Importance of zooplankton in the diet of a small fish in lagoons of the upper Paraná River floodplain, Brazil.

RUSSO¹, M.R. & HAHN², N.S.

¹ Programa de Pós-graduação e ² Universidade Estadual de Maringá – Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (Nupelia)/ Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Av. Colombo, 5790, Bl. G-90, 87020-900, Maringá, Paraná, Brasil. e-mail: ecorusso@yahoo.com.br, hahnns@nupelia.uem.br

ABSTRACT: Importance of zooplankton in the diet of a small fish in lagoons of the upper Paraná River floodplain, Brazil. Spatial and seasonal variations in the diet of Aphyocharax anisitsi (Eigenmann & Kennedy, 1903) were analysed between 2000 and 2001 in three isolated lagoons (Genipapo, Jacaré and Traíra) of the upper Paraná River floodplain. Simple seinings were performed along the marginal areas of the lagoons during the day. Analysis of 136 stomach contents was done by the volumetric method and the species was classified as predominantly zooplanktivore. Aphyocharax anisitsi feeds mainly on microcrustaceans (Cladocera and Copepoda), in addition to Decapoda larvae, insect larvae and detritus. Diet composition showed significant differences between hydrological periods and lagoons. Food resources consumed in the Genipapo lagoon during the dry period were different from those consumed in the Genipapo and Jacaré lagoons during the rainy period, and in the Traíra lagoon in the dry period. Calanoida was more consumed in the rainy period and insect larvae were consumed in the dry period. The availability of microcrustaceans did not influence the diet because the species selected most of its food resources. The ability of A. anisitsi to predate upon zooplankton suggests that this species can be an important trophic link between primary producers and top levels of the food web in the isolated lagoons of the upper Paraná River floodplain.

Key words: Aphyocharax anisitsi, planktivory, selectivity, freshwater, floodplain.

RESUMO: Importância do zooplâncton na dieta de um peixe de pequeno porte em lagoas da planície alagável do alto rio Paraná, Brasil. Foram analisadas as variações espaço-temporais na dieta de Aphyocharax anisitsi (Eigenmann & Kennedy, 1903) durante os anos de 2000 e 2001, em três lagoas isoladas (Genipapo, Jacaré e Traíra) da planície alagável do alto rio Paraná. Coletas trimestrais foram realizadas com redes de arrasto de malha simples nas regiões marginais das lagoas, no período diurno. A análise de 136 conteúdos estomacais pelo método volumétrico mostrou que a espécie consumiu predominantemente zooplâncton, sendo os mais representativos os microcrustáceos (Cladocera e Copepoda). Foram também registradas nos conteúdos estomacais, larvas de Decapoda, larvas de insetos e detrito. A composição da dieta foi significativamente diferente entre os períodos hidrológicos e lagoas. Os recursos alimentares consumidos na lagoa Genipapo durante a seca foram diferentes daqueles consumidos na lagoa Genipapo e lagoa Jacaré durante o período chuvoso, bem como na lagoa Traíra na seca. Calanoida foi mais consumido no período chuvoso e larvas de insetos no período seco. A disponibilidade dos microcrustáceos não influenciou na escolha do alimento, uma vez que a espécie selecionou a maior parte dos recursos consumidos. Estes resultados sugerem que A. anisitsi deve representar um elo trófico importante entre os produtores primários e os níveis de topo da cadeia alimentar nas lagoas isoladas da planicie de inundação do alto rio Paraná.

Palavras-chave: Aphyocharax anisitsi, planctivoria, seletividade, água doce, planície alagável.

Introduction

Zooplankton predation by fish is an important process for the dynamics of communities and also for the metabolism of ecosystem. This fact has been generating interest in studies dealing with the fishzooplankton interaction (Lazzaro, 1987). A significant number of papers on fishzooplankton interactions have taken into consideration the impact of predation by fish on zooplankton communities (Fernando & Holcik, 1982; Carvalho, 1984; Barbosa & Tundisi, 1984; Arcifa, 1984; Arcifa et al., 1986). According to Fernando (1994), great part of predation occurs upon larger zooplankton; thus, these communities are strongly reduced in size and density.

