

Scientific note

Preliminary examination of food web structure of Nicola Lake (Taim Hydrological System, south Brazil) using dual C and N stable isotope analyses

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Taim Ecological Reserve is located within the Taim Hydrological System and was created to protect a heterogeneous and productive landscape harboring exceptional biological diversity in southern Brazil. Using stable isotope ratio analyses of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), we provide a preliminary description of the food web structure, including estimates of production sources supporting fish populations and vertical trophic structure, within a representative lake of this system. A total of 21 organisms (5 macrophytes, 3 mollusks and 13 adult fishes) representing 16 species were collected for isotope analysis. Fishes had $\delta^{13}\text{C}$ values ranging from -24.30 ‰ to -28.31 ‰, showing concordance with the range of values observed for macrophytes (-25.49 to -27.10 ‰), and suggesting that these plants could be a major carbon source supporting these fishes. $\delta^{13}\text{C}$ signatures of *Corbicula* (-30.81‰) and *Pomacea* (-24.26‰) indirectly suggest that phytoplankton and benthic algae could be alternative carbon sources for some consumers. Nitrogen isotope ratios indicated approximately three consumer trophic levels. The pearl cichlid *Geophagus brasiliensis* was a primary consumer. Two catfishes (*Trachelyopterus lucenai* and *Loricariichthys anus*) were secondary consumers. Two congeneric pike cichlids (*Crenicichla lepidota* and *C. punctata*), a catfish (*Pimelodus maculatus*) and the characids *Astyanax fasciatus* and *Oligosarcus robustus* were tertiary consumers. Further studies including additional primary producers and consumers and greater sample numbers should be conducted to provide a more complete and detailed description of food web structure and dynamics within the reserve.

A Estação Ecológica do Taim está inserida dentro do Sistema Hidrológico do Taim e foi criada para proteger uma região heterogênea e produtiva no sul do Brasil, abrigando uma diversidade biológica excepcional. A partir da análise de isótopos estáveis do carbono ($\delta^{13}\text{C}$) e nitrogênio ($\delta^{15}\text{N}$), esse trabalho fornece uma descrição preliminar da estrutura da teia alimentar numa lagoa representativa desse sistema, incluindo estimativas dos produtores primários que sustentam suas populações de peixes e a estrutura trófica vertical. Um total de 21 organismos (5 macrófitas, 3 moluscos e 13 peixes adultos), representando 16 espécies, foram coletados para a análise da composição isotópica. Os peixes tiveram valores de $\delta^{13}\text{C}$ variando entre -24.30 ‰ e -28.31 ‰, com uma amplitude de variação concordante com as macrófitas (-25.49 e -27.10 ‰), sugerindo indiretamente que essas plantas poderiam ser uma fonte de carbono importante para os peixes. As assinaturas $\delta^{13}\text{C}$ de *Corbicula* (-30.81‰) e *Pomacea* (-24.26‰) sugerem que fitoplâncton e algas bentônicas podem ser outra fonte de carbono para alguns consumidores. As razões isotópicas do nitrogênio indicaram aproximadamente três níveis tróficos de consumidores. O cará *Geophagus brasiliensis* foi um consumidor primário, enquanto o penharol *Trachelyopterus lucenai* e o cascudo-viola *Loricariichthys anus* foram consumidores secundários. Duas espécies congênicas de joaninha (*Crenicichla lepidota* e *C. punctata*), o pintado *Pimelodus maculatus*, o lambari *Astyanax fasciatus* e o dentado *Oligosarcus robustus* foram consumidores terciários. Novas investigações, incluindo outros produtores primários e consumidores e um maior número de amostras, deveriam ser conduzidas para propiciar uma descrição mais completa e detalhada da estrutura e dinâmica da teia alimentar no Taim.

Key words: Subtropical wetland, Neotropical fishes, Patos-Mirim Lagoon complex, Long-Term Ecological Research (LTER), Brazilian Long Term Ecological Research (PELD).

