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Zooplankton assemblages (Copepoda and Cladocera) in a cascade of reservoirs of a large tropical river (SE Brazil)

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ABSTRACT

Zooplankton assemblages (Copepoda and Cladocera) in a cascade of reservoirs of a large tropical river (SE Brazil)

The construction of reservoirs for the production of electricity is one of the major human interferences on large tropical rivers. This study analyzes the structure of the microcrustacean assemblages (Copepoda and Cladocera) in a cascade of 8 reservoirs in the Paranapanema River. Samples were obtained during 8 campaigns through a vertical haul (from bottom to surface) with a net with 50 μm of mesh size in 19 stations distributed along the watershed (*ca.* 700 km). The 3 main tributaries were sampled downstream, just like the mouth zone ot the Paranapanema River into the Paraná River. Nineteen species of Copepoda and 56 of Cladocera were identified. This high richness confirms the importance of considering the entire watershed for the elaboration of regional inventories. The main species were *Notodiaptomus henseni*, *N. iheringi*, *Thermocyclops minutus*, *T. decipiens*, *Mesocyclops longisetus*, *M. meridianus* and *M. ogunnus*, among the copepods, and the cladocerans *Daphnia gessneri*, *Ceriodaphnia cornuta rigaudi*, *C. cornuta cornuta*, *C. silvestrii*, *Diaphanosoma spinulosum*, *D. birgei*, *D. brevireme*, *D. fluviatile*, *Moina minuta*, *Bosmina hagmanni* and *Bosminopsis deitersi*. The seasonal occurrence of the main species is discussed. A downstream increase in richness (River Continuum Concept) was not observed. The transition zones (riverine to lacustrine) and the zones connected to flooded areas and lagoons have a positive effect on the richness. Comparisons of the diaptomidae composition and dominance between decades indicate an important structural change, probably related to the increase in the trophic conditions. Two different conditions favor the increase in abundance: higher water retention time and also of the trophic conditions. Temporal and longitudinal (intra-reservoir) trends were observed but they could not be generalized. The variation of the relative abundance of the cladoceran families and *Thermocyclops* species, as well as of the Shannon diversity index, were related to the different trophic and hydrodynamic conditions in the cascade. The analysis of the microcrustacean composition and abundance has allowed the identification of important spatial patterns in the hydrographic watershed, including the effects of damming.

Key words: Zooplankton, spatial variation, temporal variation, reservoirs, hydrographic watershed.

RESUMEN

Asociaciones zooplanctónicas (Copepoda y Cladocera) en una cascada de embalses de un río tropical (SE Brasil)

La construcción de embalses para la producción de electricidad es una de las principales interferencias humanas en los grandes ríos tropicales. Este estudio analiza la estructura de las asociaciones de microcrustáceos (Copepoda y Cladocera) en una cascada de 8 embalses en el Río Paranapanema. Las muestras fueron obtenidas durante 8 campañas efectuando un arrastre vertical (de fondo a superficie) con una red de 50 μm de apertura de malla, en 19 estaciones distribuidas a lo largo de la cuenca (ca. 700 km). Los tres principales tributarios también fueron muestreados río abajo, así como la zona de desembocadura del río Paranapanema en el río Paraná. Fueron identificadas 19 especies de Copepoda y 56 de Cladocera. Esta alta riqueza confirma la importancia de considerar toda la cuenca para la elaboración de inventarios regionales de la fauna. Entre los Copepodos las principales especies fueron Notodiaptomus henseni, N. iheringi, Thermocyclos minutus, T. decipiens, Mesocyclops longisetus, M. meridianus *y* M. ogunnus, *y entre los Cladoceros* Daphnia gessneri, Ceriodaphnia cornuta rigaudi, C. cornuta cornuta, C. silvestrii, Diaphanosoma spinulosum, D. birgei, D. brevireme, D. fluviatile, Moina minuta, Bosmina hagmanni *y* Bosminopsis deitersi. *La ocurrencia estacional de las principales especies es discutida. No fue observado un incremento de la riqueza río abajo (concepto del Continuo Fluvial). Las zonas de transición (riverina a lacustre) y las zonas de conexión con áreas inundadas y lagunas tienen un efecto positivo en la riqueza. La comparación de la composición*

y dominancia de Diaptomidae entre décadas, indica un importante cambio estructural, probablemente relacionado con el incremento de las condiciones tróficas. Dos diferentes condiciones favorecen el aumento de la abundancia: incremento en el tiempo de retención del agua y también en las condiciones tróficas. Fueron observadas tendencias temporales y longitudinales (intra embalses) aunque las mismas no pueden ser generalizadas. La variación de la abundancia relativa de las familias de Cladocera *y de las especies de* Thermocyclops, *así como el índice de diversidad de Shannon, estuvieron relacionados con las diferentes condiciones tróficas e hidrodinámicas en la cascada. El análisis de la composición y la abundancia de los microcrustáceos ha permitidoidentificar importantes patrones espaciales en la cuenca hidrográfica, incluyendo los efectos de las presas.*

Palabras clave: *Zooplancton, variación espacial, variación temporal, embalses, cuenca hidrográfica.*

INTRODUCTION

The vast morphological alteration of rivers along the modern human history, such as damming, embankment and canalization, has caused the loss of the ecological function and diversity of these ecosystems (Ward, 1998; Tockner *et al.*, 1998). Since the 1990s advanced concepts of river ecology have provided the scientific foundation for a new river management strategy, including river restoration and riverine floodplain conservation (Bloesch & Sieber, 2002). In the case of large reservoirs, their construction has declined in the more developed and industrialized countries due to the unavailability of appropriate places, or changes in the economical and environmental priorities (Avakyan & Iakovleva, 1998; Kennedy, 1999). Nevertheless, in the developing countries the damming of large rivers to attend the growing energetic demand will continue to be one of the main human interferences on nature in the near future.

In Brazil, mainly in the southeast region, the series of reservoirs built up in the last decades for hydropower generation, deeply changed the countryside landscapes. Despite of the social, economical and environmental importance of the reservoir cascades, only in the 1990s studies started to be carried out in order to understand their limnological functioning (Tundisi *et al.*, 1991; Straškraba, 1994; Litvinov & Roshchupko, 1994).

Investigations of the influence of the reservoir cascades on the aquatic biota are very scarce in Brazil. Barbosa *et al.* (1999) reported marked changes in dominance of the phytoplankton assemblages along the Tietê River cascade (São Paulo). In this same system Abe *et al.* (2003) analyzed the abundance and structure of the bacterial community comparing it to those of temperate environments. Callisto *et al.* (2005) attributed the downstream increase in diversity of the benthic macro-invertebrates to the water quality improvement along the São Francisco cascade (NE Brazil). Ferrareze & Nogueira (2006) showed the influence of the alternation between lotic (free stretch) and lentic (reservoir) conditions on the structure of the phytoplankton assemblages in the Paranapanema River cascade. In the case of the zooplankton, there are studies on Copepoda Cyclopoida in the Tietê cascade (Silva & Matsumura-Tundisi, 2002) and on copepods, cladocerans and rotifers (data from 1979) (Sampaio *et al.*, 2002), and ciliates (Lansac-Toha *et al.*, 2004) in the Paranapanema cascade.

