



The role of sediment on the energy availability for fishes in the upper Paraná river floodplain

Michele de Faveri Gimenes, Alice Michiyo Takeda and Evanilde Benedito*

Universidade Estadual de Maringá, Av. Colombo, 5790, 87020-900, Maringá, Paraná, Brazil. *Author for correspondence.
E-mail: eva@pesquisador.cnpq.br

ABSTRACT. This study aimed to identify potential sources of organic matter in sediment, using stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Sediment samples were gathered from the margin and in center of three subsystems: Ivinheima, Paraná and Baía, in August/2001. The samples were fractionated granulometrically and separated by size ($< 200 \mu\text{m}$; $70\text{--}200 \mu\text{m}$; $> 70 \mu\text{m}$), prepared and sent to CENA / USP, for identifying the isotopes proportions. Significant differences were detected in the isotopic ratios of the sediment only between sampling stations. The Baía channel presented the lowest $\delta^{13}\text{C}$ values, while the highest ones were recorded in Paraná river. At this last, $\delta^{15}\text{N}$ values were negative (-14.41‰). We did not verify significant difference in isotopic composition between the particle sizes of sediment, and between the sampling points. The main sources of carbon for the sediment were C_3 macrophytes, periphyton and particulate organic carbon (POC).

Keywords: energy flow, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$.

O papel do sedimento na disponibilidade de energia para peixes da planície de inundação do alto rio Paraná

RESUMO. O presente trabalho teve por objetivo identificar as fontes potenciais de matéria orgânica do sedimento, utilizando isótopos estáveis de carbono ($\delta^{13}\text{C}$) e nitrogênio ($\delta^{15}\text{N}$). Foram coletadas amostras de sedimento das margens e do centro de três subsistemas: Ivinheima, Paraná e Baía, em agosto/2001. As amostras foram fracionadas granulometricamente e $<200 \mu\text{m}$; $70\text{--}200 \mu\text{m}$; $>70 \mu\text{m}$, e enviadas ao CENA/USP para identificação das proporções dos isótopos. Foram verificadas diferenças significativas nas razões isotópicas do sedimento apenas entre as estações de coleta. O canal Baía, exibiu s baixos valores de $\delta^{13}\text{C}$, enquanto altos valores foram registrados no rio Paraná. Nesta última estação, os valores de $\delta^{15}\text{N}$ foram negativos (-14.41‰). Não foram registradas diferenças significativas na composição isotópica entre os tamanhos de partículas do sedimento e nem entre os pontos de coleta. As principais fontes de carbono para o sedimento foram as macrófitas C_3 , perifíton e carbono orgânico particulado (COP).

Palavras-chave: fluxo de energia, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$.

Introduction

In floodplains, the matter and energy cycles involve the combination of the contributions of allochthonous and autochthonous sources that are dependent on the flood pulses (JUNK et al., 1997; MARSHALL et al., 2008). Drainage, influenced by rainfall and local anthropogenic activities, and regional drainage, made by large rivers (BEZERRA; MOZETO, 1999), promote allochthonous and autochthonous contributions that may be different within the same ecosystem.

Detritus is among the most important food sources for the food chain from tropical floodplains (WELCOMME, 1985), and one of the main link for organic matter cycling in freshwater ecosystems (WETZEL, 1975). Detritus is a general term used to

define non-living particulate material in aquatic ecosystems that comes from any trophic level, including allochthonous sources (WETZEL, 1975). It is also defined as a mixture of particulate organic matter (dead and living particles such as algae, fungi and bacteria), which is often called detrital aggregate (BOWEN, 1982; MANN, 1988). Fish are important users of this resource and create indispensable links in the food chain, as they make the resources contained in the sediment available to piscivorous species (LOPES et al., 2009).

The elucidation of the trophic dynamics in floodplains ecosystems is very important for the management of fish. The flow of organic matter through the food chain has generated a growing interest and carbon and nitrogen have been intensely

employed to determine sedimentary organic matter in biogeochemistry studies on floodplains (ALBUQUERQUE; MOZETO, 1997; HEDGES et al., 1986a and b; JEPSEN; WINEMILLER, 2007; MARTINELLI et al., 1994; MOZETO et al., 1996; RICHEY et al., 1991).

The use of carbon and nitrogen stable isotopes offers a more efficient alternative to investigate trophic relationships between plants and animals in aquatic ecosystems, permitting direct identification of the relative contributions from different autotrophic energy sources to heterotroph food chains (PETERSON; FRY, 1987). By the analysis of the isotopic composition of carbon ($\delta^{13}\text{C}$) in the organic matter of the sediment, it is possible to characterize the sources of carbon composing the detritus, e.g. plants that selectively fix the $\delta^{13}\text{C}$ isotope, through different photosynthetic ways. In the C_3 cycle (Calvin), plants discriminate CO_2 , presenting an average $\delta^{13}\text{C}$ value of -27‰ , whereas in the C_4 cycle (Hatch-Slack), a smaller discrimination occurs, presenting an average $\delta^{13}\text{C}$ value of -13‰ (LOPES; BENEDITO-CECÍLIO, 2002). Another discrimination process is observed in crassulacean acid metabolism (CAM) plants that present a specialized system of CO_2 fixation, especially to maintain a relatively positive balance of carbon in the tissues and $\delta^{13}\text{C}$ in the intermediate values of the other two cycles.