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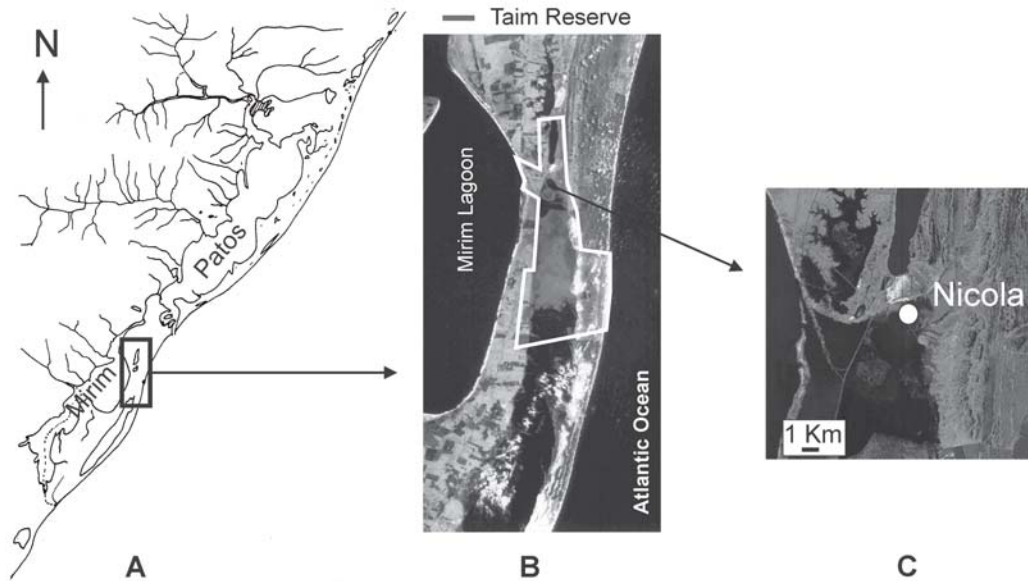


Fig. 1. Patos-Mirim Lagoon complex (ca. 14,000 Km²) (A) in southern Brazil showing the Taim Hydrological System (B) with the ecological reserve's limits (320.4 Km²) and Nicola Lake (2.45 Km²) (C).

Taim Ecological Reserve is located within a larger area called Taim Hydrological System and was created in 1978 to protect a unique freshwater wetland ecosystem in southern Brazil that had been suffering increasing anthropogenic impacts in its surroundings, such as water diversion for rice irrigation and fishing activities. The reserve encompasses a variety of habitats such as beaches, dunes, forests, grasslands and, especially, lakes and wetlands. This heterogeneous and productive landscape harbors exceptional biological diversity (Motta Marques *et al.*, 2002). In face of the above mentioned threats, it is critically important to develop baseline data on aquatic community attributes in this ecological reserve for effective conservation and management.

Fishes have been poorly investigated within Taim. Published information is restricted to taxonomic lists (Buckup & Malabarba, 1983; Grosser *et al.*, 1994; Garcia *et al.*, 2006), description of new species (Buckup, 1981; Reis, 1983) and, more recently, a feeding study (Moresco & Bemvenuti, 2005). Food web structure and dynamics in this area have not been investigated.

Based on the isotopic ratio method, we provide a preliminary description of food web structure at Nicola, a representative lake inside the reserve, including estimates of production sources supporting fish populations and vertical trophic structure. Isotopic ratios of carbon and nitrogen provide information on sources of organic matter important to consumers as well as insights about how materials are processed within trophic networks (Peterson & Fry, 1987).

Producer and consumer taxa were sampled at Nicola Lake (Taim Hydrological System) on March 25th, 2005 (Fig. 1). Our survey targeted macrofauna (fishes and mollusks) and macrophytes occurring at the study site during the day of collection. Fishes caught in Nicola Lake for isotope analysis con-

stituted a small (9 out of 42 species occurring in this site) but a representative sample of fishes inhabiting open beaches and pelagic waters in this lake (Garcia *et al.*, 2006). Floating and emergent macrophytes, snails and bivalves were collected by hand, and fishes were collected with beach seines, cast nets and gillnets. All samples were placed on ice for transport to the laboratory where they were frozen. Samples for isotopic analysis consisted of several leaves for plant species, muscle tissue (adductor) from snail and bivalve individuals, and approximately 5g of dorsal muscle tissue from individual fish. Thawed samples were inspected to remove contaminants (e.g. periphyton on leaves, bone or scales in fish tissue), rinsed with distilled water, placed in sterile Petri dishes and dried in an oven at 60°C to constant weight (minimum of 48 hrs). Dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials.