The proposal of this study was to analyze the structure of the microcrustacean assemblages in a large tropical reservoir cascade, focusing on the inter-reservoir and the intra-reservoir variability during two consecutive years. The results can contribute to a better understanding of the trophic dynamics in the reservoirs and to the improvement of the management practices in the watershed (fish biomass production, water quality/eutrophication control, habitat conservation, among others).
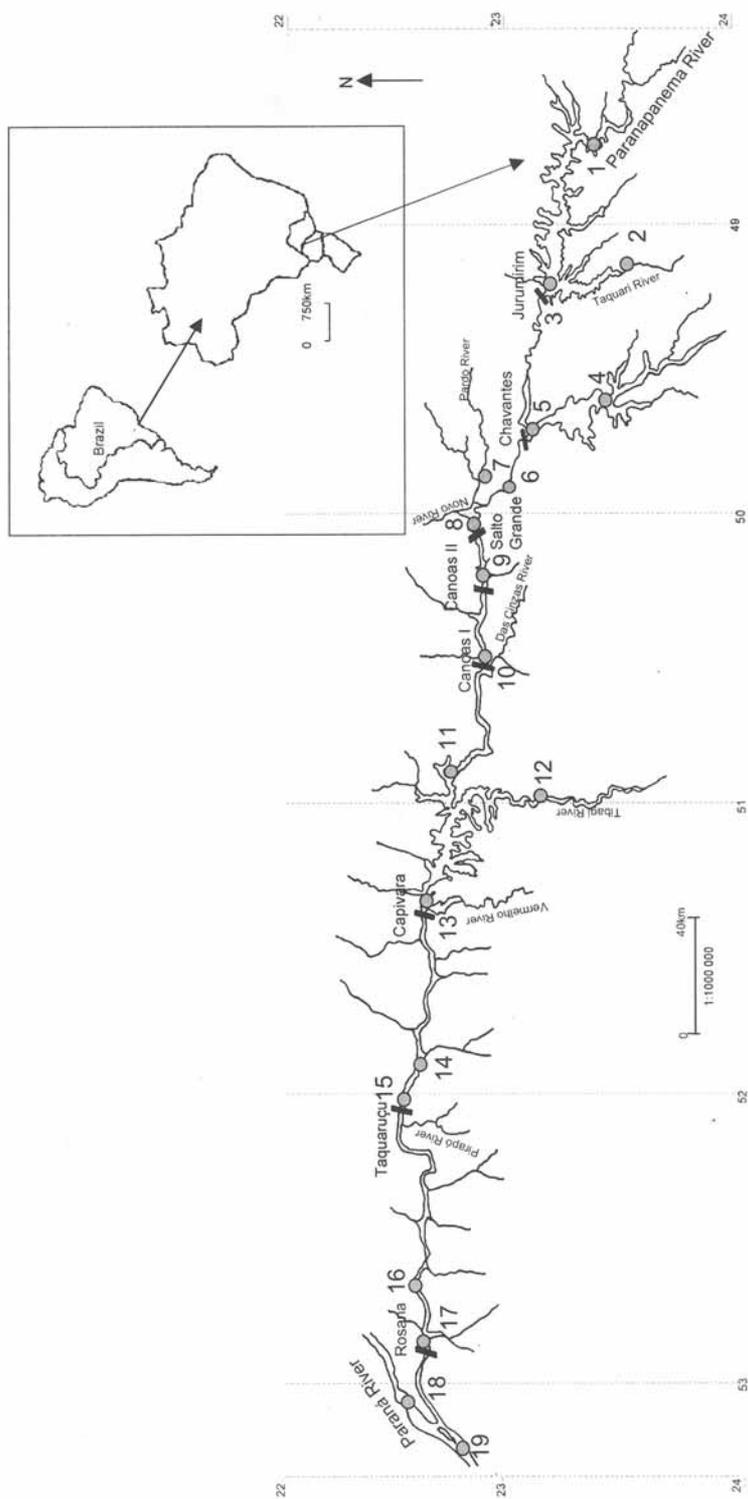
Figure 1. Geographic location of the Paranapanema River hydrographic basin and position of the sampling stations. See Table 2 for sampling stations denominations. *Localización geográfica de la Cuenca hidrográfica del Río Paranapanema y localización de las estaciones de muestreo. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

STUDY AREA

The Paranapanema River has an extension of 929 km with the headwaters (809 m a.s.l.) in the Atlantic Plateau and the mouth (239 m a.s.l.) in the Paraná River, which is the main water course of the La Plata basin, the second largest one in South America (after the Amazonian). The Paranapanema basin (100 800 km^2; 22° − 26° S and 47° − 54° W) is located between the States of São Paulo and Paraná in a transitional tropical to subtropical area (Fig. 1). During the study period the accumulated rain precipitation (mean among 8 localities distributed along the basin) was of 1241.33 mm in 2000 and 1291.2 mm in 2001. Most rains precipitate in summer, and the winter is usually dry.

The construction of the Paranapanema reservoirs for hydroelectric production started at the end of the 1950s and continued until 2005. Presently there are 11 reservoirs, 8 of which (the largest ones) have been considered in this study.

The studied reservoirs are very variable in their dimensions (12 to 576 km^2 in area) and water retention time (1.5 to 418.1 days) (Nogueira *et al.*, 2006) and their trophic status is oligo to mesotrophic (Nogueira *et al.*, 2002). However, the middle Paranapanema region is very influenced by intensive agricultural practices, receiving high loads of nutrients and sediments (Feitosa *et al.*, 2006; Jorcin & Nogueira, 2005 a, b).

Basic limnological characteristics of the reservoirs during the study period are found in Jorcin & Nogueira, (2005 a, b) and Nogueira *et al.* (2006). Figures 2 and 3 and Table 1, exhibit some limnological characteristics of the reservoir cascade.

MATERIAL & METHODS

The fieldwork was carried out in 8 sampling campaigns in 2000 and 2001 during summer (January), autumn (April), winter (July), and spring (October). The location of the 19 selected sampling stations is shown in figure 1 and their denomination in Table 2. The studied river stretch is about 700 Km long. Besides the reservoirs (Jurumirim, Chavantes, Salto Grande, Canoas I, Canoas II, Capivara, Taquaruçu, and Rosana), the mouths of the 3 main tributary rivers of the watershed (Taquari, Pardo, and Tibagi) were also sampled. Sampling in the Paranapanema mouth zone (upstream and downstream the mouth), in the Paraná River, started from the third campaign on. Except for the Canoas Complex (II and I), the reservoirs were sampled in the upstream

Table 1. Trophic state classification (Carlson Index modified by Toledo Jr. et al.) of the Paranapanema River cascade reservoirs (Data from Nogueira et al., 2002) O = Oligotrophic; M = Mesotrophic and E = Eutrohic. See Table 2 for sampling stations denominations. *Clasificación del estado trófico (Índice de Carlson modificado por Toledo Jr. et al.) de los embalses en cascada del Río Paranapanema (dados de Nogueira et al., 2002) O = Oligotrófico; M = Mesotrófico y E = Eutrófico. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*
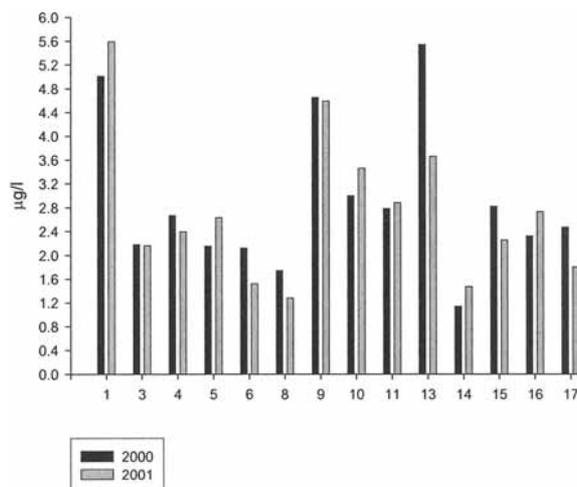
Station	January 2000 Index	Classif.	January 2001 Index	Classif.	April 2000 Index	Classif.	April 2001 Index	Classif.	July 2000 Index	Classif.	July 2001 Index	Classif.	October 2000 Index	Classif.	October 2001 Index	Classif.
1	62.35	E	64.12	E	57.61	E	51.53	M	54.79	E	56.97	E	51.84	M	59.16	E
3	51.12	M	41.91	O	47.59	M	41.37	O	47.20	M	43.17	O	42.97	O	44.31	M
4	52.52	M	46.41	M	52.72	M	44.54	M	51.96	M	44.50	M	45.23	M	43.97	O
5	48.90	M	42.50	O	49.42	M	39.65	O	47.58	M	39.74	O	41.94	O	42.70	O
6	41.92	O	42.75	O	47.34	M	41.00	O	45.59	M	44.15	M	48.57	M	39.58	O
8	56.05	E	42.74	O	46.96	M	46.57	M	48.27	M	46.49	M	46.22	M	44.66	M
9	53.98	M	55.98	E	54.80	E	46.00	M	50.75	M	46.91	M	45.12	M	52.48	M
10	52.21	M	50.19	M	53.23	M	45.97	M	52.59	M	46.56	M	41.38	O	48.80	M
11	54.18	E	55.71	E	46.43	M	42.81	O	51.08	M	47.05	M	48.55	M	47.66	M
13	52.27	M	48.44	M	54.52	E	46.01	M	48.69	M	43.55	O	50.12	M	45.86	M
14	51.80	M	40.75	O	48.88	M	45.27	M	44.13	M	46.43	M	40.17	O	43.65	O
15	49.49	M	42.10	O	49.68	M	44.11	M	44.55	M	46.91	M	45.27	M	43.62	O
16	44.02	M	50.83	M	49.52	M	47.08	M	45.85	M	48.13	M	43.76	O	43.36	O
17	45.25	M	43.64	O	45.17	M	47.36	M	48.47	M	44.29	M	44.01	M	39.35	O
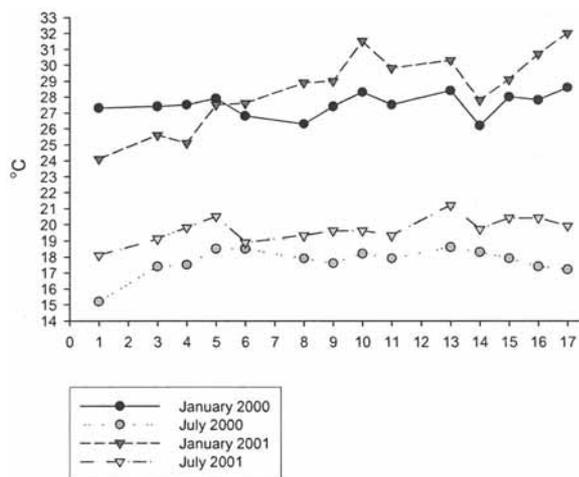
Figure 2. Temperature of the water surface during winter (July) and summer (January) in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Temperatura de la superficie del agua durante invierno y verano en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