On the other hand, $\delta^{15}\text{N}$ presents the possibility of outlining the trophic structure. This isotope does not identify primary producers like the $\delta^{13}\text{C}$, but it is consistently fractionated along the trophic web, allowing inference about the trophic position of consumers (VANDER ZANDEN et al., 1997).

In general, the organisms within the food chain reflect exactly the $\delta^{13}\text{C}$ from their energy sources, with small differences, increasing 0.2 to 1‰ at each trophic level (FRY, 1988). The increase in $\delta^{15}\text{N}$ in animals, per trophic level, is about 3.4‰ and those with $\delta^{15}\text{N}$ closer to producers are considered direct consumers of plants (POST, 2002; VANDER ZANDEN et al., 1997).

Studies focusing to trace the flow of matter and energy on the Paraná river floodplain (using stable isotopes of carbon and nitrogen) began in 2000 in the project number 558118/2009-7 CNPq-PELD (Long Term Ecological Research) with the analysis of primary producers (C_3 and C_4 plants), particulate organic carbon (POC), zooplankton and fish (LOPES et al., 2007; MANETTA; BENEDITO-CECILIO, 2003). The results revealed that the sources of carbon for the main fish species are C_3 plants. However, the origin of sediment organic

carbon from the main Paraná river floodplain subsystems was not yet investigated. Such information is important in the elucidation of the nutrient flow in the detritivore chain and indispensable for management and/or monitoring measures.

The detritivore chain includes the bottom-feeding fish species that are commercially important for the region. These benthic species remove carbon from the sediment to sustain their biomass. Frequently, analyses of the stomach contents do not permit to identify the actual source of carbon and its trophic position due to the high digestibility of the particles of organic matter present in the sediment. Thus, the present study aimed to investigate the origin of the sedimentary organic matter, which corresponds to the reservoir of organic matter for the system.

Material and methods

The study was carried out in the Paraná river basin, specifically at the upper Paraná river floodplain (Figure 1). This ecosystem presents an extensive alluvial floodplain (802,150 km^2 in Brazil). On the right bank, it has 20 km wide, with many lagoons and rivers. The lowest part of the floodplain presents a complex drainage system. This environment was divided into three subsystems (Paraná, Baía and Ivinheima). Sediment samples ($n = 46$) were obtained in August/2001 from six sampling stations, belonging to three floodplain subsystems: Paraná (Paraná river and Pau Véio Glade lagoon), Baía (Baía river and Baía channel) and Ivinheima (Ivinheima river and Finado Raimundo lagoon) ($22^\circ40'$ to $22^\circ50'S$ and $53^\circ01'$ to $53^\circ40'W$) (Figure 1). Two sampling stations were established in each of these subsystems, one in the main channel of the river, and the other in a connected lake or channel.

Sediment samples from the left bank (margin 1), center and right bank (margin 2) were taken at each sampling station (corresponding to collection points), using a modified Petersen grab. The corresponding layers were mixed within each sample in order to minimize the errors caused by the heterogeneity trait of the sediments. The samples were packed in plastic bags, tagged and stored in a freezer until the beginning of the analytical process, when they were submitted to granulometric fractionation. Three fractions were obtained: particles smaller than 70 μm , between 70 and 200 μm and larger than 200 μm . The fractionation criterion was established based on the results presented by Fugé et al. (1996) regarding the ingestion of sediment by benthic fish species.