Sub-samples were weighed to the nearest 10⁻⁶ g, pressed into Ultra-Pure tin capsules (Costech, Valencia, CA), and sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia for determination of stable isotope ratios (¹³C/¹²C and ¹⁵N/¹⁴N). Results are reported as parts per thousand (‰) differences from a corresponding standard: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Standards were carbon in the PeeDee Belemnite and molecular nitrogen gas in air. Standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ replicate analyses were 0.14‰ and 0.13‰ respectively.

Bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were used to visualize patterns of energy flow between sources and aquatic consumers. Sources of organic carbon assimilated by consumers are indicated by relative positions of taxa on the x-axis ($\delta^{13}\text{C}$ values), whereas trophic level is indicated by relative position on the y-axis ($\delta^{15}\text{N}$) (Peterson & Fry, 1987).

Previous studies have shown that $\delta^{15}\text{N}$ signatures are

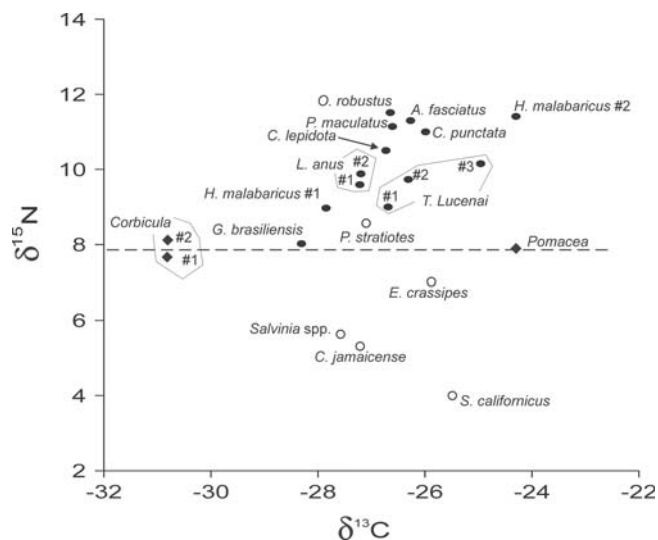


Fig. 2. Plot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for plants (○), mollusks (◇) and fishes (●) collected at Nicola Lake, Taim Hydrological System. Sources of carbon assimilated by consumers are indicated by the relative positions of taxa on the x-axis; trophic level is indicated by relative position on the y-axis. The dashed line distinguishes between producers and consumers. # symbols denotes different individuals of the same species.

accurate indicators of trophic position in aquatic systems because of predictable $\delta^{15}\text{N}$ enrichment of consumers relative to their diet (Vander Zanden & Rasmussen 1999; Post, 2002; Vanderklift & Ponsard, 2003). Considering that heavier $\delta^{15}\text{N}$ accumulates in consumers as it moves up the food web, consumers tend to be enriched by 2.5 to 3.5‰ relative to their food resources.

Thus, nitrogen isotopic distributions were used to estimate trophic positions of consumers following the method described in Post (2002) using snails and bivalves to estimate

the littoral and pelagic bases of the food web: $\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{predator}} - [\delta^{15}\text{N}_{\text{bivalve}} * \alpha + \delta^{15}\text{N}_{\text{snail}} * (1 - \alpha)]) / F$, where λ is the trophic level of consumers estimating the base of the food web (in this case $\lambda = 2$ because snails and bivalves are primary consumers), $\delta^{15}\text{N}_{\text{predator}}$ is the nitrogen signature of the consumer being evaluated, α is the proportion of carbon derived from the pelagic food web base: $\alpha = (\delta^{13}\text{C}_{\text{predator}} - \delta^{13}\text{C}_{\text{snail}}) / (\delta^{13}\text{C}_{\text{bivalve}} - \delta^{13}\text{C}_{\text{snail}})$, and F is the per trophic level fractionation of nitrogen [in this case 2.54, following the meta-analysis of Vanderklift & Ponsard (2003)]. Previous experimental studies by DeNiro & Epstein (1981), Minagawa & Wada (1984), and Vander Zanden & Ramussen (1996) suggested a fractionation value of approximately 3.4, therefore the trophic position values presented here should be considered upper estimates.

