

Isotopic fractionation and trophic position of zooplankton species in the Upper Paraná River floodplain

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(With 1 figure)

Abstract

This study aimed to evaluate the isotopic fractionation and trophic position of three zooplankton species (*Notodiaptomus amazonicus*, *Moina minuta* and *Bosmina hagmanni*) in the Upper Paraná River floodplain. We predict that phytoplankton is the main food resource used by these species. Three zooplankton samples and three phytoplankton samples were taken from each sampling site, with three to four samples collected for each species. The number of individuals for samples varied according to the body size: from 100 to 130 individuals for *Notodiaptomus amazonicus*; 150 to 200 for *Moina minuta*; and from 250 to 300 for *Bosmina hagmanni*. The isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined using mass spectrophotometer. The isotopic fractionation of ^{13}C was performed according to the relationship $\Delta = \delta^{13}\text{C}_{\text{zooplankton}} - \delta^{13}\text{C}_{\text{phytoplankton}}$. To determine the possible trophic position of these species, we used the expression $\text{TL} = (\delta^{15}\text{N}_{\text{zooplankton}} - \delta^{15}\text{N}_{\text{phytoplankton}}) / \Delta + 1$. The species showed high variation in isotopic fractionation and in trophic position in the different environments. We verified that the species use other food resources in addition to phytoplankton. The elucidation and understanding of the trophic position of the organisms based on stable isotopic analysis offers complementary information to traditional techniques. This analysis helps explain the flow of matter and energy in the food chain of floodplain aquatic environments as well as trace the trophic relationships involved in the ecological roles and strategies of distinct species.

Keywords: stable isotopes, trophic level, zooplankton, food chain.

Fracionamento isotópico e posição trófica de espécies zooplanctônicas da planície de inundação do alto rio Paraná

Resumo

O objetivo desse estudo foi avaliar o fracionamento isotópico e as posições tróficas de três espécies zooplanctônicas (*Notodiaptomus amazonicus*, *Moina minuta* e *Bosmina hagmanni*) na planície de inundação do alto rio Paraná. Pressupõe-se que o fitoplâncton seja o principal recurso utilizado por essas espécies. De cada ponto de amostragem, foram coletadas três amostras de zooplâncton e três de fitoplâncton. De cada amostra de zooplâncton, obtiveram-se de três a quatro amostras para cada uma das três espécies. O número de indivíduos, por amostra, variou dependendo do tamanho do corpo, de 100 a 130 indivíduos para *Notodiaptomus amazonicus*, de 150 a 200 para *Moina minuta* e de 250 a 300 para *Bosmina hagmanni*. Os valores dos isótopos de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ foram determinados por meio de espectrofotometria de massa. O fracionamento de $\delta^{13}\text{C}$ foi realizado de acordo com a relação $\Delta = \delta^{13}\text{C}_{\text{zooplâncton}} - \delta^{13}\text{C}_{\text{fitoplâncton}}$ e, para determinar a possível posição trófica das espécies, foi utilizada a expressão $\text{TL} = (\delta^{15}\text{N}_{\text{zooplâncton}} - \delta^{15}\text{N}_{\text{fitoplâncton}}) / \Delta + 1$. As espécies exibiram ampla variação nos fracionamentos isotópicos e nas posições tróficas calculadas para os diferentes ambientes. Constatou-se que as espécies zooplanctônicas poderiam estar utilizando outras fontes alimentares além do fitoplâncton. Em síntese, a elucidação e compreensão da posição trófica dos organismos, com base na análise de isótopos estáveis, oferecem informações complementares às técnicas tradicionais e podem auxiliar na explicação do curso da matéria e da energia na rede trófica em ambientes aquáticos de planícies de inundação, bem como determinar o papel ecológico das distintas espécies.

Palavras-chave: isótopos estáveis, nível trófico, zooplâncton, cadeia alimentar.

1. Introduction

One main application for ^{13}C and ^{15}N stable isotopes is in understanding food chain structure (Vander Zanden et al., 1997). Isotopic studies have provided a better understanding of the energy flow along food chains. In Brazil, according to Dourado and Benedito-Cecilio (2005), such surveys have yielded important results on the relationships among aquatic organisms.

The isotopic transformations involving the relative abundances of heavy and light isotopes are called fractionations, and they occur because lighter isotopes form chemical bonds that require less energy to break. Lighter isotopes are therefore generally activated more quickly and accumulate in high concentrations in nature (Dawson and Brooks, 2001).