In the floodplain of the upper Paraná River, besides the larval and juvenile fish which almost exclusively consume zooplankton (Makrakis et al., 2005), only Hypophthalmus edentatus uses solely this resource when adult, because it has filtering gill rakers (Lansac Tôha et al., 1991; Abujanra & Agostinho, 2002; Hahn et al., 2004). Even in marginal lagoons on upper Paraná River floodplain, where zooplankton is abundant, it is underexplored by adult fish (Agostinho & Júlio-Jr, 1999).

Zooplankton community in floodplains is characterized by high species richness and abundance, owing to the great heterogeneity of habitats by seasonal changes in the water level (Paggi & Paggi, 1990; Lansac-Tôha et al., 2004). In isolated lagoons of the upper Paraná River floodplain, studies on the spatial and temporal variations of zooplankton community showed that highest density values were recorded when compared with other biotopes (Lansac-Tôha et al., 2004).

Fish fauna of the littoral region of lagoons in the upper Paraná River floodplain, specially the fauna living along macrophyte banks, consists of small tetragonopterines and cheirodontines, in addition to juveniles of medium- and large-sized species (Delariva et al., 1994). Despite their abundance, little is known about the trophic interactions between these small fish and other components of the aquatic community.

Aphyocharax anisitsi (Eigenmann & Kennedy, 1903) is a small characid that reaches a maximum length of 45 mm when adult and lives in the littoral region of isolated lagoons in the upper Paraná River floodplain. In view of the high abundance of A. anisitsi and of zooplankton, the aims of this work were to investigate: i) whether small-sized fish use this resource in the lagoons; ii) whether seasonal and spatial alterations occur in the diet of this species; iii) whether food items (zooplankton taxonomic groups) are preyed upon depending on their availability in the environment.

Material and methods

Study area

Fishes were collected in three isolated lagoons near different rivers: the Genipapo lagoon, near the Paraná River, the Jacaré lagoon, near the Ivinheima River, and in the Traíra lagoon, near the Baía River (Fig. 1).

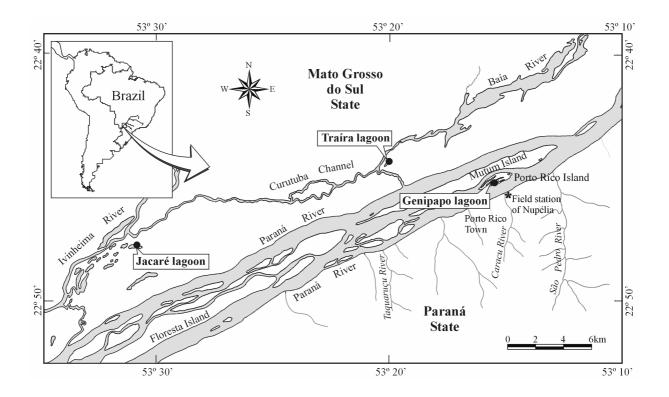


Figure 1: The sampling sites in the upper Paraná River floodplain.

Genipapo lagoon located in the Porto Rico island at 22° 45' 33.24" S; 53° 16' 5.94" W, is a temporary lagoon, with a mean depth of 0.96 m and approximately 0.06 ha area. In the littoral zone, grasses, Cyperaceae and other herbaceous plants, in addition to Croton sp. and Inga uruguensis and extensive banks of Eichhornia azurea are present. Jacaré lagoon located 22° 47' 2.04" S; 53° 29' 49.08" W, is a round-shaped lagoon with a mean depth of 2 m, length of 410 m, perimeter of 1,073 m, and 7 ha area and the littoral region is colonized predominantly by Eichhornia azurea. Traíra lagoon located 22° 44' 45.6" S; 53° 20' 21.66" W, is a small round-shaped lagoon with a mean depth of 2 m, length of 108 m, a perimeter of 292 m and 0.5 ha area. Its margins are lined with grasses, Cyperaceae and extensive banks of Eichhornia azurea, Salvinia auriculata and Pistia stratiotes.

Fish collections

Samples were taken quarterly during the years 2000 and 2001 using seining (50 m length and 0.5 cm mesh) conducted along the shoreline. All individuals were measured (standard length, cm) and weighted (total weight, g). The stomach contents were fixed in 10% formalin.

Data analysis

Abundance and biomass of A. anisitsi were described, respectively, as the number and weight of fish per 100 m^2 .