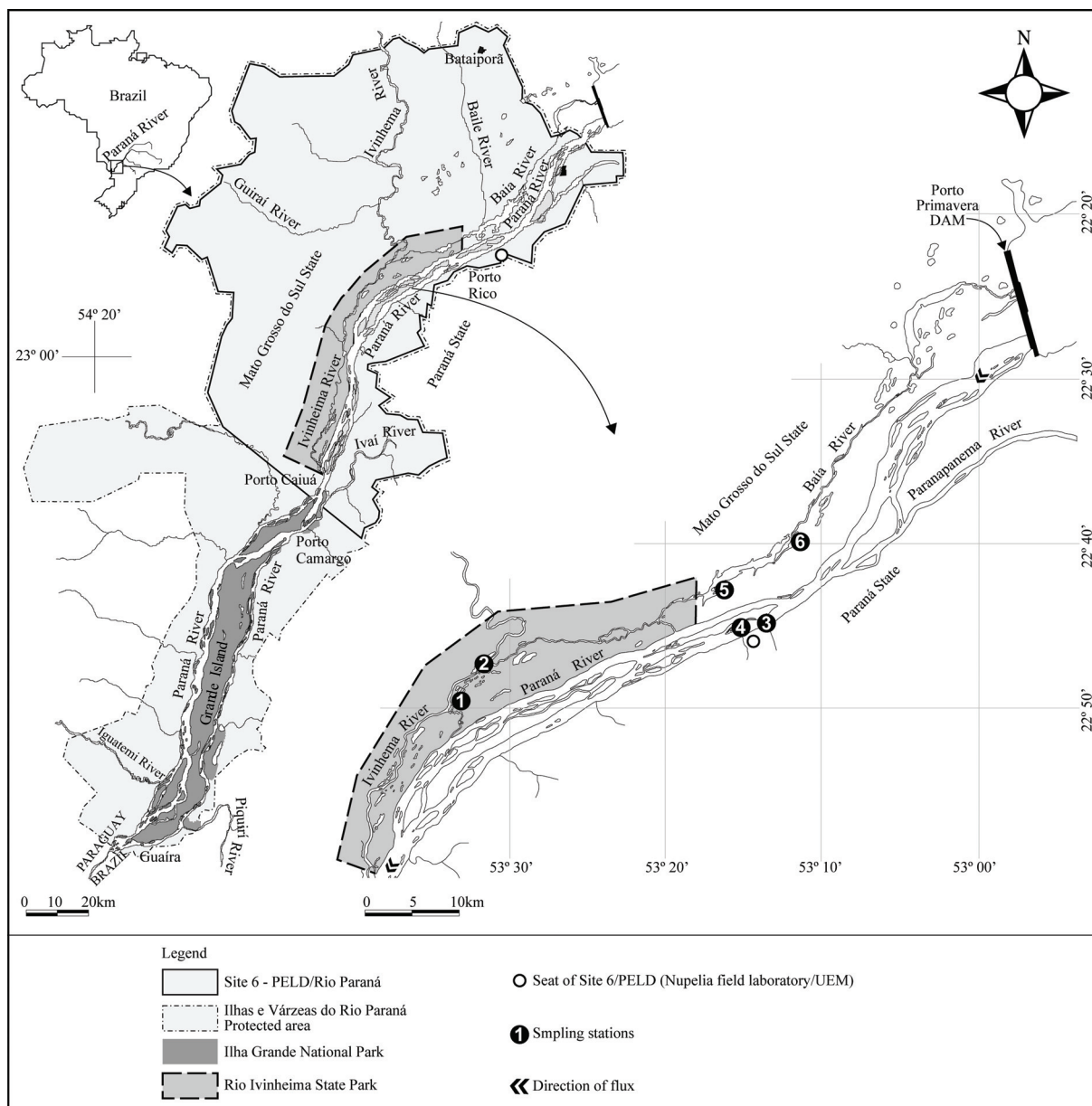


Figure 1. Sampling stations: 1) Ivinheima river; 2) Finado Raimundo lagoon; 3) Paraná river; 4) Pau Vêio Glade lagoon; 5) Baía river; 6) Baía channel.

Aiming to avoid possible contamination by inorganic carbon, the sediment samples were treated with HCL 1N. The fractions were dehydrated at 60°C to a constant weight, obtaining the dry weight. After that, the samples were homogenized in a porcelain mortar, packed in 2 mL eppendorf tubes and sent to CENA (Center for Nuclear Energy in Agriculture/São Paulo University) to determine the composition of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The carbon and nitrogen content was determined using element analysis and expressed in quantities of mass (mg) of the element per 100 mg of sample. About 1 mg of each dry sample was combusted in continuous flow by CF-IRMS (Continuous Flow Isotopic Ratio Mass

Spectrometry) in a Carlo Erba element analyzer (CHN-1110). The CO_2 and N_2 released on combustion was purified by passage through an alcohol-dry ice trap and collected with liquid N in a specially adapted high vacuum line. A secondary standard calibrated to PDB limestone was utilized to calibrate carbon isotope analyses while nitrogen isotope analyses were calibrated with atmospheric N_2 . All of the samples were analyzed in triplicate with a precision of 0.3% for carbon and 0.5% for nitrogen. Carbon and nitrogen isotope ratios were determined in a Finnigan Delta Plus mass spectrometer fitted with double inlet and double collector systems and expressed relative to the PDB and N_2 standards.

Statistical analyses were performed using STATISTICA 5.0™. Differences on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from sediment between subsystems, collection points and particle size were tested using ANOVA at a 5% significance level. With the aim of identifying the origin of the organic matter present in the sediment, their isotopic values were compared with those values from primary producers (C3 macrophyte, C4 plant, C3 plant, CAM plant, phytoplankton, periphyton) and particulate organic carbon (POC) (BENEDITO-CECÍLIO et al., 2004).