A total of 21 organisms (5 macrophytes, 3 mollusks and 13 adult fishes) representing 16 species was collected for isotope analysis (Table 1). Macrophytes showed higher between-taxon variation in $\delta^{15}\text{N}$ (4.00 to 8.57‰) than $\delta^{13}\text{C}$ (-25.49 to -27.10‰) signatures (Fig. 2). Floating macrophytes (*Pistia stratiotes*, *Eichhornia crassipes*, *Salvinia* spp.) were more enriched in $\delta^{15}\text{N}$ than emergent macrophytes (*Cladium jamaicense*, *Scirpus californicus*). The floating macrophyte *P. stratiotes* had $\delta^{15}\text{N}$ values that surpassed values of some consumers (both mollusks and the fish *Geophagus brasiliensis*). The two mollusks (*Corbicula* and *Pomacea*) had similar $\delta^{15}\text{N}$ values (around 8‰) but contrasting $\delta^{13}\text{C}$ signatures, with *Corbicula* showing a lighter signature (-30.81‰ mean value) compared to *Pomacea* (-24.26‰). Fishes had $\delta^{13}\text{C}$ values ranging from -24.30‰ to -28.31‰, showing concordance with the range of values observed for macrophytes (-25.49 to -27.10‰), and suggesting that these plants could be a major carbon source supporting these fishes (Fig. 2; Table 1).

Macrophytes revealed a $\delta^{13}\text{C}$ range concordant with values reported in the literature for terrestrial plants using the C_3

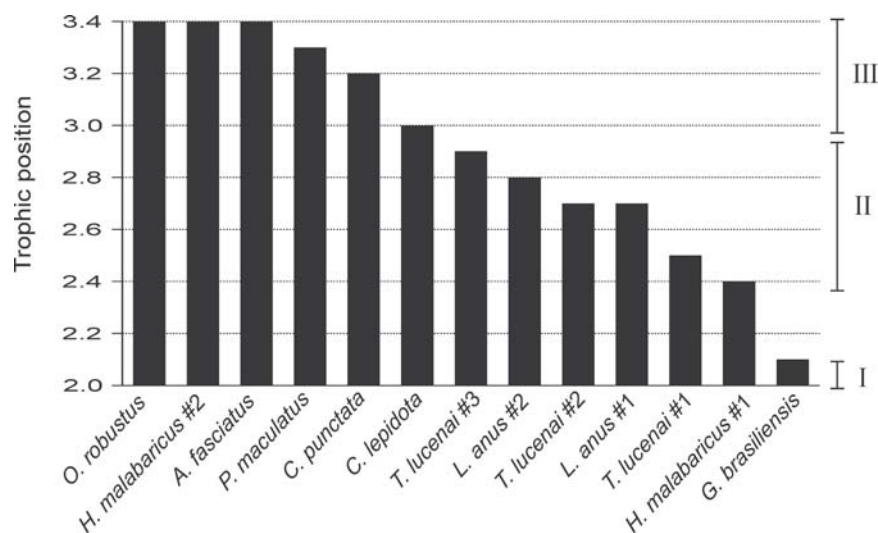


Fig. 3. Trophic position estimates of fishes collected at Nicola Lake, Taim Hydrological System. # symbols denotes different individuals of the same species.

Table 1. Taxonomic status and total length (TL mm) of the individuals collected at Nicola Lake, Taim Hydrological System. # symbols denotes different individuals of the same species.

Family	Species	TL (mm)
Fishes		
Cichlidae	<i>Geophagus brasiliensis</i>	190
	<i>Crenicichla lepidota</i>	165
	<i>Crenicichla punctata</i>	190
Erythrinidae	<i>Hoplias malabaricus</i> #1	375
	<i>H. malabaricus</i> #2	226
Auchenipteridae	<i>Trachelyopterus lucenai</i> #1	205
	<i>T. lucenai</i> #2	210
	<i>T. lucenai</i> #3	245
Pimelodidae	<i>Pimelodus maculatus</i>	305
Loricariidae	<i>Loricariichthys anus</i> #1	386
	<i>L. anus</i> #2	239
Characidae	<i>Oligosarcus robustus</i>	172
	<i>Astyanax fasciatus</i>	123
Mollusks		
Corbiculidae	<i>Corbicula</i> sp.	
Ampullariidae	<i>Pomacea</i> sp.	
Floating macrophytes		
Araceae	<i>Pistia stratiotes</i>	
Pontederiaceae	<i>Eichhornia crassipes</i>	
Salviniaceae	<i>Salvinia</i> sp.	
Emergent macrophytes		
Cyperaceae	<i>Cladium jamaicense</i>	
	<i>Scirpus californicus</i>	

