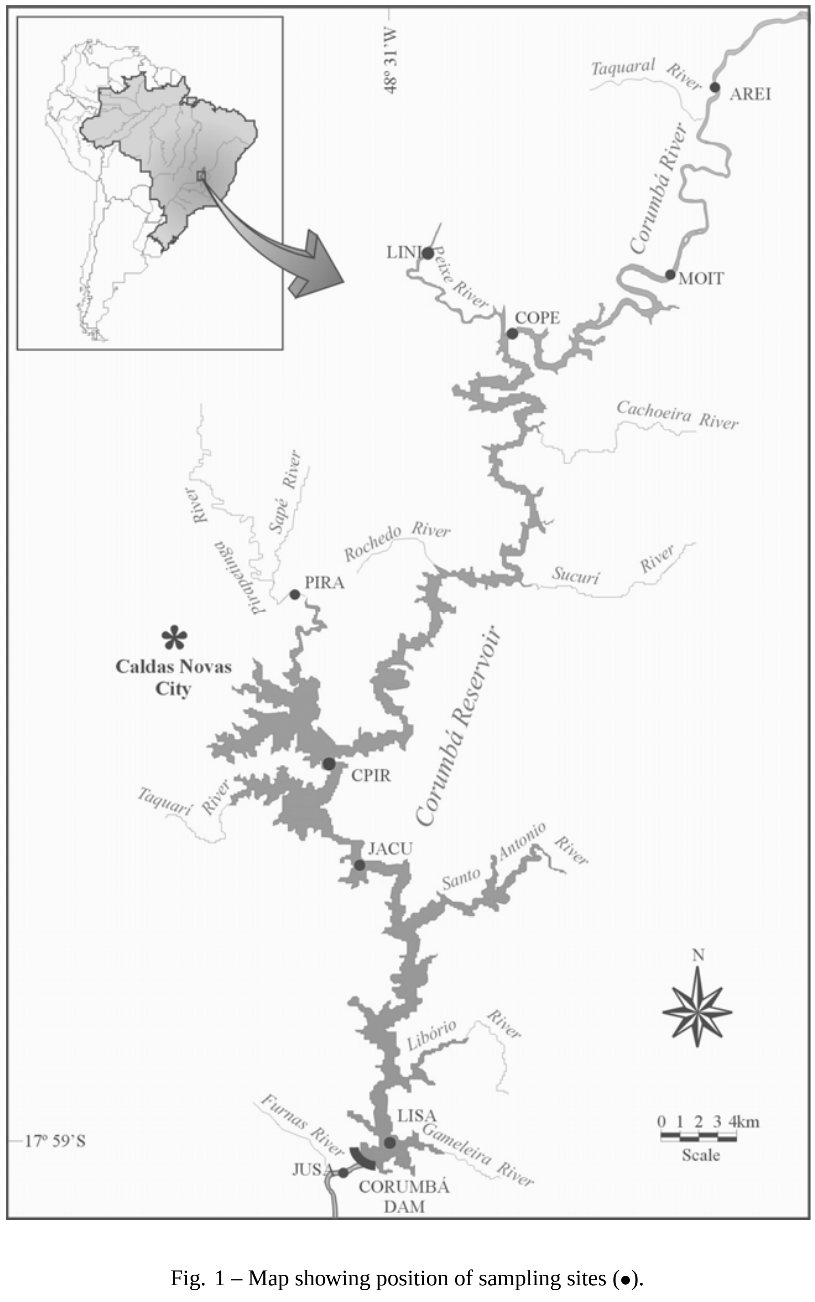

Fig. 1 – Map showing position of sampling sites (•).

level. Based on this criterion, results of phytoplankton were limited to the inner areas of the reservoir (about 40km above the dam), because this area presented the higher abundance of zooplankton (Velho et al. 2001). Samples were dried at 60°C and sent to the Institute of Ecology and Analytic Chemistry Laboratory in Georgia, USA, and to the Stable Isotope Facility – Department of Agronomy and Range Science in California, USA, for determination of δ^{13}C and δ^{15}N ratios by mass spectrometer.