Results

On the Paraná river floodplain, significant differences were observed between the carbon isotopic composition ($\delta^{13}\text{C}$) in the sediment samples from the sampling stations (ANOVA; $p = 0.049$).

Based on the mean values, the Baía channel was verified to be the most depleted in $\delta^{13}\text{C}$ (-27.5‰); whereas the Paraná river was recorded to be the most enriched (-24.3‰) (Figure 2).

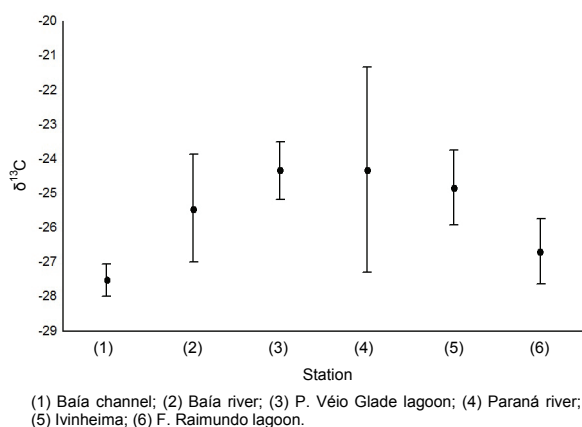


Figure 2. Mean values and standard error from the carbon isotopic composition ($\delta^{13}\text{C}$) in the sampling stations (Baía channel $n = 9$; Baía river $n = 9$; P. Véio Glade lagoon $n = 9$; Paraná river $n = 3$; Ivinheima river $n = 7$; F. Raimundo lagoon $n = 9$).

In relation to the collection points, no significant differences were verified. Meantime, the samples from the center presented mean values slightly more enriched in $\delta^{13}\text{C}$ than the other points of the transect in the sampled environments (Figure 3).

Although significant differences were not registered between the particle sizes, the highest mean value $\delta^{13}\text{C}$ was verified in the samples with large granulometric diameter ($> 200 \mu\text{m}$) (Figure 4).

Regarding the isotopic composition of nitrogen ($\delta^{15}\text{N}$), significant differences were detected between the sediment samples from the sampling stations (ANOVA: $\text{DF} = 5$; $F = 15.45$; $p = 0.000$).

The proportions of $\delta^{15}\text{N}$ ranged from 0.83 to 4.31‰ in the Baía river, 1.61 to 3.28‰ in the Baía channel, 4.49 to 6.34‰ in the Pau Véio Glade lagoon, -9.6 to -23.5‰ in the Paraná river, 3.62 to 7.42‰ in the Ivinheima river and 1.14 to 3.32‰ in the Finado Raimundo lagoon. The Pau Véio Glade lagoon presented the highest mean value (5.6‰), while the lowest one was observed in the Paraná river (-14.4‰) (Figure 5).

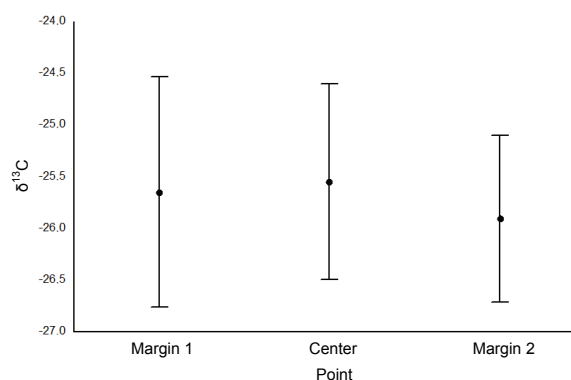


Figure 3. Mean values and standard error from the carbon isotopic composition ($\delta^{13}\text{C}$) in the collection points (center $n = 14$; margin 1 $n = 16$; margin 2 $n = 16$).

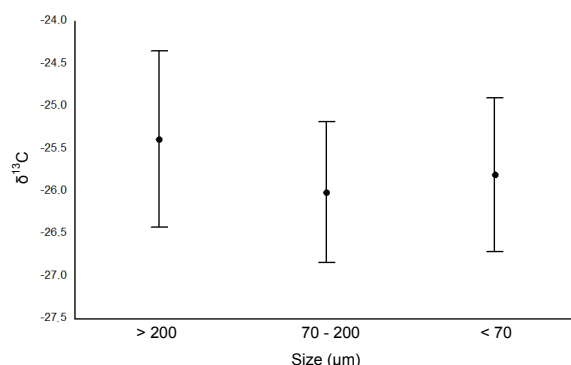


Figure 4. Mean values and standard error from the carbon isotopic composition ($\delta^{13}\text{C}$) in the particles sizes of sediment ($< 70 \mu\text{m}$ $n = 14$; $70\text{-}200 \mu\text{m}$ $n = 14$; $> 200 \mu\text{m}$ $n = 18$).

