

# Spatial variation in the stable isotopes of <sup>13</sup>C and <sup>15</sup>N and trophic position of *Leporinus friderici* (Characiformes, Anostomidae) in Corumbá Reservoir, Brazil

ALEXANDRE L. PEREIRA<sup>1</sup>, EVANILDE BENEDITO<sup>2</sup> and CÁSSIA M. SAKURAGUI<sup>3</sup>

<sup>1</sup>Departamento de Agronomia, Universidade Estadual de Maringá
 Avenida Colombo, 5790, 87020-900 Maringá, PR, Brasil
<sup>2</sup>Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, Departamento de Biologia
Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá
 Avenida Colombo, 5790, 87020-900 Maringá, PR, Brasil
<sup>3</sup>Departamento de Biologia, Universidade Estadual de Maringá
 Avenida Colombo, 5790, 87020-900 Maringá, PR, Brasil

Manuscript received on August 11, 2005; accepted for publication on August 8, 2006; presented by Lucia Mendonça Previato

#### 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<sub>4</sub> plants calculated integrating the variation of plants and fish were 47.7% and 2.4%, respectively. Among C<sub>3</sub> 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 2<sup>nd</sup> (a) and to the 3<sup>rd</sup> (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 (Van-

Correspondence to: Alexandre Leandro Pereira

E-mail: alexmga@yahoo.com.br

der 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).

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<sup>2</sup>, a total volume of  $1500 \times 106 \text{ m}^3$ , 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  $25\mu m$ - and  $75\mu m$ -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  $1^{\circ}$ c fractionation per trophic

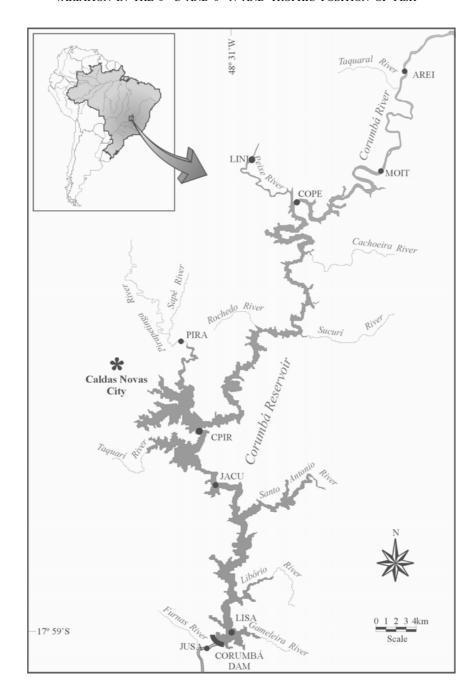


Fig. 1 – Map showing position of sampling sites ( $\bullet$ ).

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  $\delta^{13}$ C and  $\delta^{15}$ 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 =  $-29,4^{\circ}/\circ\circ$ ) was used to calculate the maximum contribution of  $C_4$  plants, while the less negative group (periphyton =  $-21,6^{\circ}/\circ\circ$ ) 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):

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

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<sup>th</sup> food item;

Tn = trophic position of n<sup>th</sup> 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%  $\pm 1.7$  (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.

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

TABLE I

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

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 ( $-2.7^{\circ}/\circ \circ \pm 0.7$ ), but phytoplankton was the more negative group ( $-29.3^{\circ}/\circ \circ \pm 1.6$ ). 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 ( $-21.6^{\circ}/\circ \circ$ ;  $\pm 3.4$ ). Nevertheless, planktonic and periphytic algae presented more positive average values if compared with those registered for the Amazonian

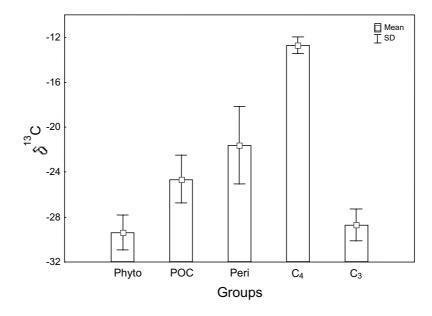


Fig. 2 – Means Values and standard deviation (SD) of  $\delta^{13}$ C for C<sub>3</sub> plants, C<sub>4</sub> grasses, phytoplankton (phyto), periphyton (peri) and POC (Particulate Organic Carbon) sampled in the area of influence of Corumbá Reservoir (source: Benedito-Cecilio et al. 2004).