To determine the relative importance of C_4 plants as source of carbon for adults *L. friderici*, the following equation was used (Forsberg et al. 1993):

$$\%C_4 = \left[1 - \frac{\delta^{13}C_{fish} - \delta^{13}C_{c4}}{\delta^{13}C_{c3} - \delta^{13}C_{c4}}\right] \times 100$$

where:

$\%C_4$ = C_4 plants contribution;
$\delta^{13}C_{fish}$ = mean value of $\delta^{13}C$ for *L. friderici*;
$\delta^{13}C_{C3}$ = mean value of $\delta^{13}C$ for C_3 plants;
$\delta^{13}C_{C4}$ = mean value of $\delta^{13}C$ for C_4 plants.

According to defined mean values of carbon for the groups of plants of the area of influence of Corumbá Reservoir (Benedito-Cecilio et al. 2004), the most negative group (phytoplankton = –29,4‰) was used to calculate the maximum contribution of C_4 plants, while the less negative group (periphyton = –21,6‰) was used to calculate the minimum contribution. The percentage of the carbon originated from C_3 plants, by definition, was $\%C_3 = (\%C_4) - 100$.

Trophic position (TP) based on $\delta^{15}N$ was calculated according to formula (Vander Zanden et al. 1997):

$$TP = \left\{\frac{(\delta^{15}N_{fish} - 5.7)}{3.4}\right\} + 1$$

where:

$\delta^{15}N_{fish}$ = mean value of $\delta^{15}N$ for *L. friderici*;
5.7 = average $\delta^{15}N$ for vascular plants;
3.4 = increase of trophic level for $\delta^{15}N$.

The enrichment of $\delta^{15}N$ was calculated in 3.4‰ for trophic level (Fry 1988, Vander Zanden et al. 1997). Diet of the species was described in Hahn et al. (2004). Diet-based mean trophic position (MTP) was estimated by the formula (Winemiller 1990, Vander Zanden and Rasmussem 1996):

$$MTP = \Sigma\,(Cn \cdot Tn) + 1$$

where:

Cn = percentage contribution of the n^{th} food item;
Tn = trophic position of n^{th} food item.

Values of the trophic position estimated for items ingested by the species were: 3 – carnivorous-prey; 2.5 – omnivorous-prey; 2 – herbivorous-prey; 1 – for primary producers (Vander Zanden et al. 1997).

RESULTS AND DISCUSSION

For adult *L. friderici* (Ls above 17.5 cm), the $\delta^{13}C$ mean value and standard deviation was –21.4‰ ± 1.7 (Table I). In Central Amazon, isotopic values superior to that were verified for *Schizodon fasciatus* (–18.8‰), and an average of –28.8‰ for the entire fish assemblage (Forsberg et al. 1993). The low value could be related to the formation of Corumbá Reservoir that influenced the access to the sources of energy for the species. The analysis of stomach content, in river phase and immediately after Corumbá Reservoir filling (Ferreira et al. 2002, Luz-Agostinho et al. 2006), demonstrated variations in diet of species. In the river phase, the item fish was predominant in those the diet, whereas in the reservoir phase *L. friderici* ingested, basically, plants and a small proportion of fish and insects. These findings are reinforced by Andrian et al. (1994) for the Paraná River floodplain, which classified the species as opportunist.

TABLE I

Means values of $\delta^{13}C$ and $\delta^{15}N$ (‰) for *L. friderici* sampled in the area of influence of Corumbá Reservoir (n = number of specimens, SD = standard deviation).