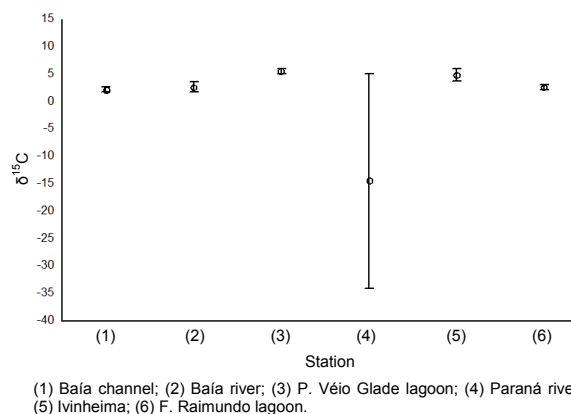


Figure 5. Mean values and standard error from the nitrogen isotopic composition ($\delta^{15}\text{N}$) in the sampling stations.

Between margin and center, no significant differences were found in the proportion of $\delta^{15}\text{N}$ at any of the collection stations, evidencing the homogeneity over the transversal transect of the river, despite the samples from the center presented mean values slightly higher than the other collection points (Figure 6).

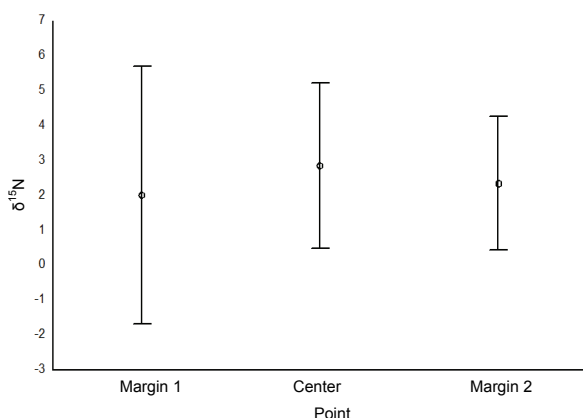


Figure 6. Mean values and standard error from the nitrogen isotopic proportion ($\delta^{15}\text{N}$) in the collection points.

Particles larger than $200\ \mu\text{m}$ presented very low $\delta^{15}\text{N}$ values, contrasting the other sizes ($70\text{--}200\ \mu\text{m}$ and smaller than $70\ \mu\text{m}$) whose mean values were estimated around 3.5‰ (Figure 7).

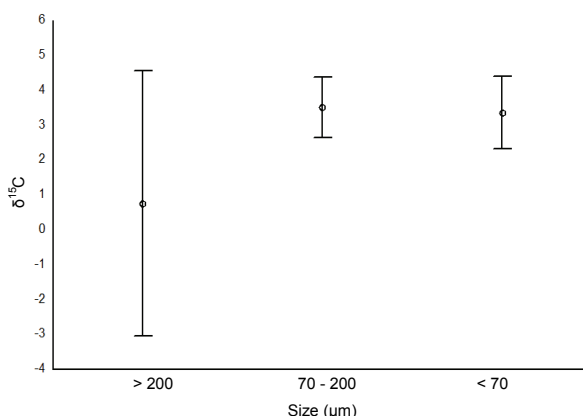


Figure 7. Mean values and standard error from the nitrogen isotopic composition nitrogen ($\delta^{15}\text{N}$) in the particles sizes of sediment.

The Figure 8 represents the isotopic proportions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the different potential sources of sedimentary organic matter. We verified that the sediment was basically composed by C_3 macrophytes, periphyton and POC, the last two presenting higher overlap values. Concerning $\delta^{15}\text{N}$, all primary producers overlapped the sediment values (1.50‰ CAM to 5.50‰ POC).

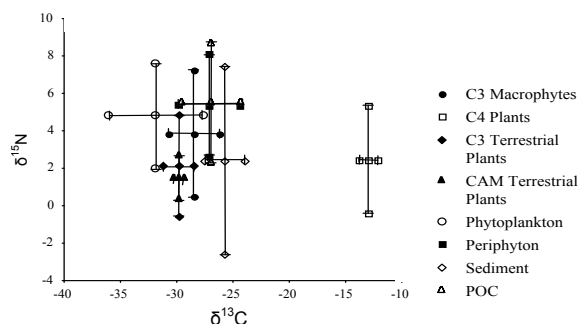


Figure 8. Mean values and confidence interval of the isotopic composition of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the sources of organic matter in the sediment (BENEDITO-CECÍLIO et al., 2004).

Discussion

The Paraná river floodplain presents a variety of biotic and abiotic conditions that causes the heterogeneity in the sediment composition at each site, as observed through the isotopic values of carbon and nitrogen. This fact is due to the complexity of the dynamics of the organic matter in this ecosystem, which is even more enriched during the rainy period. With the increase in the water level, the allochthonous organic matter is carried to the interior of the rivers and lakes. There is growing evidence from streams (KAWAGUCHI et al., 2003; NAKANO; MURAKAMI, 2001), rivers (FINLAY et al., 2002) and a few lakes (CARPENTER et al., 2005; JANSSON et al., 2007; MEHNER et al., 2005) suggesting that allochthonous carbon sources are important subsidies for fish production.