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  $\delta^{13}$ 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  $\delta^{13}$ C from downstream to upstream. Similarly, Thomas and Cahoon (1993) demonstrated significant differences in the ratio of  $\delta^{13}$ C and 15N for fish in coral reefs. For L. friderici, although significant spatial differences in  $\delta^{13}N$  were not been identified (F<sub>2.12</sub> = 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. frid-erici* 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  $\delta^{13}$ 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<sup>13</sup>C of C<sub>4</sub> 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 CO2 and present higher values of  $\delta^{13}$ 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  $\delta^{13}$ C.

The inverse tendency verified for phytoplankton seems to be associated to diel variations in  $^{13}\text{CO}_2$  concentration (Martinelli et al. 1991). Jackson and Harkness (1987) found spatial variation in  $\delta^{13}\text{C}$  for plants. Such variations may happen due to environmental alterations induced in plant physiology, which means that,  $\delta^{13}\text{C}$  values could be related to environmental conditions (tem-

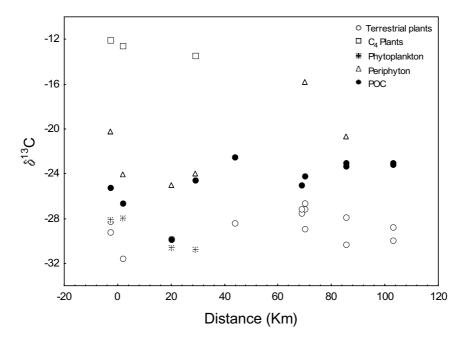


Fig. 3 – Spatial variation of  $\delta^{13}C$  in leaves of the riparian vegetation, C4 plants, zooplankton, periphyton, POC in the area of influence of Corumbá Reservoir: 0 = dam; distance > 0 = upstream; distance < 0 = downstream (source: Benedito-Cecilio et al. 2004).

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 2<sup>nd</sup> trophic level, b = trophic position based on prey occupying the 3<sup>rd</sup> 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 2<sup>nd</sup> (a) and to the 3<sup>rd</sup> (b) trophic levels (Table II).

Determination of trophic position based on diet, compared to the use of  $\delta^{15}$ N, involves distinctions in the way as these methods integrate variations in trophic positions (Vander Zanden et al. 1997). The  $\delta^{15}$ 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  $\delta^{15}$ 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  $\delta^{15}N$ , 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.

#### ACKNOWLEDGMENTS

We are grateful to M.F.A and L.C. Gomes for valuable comments, to Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUPELIA) and FURNAS Centrais Elétricas S.A. for infrastructural support and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for the scientific iniciation scholarship to ALP.

## RESUMO

Isótopos estáveis de carbono ( $\delta^{13}$ C) e nitrogênio ( $\delta^{15}$ 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<sub>4</sub>, 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  $\delta^{15}$ 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.

# REFERENCES

AGOSTINHO AA, BORGHETTI JR, DOMANINSKI CM, OKADA EK AND NOGUEIRA SVG. 1989. Produção pesqueira e situação da pesca no reservatório de Itaipu. In: 18° SEMINÁRIO NACIONAL DE GRANDES BARRAGENS, Foz do Iguaçu, PR, Brasil.