Environment	N	$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$
River	4	-21.8 ± 2.3	9.0 ± 1.0
Reservoir	4	-21.4 ± 1.4	9.7 ± 1.2
Downstream	4	-21.1 ± 1.7	11.3 ± 1.7
Mean values		-21.4 ± 1.7	10.0 ± 1.6

Isotopic variations of $\delta^{13}C$ for primary producers analyzed by Benedito-Cecilio et al. (2004) in the same area are presented in the Figure 2. C_4 plants were strongly enriched in $\delta^{13}C$ (–2.7‰ ± 0.7), but phytoplankton was the more negative group (–29.3‰ ± 1.6). Phytoplankton carbon is usually lighter than vascular plants carbon (Hamilton and Lewis 1992, Victoria et al. 1992). However, in the area studies C_3 plants (riparian vegetation, C_3 grasses, periphyton and phytoplankton) presented significant different isotopic ratios ($F_{3,22} = 22.59$; $p < 0.001$). Periphyton presented positive values of $\delta^{13}C$ (–21.6‰ ; ± 3.4). Nevertheless, planktonic and periphytic algae presented more positive average values if compared with those registered for the Amazonian

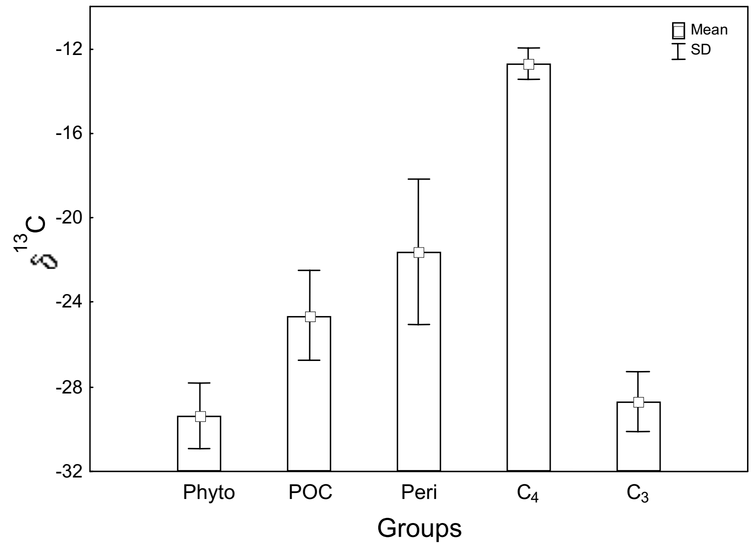

Fig. 2 – Means Values and standard deviation (SD) of δ^{13}C for C_3 plants, C_4 grasses, phytoplankton (phyto), periphyton (peri) and POC (Particulate Organic Carbon) sampled in the area of influence of Corumbá Reservoir (source: Benedito-Cecilio et al. 2004).

basin, where mean values were –33.3 and –26.2‰, respectively (Araújo-Lima et al. 1986).

Spatial variations were not identified in the composition of δ^{13}C for adult *L. friderici* (Table I). Large variance was detected for isotopic values of carbon in lotic environments. Spatial differences in isotopic ratio for adults *Colossoma macropomum* and *Prochilodus nigricans* were verified by Benedito-Cecilio et al. (2000) in Central Amazon, where the authors observed depletion of δ^{13}C from downstream to upstream. Similarly, Thomas and Cahoon (1993) demonstrated significant differences in the ratio of δ^{13}C and 15N for fish in coral reefs. For *L. friderici*, although significant spatial differences in δ^{13}N were not been identified ($F_{2,12}$ = 3.18; $p > 0.05$), values were greater downstream from the dam (Table I). In spite of differences were not significant, the species may be adopting specific trophic strategy for each environment. This is confirmed if we consider that fish sampled downstream consumed more (Luz-Agostinho et al. 2006), denoting the use of protein originated from superior trophic levels.

Variations in the isotopic composition of *L. friderici* can also be due to the spatial variability in the isotopic ratio of the same food item. The spatial analysis, relative to the distance of to the dam, of the isotopic variations of δ^{13}C for primary producers is presented by Benedito-Cecilio et al. (2004) (Figure 3). Although the studied area was relatively short (100 km), spatial correlations were detected for phytoplankton (r = 0.97; $p < 0.05$) and POC (r = 0.65; $p < 0.05$). In the system Solimões-Amazonas (between Tefé and Santarém), spatial differences were also verified in δ^{13}C of C_4 macrophytes (Benedito-Cecilio et al. 2000). Gradients of carbon stable isotopes can exist in ecosystems and this may have influenced the isotopic ratios of plants. The upstream stretches, not impacted by the reservoir, are 1.5 to 2 times more saturated in CO_2 and present higher values of δ^{13}C than downstream (Lajtha and Marshall 1994). POC, which is composed by organic carbon originated from parts of plants and animals, can represent that reduction in the downstream values of δ^{13}C.