Nevertheless, the action of the Paraná river on the dynamics of the lentic, semilotic and lotic subsystem occurs through a dilution effect from the river on the "várzea" (THOMAZ et al., 1997). In this way, during the dry period analyzed in this study, the Paraná River was the most enriched in $\delta^{13}\text{C}$ (mean values) and the most depleted in $\delta^{15}\text{N}$ (mean values). This means that this environment is poor in organic matter compounded basically by proteins. Furthermore, there is the adsorption incapacity of the sediment particles ($> 200\ \mu\text{m}$), which are of sandy origin and easily washed by the water current. The most enriched $\delta^{13}\text{C}$ values indicate that the organic matter consists of very positive sources of carbon, with probable contribution from C_4 plants, which are found in some stretches of the Paraná subsystem.

In relation to the collection points, we observed that the margins presented mean values more depleted in $\delta^{13}\text{C}$ than the center, indicating the probable influence from terrestrial plants (riparian vegetation) at this point, which tends to decrease the isotopic value (mean values around -29.8‰).

The absence of differences between the analyzed mean values of $\delta^{13}\text{C}$ for the different particle size, suggests that the organic matter associated with the particle sizes from the sediment have the same origin. The great isotopic variability of the particles larger than $200\ \mu\text{m}$ is due to the high quantity of large-sized detritus that is mixed with sediment during granulometric separation. Thus, although the size selection occurs for the particle of sediment ingested by benthic fishes (FUGI et al., 1996), there is no difference in the composition of the organic matter adsorbed to the different diameter particles. This suggests that the selective ingestion is related to the proportion of organic matter, which is different for the different particles sizes of sediment (GIMENES et al., 2004).

The $\delta^{13}\text{C}$ values of the sediment coincided with the mean values of this isotope verified in C_3 macrophytes, periphyton and POC, confirming that the main sources of sedimentary carbon present autochthonous origins. On the other hand, the POC is compounded by parts of plants and animals, besides microorganisms (LOPES; BENEDITO-CECÍLIO, 2002). Moreover, we observed that, through the graphics, the POC isotopic values overlap every plant group except C_4 plants that are scarce on the Paraná river floodplain. These plants are represented by grasses situated in the marginal region from water bodies (LOPES et al., 2007), unlike the observed in the Amazon (FORSBERG et al., 1993). Consequently, the allochthonous sources, mainly C_3 riparian vegetation and CAM, compose the sediment through POC.

Recent studies in the Amazon region (ARAÚJO-LIMA et al., 1986; FORSBERG et al., 1993; HAMILTON, 1992), using carbon stable isotopes, evidenced the importance of algae in the detritivore food chain. These results contradict traditional interpretations that indicate that detritus originating from vascular plants (including C_4 plants) is one of the main sources of carbon for the food chain in flooding areas (HOWARD-WILLIAMS; JUNK, 1976; SOARES et al., 1986). In ecosystems like the mangrove swamp at Sepetiba Bay (Rio de Janeiro State), the main sources of organic carbon in the sediment are tree leaves (LACERDA et al., 1986).

The general mean value of $\delta^{15}\text{N}$ in the sediment at the Paraná river floodplain was 2.4‰ ; therefore, probably the main sources of organic matter in the sediment belong to the base of the food chain. POC and periphyton presented higher mean values than the sediment because they include organisms like protozoans, rotifers and microcrustaceans, as well as primary producers.

The distinction between the isotopic values of carbon and nitrogen allows the achievement of essential information about some processes like photosynthetic routes and energy mechanisms (determination of contributions from primary producers and consumers in the food chain). Identification of such processes is necessary to the understanding of the origin and destination of the resources in aquatic environments and to the taking of coherent management measures regarding the energy flow along the trophic web.

Conclusion

In summary, for the studied period, the energy sources available for detritivore organisms are originated from autochthonous sources. The energy availability and nutrient cycling need to be elucidated; since the detritivorous species are abundant, in number and biomass. Furthermore, our results evidenced the need for further studies concerning the detritus from floodplain subsystems, in order to better understand the aquatic food chain.

Acknowledgements

The authors wish to express their gratitude to Research Nucleus in Limnology, Ichthyology and Aquiculture (Nupelia) for logistic support, discussion of results and text review.