These isotopic signatures motivate ecologists to identify the flow of energy in the food chains composed of different trophic levels, where the number of levels represents the energy or nutrient transferences among the organisms (Lindeman, 1942). The efficiency of this energy transference describes several aspects of the structure of one ecosystem, including the number of trophic levels, the relative importance of detritivorous and herbivorous, the equilibrium values of biomass, the accumulated detritus, and the rates of material exchange (Ricklefs, 2003).

To trace this energy flow, we must understand the existing interrelations of a community, and stomach content analyses are often used to this end. However, the ingested food never represents those assimilated because items digested quickly cannot be identified through these methods (Jepsen, 1999), which are restricted to identifying food chain components. For both C and N isotopes, it is therefore essential to consider changes related to nutritional stress, reproductive activity, migratory behaviour (since migratory species may present a signal different from existing sources in the location where they were collected), and the developmental stage of the organism (Vander Zanden and Rasmussen, 2001; Benedito-Cecilio and Araújo-Lima, 2002).

In addition, it is difficult to obtain trustworthy interpretations of isotopic data because it requires understanding the isotopic fractionation that occurs between the diet and the consumer, as small organic changes affect trophic level estimations and the contributions of different producer sources (McCutchan et al., 2003).

Zooplankton is the principal link in energy transfer between other trophic levels, making it is extremely important to study the isotopic variability of zooplankton (Santana et al., 2009). Such studies can complement knowledge obtained through traditional methods, including stomach content analysis.

In the floodplain of the upper Paraná River, studies have demonstrated high zooplanktonic biodiversity and its seasonal and spatial heterogeneity, as well as relations with other biota especially microbial (Lansac Tôha et al., 2009; Bonecker et al., 2009). The results of these studies

emphasize the need to investigate the complexity of zooplankton dynamics through stable isotope analysis.

This study aimed to determine the isotopic fractionation between the phytoplankton and three zooplankton species, *Notodiptomus amazonicus* (Wright, 1935), *Bosmina hagmanni* Stingelin, 1904 and *Moina minuta* Hansen, 1899, and investigate the trophic position of these species in five lakes from the Upper Paraná River floodplain in the Paraná and Baía subsystems. The general hypothesis of the study predicts that phytoplankton is the main autotrophic source used by three analysed species, independent of sampled locations.

2. Material and Methods

2.1. Study area

Zooplankton and phytoplankton samplings were collected in the Upper Paraná River floodplain (22° 40' to 22° 50' S and 53° 10' to 53° 40' W) in May 2007, the rainy period which annually boasts the highest recorded number of zooplankton species (Lansac-Tôha et al., 2004, 2009).

Zooplankton was sampled in two subsystems totalling five sampling stations. In the Baía subsystem, samplings were performed in Porcos, Guaraná and Maria Luiza lakes. In the Paraná subsystem, samplings were undertaken in Garças Lake and Leopoldo Backwater (Figure 1).

Porcos Lake has an elongated shape, a mean depth of 2.3 m and a length of 781.3 m, and it is directly connected to the Baía River through a 60-m wide channel. Its banks are 1 m above river level and are dominated by cyperaceans (*Cyperus*) and few bushes (20%). Guaraná Lake presents a rounded shape, a mean depth of 2.1 m and a length of 386.5 m. The connection with the Baía River is 70 m long and 18 m wide. Here aquatic macrophytes predominate and the banks are covered by grasses (95%) and bushes (5%). Maria Luiza Lake is an elongated shape and connects to the Baía River through a small channel. This lake is 693.3 m long and has a mean depth of 3.3 m. This environment is located in a "várzea" field, and vegetation is composed of grasses and cyperaceans with few bushes such as azedinha, tucum and *Inga uruguensis* Hook et Arn. (UEM et al., 2002).

Garças Lake is situated beside the main Paraná River channel. Among the sampling stations, this lake is the longest (2,128 m) with a mean depth of 2 m. Its banks are covered by grasses and riparian vegetation. Leopoldo Backwater has a mean depth of 3.1 m and is 966.2 m long, with a 15-m wide channel connection to the Paraná River. Banks are covered by forest (100%), which consists mostly of *Bambusa guadua* Humb et Bonpl. and *Croton*, *Cecropia*, *Inga* (UEM et al., 2002).