Figure 3. Chlorophyll a concentration (water column mean) in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Concentración de clorofila a (promedio de la columna de agua) en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

(riverine) and near the dam (lacustrine zone). The zooplankton samples were collected using a conical net (30 cm mouth diameter and 50 μm mesh size) and vertical hauls from near the bottom (*ca.* 1 m) to the surface. In each point/period an additional sample for qualitative analysis was collected. In very shallow/lotic environments the zooplankton was sampled directly from the surface, filtering a known water volume (150 L) (graduated pail).

Among cladocerans the Chydoridae, Ilyocryptidae, and Macrothricidae were grouped as "others" (for graphical representation), due to their low representativeness in the limnetic zones focused on in this work.

Samples were fixed and preserved in 4 % formaldehyde, and are deposited in the Freshwater Invertebrate Collection of the Department of Zoology, Biosciences Institute of the State University of São Paulo (campus of Botucatu). Specimens of most identified species were also deposited at the Crustacea Collection of the Museu de Zoologia-Universidade de São Paulo (MZUSP Crustacean Collection No 18396 to 18418). For

Table 2. Numerical denomination of the sampling stations of the Paranapanema River cascade reservoirs. *Denominación numérica de las estaciones de muestreo de los embalses en cascada del Río Paranapanema.*

Stations	Abbreviation	Location	Station	Abbreviation	Location
1	UJ	Upstream of Jurumirim Reservoir	11	UC	Upstream of Capivara Reservoir
2	TR	Taquari River	12	TiR	Tibagi River
3	DJ	Dam zone of Jurumirim Reservoir	13	DC	Dam zone of Capivara Reservoir
4	UCh	Upstream of Chavantes Reservoir	14	UT	Upstream of Taquaruçu Reservoir
5	DCh	Dam zone of Chavantes Reservoir	15	DT	Dam zone of Taquaruçu Reservoir
6	USG	Upstream of Salto Grande Reservoir	16	UR	Upstream of Rosana Reservoir
7	PR	Pardo River	17	DR	Dam zone of Rosana Reservoir
8	DSG	Dam zone of Salto Grande Reservoir	18	UPM	Upstream of Paranapanema river mouth
9	CII	Dam zone of Canoas II Reservoir	19	DPM	Downstream of Paranapanema river mouth
10	CI	Dam zone of Canoas I Reservoir			

the quantitative analyses, a minimum of juveniles, adult individuals and 100 nauplii were was counted per sample and in case of low abundance the entire sample was analyzed.

The diversity of the zooplankton assemblages was determined by the Shannon Index ($\log_2$). A cluster analysis (1-Pearson r) was performed (PC-Ord) (McCune & Mefford, 1995) based on the zooplankton similarity (composition and abundance).

RESULTS

Composition and Richness

The list of the 74 taxa found in the zooplankton samples of the Paranapanema River is shown on Table 3. Cladocera was represented by 56 species (2 Moinidae, 3 Bosminidae, 5 Sididae, 11 Daphiniidae, 2 Ilyocryptidae, 2 Macrothricidae, 11 Chydorinae and 20 Aloninae) and Copepoda by 19 species (6 Diaptomidae, 12 Cyclopidae and 1 Ergasilidae).

Among the copepods, the main species in terms of abundance and frequency of occurrence, were the diaptomidae *Notodiaptomus henseni* and *N. iheringi* as well as the cyclopidae *Thermocyclops minutus*, *T. decipiens*, *Mesocyclops longisetus*, *M. meridianus*, and *M. ogunnus*.

The main cladoceran species were the Daphiniidae *Daphnia gessneri*, *Ceriodaphnia cornuta rigaudi*, *C. cornuta cornuta*, and *C. silvestrii*; the Sididae *Diaphanosoma spinulosum*, *D. birgei*, *D. brevireme*, and *D. fluviatile*; the Moinidae *Moina minuta* and the Bosminidae *Bosmina hagmanni* and *Bosminopsis deitersi*.

The species richness per sampling station is shown in figure 4. The highest means were calculated for UJ (15.5 taxa) and DR (15 taxa). Considering individual samples, the maximum richness was found at UJ (24 taxa in April 2001). The sampling stations with lower mean values for richness were PR (6.3 taxa), USG (9.1 taxa) and UPM (9.7 taxa). A seasonal pattern of variation for zooplankton richness was not detected. The number of species observed in 2000, mainly in spring, was slightly higher than in 2001.
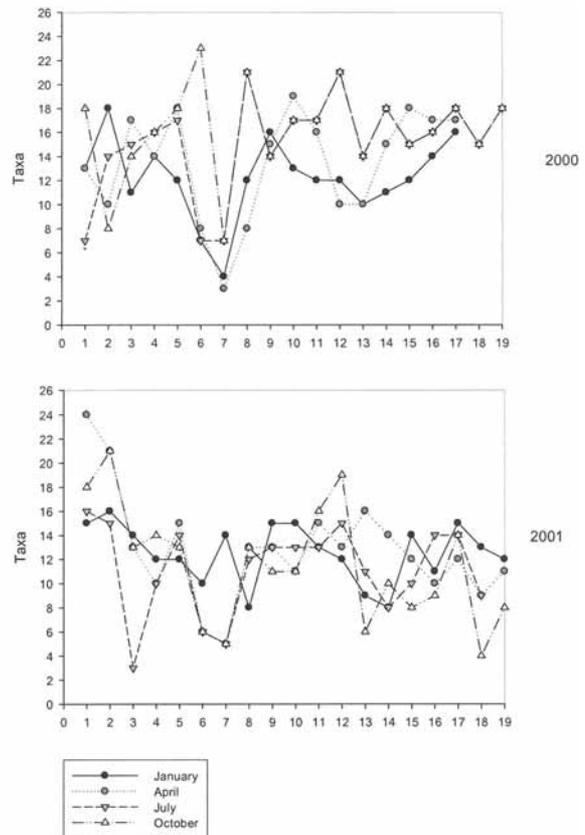
Figure 4. Taxonomical richness of the planktonic microcrustaceans in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Riqueza taxonomica de los microcrustáceos planctonicos en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

Absolute abundance

The lowest microcrustacean abundance (mean was 148 ind/m^3) was found at the station PR. Very low values per sample were recorded at this station (9 and 28 ind/m^3 in April 2000 and July 2001, respectively). Relatively low values of abundance were also observed at the sampling stations of Salto Grande (means were 890 and 1206 ind/m^3 at upstream and dam zones, respectively). The highest abundance value (mean was 25 648 ind/m^3) was obtained at the TR station.