Stomach contents were analyzed by volumetric method (i.e., the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents) (Hyslop, 1980), using graduated test tubes, and a counting glass plate (Hellawell & Abel, 1971). Food items were determined to the most detailed taxonomic level possible.

An ordination method was used to summarize feeding data. According to Pielou (1984), the detrended correspondence analysis (DCA) is an ordination method designed to remove some sources of error such as the arch effect and the scale contraction effect at the end of axis. This method is suitable for nonlinear data and this procedure reveals intrinsic patterns. Specifically, it was used DCA (Hill & Gauch, 1980) to ordinate the diet of fish according to the items ingested in each period (dry and rainy periods) and in each lagoon (Genipapo, Jacaré and Traíra). Scores of this ordination were generated and submitted to a two way analysis of variance (ANOVA) since that it is difficult to meet ANOVA assumptions the normality by Shapiro Wilk's test and the homogeneity of variance by Levene's test, using crude data. When assumptions were not met, scores were square root transformed.

In order to verify whether A. anisitsi was selective with respect to zooplankton predation, we applied the Electivity Index (Ivlev, 1961): $E_i = (r_i - p_i)/(r_i + p_i)$, where: $E_i =$ electivity of the food item i; r_i : ratio of consumed items; p_i : ratio of available items.

Results

Among the three lagoons, Genipapo and Jacaré showed similar number (ind/ 100 m²) and biomass (g/100 m²) of A. anisitsi, with values of 137 and 77 for the first, and 139 and 75 for the second, respectively. But for the Traíra lagoon, these values were 46 and 24.

The analysis of 136 stomach contents showed that the diet in this species consisted predominantly of microcrustaceans in the three lagoons, particularly during the rainy period. During the dry period, plankton resource was only important at the Traíra lagoon. Insects were equally important than zooplankton in Genipapo lagoon and more important than zooplankton in Jacaré lagoon (Fig. 2).

The diet was represented by different taxa of Cladocera, Copepoda, Ostracoda, and Conchostraca, Decapoda larvae, and insect larvae, such as Chaoboridae and Chironomidae. Detritus was always present in the stomach contents (Tab. I).

In the Genipapo lagoon, the more frequently exploited resources were larvae of the shrimp Macrobrachium amazonicum (35.79%) and Calanoida (24.98%) during the rainy period, and Chironomidae larvae (37.28%), and Cladocera (Macrothryx sp.) and Cyclopoida, which together represented 25% of the diet during the dry period. In the Jacaré lagoon, Calanoida was predominant in more than 60% of the diet during the rainy period, while Chaoboridae larvae were predominant (48.42%) during the dry period. In the Traíra lagoon, Calanoida was the most consumed food item in both periods (86.52% in rainy period and 78.26% in dry period) (Tab. I).

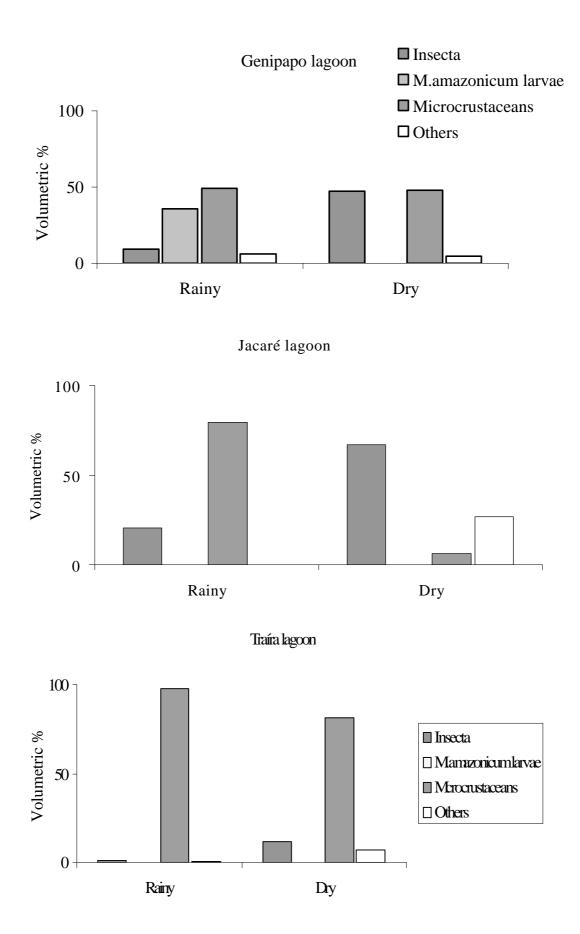


Figure 2: Volumetric ratio of the main food resources consumed by Aphyocharax anisitsi, in three isolated lagoons in the upper Paraná River floodplain, during the rainy and dry periods.