- AGOSTINHO AA, JÚLIO JR HF AND BORGHETTI JR. 1992. Considerações sobre os impactos dos represamentos na ictiofauna e medidas para sua atenuação Um estudo de caso: Reservatório de Itaipu. Unimar 14: 89–107.
- AGOSTINHO AA, JÚLIO JR HF AND PETRERE JR M. 1994. Itaipu reservoir (Brazil): impacts of the impoudment of the fish fauna and fisheries. In: Cowx IG (Ed), Rehabilitation of freshwater fisheries, Oxford: Fishing News Books, p. 171–184.
- AGOSTINHO AA, MIRANDA LE, BINI LM, GOMES LC, THOMAZ SM AND SUZUKI HI. 1999. Patterns of Colonization in Neotropical reservoirs, and Prognoses on Aging. In: TUNDISI JG AND STRASKRABA M (Eds), Theoretical Reservoir Ecology and its Applications, International Institute of Ecology, São Carlos, SP, Brazil, p. 227–265.
- ANDRIAN IF, DÓRIA CRC, TORRENTE G AND FERRETI CM. 1994. Espectro alimentar e similaridade na composição da dieta de quatro espécies de *Leporinus* (Characiformes, Anostomidae) do rio Paraná (22°10-22°50′/53°40′W), Brasil. Unimar 16: 97–106.
- ANGRADI TR. 1994. Trophic linkages in the lower Colorado River: multiple stable isotope evidence. J N Am Benthol Soc 13: 479–495.
- ARAÚJO-LIMA CARM, FORSBERG BR, VICTORIA R AND MARTINELLI LA. 1986. Energy sources for detritivorous fishes in the Amazon. Science 234: 1256–1258.
- BENEDITO-CECILIO E, AGOSTINHO AA, JÚLIO JR HF AND PAVANELLI CS. 1997. Colonização ictiofaunística do reservatório de Itaipu e áreas adjacentes. Rev Bras Zool 14: 1–14.
- BENEDITO-CECILIO E, ARAÚJO-LIMA CARM, FORSBERG BR, BITTENCOURT MM AND MARTINELLI LC. 2000. Carbon sources of Amazonian fisheries. Fish Manag Ecol 7: 305–315.
- BENEDITO-CECILIO E, PEREIRA AL AND SAKURAGUI CM. 2004. Effect of size on the energy acquired in species of the fish from a neotropical reservoir, Brazil. Environ Biol Fishes 7: 313–320.
- BENEDITO-CECILIO E, PEREIRA AL, BALERONI H AND FARIA ACEA. 2005. Effects of habitat on physiological indicators in *Leporinus friderici* (Pisces, Anostomidae) in the influence area of the Corumbá Reservoir, Goiás, Brazil. Acta Limnol Bras 17: 71–79.
- CASWELL H, REED F, STEPHENSON SN AND WERNWE PA. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. Am Nat 107: 465–480.

- FARQUHAR GD, EHLERINGER JR AND HUBICK KT. 1989. Carbon isotope discrimination and photosynthesis. Ann Rev Plant Physiol Plant Mol Biol 40: 503–537.
- FERREIRA A, HAHN NS AND DELARIVA RL. 2002. Ecologia alimentar de *Piabina argentea* (Teleostei, Tetragonopterinae) nas fases de pré e pós-represamento do rio Corumbá. Ecol Monogr Acta Limnol Bras 14: 43–52.
- FORSBERG BR, ARAÚJO-LIMA CARM, MARTINELLI LA, VICTORIA RL AND BONASSI JA. 1993. Autotrophic carbon sources for fish of the Central Amazon. Ecology 74: 643–652.
- FRANCE RL. 1997. Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. Ecol Freshw Fish 6: 78–83.
- FRY B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic compositions. Limnol Oceanogr 33: 1182–1190.
- FRY B AND SHERR EB. 1984.  $\delta^{13}$ C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib Mar Scien 27: 13–47.
- HAHN NS, FUGI R AND ANDRIAN IF. 2004. Trophic ecology of fish assemblages. In: THOMAZ SM, AGOSTINHO AA AND HAHN NS (Eds), The upper Paraná River and its floodplain: physical aspects, ecology and conservation. Leiden: Backhuys Publishers, p. 381–393.
- HAMILTON SK AND LEWIS WM. 1992. Stable carbon and nitrogen isotopes in algae and detritus from the Orinoco River floodplain, Venezuela. Geochim Cosmochim Acta 56: 4237–4246.
- HOBSON KA AND WASSENAAR LI. 1999. Stable isotope ecology: an introduction. Oecologia 120: 312–313.
- JACKSON D AND HARKNESS DD. 1987. The use and interpretation of  $\delta^{13}$ C values as a means of stablishing dietary composition. Oikos 48: 258–264.
- JENNINGS S, REÑONES O, MORALES-NIN B, POLUNIN NVC, MORANTA J AND COLL J. 1997. Spatial variation in the <sup>15</sup>N and <sup>13</sup>C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. Mar Ecol Prog Ser 146: 109–116.
- KEOUGH JR, SIERSZEN ME AND HAGLEY CA. 1996. Analysis of a lake superior coastal food web with stable isotope techniques. Limnol Oceanogr 41: 136–146.
- LAJTHA K AND MARSHALL JD. 1994. Sources of variation in the stable isotopic composition of plants. In: MICHENER RH AND LAJTHA K (Eds), Stable Isotopes in ecology and environmental science, Oxford: Blackwell, p. 1–21.