The copepod abundance was higher in the first two reservoirs of the cascade (Jurumirim and Chavantes), followed by an accentuated decline in the Salto Grande Reservoir. An abun-

Table 3. Microcrustacean assemblage composition (Cladocera and Copepoda) of the Paranapanema River cascade reservoirs. *Composición del agrupamiento de los microcrustáceos (Cladocera y Copepoda) de los embalses en cascada del Río Paranapanema.*

Cladocera

Sididae

　　Diaphanosoma birgei Korineck, 1981
　　Diaphanosoma brevireme Sars, 1901
　　Diaphanosoma fluviatile Hansen, 1899
　　Diaphanosoma spinulosum Herbst, 1967
　　Latonopsis australis Sars, 1888

Daphniidae

　　Ceriodaphnia cornuta cornuta Sars, 1886
　　Ceriodaphnia cornuta cf *intermedia* Sars, 1886
　　Ceriodaphnia cornuta rigaudi Sars, 1886
　　Ceriodaphnia silvestrii Daday, 1902
　　Daphnia gessneri Herbst, 1967
　　Daphnia ambigua Scourfield, 1947
　　Scapholeberis armata (Herrick, 1882)
　　Simocephalus latirostris Stingelin, 1906
　　Simocephalus serrulatus (Koch, 1841)
　　Simocephalus punctatus Orlova-Bienkowskaja, 1998
　　Simocephalus vetulus (O. F. Müller, 1776)

Moinidae

　　Moina micrura Kurz, 1874
　　Moina minuta Hansen, 1899

Bosminidae

　　Bosmina longirostris (O. F. Müller, 1785)
　　Bosmina hagmanni Stingelin, 1904
　　Bosmina tubicen Brehm, 1953
　　Bosminopsis deitersi Richard, 1895

Ilyocryptidae

　　Ilyocryptus spinifer Herrick, 1882
　　Ilyocryptus sordidus (Liévin, 1848)

Macrothricidae

　　Macrothrix spinosa King, 1853
　　Macrothrix superaculeata (Smirnov, 1992)

Chydoridae
Chydorinae

　　Alonella daday (Birge, 1990)
　　Alonella hamulata (Birge, 1879)
　　Alonella cf *hamulata* (Birge, 1879)
　　Chydorus eurynotus Sars, 1901
　　Chydorus pubescens Sars, 1901
　　Chydorus sphaericus sens. lat.
　　Chydorus sp Leach, 1816
　　Disparalona acutirostris (Birge, 1879)
　　Dunhevedia odontoplax Sars, 1901
　　Pleuroxus sp$_1$ Baird, 1843
　　Pleuroxus sp$_2$ Baird, 1843

Aloninae

　　Acroperus harpae Bardi, 1843
　　Alona glabra, Sars, 1901
　　Alona cf *cambouei* Guerne & Richard, 1893
　　Alona davidi Richard, 1895
　　Alona guttata Sars, 1862
　　Alona cf *incredibilis* Smirnov, 1984
　　Alona cf *poppei* Richard, 1897
　　Alona quadrangularis (O. F. Muller, 1875)
　　Alona rectangula Sars, 1861
　　Alona sp. Baird, 1843
　　Alona intermedia Sars, 1862
　　Biapertura verrucosa Sars, 1901
　　Biapertura intermedia Sars, 1862
　　Camptocercus dadayi Stingelin, 1913
　　Euryalona orientalis (Daday, 1898)
　　Graptoleberis testudinaria (Fisher, 1851)
　　Kurzia polyspina Hudec, 2000
　　Leydigia ciliata Gauthier, 1939
　　Leydigia schubarti Brehm & Thomsen, 1936
　　Notoalona sculpta (Sars, 1901)

Copepoda

Diaptomidae

　　Argyrodiaptomus azevedoi Wright, 1935
　　Argyrodiaptomus furcatus (Sars, 1901)
　　Notodiaptomus henseni Dahl, 1894
　　Notodiaptomus iheringi Wright, 1935
　　Notodiaptomus deitersi (Poppe, 1891)
　　Diaptomidae not identified

Cyclopidae

　　Eucyclops cf *serrulatus* (Fischer, 1851)
　　Eucyclops sp. *Mesocyclops longisetus* (Thiébaud, 1914)
　　Mesocyclops meridianus Kiefer, 1926
　　Mesocyclops ogunnus Onabamiro, 1957
　　Metacyclops mendocinus (Wierzejski, 1892)
　　Microcyclops anceps anceps (Richard, 1897)
　　Paracyclops chiltoni (Thomson, 1882)
　　Thermocyclops decipiens (Kiefer, 1929)
　　Thermocyclops minutus (Lowndes, 1934)
　　Thermocyclops inversus (Kiefer, 1936)
　　Tropocyclops prasinus meridionalis (Kiefer, 1931)
　　Cyclopidae not identified

Ergasilidae

　　Ergasilus sp. Nordmann, 1832

dance recovery occurred in the reservoirs of the middle Paranapanema River (Canoas II, Canoas I, and Capivara), followed by a new decrease in Taquaruçu and a recovery in the last reservoir (Rosana). In general the lowest copepod abun-

dances were recorded in Salto Grande Reservoir and in its main tributary, PR (minimum of 8 ind/m^3 in July 2001). A relatively low abundance was also seen in the UJ (January, April, July and October of 2000). The stations UCh

and UC were the ones where the copepod abundance remained high (about 5000 ind/m^3 or even more) in most sampling periods, followed by TR. In this last station the highest abundance (32 387 ind/m^3 in April 2000) was observed. The abundance of copepods increased in summer, mainly due to the nauplii contribution, when high values (5 000 ind/m^3 or even more) were recorded (at 9 sampling stations in January 2000 and at 11 sampling stations in January 2001). During the winter, there was a decrease, especially in July 2000, and only 3 stations showned relatively high abundance of copepods.

The noticeable diminution of the copepod larval stages in Salto Grande Reservoir (sometimes also in the Canoas complex) showed to be a recurrent pattern. The maximum nauplii abundance was recorded in TR in April 2000 (about 30 000 ind/m^3), with similar proportion between Calanoida and Cyclopoida.

In general the nauplii of Cyclopoida were more abundant than the nauplii of Calanoida. This trend was not observed among the juveniles, and the copepodids of calanoids were relatively as abundant as those of cyclopoids. As seen for nauplii, the copepodid abundance also exhibited a diminution in the region of Salto Grande and Canoas Complex Reservoirs, and less frequently in Taquaruçu, and UR. The highest copepodid abundances (7361 and 5925 ind/m^3 of calanoids and cyclopoids, respectively) were observed in the DPM (Paraná River) in April 2000. As to the juveniles, the main seasonal variation was the decrease occurred in the winter of 2001.

The abundances of cladocerans were low at the first sampling point (UJ) (except for October 2001), in the Salto Grande/River Pardo and at UT. Conversely, higher abundances were observed in the middle Paranapanema – mainly in CI and UC. The maximum cladoceran abundance among the reservoir sampling stations was about 30 000 ind/m^3, recorded in CI during October 2000. In the rivers, the cladoceran abundances were highly variable. In PR it was always low and the maximum occurred at TR (October 2000), with 118 636 ind/m^3. In 2000 there was a marked seasonal variation in the Cladocera abundance, with higher numbers in summer and spring and