Table I: Diet composition and volumetric proportion of food items consumed by Aphyocharax anisitsi in isolated lagoons of the upper Paraná River floodplain, in the rainy and dry periods. Numbers in boldface indicate the main food items.

Lagoons Periods	Genipapo		Jacaré		Traíra	
	Rainy (n=13)	Dry (n=48)	Rainy (n=18)	Dry (n= 22)	Rainy (n=6)	Dry (n=29)
Cladocera						
Alona sp.	0.09	4.63				0.01
Bosmina sp.	0.06		0.81	0.17		0.17
Chidorus sp.		0.61				
Diaphanosoma sp.	6.86				0.03	
llyocryptus sp.		0.52				
Leydigia sp.		3.09				
Leydigiopsis sp.		O.11				
Macrothryx sp.		12.26				
Moina sp.	11.36	0.51				0.01
Pleuroxus sp.		0.01				
Simocephalus sp.		6.70				
Copepoda						
Calanoida	24.98	3.39	61.52	4.02	86.52	78.26
Cyclopoida	5.31	12.72		1.01	11.21	0.30
Harpacticoida			15.18			
Non-planktonic crustaceans	;					
Ostracoda		3.70				0.07
Conchostraca		0.68		0.67		0.31
Other crustaceans						
M. amazonicum (larvae)	35.79					
Insecta						
Chaoboridae (larvae)		0.58	4.34	48.42		1.48
Chironomidae (larvae)		37.28	6.78	18.23		6.20
Detritus	15.56	13.19	11.38	27.49	2.25	13.20

The results of the spatial and seasonal ordination of the diet are shown in Figure 3 A and B. Scores obtained by DCA were: axis 1= DCA1 (eigenvalue = 0.84) and axis 2= DCA2 (eigenvalue = 0.43). The first two axes were retained for interpretation, because they presented eigenvalues greater than 0.20 (as recommended by Matthews, 1998). This analysis showed that the diet is differentiated mainly as a function of periods, not sampling sites. Thus, food items more important for the ordination during the rainy period were (negatively in DCA1), Calanoida, M. amazonicum, and Moina sp., in all lagoons, and during the dry period were (positively in DCA1) Simocephalus, Pleuroxus, and Chidorus in both Genipapo and Jacaré lagoons. On the

other hand, on DCA2, resources consumed in dry period (Macrothryx, Ilyocryptus, Leydigia and Leydigiopsis) and during the rainy period (Cyclopoida), respectively, in the Genipapo and Traíra lagoons, influenced negatively the ordination, and the item consumed in rainy period (Harpacticoida) in the Genipapo and Jacaré lagoons, influenced positively the ordination.

Significant Interactions between lagoons and periods were no found along axis 1 ($F_2 = 0.97$; P = 0.41); therefore, the influence of each factor was evaluated separately. Significant differences were detected in the temporal scale only ($F_1 = 4.67$; P = 0.04; axis 1), indicating that the resources consumed depended on sampling period. Significant interactions occurred between lagoons and