2.2. Field samplings

Three zooplankton samples were collected from each sampling site using a plankton net (68 μm). Three phytoplankton samples were taken with a phytoplankton net (15 μm) at each locale, filtered in a Kitasato system, and retained in glass fibre filters (Whatman SeS GF 52-C) that had been sterilised in a muffle furnace for 5 hours at 450 °C.

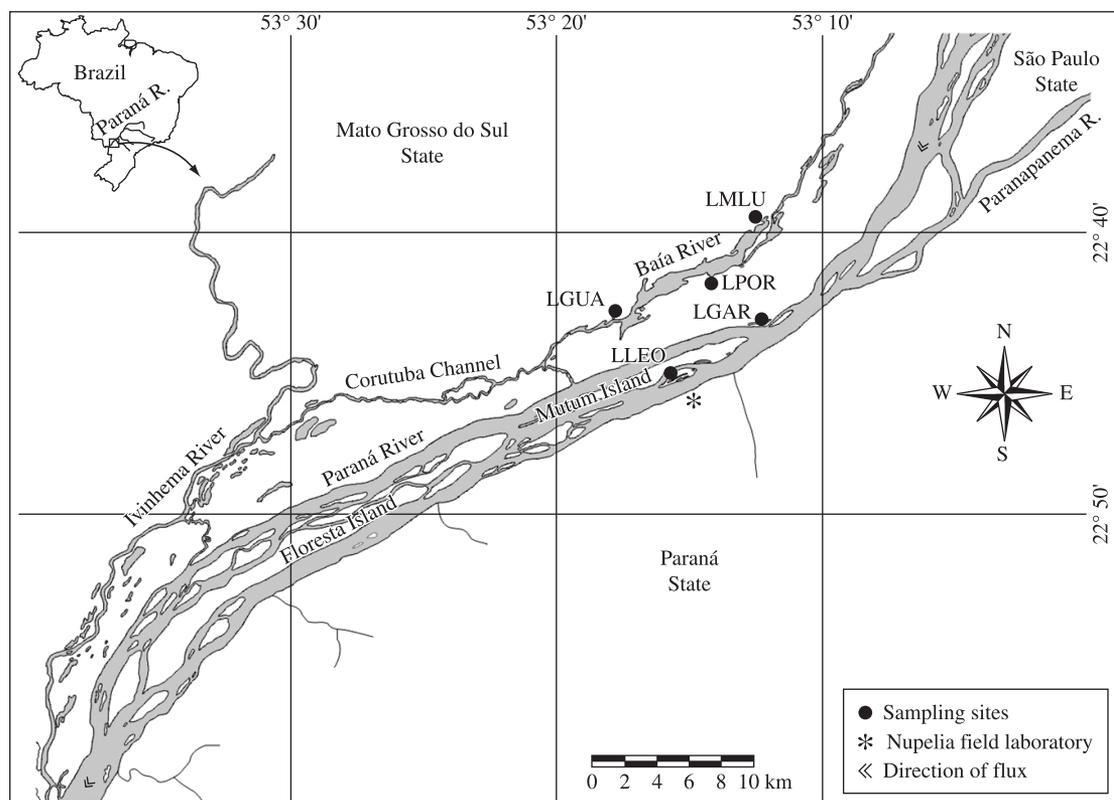


Figure 1. Location of sampling stations in the Upper Paraná River floodplain: LGAR = Garças Lake, LGUA = Guaraná Lake, LPO = Porcos Lake, LMLU = Maria Luiza Lake, LLEO = Leopoldo Backwater.

The sampled material was taken to the Laboratory of Energetic Ecology from the Universidade Estadual de Maringá, where the identification and sorting of zooplankton species were performed. From each sample, we obtained three to four samples for each one of the three zooplankton species studied. The number of individuals varied according to body size, with 100 to 130 individuals for *Notodiptomus amazonicus*, 150 to 200 for *Moina minuta*, and from 250 to 300 for *Bosmina hagdmani*.

The zooplankton and phytoplankton samples were then dried at 50 °C in an oven with forced circulation for about 48 hours and sent to the Centro de Isótopos Estáveis do Instituto de Biociências at the Universidade Estadual Paulista (Unesp/Botucatu-SP) to determine $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotopic ratios with a mass spectrophotometer, calculated according to the following equation: $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$; where: $R = ^{15}\text{N} : ^{14}\text{N}$ (Peterson and Fry, 1987).