decreases in autumn and winter. In 2001, this tendency was not observed, and a relatively low abundance was seen in winter and spring.
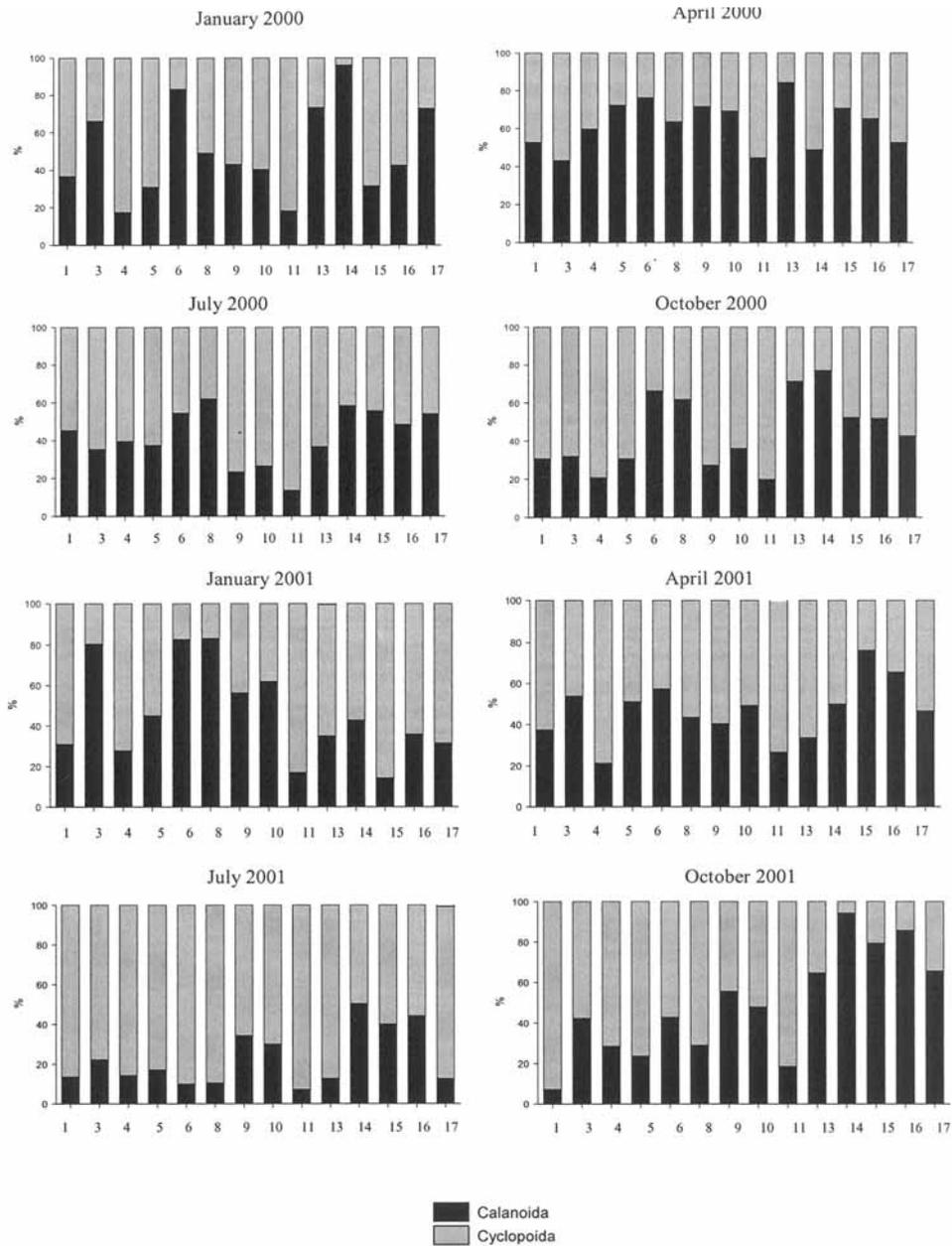
Relative abundance

The relative Calanoida/Cyclopoida abundance in the sampling stations, including all the development stages, is shown in figure 5. In general, considering both study years, the cyclopoids were proportionally more abundant in winter and the calanoids in summer/autumn.

In the rivers, the cyclopoids were generally dominant in relation to the calanoids.

The relative abundance among families of Cladocera (Sididae, Daphniidae, Moinidae, Bosminidae and Others) is shown in figure 6. A higher proportion of Sididae was observed in the reservoirs located upstream the cascade, reaching about 80 % of the cladocerans at the stations DJ, Uch, and USG. Then, a conspicuous decrease of Sididae occurred at the beginning of the middle Paranapanema stretch (Salto Grande, Canoas II and Canoas I). Only in January 2000 a noticeable increase in Sididae abundance was recorded in the middle-lower river reservoirs, reaching about 80 % and 70 % of the Cladocera at DC and UT, respectively. In the winter there was a remarkable decrease in the proportion of Sididae, which continued until the spring of 2001.

The Daphniidae were proportionally less abundant in the reservoirs of the middle Paranapanema. In January 2000 and in July and October 2001 this trend was more evident. In the last sampling period (October 2001) the Daphniidae (mainly *D. gessneri*) represented 86 to 100 % of all cladocerans in the stretch between the DC and DR. This group was not found in Salto Grande Reservoir in July 2000 (upstream zone) or April 2001 (dam zone) and only in January of 2001 they were found with an expressive abundance in all reservoirs.

A higher relative abundance of the Moinidae was found in the middle, and occasionally in the lower, Paranapanema reservoirs. The higher proportion of Moinidae in relation to the total cladocerans was about 60 % (UC-January 2000; CI-October 2000; DT-January 2001 and CII-October
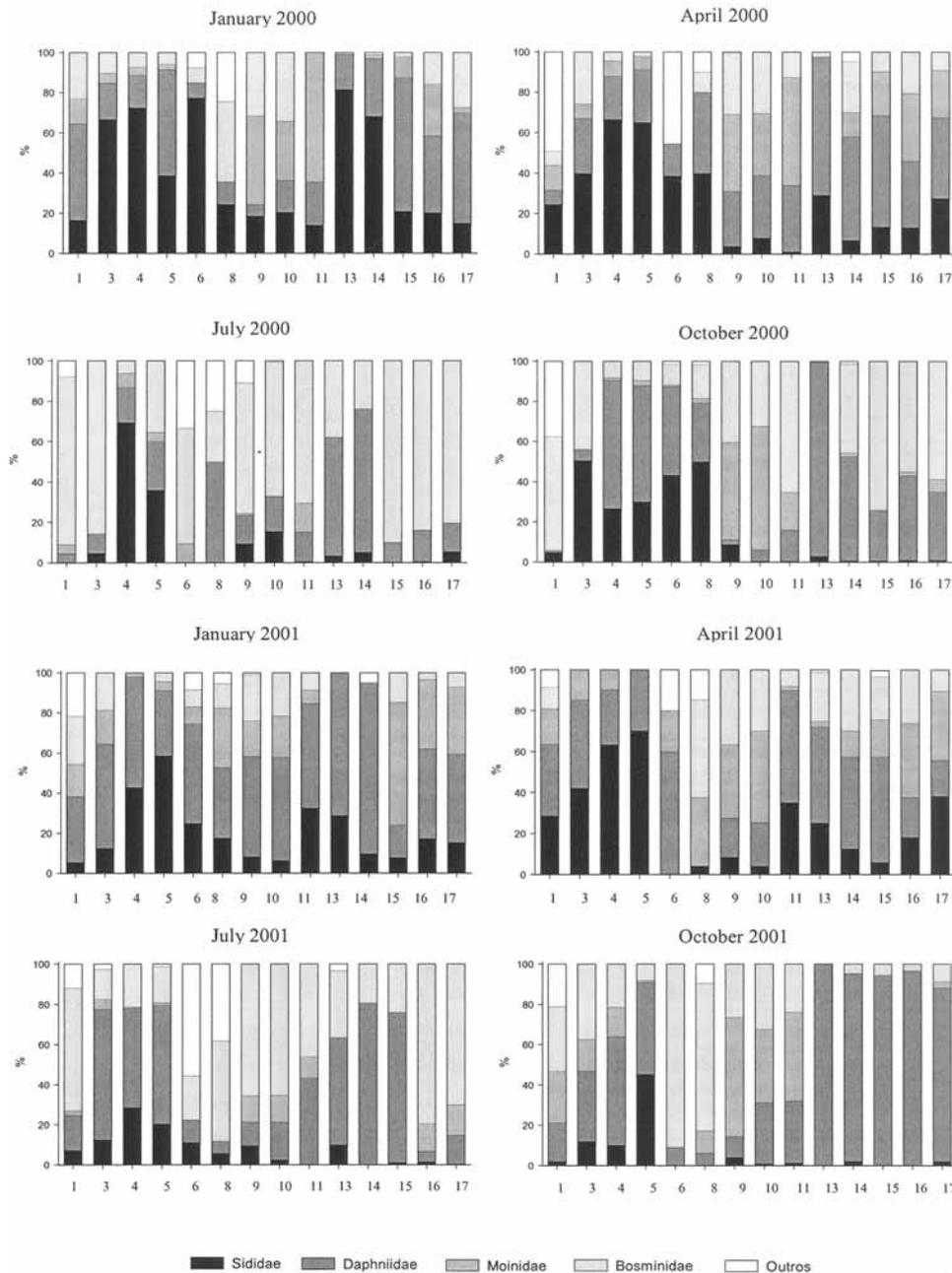
Figure 5. The relative abundance of calanoid and cyclopoid copepods in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Abundancia relativa de copepodos calanoides y ciclopoides en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

2001). During the winter samplings, both 2000 and 2001, the proportion of Moinidae was very low, with a maximum of 14 % recorded at UC in July 2000 and UR July 2001.