photosynthetic pathway (-23 ‰ and -30 ‰, Smith & Epstein, 1971; -26.8 ‰ and 28.9 ‰, Deegan & Garritt, 1997) rather than the relatively enriched signatures shown by species that employ the C₄ photosynthetic pathway (between -12.9 ‰ and -15.8 ‰, Deegan & Garritt, 1997; -10 ‰ and -16 ‰, Forsberg *et al.*, 1993). In contrast with few C₄ emergent grasses (*e.g.*, *Zizaniopsis bonariensis*), which were not sampled in this study, most aquatic macrophytes inhabiting Taim freshwater wetlands seemed to be C₃ plants (Motta Marques *et al.*, 1997). High concordance between δ¹³C values of these primary producers and consumers suggests that analyzed macrophytes could constitute a major carbon source supporting aquatic consumers at Nicola Lake. In the Baía River (Paraná River floodplain, Brazil), Manetta and collaborators (2003), found that C₃ plants seem to be the main carbon source for the ichthyofauna.

However, the contrasting δ¹³C signatures of the two mollusks (*Corbicula*: -30.81 ‰ and *Pomacea*: -24.26 ‰), which constituted the extremes values observed for the δ¹³C signatures, also suggests that phytoplankton and benthic algae could be alternative carbon sources. Based on diet studies of congeneric species (Fellerhoff, 2002; Kasai *et al.*, 2006), we hypothesize *Corbicula* δ¹³C signatures reflect the isotopic composition of seston (phytoplankton, suspended detritus and bacteria) and *Pomacea* reflect δ¹³C largely derived from benthic algae. Phytoplankton and benthic algae have been shown to

be important carbon sources supporting aquatic food webs in a variety of habitats (*e.g.* Araujo-Lima *et al.*, 1986; Post, 2002; Vander Zanden & Vadeboncoeur, 2002; Kang *et al.*, 2003).

Nitrogen isotope ratios estimated four trophic levels at Nicola Lake (Fig. 2 and 3). The cichlid *G. brasiliensis* approximated the second trophic level (primary consumers, trophic position = 2.1), clustering together with suspension feeder *Corbicula* and grazer *Pomacea*. The black catfish *T. lucenai* and the armored catfish *L. anus*, had intermediate trophic position values (between 2.4 and 3.0). Pike cichlids *Crenicichla lepidota* and *C. punctata*, Bloch's catfish *Pimelodus maculatus*, trahira *H. malabaricus* (individual #2), and the characids *Astyanax fasciatus* and *Oligosarcus robustus* occupied the third trophic level (from 3.0 to 3.4).

These results provided a first glance at vertical trophic structure at Nicola Lake. Although some species had intermediate trophic positions, our results suggested approximately three consumer trophic levels. The pearl cichlid, *Geophagus brasiliensis*, was a primary consumer. Two catfishes (*T. lucenai* and *L. anus*) were secondary consumers. Two congeneric pike cichlids (*Crenicichla lepidota* and *C. punctata*), a catfish (*Pimelodus maculatus*) and the characids *Astyanax fasciatus* and *Oligosarcus robustus* were tertiary consumers.

Stomach contents analysis performed on these species at Taim (Moresco & Bemvenuti, 2005) and elsewhere in Brazil (Arcifa & Meschiatti, 1993; Hahn *et al.*, 2004; Cassemiro *et al.*, 2005) largely corroborated the trophic positions obtained by the isotopic ratio method. The pearl cichlid fed on detritus/sediment, aquatic insects, fish and fish scales in a shallow eutrophic reservoir, Monte Alegre Lake, São Paulo state (Arcifa & Meschiatti, 1993). In the Iguaçú River (Paraná state), the pearl cichlid diet is composed mainly of detritus/sediment, micro-crustaceans, insects, fish, algae and vascular plants (Cassemiro *et al.*, 2005). Within the Taim Ecological Reserve, black catfish *T. lucenai* has a diet composed mainly of insects and fish, followed by mollusks and crustaceans. This species also seems to be an opportunistic forager, as evidenced by the occurrence of the blind-snake *Amphisbaena darwini* in the stomach of one individual (Moresco & Bemvenuti, 2005). The armored catfish *Loricariichthys* sp. from the Upper Paraná River floodplain fed mostly on detritus, sediments and insects, plus lesser amounts of other invertebrates and algae (Hahn *et al.*, 2004). Cassemiro *et al.* (2005) found that trahiras and pike cichlids at rio Iguaçú were piscivores, and catfish of the genus *Pimelodus* fed mostly on fish and micro-crustaceans.