- LOPES CA, BENEDITO-CECILIO E AND AGOSTINHO AA. 2000. The reproductive strategy of *Leporinus friderici* (Characiformes, Ansotomidae) in the Paraná River basin: the effect of reservoirs. Rev Brasil Biol 60: 255–266.
- LUZ-AGOSTINHO KDG, BINI LM, FUGI R, AGOSTINHO AA AND JÚLIO JR HF. 2006. Food spectrum and trophic structure of the ichthyofauna of Corumbá reservoir, Paraná river Basin, Brazil. Neotr Ichth 4: 61–68.
- MARTINELLI LA, DEVOL AH, VICTORIA RL AND RICHEY JE. 1991. Stable carbon isotope variation in  $C_3$  and  $C_4$  plants along the Amazon River. Nature 353: 57–59.
- MCARTHUR JV AND MOORHEAD KK. 1996. Chraracterization of riparian species and stream detritus using multiple stable isotopes. Oecology 107: 232–238.
- McClelland JW and Valiela I. 1998. Changes in food web structure under the influence of increase anthropogenic nitrogen inputs to estuaries. Mar Ecol Prog Ser 168: 259–271.
- PETERSON BJ AND FRY B. 1987. Stable isotopes in ecosystem studies. Ann Rev Ecol Syst 18: 293–320.
- THOMAS CJ AND CAHOON LB. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. Mar Ecol Prog Ser 95: 19–24.
- VANDER ZANDEN MJ AND RASMUSSEN JB. 1996. A trophic position model of pelagic food webs: impact on contaminant biomagnification in lake trout. Ecol Monogr 66: 451–477.

- Vander Zanden MJ, Cabana G and Rasmussen JB. 1997. Comparing trophic position of calculated using stable nitrogen isotope ratios ( $\delta^{15}$ N) and literature dietary data. Can J Fish Aquat Sci 54: 1142–1158.
- VAZZOLER AEAM, AGOSTINHO AA AND HAHN NS. 1997 A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Maringá, PR, Brasil, EDUEM, 460 p.
- VELHO LFM, LANSAC-TÔHA FA, BONECKER CC, BINI LM AND ROSSA DC. 2001. The longitudinal distribution of copepods in Corumbá Reservoir, State of Goiás, Brazil. Hydrobiologia 453/454: 385–391.
- VICTORIA RL, MARTINELLI LA, TRIVELIN PCO, MAT-SUI E, FORSBERG BR, RICHEY JE AND DEVOL AH. 1992. The use of the stable isotopes in studies of nutrient cycling: carbon isotope composition of Amazon Varzea sediments. Biotropica 24: 240–249.
- WASLIEN CI. 1979. Unusual sources of proteins for man. Crit Rev Food Sci Nutr 6: 77–151.
- WINEMILLER KO. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol Monogr 60: 331–367.