The spatial distribution of Bosminidae was variable, and no defined pattern could be identi-

fied. However, the presence of these animals was generally low in the stretch between the Reservoirs of Chavantes and Salto Grande (upstream zone). Seasonally, the proportion of Bosminidae remarkably increased during winter. In July 2000 the Bosminidae reached 80 % of the cladocerans,
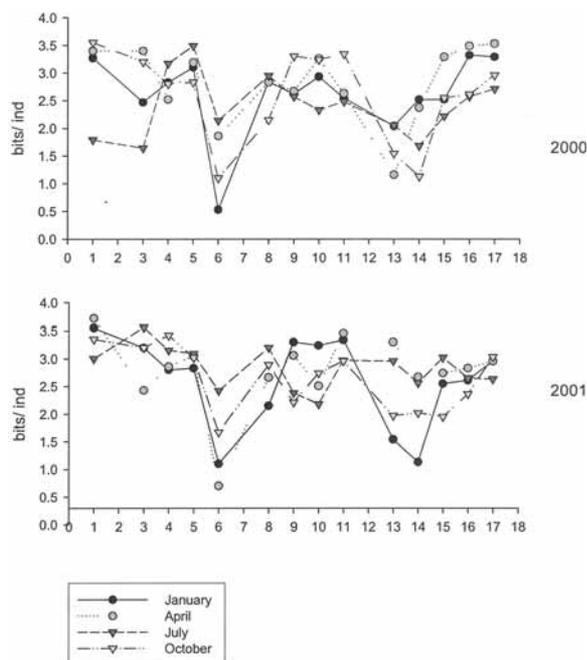
Figure 6. The relative abundance of cladoceran families in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Abundancia relativa de familias de cladoceros en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

or even more, in different sampling stations, either in the high (UJ and DJ) or in the low (DT, UR DR) Paranapanema River.

Cladoceran families which are typical of littoral habitats (Chydoridae, Ilyocryptidae, and Macrothricidae (Others) were proportionally more abundant at UJ (50 % in April 2000 and 40 % in October 2000) and Salto Grande Reser-

Figure 7. Shannon diversity index for microcrustacean assemblages in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Índice de diversidad de Shannon para los agrupamientos de microcrustáceos en la casada de embalses del río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

voir (60 % at upstream zone-July 2001 and 40 % at dam zone in July 2001), and eventually (July 2000) at CII and CI sampling stations.

The proportion of the cladoceran families in the rivers' sampling stations was quite variable. But the relative abundance of Sididae was always very low, especially during winter/spring.

Diversity

The zooplankton diversity (Shannon Index) along the reservoir cascade is shown in figure 7. Spatially, there was a tendency for diversity diminution in the regions of Salto Grande/River Pardo and Capivara/Taquaruçu. In the reservoirs of the high (Jurumirim and Chavantes) and low (Rosana) river stretches, diversity was high when compared to the ones of the middle Parana-panema. TR (3.75 bits/ind in January 2000) and UJ (3.72 bits/ind in April 2001) exhibited the highest values of diversity. Nevertheless, the station RT also was affected by one of the low-

est diversity values (0.76 bits/ind in October 2000). Among the reservoirs the lowest diversity was calculated for USG (0.53 bits/ind in January 2000). Seasonally, the diversity was higher in summer/autumn and decreased in winter/spring.
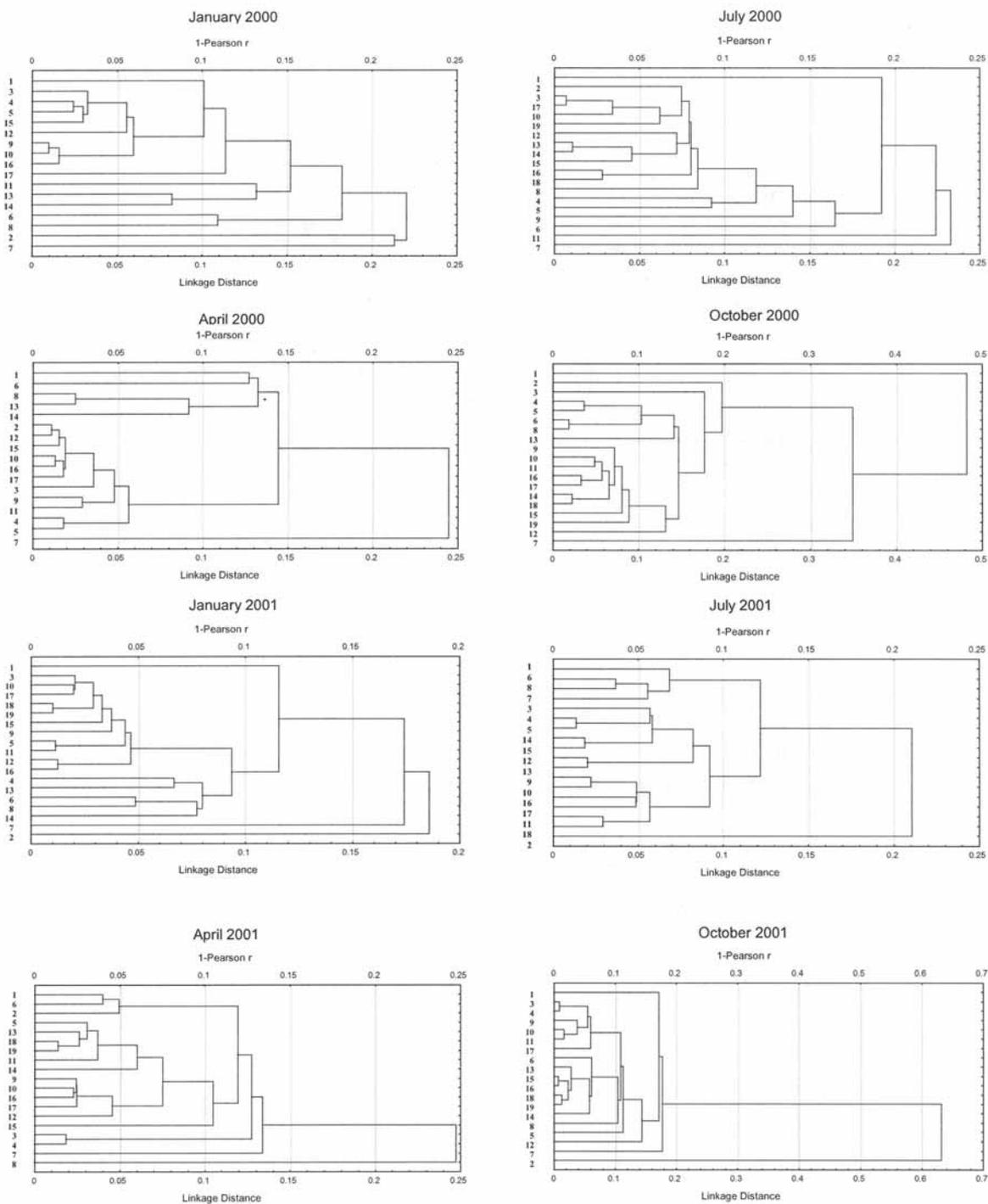
Similarity

The results of the cluster analysis are shown in figure 8. Extreme differences in the zooplankton structure were detected between the most upstream sampling station-UJ, and the Rivers Pardo and Taquari, which sometimes were closely associated. The main groups in terms of zooplankton similarity were: Canoas Complex (CII and CI) in January 2000 and April, July and October 2001; CI-UC in October 2000 and October 2001; UCh and DCh in January, April, July and October 2000 and July 2001. In some periods this last group was also linked to the DJ (January 2000 and April and October 2001); USG and DSG were closely grouped in October 2000 and July 2001; UR and DR in October 2001 and UPM and DPM, in the Paraná River, during January, April and October 2001.