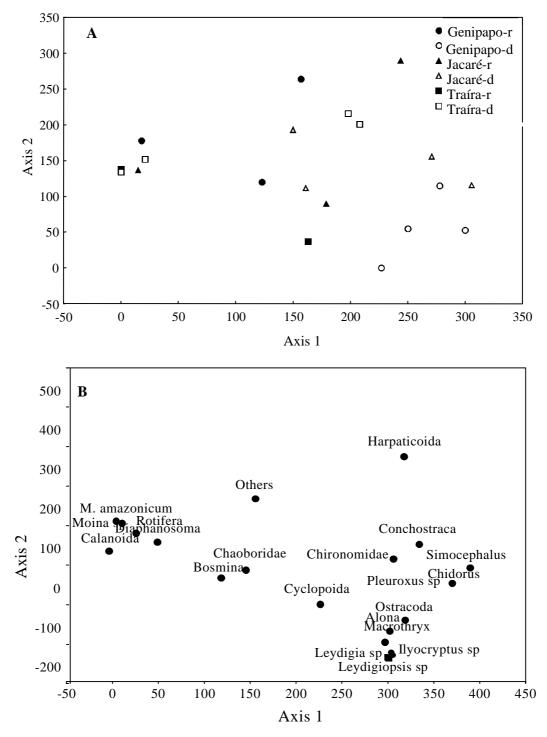
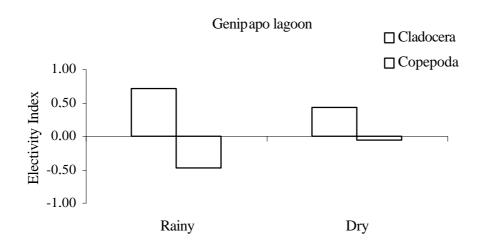


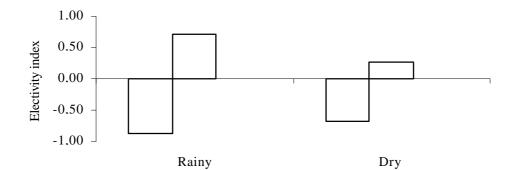
Figure 3: Scores derived from correspondence analysis, with removal of the arch effect (DCA), considering A) sites and sampling periods (r = rainy period; d = dry period); B) feeding items consumed by Aphyocharax anisitsi.

periods in axis 2 ($F_2 = 4.79$; P = 0.03; axis 2), indicating that the resources consumed in the Genipapo lagoon during the dry period were different from those consumed in the Genipapo (Duncan P= 0.03) and Jaca-ré lagoons (Duncan P=0.04) during the rainy period, and in the Traíra lagoon (Duncan P= 0.04) in the dry period.

Aphyocharax anisitsi was selective in ingesting zooplankton in all lagoons and in both periods (Fig. 4). In the Genipapo lagoon, the species positively consumed Cladocera in the rainy and dry periods. Copepoda were positively consumed in the Jacaré and Traíra lagoons, in both the rainy and dry periods.









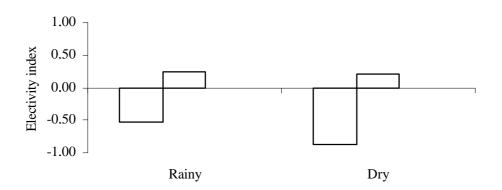


Figure 4: Electivity index of food resources consumed by Aphyocharax anisitsi, relative to available resources, in three isolated lagoons in the upper Paraná River floodplain, during the rainy and dry periods.

Discussion

The isolated shallow lagoons in the upper Paraná River floodplain are characterized by high phosphorus and chlorophyll a concentrations due to daily mixing water column and inputs of nutrients from sediment (Thomaz et al., 1997). Greater density, biomass, and richness of smallsized, short-life-cycle fishes were recorded in the years 2000 and 2001 in isolated lagoons, than those connected with the river (Petry et al., 2003). Aphyocharax anisitsi was the fifth most-captured species in the all lagoons of this floodplain in another study, including the Traíra, Jacaré and Genipapo lagoons (Agostinho, personal communication).

The diet of this species, based mainly on microcrustaceans, indicates a strong tendency to zooplanktivory in the three lagoons. Microcrustaceans were recorded at high densities in collections made concurrently with this study (Lansac-Tôha et al., 2004). These organisms show an association with aquatic plants, where they find shelter against excessive predation (Scheffer, 1998). addition In to microcrustaceans, Chaoboridae larvae were dominant in stomach contents in the Genipapo lagoon during the dry period. These insects are planktonic during the larval stage (Esteves, 1998). These records are strong indications that A. anisitsi is a surface feeder, preferentially zooplanktivorous, and may, in the case of lagoons, be acquiring food among the aquatic vegetation. Except Calanoida, Chaoboridae larvae, and the Cladocera Bosmina and Moina the other consumed taxa are typical members of littoral regions, living mainly among macrophytes, where they feed on periphyton (Green, 1985). Marginal regions of floodplain lagoons play an important role in the zooplankton community, as they promote greater habitat richness and offer more available food, due to the massive presence of extensive macrophyte banks (Green, 1985). According to Rainyzel (1990) the most significant interactions between fish and zooplankton occur in the littoral zone. Loureiro-Crippa (personal communication) also characterized A. anisitsi as zooplanktivorous in some lagoons of the Paraná River floodplain. Studies performed by Pouilly et al. (2004) on the trophic structure of fish in eight lagoons on the Mamoré River floodplain in Bolivia regarded A. anisitsi as a zooplanktivorous species, since it consumed aquatic invertebrates, as Cladocera, Copepoda, and Rotifera. Then, this fish may be considered a trophic specialist. So far, only Hypophthalmus has been referred edentatus as zooplanktivorous fish in the upper Paraná River floodplain (Lansac Tôha et al., 1991; Abujanra & Agostinho, 2002; Hahn et al., 2004).