The values of isotopic ratios were expressed in delta (δ) and in parts per thousand (‰), relative to the international standard (Peterson and Fry, 1987) *PeeDee Belemnite* (PDB) (Roland et al., 2005).

The isotopic fractionation of ^{13}C was performed according to the relationship determined by Michener and Schell (1994): $\Delta = \delta^{13}\text{C}_{\text{zooplankton}} - \delta^{13}\text{C}_{\text{phytoplankton}}$ and negative results were presented in module. To determine the possible trophic position of these species, we used the ^{15}N fractionation

proposed by Vander Zanden et al. (1997), of 3.4‰ by trophic level. Thus: $\text{TL} = (\delta^{15}\text{N}_{\text{zooplankton}} - \delta^{15}\text{N}_{\text{phytoplankton}}) / \Delta + 1$, where: $\delta^{15}\text{N}_{\text{zooplankton}}$ = isotopic value from zooplankton nitrogen; $\delta^{15}\text{N}_{\text{phytoplankton}}$ = isotopic value from primary producer nitrogen; Δ = fractionation of 3.4‰ (Vander Zanden et al., 1997); 1 = one trophic level above the primary producer.

3. Results

3.1. Isotopic fractionation

The $\delta^{13}\text{C}$ fractionation between phytoplankton and zooplankton was highly variable between the sampling stations and values were considered in module. For the same species (*B. hagdmani*), the amplitude was around 9.5‰ between environments where species presented the lowest and the highest fractionation. These results are presented in Table 1.

Among the analysed species in the module, *N. amazonicus* had the highest isotopic fractionation (7.02‰) in Guaraná Lake, while the lowest value for this species (1.96‰) was in Porcos Lake. The lowest fractionation for *B. hagdmani* ($-6.04‰$) was observed in Leopoldo Backwater and the highest value (3.51‰) in Garças Lake. *Moina minuta* did not show extreme fractionation values, with the lowest ($-3.77‰$) in Guaraná Lake and the highest (3.17‰) also in Garças Lake (Table 1).

Table 1. Isotopic fractionation between phytoplankton and the three zooplankton species by sampling station in the Upper Paraná River floodplain. The value was used in module (| |). LGAR = Garças Lake, LGUA = Guaraná Lake, LPOR = Porcos Lake, LMLU = Maria Luiza Lake, LLEO = Leopoldo Backwater.

Sites/species	<i>Moina minuta</i>	<i>Bosmina hagmanni</i>	<i>Notodiptomus amazonicus</i>
LGAR	3.17‰	3.51‰	3.35‰
LGUA	-3.77‰	0.27‰	7.02‰
LPOR	0.14‰	0.77‰	1.96‰
LMLU	-0.42‰	-0.37‰	2.29‰
LLEO	2.66‰	-6.04‰	2.53‰

3.2. $-(\delta^{15}N)$ – Trophic position

Determining trophic position was only possible for *M. minuta* and *N. amazonicus*. We could not obtain an isotopic signal for *B. hagmanni* considering the small size of this species (290 to 400 μm ; Elmoor-Loureiro, 1989). Despite using 250 to 300 individuals per sample of *B. hagmanni*, the spectrophotometer was not sensitive enough to identify the isotopic values. For *M. minuta*, the trophic position was not determined in the Guaraná and Maria Luiza lakes due to low numbers of samples. The possible trophic positions for *N. amazonicus* showed similar values in most of these environments, whereas *M. minuta* showed greater variation in the different environments (Table 2).

By analysing each sampled location, we found that none of the species showed the same pattern of fractionation in relation to the other species.

The highest trophic position was verified for *N. amazonicus* (3.7) in Guaraná Lake, and this same species occupied a similar trophic position in all the environments. *M. minuta* had a higher position in Porcos Lake (2.3) and a lower position in Leopoldo Backwater (0.6) (Table 2).