DISCUSSION

The richness of microcrustacean taxa found during the present study, 74, is about double the maximum value obtained in previous individual analyses of the zooplankton assemblages carried out in the Paranapanema River (Nogueira, 2001; Sampaio *et al*., 2002; Panarelli *et al*., 2003; Martins & Henry, 2004). This high richness was positively influenced by the spatially wide sampling design, with almost simultaneous observations over the whole watershed.

The higher proportion of Cladocera (56 in relation to Copepoda (19 species) observed in the Paranapanema reservoir cascade follows the tendency observed in other regional studies on planktonic microcrustaceans (Rocha *et al*., 2002). However, it is important to note that this is not an exclusive pattern for the neotropics. Studies in the Amazonian region (Robertson & Hardy, 1984) and middle Paraná (Paggi & José

Figure 8. Similarity among the sampling stations (cluster analysis) on the basis of microcrustacean assemblages structure in the Paranapanema River cascade reservoirs. See Table 2 for sampling stations denominations. *Similaridad entre las estaciones de muestreo (análisis cluster) con base en la estructura de los agrupamientos de los microcrustáceos en la cascada de embalses del Río Paranapanema. Ver Tabla 2 por denominaciones de las estaciones de muestreo.*

de Paggi, 1990) have demonstrated that Copepoda can also be of a major importance in terms of richness (about 40 to 50 species).

The highest microcrustacean richness per sample was observed in the transitional river/reservoir zones (24 taxa at Upstream of Jurumirim in April 2001; 23 at Upstream of Salto Grande in October 2000; 21 taxa at River Taquari mouth in April 2001 and October 2001). These results indicate that intermediate hydrodynamic conditions - transition between lotic and lentic habitats, seems to favor the microcrustacean assemblages in terms of species richness. Probably two different communities are co-existing, the riverine and the lacustrine. It is also important to consider that these regions are generally connected (temporally or permanently) to lateral floodplain lagoons, being positively influenced by the typical high diversity found in these habitats (Lachavanne, 1997). Nevertheless, our results also showed (high mean standard deviations) that in these transitional river/reservoir regions, the temporal variability in richness is very high (e.g. Upstream of Jurumirim, River Taquari mouth, Upstream of Salto Grande). This certainly occurs because in these areas there is a pronounced water level variation (seasonal or operational), which could represent a stressing factor for the zooplankton assemblages.

Considering the mean values among sampling periods, relatively high numbers of taxa were observed at different points distributed along the watershed, such as the upstream zone of the first reservoir (15.5 taxa) as well as the dam zone of the last reservoir (15.0 taxa), separated from one another by about 500 Km. This demonstrates that the expected longitudinal increase in richness (Vannote *et al.*, 1980), as observed for fish in this same river (Carvalho *et al.*, 1998; Britto & Carvalho, 2006), is not applicable for the microcrustaceans. Hart (1996) observed a downstream increase of cladoceran richness only between the first and second reservoirs of the Mgeni River cascade in South Africa, but the tendency was not progressive down the river.

When compared with previous studies, the present composition and dominance among diaptomidae in the Paranapanema reservoirs indicates the occurrence of important structural changes in the zooplankton assemblage. In this study *Notodiaptomus iheringi* and *N. henseni* were the main species and *N. conifer* was never found. This last species was one of the most frequent in the Paranapanema reservoirs during the late 1970s (Sampaio *et al.*, 2002), and was still present in relative high numbers in the beginning of the 2000's, at least in the region of Jurumirim (Nogueira, 2001; Mitsuka & Henry, 2002). Another important species in the past, *Argyrodiaptomus furcatus*, has presently a minor contribution. Changes in the composition of Calanoida fauna over the last three decades in the reservoirs of the State of São Paulo are discussed by Matsumura-Tundisi & Tundisi (2003). The authors consider that the substitution of species may be related to the progressive increase of the electric conductivity and alterations in the ionic composition of the water, reflecting the advance of eutrophication.

In terms of composition and richness our data also shows that the entrance of the Paranapanema could contribute to the increase of the microcrustaceans richness in the Paraná River. Except in one sampling period (January 2001), the richness was higher in samples collected downstream the Paranapanema mouth (mean of 13.4 taxa) than in those from upstream (mean of 9.7 taxa). A comparative analysis between two other studies also indicates this trend. In the downstream of the Paranapanema River mouth, in the Paraná River and associated floodplain areas, Lansac-Tôha *et al.* (2004) found 49 species of Cladocera and 15 of Copepoda. Almost the same number of Copepoda, 14 taxa, but lower value for Cladocera, 21 taxa, were identified by Sendacz & Monteiro Junior (2003) in the Paraná River stretch, and adjacent ecosystems (tributary rivers and lagoons), located upstream of the Paranapanema mouth, an area presently flooded by the construction of the Porto Primavera dam. Thus, it is possible to assume that each major lateral river (e.g. Grande, Tietê, Paranapanema, Iguaçu, Paraguai and Uruguai) has an important role in maintaining the biodiversity of the Paraná River-La Plata basin.

A higher abundance of microcrustaceans was frequently observed in the large and oligotrophic (Table 1) first two reservoirs of the Paranapanema cascade. In some sampling periods the

abundance was also high in reservoirs of the middle/low stretch of the river. The factors stimulating the zooplankton growth should be, in the first case, the increase in the water retention time (minimum mean of 387 days), and in the second case the increase in the trophic conditions (Table 1 and Fig. 3). The highest abundance (mean of 14 341 ind/m^3) was calculated for Canoas I, a reservoir located in the middle Paranapanema where the trophic conditions tend to be higher (Nogueira *et al*., 2002; Jorcin & Nogueira, 2005a, b; Nogueira *et al*., 2006). This result is in agreement with those of Lânsac-Toha *et al.* (2004), who verified that the ciliate abundance along the Paranapanema cascade did not corroborate the hypothesis of a decreasing density and biomass due to an expected downriver oligotrophication (Tundisi *et al*., 1991; Armengol *et al*., 1999; Abe *et al*., 2003).

A remarkable diminution of the microcrustacean abundance was always observed in Salto Grande Reservoir/Pardo River (mean of 1200 ind m^{-3} at USG; 890 ind/m^3 at DSG and 148 ind/m^3 at PR). The predominance of riverine conditions (mean RT between 1.3 to 1.5 days in Salto Grande) is probably the main factor explaining the low abundance. Despite of the high input of point and non point loads of nutrients in this reservoir (Feitosa *et al*., 2006), the predictable bottom up effects with the magnification of plankton populations are suppressed by the intense water flow. Studying a large reservoir in central Brazil, Velho *et al*. (2001) also concluded that the hydrology was the primary process controlling the spatial distribution of copepods.

In the first studied summer (January 2000) the microcrustaceans reached high abundance (*ca.* 10 000 ind/m^3 or even more) in a higher number of sampling stations and a sharp decline occurred during the winter (July 2000), with only one sampling station exhibiting an abundance near to 10 000 ind/m^3. However, these seasonal differences on abundance were not recurrent in the following study year.

Higher microcrustacean abundance downstream of Paranapanema mouth (mean value of 14 292 ind/m^3) compared to the upstream of Paranapanema mouth (mean value of

10 963 ind/m^3), as discussed for richness, could also be indicative of the importance of this river entrance on the zooplankton assemblage structure of the Paraná River. However it is important to note that data from these sampling points were highly variable.

In reservoirs, the zooplankton populations are affected by passive transport produced by water renewal, besides the autochthonous processes depending on the biology and ecology of the different species and intrinsic water characteristics (Armengol *et al*., 1988). Explanation for the longitudinal variation in abundance should combine information on the influence of advective loss (more important in lotic conditions) and compensation by reproductive rates (more important in lentic conditions) (Marzolf, 1990).