The two analyzed trahira specimens from Taim had different trophic positions (2.4 and 3.4). We speculated that this apparent incongruent pattern could be associated with diet changes during ontogeny. The smaller trahira (226 TL mm) likely had a higher trophic position because it fed on small insectivorous characins. The larger trahira (375 mm) may have fed heavily on relatively larger detritivorous fishes. In the Venezuelan llanos trahira experience ontogenetic diet shifts from invertebrate feeding by small juveniles to piscivory by

subadult and adult size classes (Winemiller, 1989). Large adults fed heavily on detritivorous characiforms (Winemiller, 1996).

Despite the low number of samples analyzed and lack of adequate sample replication, our study provides a first preliminary estimate of food web structure within Taim Ecological Reserve. Further food web studies in Taim's wetlands should include additional primary producers (*e.g.*, phytoplankton, benthic microalgae) and consumers (*e.g.*, benthic invertebrates, zooplankton and other fish species) to provide a more complete and detailed description of food web structure and dynamics. The isotopic ratio method could also be used to investigate ontogenetic changes in diet (Genner *et al.*, 2003), temporal and spatial variation (Deegan & Garritt, 1997; Dalerum & Angerbjorn, 2005) and material transfers associated with animal movements (Cunjak *et al.*, 2005; Herzka, 2005). Stable isotope analyses have been underutilized in investigations of food web structure within protected areas in Brazil. Compared to the more common method of stomach contents analysis, the stable isotope method yields estimates of trophic structure without requiring large sample sizes, a significant advantage when studying protected ecosystems.