Strong seasonal influence on the composition and amount of zooplankton consumed was recorded in the three lagoons of the upper Paraná River floodplain. Copepoda were heavily preyed upon during the rainy period, although concurrent study with these organisms showed that they were more abundant during the dry period in the three isolated lagoons (Lansac-Tôha et al., 2004). On the other hand, Cladocera, which were consumed predominantly in the rainy period, were also more abundant in the three lagoons (Lansac-Tôha et al., 2004).

Differences in diet were more related to food composition, when comparing the individuals of the three lagoons, since A. anisitsi consumed different zooplankton groups (Cladocera and Copepoda). Electivity values showed that selection of zooplankton type occurred in the different lagoons.

Despite the high biomass of protozoans and Rotifera in tropical lentic environments (Lazzaro, 1987; Fernando, 1994; Esteves, 1998), as well as in the upper Paraná River floodplain (Lansac-Tôha et al., 2004), A. anisitsi seems to have a preference for microcrustaceans. According to Zaret (1972), this behavior is typical of visual predators that "catch" their items in the water column, and this seems to be the case also with A. anisitsi. But, protozoans are more easily digested and were no found in stomachs of the fish. However, Rotifera that have a non-digestible shell were seldom found.

A reason for the little understanding on the use of zooplankton by freshwater fish appears to be that most investigations specifically considered the interactions between pelagic fish x pelagic zooplankton (Barbosa & Tundisi, 1984; Arcifa, 1984) and there are indications that the fishzooplankton interaction in tropical environments has a solely feature. Then, large part of the interactions are neither related to medium- and large-sized fishes, nor with the pelagic compartment of aquatic environments. In fact, interactions mainly occur among small fishes that feed preferentially on the littoral.

Thus, A. anisitsi is a selective zooplankton predator, changing the type of food according to seasonal availability. These results constitute strong evidence that A. anisitsi is an important trophic link in these lagoons, acting between primary producers and top levels of the food chain.

Acknowledgments

We express our appreciation to Nupélia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura), to the PELD project (Pesquisas Ecológicas de Longa Duração – site 6; Proc. n° 520026/1998-5), and to PEA (Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais) for their financial support and infrastructure.

References

- Abujanra, F. & Agostinho, A.A. 2002. Dieta de Hypophthalmus edentatus (Spix, 1829) (Osteichthyes, Hypophthalmidae) e variações de seu estoque no reservatório de Itaipu. Acta Sci., 24:401-410.
- Agostinho, A.A. & Júlio Jr., H.F. 1999. Peixes da bacia do alto rio Paraná. In: McConnell, L. (ed.) Estudos ecológicos de comunidades de peixes tropicais. Edusp, São Paulo. p.374-399.
- Arcifa, M.S. 1984. Zooplankton composition in ten reservoirs in Southern Brazil. Hydrobiologia, 113:137-145.
- Arcifa, M.S., Northcote, T.G. & Froehlich, O. 1986. Fish-zooplankton interactions and their effects on water quality of a tropical Brazilian reservoir. Hydrobiologia, 139:49-58.
- Barbosa, P.M.M. & Tundisi, T.M. 1984. Consumption of zooplanktonic organisms by Astyanax fasciatus Cuvier, 1819 (Osteichthyes, Characidae) in Lobo (Broa) reservoir, São Paulo, S.P., Brazil. Hydrobiologia, 113:171-181.
- Carvalho, M.L. 1984. Influence of predation by fish and water turbidity on a Daphnia gessneri population in a Amazonian floodplain lake, Brazil. Hydrobiologia, 113:1-13.
- Delariva, R.L., Agostinho, A.A. Nakatani, K. & Baumgartner, G. 1994. Ichthyofauna associated to aquatic macrophytes in the upper Paraná River floodplain. Rev. Unimar, 16:41-60.
- Esteves, F.A. 1998. Fundamentos de Limnologia. Interciência, Rio de Janeiro. 602p.
- Fernando, C.H. & Holcik, J. 1982. The nature of fish communities: a factor influencing the fishery potential and yields of tropical lakes and reservoirs. Hydrobiologia, 97:127-140.
- Fernando, C.H. 1994. Zooplankton, fish and fisheries in tropical freshwaters. Hydrobiologia, 272:105-123.
- Green, J. 1985. Horizontal variations in associations of zooplankton in Lake Kariba. J. Zool., 206:225-239.
- Hahn, N.S., Fugi, R. & Andrian, I.F. 2004. Trophic ecology of the fish assemblages.