References

- ALBUQUERQUE, A. L. S.; MOZETO, A. A. C:N:P ratios and stable carbon isotope compositions as indicators of organic matter sources in a riverine wetland system (Mojí-Guaçu river, São Paulo-Brazil). *Wetlands*, v. 17, n. 1, p. 1-9, 1997.
- ARAÚJO-LIMA, C. A. R. M.; FORSBERG, B. R.; VICTORIA, R.; MARTINELLI, L. Energy sources for detritivorous fishes in the Amazon. *Science*, v. 234, n. 4781, p. 1256-1258, 1986.
- BENEDITO-CECÍLIO, E.; LOPES, C. A.; MANETTA, G. I.; GIMENES, M. F.; FARIA, A. C. E. A.; DOURADO, E. C. S.; PINHEIRO, R. P.; MARTINELLI, L. A. Trophic structure of the fish assemblage in the floodplain of the upper Paraná river: stable isotopes. In: AGOSTINHO, A. A.; RODRIGUES, L.; GOMES, L. C.; THOMAZ, S. M.; MIRANDA, L. E. (Ed.). *Structure and functioning of the Parana River and its floodplain LTER - SITE 6 (PELD sítio 6)*. Maringá: Eduem, 2004. p. 151-156.
- BEZERRA, M. A. O.; MOZETO, A. A. Deposição de carbono orgânico na planície de inundação do rio Paraguai durante o Holoceno Médio. *Oecologia Brasiliensis*, v. 12, n. 1, p. 155-171, 1999.
- BOWEN, S. H. Feeding, digestion and growth-qualitative considerations. In: PULLIN, R. S. V.; LOWE-

- MCCONNELL, R. (Ed.). **The biology and culture of tilapias**. Manila: ICLARM, 1982. p. 141-156.
- CARPENTER, S.; COLE, J.; PACE, M.; VAN de BOGERT, M.; BADE, D.; BASTVIKEN, D.; GILLE, C.; HODGSON, J.; KITCHELL, J.; KRITZBERG, E. Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. **Ecology**, v. 86, n. 10, p. 2737-2750, 2005.
- FINLAY, J.; KHANDWALA, S.; POWER, M. Spatial scales of carbon flow in a river food web. **Ecology**, v. 83, n. 7, p. 1845-1859, 2002.
- FORSBERG, B. R.; ARAÚJO-LIMA, C. A. R. M.; MARTINELLI, L. A.; VICTORIA, R. L.; BONASSI, J. A. Autotrophic carbon sources for fish of the Central Amazon. **Ecology**, v. 74, n. 3, p. 643-652, 1993.
- FRY, B. Food web structure on Georges bank from stable C, N and S isotopic compositions. **Limnology and Oceanography**, v. 33, n. 5, p. 1182-1190, 1988.
- FUGI, R.; HAHN, N. S.; AGOSTINHO, A. A. Feeding styles of five species of bottom-feeding fishes of the high Paraná River. **Environmental Biology of Fishes**, v. 46, n. 3, p. 297-307, 1996.
- GIMENES, M. F.; BENEDITO-CECÍLIO, E.; TAKEDA, A. M.; VISMARA, M. R. Availability of sedimentary organic matter for benthic fishes of the upper Paraná river floodplain. **Acta Scientiarum. Biological Sciences**, v. 26, n. 2, p. 181-187, 2004.
- HAMILTON, S. K. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotope. **Oecologia**, v. 89, n. 3, p. 324-330, 1992.
- HEDGES, J. I.; CLARK, W. A.; QUAY, P. D.; RICHEY, J. E.; DEVOL, A. H.; SANTOS, U. M. Compositions and fluxes of particulate organic material in the Amazon river. **Limnology and Oceanography**, v. 31, n. 4, p. 717-738, 1986a.
- HEDGES, J. I.; ERTEL, J. R.; QUAY, P. D.; GROOTES, P. M.; RICHEY, J. E.; DEVOL, A. H.; FARWELL, G. W.; SCHMIDT, F. W.; SALATI, E. Organic carbon-14 in the Amazon river system. **Science**, v. 231, n. 4742, p. 1129-1130, 1986b.
- HOWARD-WILLIAMS, C.; JUNK, W. J. The decomposition of aquatic macrophytes in the floating meadows of a Central Amazonian várzea lake. **Biogeographica**, v. 7, n. 1, p. 115-123, 1976.
- JANSSON, M.; PERSSON, L.; DE ROOS, A.; JONES, R.; TRANVIK, L. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. **Trends in Ecology and Evolution**, v. 22, n. 6, p. 316-322, 2007.
- JEPSEN, D. B.; WINEMILLER, K. O. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. **Ecology of Freshwater Fish**, v. 16, n. 3, p. 267-281, 2007.
- JUNK, W. J.; SOARES, M. G. M.; SAINT-PAUL, U. The fish. In: JUNK, W. J. (Ed.). **The Central Amazon Floodplain**. Ecological Studies. Berlin Heidelberg: Springer-Verlag, 1997. p. 385-408.
- KAWAGUCHI, Y.; TANIGUCHI, Y.; NAKANO, S. Terrestrial invertebrate inputs determine the local abundance of stream fish in a forested stream. **Ecology**, v. 84, n. 3, p. 701-708, 2003.
- LACERDA, L. D.; REZENDE, C. E.; MARTINELLI, L. A.; OVALLE, A. R. C.; MOZETTO, A. A.; NOGUEIRA, F. B.; VICTORIA, R. L.; ARAGON, G. T.; CUNHA, C. T.; SILVA, C. A. R. Composição isotópica de carbono em componentes de um ecossistema de manguezal na Baía de Sepetiba, Rio de Janeiro. **Ciência e Cultura**, v. 38, n. 10, p. 1714-1717, 1986.
- LOPES, C. A.; BENEDITO-CECÍLIO, E. Variabilidade isotópica ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) em produtores primários de ambientes terrestres e de água doce. **Acta Scientiarum. Biological Sciences**, v. 24, n. 2, p. 303-312, 2002.
- LOPES, C. A.; BENEDITO-CECÍLIO, E.; MARTINELLI, L. A.; MOREIRA, M. Z. Energy sources for explorator of bottom fish, *Prochilodus lineatus* (Prochilodontidae, Characiformes), in neotropical region. **Journal of Fish Biology**, v. 70, n. 5, p. 1649-1659, 2007.
- LOPES, C. A.; BENEDITO, E.; MARTINELLI, L. A. Trophic position of bottom-feeding fish in the upper Paraná river floodplain. **Brazilian Journal of Biology**, v. 69, suppl. 2, p. 573-581, 2009.
- MANETTA, G. I.; BENEDITO-CECÍLIO, E. Aplicação da técnica de isótopos estáveis na estimativa da taxa de turnover em estudos ecológicos: uma síntese. **Acta Scientiarum. Biological Sciences**, v. 25, n. 1, p. 121-129, 2003.
- MANN, K. H. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. **Limnology and Oceanography**, v. 33, n. 4, p. 910-930, 1988.
- MARSHALL, B. G.; FORSBERG, B. R.; THOMÉ-SOUZA, M. J. F. Autotrophic energy sources for *Paracheirodon axelrodi* (Osteichthyes, Characidae) in the middle Negro river, Central Amazon, Brazil. **Hydrobiologia**, v. 596, n. 1, p. 95-103, 2008.
- MARTINELLI, L. A.; VICTORIA, L.; FORSBERG, B. R. Isotopic composition of majors carbon reservoirs in the Amazon floodplain. **International Journal of Ecology and Environmental Sciences**, v. 20, n. 1, p. 31-46, 1994.
- MEHNER, T.; IHLAU, J.; DOERNER, H.; HOELKER, F. Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? **Limnology and Oceanography**, v. 50, n. 6, p. 2022-2031, 2005.
- MOZETO, A. A.; NOGUEIRA, F. M.; SOUZA, M. H. A.; VICTORIA, R. L. C3 and C4 grasses distribution along soil moisture gradient in surrounding areas as the lobo Dam (São Paulo, Brazil). **Anais da Academia Brasileira de Ciência**, v. 68, n. 1, p. 113-121, 1996.
- NAKANO, S.; MURAKAMI, M. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. **Proceedings of the National Academy of Sciences**, v. 98, n. 1, p. 166-179, 2001.
- PETERSON, B. J.; FRY, B. Stable isotopes in ecosystem studies. **Annual Review on Ecology and Systematics**, v. 18, n. 18, p. 293-320, 1987.