Our results showed some conspicuous increases of zooplankton abundance towards the dam (e.g. Jurumirim, Capivara and Taquaruçu in January 2000; Rosana in April 2000; Capivara and Rosana in October 2000 and Rosana in January 2001). Velho *et al*. (2001), studying copepod distribution in Corumbá Reservoir (Central Brazil), also observed abundance increases, albeit not linearly, towards the lacustrine zone. The authors considered that hydrology is the primary process that controls the copepod abundance. The negative influence of the lotic conditions on abundance was also reported by Mitsuka & Henry (2002) when analyzing the fate of Copepoda populations downstream the lacustrine (dam) zone of Jurumirim. However, the increase towards the dam was not the only spatial tendency observed in our results. Some considerable longitudinal decreases in abundance, mainly in July and October 2001, (Jurumirim, Chavantes, Capivara), as well as similar values between upstream and dam zones (e.g. Salto Grande except in January 2001), were also seen. Casanova & Henry (2004) observed that the presence of lateral lakes changed the longitudinal gradient pattern of copepod abundance in the transitional river-reservoir zone of Jurumirim.

The spatial variation on Copepoda abundance followed the same tendencies observed for the total microcrustaceans. This occurred because they were always numerically

dominant in relation to cladocerans, mainly due to the contribution of the initial development stages (nauplii and copepodids). Except for October 2000, the lowest abundances of copepods were always recorded in the Salto Grande Reservoir and its main tributary-the Pardo River, probably related to the high flow conditions. This is probably also the cause for the low copepod abundance frequently seen in the upstream of Jurumirim.

The calanoids and cyclopoids co-existed in all sampling points. Temporally, there was a diminution of the calanoids in relation to the cyclopoids during the winter (July 2000 and July 2001). A higher abundance of cyclopoids in winter, mainly *T. minutus*, and calanoids in summer, mainly *N. iheringi*, was already reported by Panarelli *et al*. (2001) for Jurumirim Reservoir. Spatially the proportion between calanoids and cyclopoids varied widely. The downstream increase of the calanoid abundance, especially of *Notodiaptomus* in certain periods, seemed to be positively correlated to the temperature (Fig. 2). According to Hart (1992) the temperature changes influenced the dominance between two calanoid species in the cascading reservoirs of Mgeni River (South Africa).

The cyclopoids did not increase in abundance in the more eutrophic reservoirs, as could be expected (Tundisi & Matsumura-Tundisi, 1990; Silva & Matsumura-Tundisi, 2002; Sendacz *et al*., 2006). Cyclopoids can feed on large colonial blue-green algae, common in eutrophic systems (Matsumura-Tundisi *et al*., 1997), since they are raptorial. Nogueira (2001), verified a clear longitudinal gradient of the relation Calanoida/Cyclopoida in Jurumirim Reservoir, with the cyclopoida dominating the more riverine and eutrophic compartments.

Nevertheless, when data of Cyclopoida were analyzed at the species level it was seen that *Thermocyclops minutus* was more abundant in the larger and more oligotrophic reservoirs of the upper cascade (Jurumirim and Chavantes), alternating with *T. decipiens*, which was more numerous in the more eutrophic reservoirs of the middle cascade. These observations corroborate the hypothesis that these two species could be considered as good trophic state bio-indicators in

the neotropics (Reid, 1989; Silva & Matsumura-Tundisi, 2002). Nogueira & Panarelli (1997) suggested that, during periods when *T. minutus* and *T. decipiens* co-occur in similar numerical proportion, they could minimize competition through vertical segregation in the water column.

Cyclopoid nauplii were more abundant than calanoid nauplii in most sampling sites and periods, but in relation to the juvenile stages, the proportion of calanoids increased. These results indicate that the cyclopoids could be considered as *r*-selected (colonialist) with a high reproductive rate but a low survival rate for the larval stages. The calanoid eggs are bigger than the cyclopoid ones, considering the species found in the samples, and this could be the primary (nutritional) factor assuring a higher survival rate of the calanoid larvae (K-selected organisms). The highest abundance of nauplii (30 000 ind m^{-3}), with similar proportion of cyclopoids and calanoids, was observed in the Taquari River mouth (April 2000). This is a typical floodplain area, and the results indicate that the adjacent wetlands/lagoons can have an important role for the recruitment of copepod populations. This hypothesis was also considered by Casanova & Henry (2004) for the Jurumirim Reservoir upper stretch (river-reservoir transitional zone).

A higher proportion of Sididae was seen in the larger and more oligotrophic reservoirs (Tab. 1) of the upper Paranapanema cascade, frequently represented by different species of *Diaphanosoma*, simultaneously. However the maximum peak of *D. spinulosum* (*ca.* 3000 ind/m^3) was observed in the most productive reservoir in the river middle stretch (Capivara) in January 2000. Nogueira (2001) considered *D. birgei* as the main cladoceran species in Jurumirim, with a distribution more associated to the lacustrine zones.

Another important spatial tendency among cladocerans along the cascade was the increase of the smaller microcrustaceans Moinidae (*Moina minuta*) and Bosminidae (*Bosmina hagmani* and *Bosminopsis deitersi*) in the middle of the cascade, under more eutrophic conditions (Table 1 and Fig. 3). It has been shown that in Jurumirim the distribution of *M. minuta*, associ-

ated with *B. deitersi*, was more abundant in the upper and more eutrophic compartments (e.g. higher chlorophyll concentration-Fig. 3) and that *B. deitersi* did not occur in the deeper lacustrine zone (Nogueira, 2001; Panarelli *et al.*, 2003). The progressive importance of small-bodied cladocerans down the cascade, intra and inter-generically, was also observed by Hart (1992; 1996) in the Mgeni River (South Africa). The author considered that the changes were primarily related to rising water temperature. This explanation is also a possibility to be considered in our results, as a longitudinal (downstream) increase in temperature is especially evident in summer (Fig. 2). Nevertheless, other factors such as trophy and water retention time should necessarily be considered.

For Daphniidae, another important limnetic family, no regular variation pattern along the Paranapanema cascade could be identified. The two main species *C. cornuta* and *D. gessneri* found in the samples are not considered as good indicators of distinct environmental conditions, as they are physiologically and morphologically adapted to live along oligo-hypereutrophic conditions (Sampaio *et al.*, 2002).

The Shannon diversity index appeared as an efficient tool to evaluate the structural complexity of the microcrustacean assemblages. A consistent diversity decrease in the regions of Salto Grande (minimum of 0.53 bits/ind in January 2000) and dam zone of Capivara (minimum of 1.16 bits/ind in April 2000) was observed, and certainly it is related to two different factors: very low water retention time and eutrophication process (Table 1), respectively. Conversely, higher values of diversity, around 3.5 bits/ind, were recorded in the first large and oligotrophic reservoirs (Jurumirim and Chavantes) (Table 1). The characteristic low richness/diversity among the microcrustaceans of the Salto Grande Reservoir was not noticed during the 1970s (Sampaio *et al.*, 2002). This fact is a sensitive indicator of the negative influence of the water quality impoverishment during the last two or three decades.

Some limnological studies have demonstrated that larger reservoirs of the Paranapanema basin are spatially very complex (Henry & Maricatto,

1996; Nogueira *et al.*, 1999; Nogueira, 2000). However, along the reservoirs main axes, no clear pattern of microcrustacean diversity variation could be identified. The number of times that the diversity increased towards the dam is similar to the number of times that the diversity decreased in this same direction. Less frequently it remained similar between the two zones. The first tendency was observed mainly in the larger reservoirs (Jurumirim and Capivara), but the second one was seen in two very distinctive reservoirs: Chavantes (large) and Salto Grande (small). The third tendency was generally observed in Taquaruçu and Rosana, two relatively large but not dendritic reservoirs and also with relatively low water retention time, 8-20 days (Nogueira *et al.*, 2006).

The analysis on the faunistic similarity showed important spatial patterns, which were recurrent in time. Some consistent ecological groups were the ones representing reservoirs with high flow and mesotrophic condition (Canoas II and I; Canoas I and Upstream of Capivara); larger, deeper an more oligotrophic reservoirs (Upstream and Dam of Chavantes, eventually linked to the Dam of Jurumirim); very low water retention time reservoir and meso-eutrophic condition (Upstream and Dam of Salto Grande); low to medium water retention time and oligo-mesotrophic condition (Upstream and Dam of Rosana; Dam of Taquaruçu and Upstream of Rosana) and Paraná/Paranapanema confluence (Upstream and Downstream of Paranapanema River mouth). Thus, the results show that it is possible to use data on the microcrustacean assemblage structure (composition and abundance) as an indicator of distinct environmental conditions in large dammed rivers.

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