In: Thomaz, S.M., Agostinho, A.A. & Hahn, N.S. (eds.) The upper Paraná River and its floodplain: physical aspects, ecology and conservation, Backhuys Publishers, Leiden. p.247-269.

- Hellawell, J. & Abel, R. 1971. A rapid volumetric method for the analysis of the food of fishes. J. Fish Biol., 3:29-37.
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio, 42:47-58.
- Hyslop, E.M.S. 1980. Stomach contents analysis – a review of methods and their application. J. Fish Biol., 17:411-429.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven. 302p.
- Lansac-Tôha, F.A., Lima, A.F., Hahn, N.S. & Andrian, I.F. 1991. Composição da dieta alimentar de Hypophthalmus edentatus Spix, 1892 (Pisces, Hypophthalmidae) no reservatório de Itaipu e no rio Ocoí. Rev. Unimar, 13:147-162.
- Lansac-Tôha, F.A., Bonecker, C.C. & Velho, LFM 2004. Composition, species richness and abundance of the zooplankton community. In: Thomaz, S.M., Agostinho, A.A. & Hahn, N.S. (eds.) The upper Paraná River and its floodplain: physical aspects, ecology and Backhuys Publishers, conservation. Leiden. p.146-180.
- Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia, 146:97-167.
- Makrakis, M.C., Nakatani, K., Bialetzki, A., Sanches, P.V., Baumgartner, G. & Gomes, L.C. 2005. Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu reservoir, Brazil. Environ. Biol. Fishes, 72:99-107.
- Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, New York. 756p.
- Paggi, J.C. & Paggi, J. 1990. Zooplâncton de ambientes lóticos e lênticos do rio Paraná médio. Acta Limnol. Bras., 3:685-719.
- Petry, A.C., Agostinho, A.A. & Gomes, L.C. 2003. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. Neotrop. Ichthyol., 1:111-120.
- Pielou, E.C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley & Sons, New York. 263p.

- Pouilly, M., Yunoki, T., Rosales, C. & Torres, L. 2004. Trophic structure of fish assemblages from Mamoré River floodplain lakes (Bolivia). Ecol. Freshwater Fish, 13:245-257.
- Rainyzel, R.G. 1990. Land-water interfaces: metabolic and limnological regulators. Int. Ver. Theor. Angew. Limnol. Verh., 24:6-24.
- Scheffer, M. 1998. Ecology of shallow lakes. Chapman & Hall, London. 357p.
- Sheldon, A.L. & Meffe, G.K. 1993. Multivariate analysis of feeding relationships of fishes in blackwater streams. Environ. Biol. Fishes, 37:161-171.
- Thomaz, S.M., Roberto, M.C. & Bini, L.M. 1997. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. In: Vazzoler, A.E.A.M., Agostinho, A.A. & Hahn, N.S. (eds.) A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos. Eduem, Maringá. p.73-102.
- Zaret, T.M. 1972. Predators, invisible prey, and the nature of polymorphism in Cladocera (Class Crustacea). Limnol. Oceanogr., 17:171-184.

Received: 01 September 2006 Accepted: 20 November 2006