The inverse tendency verified for phytoplankton seems to be associated to diel variations in $^{13}CO_2$ concentration (Martinelli et al. 1991). Jackson and Harkness (1987) found spatial variation in δ^{13}C for plants. Such variations may happen due to environmental alterations induced in plant physiology, which means that, δ^{13}C values could be related to environmental conditions (tem-

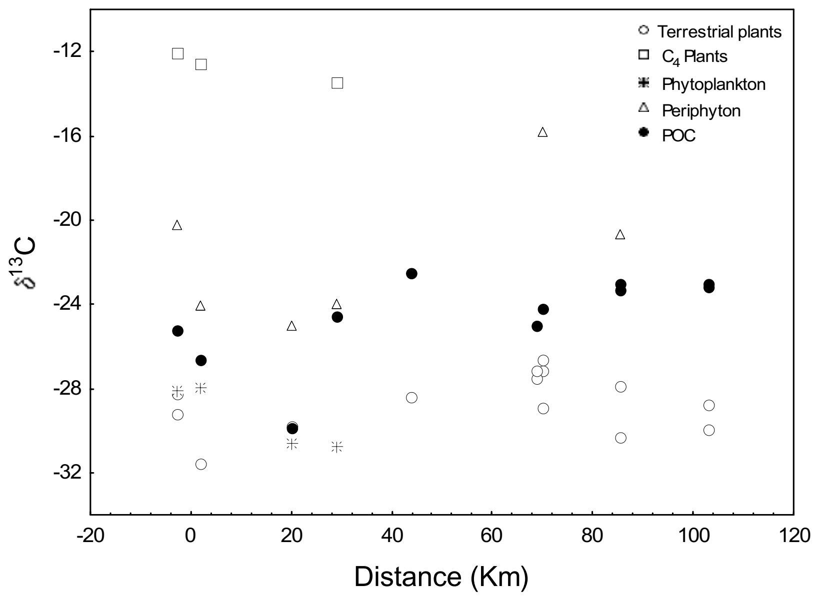

Fig. 3 – Spatial variation of $\delta^{13}C$ in leaves of the riparian vegetation, C4 plants, zooplankton, periphyton, POC in the area of influence of Corumbá Reservoir: $0 =$ dam; distance $> 0 =$ upstream; distance $< 0 =$ downstream (source: Benedito-Cecilio et al. 2004).

perature, salinity, seasonality) and to geographical and temporal variations. All these have potential to induce alterations in plant metabolism.

In Corumbá Reservoir, the maximum and minimum contribution of C4 plants, for adults of *Leporinus friderici*, calculated integrating the variation of plants and fish were 47.7% and 2.4%, respectively. This is an expressive contribution of carbon from C4 plants, if compared to the fish assemblages studied in Central Amazon. In that ecosystem, only four species presented maximum contribution of C_4 plants superior to 38%. The largest proportion of C_3 carbon in adult fish could be, however, due to the preferential consumption of C_3 plants (Forsberg et al. 1993).

The low digestibility and the diminished nutritional value of C_4 plants for herbivores were demonstrated by Caswell et al. (1973). On the other hand, algal protein is highly nutritive and easily assimilated by most animals (Waslien 1979). Among C_3 plants, periphyton presented closer isotopic values to those observed for fishes, corresponding to an important carbon source to *L. friderici*.

The intra specific variability in trophic position for the species, calculated from the obtained values of $\delta^{15}N$ (Vander Zanden et al. 1997) and diet data (Luz-Agostinho et al. 2006), are presented in Table II. The proportion of ingested plant item is larger in rivers upstream from the reservoir (42.7%), which justifies the smaller trophic level among there. However, in the reservoir, the ingestion of fish was 81.4%, while ingested plants contributed with 18.6%. Downstream from the dam, participation of plant item was even smaller (14.4%).