4. Discussion

The isotopic fractionation in organismal tissue varies according to food consumed, which comes from different sources (Adams and Sterner, 2000). In the present study, the isotopic fractionation was quite distinct among species in the different sampling stations. In studies in the Amazon, Benedito-Cecilio et al. (2000) registered a $\delta^{13}\text{C}$ mean value of -36.2‰ for the zooplankton. This value was considered the isotopic fractionation to be 1‰ by trophic level (De Niro and Epstein, 1978, Fry and Sherr, 1984), and they

similarly estimated the phytoplankton value as -37.2‰. A similar value was found in Venezuelan lakes (Hamilton and Lewis, 1992). The present study showed that the isotopic fractionation between phytoplankton and their consumers varied from -6.04‰ to 7.02‰ for carbon. Based on this result, we suspect that zooplankton compete with components of the microbial food chain for those resources. Considering that zooplankton may explore distinctly the autochthonous and allochthonous resources (Matthews and Mazunder, 2006) as well as bacteria (Bastviken et al., 2003), which have varied isotopic ratios, the use of 1‰ fractionation, established by De Niro and Epstein (1978) and by Fry and Sherr (1984) is difficult in neotropical food web studies.

Some authors have concluded that algae are the main energy source for planktonic food chains (Forsberg et al., 1993, Vaz et al., 1999, Benedito-Cecilio et al., 2000, Finlay, 2001). Nevertheless, phytoplankton may not explain adequately the impoverishment observed in zooplankton $\delta^{13}\text{C}$ values. Other studies (Jones et al. 1999, Bastviken et al., 2003) registered isotopic values ranging from -42 to -25‰. The authors suggest that methanotrophic bacteria might be significant sources of zooplankton nutrition (Hessen and Nygaard, 1992). These bacteria develop in environments rich in dissolved organic carbon during the rainy period (Calheiros and Hamilton, 1998) due to the accumulation of allochthonous organic matter and low levels of oxygen, conditions that facilitate methanogenesis (Bastviken et al., 2003). These bacterioplankton are assimilated by filter feeding organisms as reflected in their low $\delta^{13}\text{C}$ values (Calheiros, 2003).

Regarding nitrogen, 3.4‰ is the fractionation proposed by Vander Zanden et al. (1997) in estimating possible trophic position for species in each sampled environment.

Table 2. Trophic position estimate of zooplankton species by sampling station. LGAR = Garças Lake, LGUA = Guaraná Lake, LPOR = Porcos Lake, LMLU = Maria Luiza Lake, LLEO = Leopoldo Backwater.

Sites/species	<i>Moina minuta</i>	<i>Notodiptomus amazonicus</i>
LGAR	1.0	1.8
LGUA	...	3.7
LPOR	2.3	1.6
LMLU	...	1.8
LLEO	0.6	1.5

The highest trophic level was observed for *N. amazonicus* (3.7) in Guaraná Lake and this species presented a similar trophic position in the rest of the environments (on average 1.67). Nevertheless, only one sample of this species was collected in this lake which may explain the high mean isotopic value. On the other hand, this species is a calanoid copepod, a selective omnivorous filter feeding organism that mainly feeds on phytoplankton and detritus (Margalef, 1983, Reynolds, 1984).

Moina minuta represented extreme trophic positions, with the highest was observed in Porcos Lake (2.3) and the lowest in Leopoldo Backwater (0.6), followed by Garças Lake (1.0). Here the species is possibly acting between the first and the second trophic level in Leopoldo Backwater and Garças Lake, and between the second and the third level in Porcos Lake. Such variation was also recorded in Arctic lakes by Kling et al. (1992), who reported that when the herbivorous copepod *Diaptomus pribilofensis* was present, the predator *Heterocope septentrionalis* fed preferentially on *Diaptomus* instead of only algae (Luecke and O'Brien, 1983). However, this observation was not recorded in all studied lakes, with *Heterocope* showing a preference for algae, and only rarely was *Heterocope* a restricted predator in these environments. The fact that *M. minuta* presents trophic position close to 2 may also be associated with the wide food range of cladocerans, which are filter feeding organisms that ingest particles of varied size, including nanoplankton, detritus, bacteria and phytoplankton (Margalef, 1983, Reynolds, 1984). Kling et al. (1992) emphasize that the relative enrichment between the predator zooplankton and its prey is not well known because in natural systems this relationship depends on extending the omnivorous character of these organisms. These authors observed variations in the absolute isotopic value among the systems depending on the basis of the food chain, and highlighted the difficulties inherent in estimations from mixed food sources of several origins. In this study, the absence of bacterioplankton hindered the determination of the trophic position based on the relationship proposed by Vander Zanden et al. (1997).