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Literature Cited

- Araujo-Lima, C. A. R. M., B. R. Forsberg, R. L. Victoria & L. A. Martinelli. 1986. Energy sources for detritivorous fishes in the Amazon. *Science*, 234: 1256-1258.
- Arcifa, M. S. & A. J. Meschiatti. 1993. Distribution and feeding ecology of fishes in a Brazilian reservoir – Lake Monte Alegre. *Interciência*, 18: 302-313.
- Buckup, P. A. & L. R. Malabarba. 1983. A list of the fishes of the Taim Ecological Station, RS, Brazil. *Iheringia, Série Zoologia*, 63: 103-113.
- Buckup, P. A. 1981. *Microlepidogaster taimensis* sp. n., novo Hypoptopomatinae da Estação Ecológica do Taim, Rio Grande do Sul, Brasil (Ostariophysi, Loricariidae). *Iheringia, Série Zoologia*, 60: 19-31.
- Cassemiro, F. A. S., N. S. Hahn & R. L. Delariva. 2005. Estrutura trófica ao longo do gradiente longitudinal do reservatório de Salto Caxias (Rio Iguaçu, Paraná, Brasil), no terceiro ano após o represamento. *Acta Scientiarum*, 27(1): 63-71.
- Cunjak, R. A., J. M. Roussel, M. A. Gray, J. P. Dietrich, D. F. Cartwright, K. R. Munkittrick & T. D. Jardine. 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144: 636-646.
- Dalerum, F. & A. Angerbjorn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*, 144: 647-658.
- Deegan, L. A. & R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series*, 147: 31-47.
- DeNiro, M. J. & S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta*, 45: 341-351.
- Fellerhoff, C. 2002. Feeding and growth of apple snail *Pomacea lineata* in the Pantanal wetland, Brazil - A stable isotope approach. *Isotopes in Environmental and Health Studies*, 38(4): 227-243.
- Forsberg B. R., C. A. R. M. Araújo-Lima, L. A. Martinelli, R. L. Victoria & J. A. Bonassi. 1993. Autotrophic carbon sources for fish of the central Amazon. *Ecology*, 74: 643-652.
- Garcia, A. M., M. A. Bemvenuti, J. P. Vieira, D. M. L. Motta Marques, M. D. M. Burns, A. Moresco & M. V. Condini. 2006. Checklist comparison and dominance patterns of the fish fauna at Taim Wetland, South Brazil. *Neotropical Ichthyology*, 4(2): 261-268.
- Genner, M. J., S. J. Hawkins & G. F. Turner. 2003. Isotopic change throughout the life history of a lake malawi cichlid fish. *Journal of Fish Biology*, 62: 907-917.
- Grosser, K. M., W. R. Koch & S. Drugg-Hahn. 1994. Ocorrência e distribuição de peixes na estação ecológica do Taim, Rio Grande do Sul, Brasil, (Pisces, Teleostomi). *Iheringia, Série Zoologia*, 77: 89-98.
- Hahn, N. S., R. Fugi, & I. F. Andrian. 2004. Trophic ecology of the fish assemblages. Pp. 247-269. In: Thomaz, S. M., A. A. Agostinho, N. S. Hahn (Eds.). *The Upper Paraná river and its floodplain: physical aspects, ecology and conservation*. Leiden, The Netherlands.
- Herzka, S. Z. 2005. Assessing connectivity of estuarine fishes based on stable isotope ratio analysis. *Estuarine, Coastal and Shelf Science*, 64: 58-69.
- Kang, C. K., J. B. Kim, K. S. Lee, P. Y. Lee & J. S. Hong. 2003. Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. *Marine Ecology Progress Series*, 259: 79-92.
- Kasai, A., H. Toyohara, A. Nakata, T. Miura & N. Azuma. 2006. Food sources for the bivalve *Corbicula japonica* in the foremost fishing lakes estimated from stable isotope analysis. *Fisheries Science*, 72: 105-114.
- Manetta, G. L., E. Benedito-Cecilio & M. Martinelli. 2003. Carbon sources and trophic position of the main species of fishes of Baía River, Paraná River floodplain, Brazil. *Brazilian Journal of Biology*, 63(2): 283-290.
- Minagawa, M. & E. Wada. 1984. Stepwise enrichment of n-15 along food-chains - further evidence and the relation between delta-n-15 and animal age. *Geochimica Et Cosmochimica Acta*, 48: 1135-1140.
- Moresco, A. & M. A. Bemvenuti. 2005. Morphologic features and feeding analysis of the black catfish *Trachelyopterus lucenai* Bertoletti, Pezzi da Silva & Pereira (Siluriformes, Auchenipteridae). *Acta Limnologica Brasiliensis*, 17(1): 37-44.
- Motta Marques, D. M. L., B. Irgang & S. G. T. Giovannini. 1997. A importância do hidroperíodo no gerenciamento de água em terras úmidas (*wetlands*) com uso múltiplo – o caso da Estação Ecológica do Taim. *Anais do XII Simpósio Brasileiro de Recursos Hídricos*, Vitória (ES), 1-8.

- Motta Marques, D. M. L., C. Tucci, D. Calazans, V. L. M. Callegaro & A. Villanueva. 2002. O Sistema Hidrológico do Taim - site 7. Pp. 125-144. In: Seeliger, U., C. V. Cordazzo & F. Barbosa (Eds.) Os sites e o programa Brasileiro de pesquisas ecológicas de longa duração. Belo Horizonte, MCT-CNPq, 184p.
- Peterson, B. J. & B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology Evolution and Systematics, 18: 293-320.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecology, 83: 703-718.
- Reis, R. E. 1983. *Rineloricaria longicauda* e *Rineloricaria quadrensis*, duas novas espécies de Loricariinae do sul do Brasil (Pisces, Siluriformes, Loricariidae). Iheringia, Série Zoologia, 62: 61-80.
- Smith, B. N. & S. Epstein. 1971. 2 categories of C-13/C-12 ratios for higher plants. Plant Physiology, 47: 380
- Vander Zanden, M. J. & J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecological Monograph, 66: 451-477.
- Vander Zanden M. J. & J. B. Rasmussen. 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. Ecology, 80: 1395-1404.
- Vander Zanden, M. J. & Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, 83: 2152-2161.
- Vanderklift, M. A. & S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. Oecologia, 136: 169-182.
- Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. Environmental Biology of Fishes, 26: 177-199.
- Winemiller, K.O. 1996. Factors driving spatial and temporal variation in aquatic floodplain food webs. Pp. 298-312. In: Polis, G. A. & K. O. Winemiller (Eds.). Food Webs: Integration of Patterns and Dynamics. New York, Chapman and Hall, 475p.

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