TABLE II

Trophic position (TP) based on diet composition and $\delta^{15}N$ for *L. friderici* (a = trophic position based on prey occupying the 2nd trophic level, b = trophic position based on prey occupying the 3rd trophic level).

		TP diet	
Environment	TP $\delta^{15}N$	a	b
River	2.0	2.8	3.4
Reservoir	2.2	2.8	3.6
Downstream	2.7	2.9	3.7

Trophic position indicates how many times the biomass consumed by an organism have been metabolized along the food chain (Vander Zanden et al. 1997). In this case, the omnivorous behavior of the species, a characteristic of tropical ecosystems complexity, makes difficult the understanding of energy flow and mass transfer in aquatic ecosystems. The trophic position variability of the species can be attributed to the following factors or even to the combination of both: i) high flexibility in feeding species, already justified by Andrian et al. (1994) for the Paraná River floodplain, and ii) variation in the trophic position of preys. In this last case, the difficulty to identify prey is due to a characteristic of the species that removes pieces of fishes when feeding. This impedes the determination of the prey trophic level (Luz-Agostinho et al. 2006). For an appropriate correction of this variation, experimentations to quantify the degree of trophic flexibility and to determine preferential prey are fundamental. Although the trophic position calculated with diet data was proportional to the one calculated with 15N values, the former elevated the trophic level of *L. friderici* in the food web, because estimated trophic positions were based on fish items belonging to the 2nd (a) and to the 3rd (b) trophic levels (Table II).

Determination of trophic position based on diet, compared to the use of δ^{15}N, involves distinctions in the way as these methods integrate variations in trophic positions (Vander Zanden et al. 1997). The δ^{15}N presents, in a more robust way, the integration in longer time, through the food web, the energy assimilated by lower trophic levels. However, a better estimate of the results obtained with δ^{15}N is only possible based on diet composition.

Results obtained with the use of isotopes made possible a better understanding of the role of *L. friderici* in the flow of energy in the food web of the area of Corumbá Reservoir influence. The primary sources of carbon for the species, after the first year reservoir filling, were constituted by periphyton and C_4 grasses. Although studies have not been conducted in the river phase, such sources might not have been the same during the two phases (before and after the formation of the reservoir), once the diet of the species presented similar item, but in different relative importance in the reservoir phase. On the other hand, trophic position of the species, in the adult phase, based on diet data and δ^{15}N, ranks it above the second trophic level. However, the pattern of carbon flow and trophic dynamics in juveniles of this species may be distinct to those presented in this work.

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RESUMO

Isótopos estáveis de carbono (δ^{13}C) e nitrogênio (δ^{15}N) foram utilizados para descrever as fontes de energia e a posição trófica de adultos de *Leporinus friderici* na área do reservatório de Corumbá, Brasil. As amostras foram coletadas entre abril de 1999 e março de 2000. Variações espaciais não foram identificadas quanto à composição isotópica da espécie. As contribuições máximas e mínimas das plantas C_4, foram de 47,7% e 2,4%, respectivamente. Entre as plantas C_3, o perífiton correspondeu a uma das mais importantes fontes de carbono para a espécie, pois seus valores isotópicos foram os mais próximos àqueles observados para os peixes. A proporção ingerida do item vegetal foi maior em rios localizados a montante do reservatório (42,7%), justificando a menor posição trófica registrada para a espécie entre os ambientes estudados, enquanto no reservatório esta proporção foi de 18,6%, sendo que o item peixes atingiu 81,4%. A jusante do reservatório, a participação das plantas foi ainda menor, atingindo 14,4%. Embora a posição trófica da espécie, calculada com os dados de dieta, fossem proporcionais àqueles calculados com os valores de δ^{15}N, os primeiros elevaram o nível trófico de *L. friderici* na cadeia alimentar, pois estas foram baseadas nos itens peixe, cujas espécies pertenciam ao segundo e ao terceiro nível trófico.

Palavras-chave: isótopos estáveis, reservatório, *Leporinus friderici*, teia alimentar.

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