In the present study, we rejected the null hypothesis of the absence of interspecific and spatial variations in zooplankton community. The complexity in zooplankton dynamics examined using stable isotopes and fractionation estimations may vary depending on physiological and environmental factors. Further studies focusing on bacterioplankton are necessary for a more reliable determination of the different trophic levels of the planktonic food chain. The wide isotopic variation in zooplankton emphasizes the need to develop methods to study the trophic structure of environments subject to constant changes, namely tropical aquatic systems. The elucidation and understanding of the trophic positions of these organisms, based on traditional techniques (stomach content analysis) and stable isotopic analysis offer complementary insights into the flow of matter and energy in floodplain aquatic environment food chains as well the trophic relations involved in the ecological strategies roles distinct species.

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References

- ADAMS, TS. and STERNER, RW., 2000. The effect of dietary nitrogen on trophic level ^{15}N enrichment. *Limnology and Oceanography*, vol. 45, no. 3, p. 601-607.
- BASTVIKEN, D., EJLERTSSON, J., SUNDH, I. and TRANVIK, L., 2003. Methane as a source of carbon and energy for lake pelagic food webs. *Ecology*, vol. 84, no. 4, p. 969-981.
- BENEDITO-CECILIO, E. and ARAÚJO-LIMA, CARM., 2002. Variation in the carbon isotope composition of *Semaprochilodus insignis*, a detritivorous fish associated with oligotrophic and eutrophic Amazonian rivers. *Journal of Fish Biology*, vol. 60, no. 6, p. 1603-1607.
- BENEDITO-CECILIO, E., ARAÚJO-LIMA, CARM., FORSBERG, BR. and BITTENCOURT, MM., 2000. Carbon sources of Amazonian fisheries. *Fisheries Management and Ecology*, vol. 7, no. 4, p. 305-315.
- BONECKER, CC., AOYAGUI, ASM. and SANTOS, RM., 2009. The impact of impoundment on the rotifer communities in two tropical floodplain environments: interannual pulse variations. *Brazilian Journal of Biology*, vol. 69, no. 2 (Suppl.), p. 529-537.
- CALHEIROS, DF., 2003. *Influência do pulso de inundação na composição isotópica ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) das fontes primárias de energia na planície de inundação do rio Paraguai (Pantanal-Paraguai)*. São Paulo: Universidade de São Paulo. 186 p. Tese de Doutorado.
- CALHEIROS, DF. and HAMILTON, SK., 1998. Limnological conditions associated with natural fish kills in the Pantanal wetland of Brasil. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, vol. 26, no. 5, p. 2189-2193.
- DAWSON, TE. and BROOKS, PD., 2001. Fundamentals of stable isotope chemistry and measurement. In UNKOVICH, M., PATE, J., McNEILL, A. and GIBBS, DJ., Ed. *Stable isotope techniques in the study of biological processes and functioning of ecosystems*. Dordrecht: Kluwer. 289 p.
- DE NIRO, MJ. and EPSTEIN, S., 1978. Carbon isotopic evidence for different feeding patterns in two *Hyrax* species occupying the same habitat. *Science*, vol. 201, no. 8, p. 908-908.
- DOURADO, ECS. and BENEDITO-CECILIO, E., 2005. *Ecologia energética de peixes: influência de fatores abióticos e bióticos*. Maringá: Eduem. 56 p.
- ELMOOR-LOUREIRO, LMA., 1989. Ciclomorfose em *Bosmina* (Crustacea, Cladocera) no lago Paranoá, Brasília. *Revista Brasileira de Zoologia*, vol. 6, no. 1, p. 37-48.
- FINLAY, JC., 2001. Stable-Carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology*, vol. 82, no. 4, p. 1052-1064.
- FORSBERG, BR., ARAÚJO-LIMA, CARM., MARTINELLI, LA., VICTORIA, RL. and BONASSI, JA., 1993. Autotrophic carbon sources for fish of the central Amazon. *Ecology*, vol. 74, no. 3, p. 643-652.