- POST, D. M. Using stable isotopes to estimate trophic position: models, methods, and assumptions. **Ecology**, v. 83, n. 3, p. 703-718, 2002.
- RICHEY, J. E.; VICTORIA, R. L.; SALATI, E.; FORSBERG, B. R. The biogeochemistry of a major river system: The Amazon case study. In: DEGENS, E. T.; Kempe, S.; RICHKEY J. E. (Ed.). **Biogeochemistry of major world rivers**. New York: John Wiley and Sons, 1991. p. 245-263.
- SOARES, M. G. M.; ALMEIDA, R. G.; JUNK, W. J. The trophic status of the fish fauna in Lago Camaleão, a macrophyte dominated floodplain lake in the middle Amazon. **Amazoniana**, v. 9, n. 4, p. 511-526, 1986.
- THOMAZ, S. M.; ROBERTO, M. C.; BINI, L. M. Fatores limnológicos e clorofila-a: caracterização dos habitats e influência do pulso de inundação. In: VAZOLLER, A. E. A. M.; AGOSTINHO, A. A.; HAHN, N. S. (Ed.). **A planície de inundação do alto rio Paraná**. Maringá: Eduem, 1997, p. 71-100.
- VANDER ZANDEN, M. J.; CABANA, G.; RASMUSSEN, J. B. Comparing trophic position of calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 54, n. 5, p. 1142-1158, 1997.
- WELCOMME, R. L. **River Fisheries**. FAO Fisheries Technical Paper, 1985.
- WETZEL, R. G. **Limnology**. Philadelphia: W. B. Saunders Company, 1975.
- Received on February 3, 2010.*
Accepted on October 8, 2010.
- License information: This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.