- FRY, B. and SHERR, EB., 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science*, vol. 27, no. 1, p. 13-47.
- HAMILTON, SK. and LEWIS Jr., WM., 1992. Stable carbon and nitrogen isotopes in algae and detritus from the Orinoco river floodplain, Venezuela. *Geochimica et Cosmochimica Acta*, vol. 56, no. 12, p. 4237-4246.
- HESSEN, DO. and NYGAARD, K., 1992. Bacterial transfer of methane and detritus: implications for the pelagic carbon budget and gaseous release. *Archives für Hydrobiologie*, vol. 37, p. 139-148.
- JEPSEN, DB., 1999. *Analysis of trophic pathways in freshwater ecosystems using stable isotope signatures*. Texas: Texas A & M University, 148 p. Doctor Thesis.
- JONES, RI., GREY, J., SLEEP, D. and ARVOLA, L., 1999. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos*, vol. 86, no. 1, p. 97-104.
- KLING, WG., FRY, B. and O'BRIEN, WJ., 1992. Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology*, vol. 73, no. 2, p. 561-566.
- LANSAC-TÔHA, FA., BONECKER, CC., VELHO, LFM., 2004. Composition, species richness and abundance of the zooplankton community. In THOMAZ, SM., AGOSTINHO, AA. and HAHN, NS., Ed. *The Upper Paraná River and its floodplain: physical aspects ecology and conservation*. Leiden: Backhuys Publishers. p. 145-190.
- LANSAC-TÔHA, FA., BONECKER, CC., VELHO, LFM., SIMÕES, NR., DIAS, JD., ALVES, GM. and TAKAHASHI, EM., 2009. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology*, vol. 69, no. 2 (Suppl.), p. 539-549.
- LINDEMAN, RL., 1942. The trophic dynamic aspect of ecology. *Ecology*, vol. 23, no. 4, p. 399-418.
- LUECKE, C. and O'BRIEN, WJ., 1983. The effect of *Heterocope* predation on zooplankton communities in arctic ponds. *Limnology and Oceanography*, vol. 28, no. 2, p. 367-377.
- MARGALEF, R., 1983. *Limnologia*. Barcelona: Ediciones Omega. 952 p.
- MATTHEWS, B. and MAZUNDER, A., 2006. Habitat specialization and the exploitation of allochthonous carbon by zooplankton. *Ecology*, vol. 87, no. 11, p. 2800-2812.
- McCUTCHAN, JH., LEWIS, WM., KENDALL, C. and McGRATH, CC., 2003. Variation in the trophic shift for stable isotope ratios of carbon, nitrogen, and sulphur. *Oikos*, vol. 102, no. 2, p. 378-390.
- MICHENER, RH. and SCHELL, DM., 1994. *Stable isotope ratios as tracers in marine aquatic food webs*. In LAJTHA, H. and MICHENER, RH., Ed. *Stable isotopes in ecology and environmental science*. Oxford: Blackwell Scientific. cap.7, p. 138-157.
- PETERSON, BJ. and FRY, B., 1987. Stable isotopes in ecosystem studies. *Annual Reviews and Ecology Systematics*, vol. 18, p. 293-320.
- REYNOLDS, CS., 1984. *The ecology of freshwater phytoplankton*. Cambridge: Cambridge University Press. 398 p.
- RICKLEFS, RR., 2003. *A economia da natureza*. Rio de Janeiro: Guanabara Koogan. 503 p.
- ROLAND, F., CÉSAR, D. and MARINHO, M., 2005. *Lições de limnologia*. São Carlos: RiMa. 532 p.
- SANTANA, ARA., LANSAC-TÔHA, FA. and BENEDITO, E., 2009. Variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in three zooplankton species from Upper Paraná River floodplain. *Zoologia*, vol. 26, no. 4, p. 725-732.
- Universidade Estadual de Maringá - UEM, Núcleo de Pesquisas em Limnologia e Aquicultura - NUPELIA, Pesquisas Ecológicas de Longa Duração - PELD and Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPQ, 2002. *A planície alagável do alto rio Paraná: estrutura e processos ambientais*. Maringá: PELD/CNPq. Site 6: Relatório técnico. Available from: <http://www.peld.uem.br/Relat2002/pdf/comp_fisico_locais.pdf>. Access in: 4 nov. 2007.
- VANDER ZANDEN, MJ. and RASMUSSEN, JB., 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography*, vol. 46, no. 8, p. 2061-2066.
- VANDER ZANDEN, MJ., CABANA, G. and RASMUSSEN, JB., 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 54, no. 5, p. 1142-1158.
- VAZ, MM., PETRERE Jr., M., MARTINELLI, LA. and MOZETO, AA., 1999. The dietary regime of detritivorous fish from the river Jacaré Pepira, Brazil. *Fisheries Management and Ecology*, vol. 6, no. 2, p. 121-132.