

LONGITUDINAL DISTRIBUTION OF COPEPODA POPULATIONS IN THE TRANSITION ZONE OF PARANAPANEMA RIVER AND JURUMIRIM RESERVOIR (SÃO PAULO, BRAZIL) AND INTERCHANGE WITH TWO LATERAL LAKES

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ABSTRACT

Longitudinal changes in composition, abundance, and distribution of copepods were studied at the transition zone of Paranapanema River-Jurumirim Reservoir (SP, Brazil). The interchange of biotic material between marginal lakes and the river system was also examined. Water samples were obtained from 6 stations along a stretch of 13 km of the Paranapanema River, from an upstream reach with high water velocity up to the river mouth into Jurumirim Reservoir. Two other sites in lateral lakes were also sampled. Nine copepod taxa were identified: 3 calanoids (*Argyrodiaptomus furcatus* Sars, *Notodiaptomus iheringi* Wright, and *N. conifer* Sars) and 6 cyclopoids (*Eucyclops* Claus, *Microcyclops* Claus, *Mesocyclops longisetus* Thiébaud, *Thermocyclops decipiens* Fischer, *T. minutus* Lowndes, and *Paracyclops* Claus). Harpacticoids were also collected. Calanoid and cyclopoid nauplii and copepodids, and harpacticoids were the most abundant organisms. In general, there was a longitudinal decrease in copepod abundance, whereas an increase was detected near the lakes. The abundance of most copepods was inversely correlated with current velocity and suspended solids. Higher abundance was observed in the river main course during the rainy season, during which there is a higher connectivity between the lakes and the main river. This promotes exportation of biologic material from marginal lakes to the river system, a biotic exchange reflecting the importance of marginal lakes to the river community structure.

Key words: Copepoda, longitudinal distribution, river, lakes, floodplain.

RESUMO

Distribuição longitudinal de Copepoda na região de transição rio–reservatório (rio Paranapanema–Represa de Jurumirim, SP) e influência de duas lagoas laterais

O presente estudo foi realizado na zona de desembocadura do rio Paranapanema, na Represa de Jurumirim, visando a verificar as mudanças longitudinais na composição, abundância e distribuição dos Copepoda e a analisar a influência de lagoas laterais na exportação de material biótico para o rio. Foram amostrados 6 pontos no rio (trecho de 13 km), desde um local mais a montante, com alta velocidade da correnteza, até um local com características mais lênticas, na desembocadura do rio na represa, além de duas lagoas conectadas ao rio. Foram identificados 9 taxa: 3 Calanoida (*Argyrodiaptomus furcatus* Sars, *Notodiaptomus iheringi* Wright e *N. conifer* Sars) e 6 Cyclopoida (*Eucyclops* Claus, *Microcyclops* Claus, *Mesocyclops longisetus* Thiébaud, *Thermocyclops decipiens* Fischer, *T. minutus* Lowndes e *Paracyclops* Claus), além de representantes da ordem Harpacticoida.

Os organismos mais abundantes foram as fases de desenvolvimento nauplius e copepoditos, de Calanoida e Cyclopoida e os Harpacticoida. De forma geral, observou-se diminuição na abundância dos Copepoda, do ponto 1 ao ponto 5, aumentando, porém, no ponto 6 e nas lagoas marginais. A maioria dos Copepoda mostrou relação inversa com a velocidade da corrente e o material em suspensão. Sazonalmente, as maiores abundâncias no canal do rio foram observadas no período chuvoso, refletindo a importância das lagoas laterais na estrutura da comunidade do rio, visto que nesse período ocorre maior conexão entre os ambientes, acarretando a exportação de material biológico das lagoas para o rio.

Palavras-chave: Copepoda, distribuição longitudinal, rios, lagoas, planície de inundação.

INTRODUCTION

In rivers, zooplankton density is usually believed to be low (Greenberg, 1964; Hynes, 1970). However, there are studies reporting high densities of zooplankton in lotic environments, both regulated and unregulated (Winner, 1975; Steveninck *et al.*, 1992; Kobayashi *et al.*, 1998).

Factors controlling spatial and temporal variations in zooplankton density in river systems have been focused on to determine the effects of abiotic factors on lotic communities, but also to show the importance of zooplankton in nutrient transferring and recycling (especially carbon, phosphorus, and nitrogen) in aquatic systems (Kobayashi *et al.*, 1998).

Several studies on zooplankton longitudinal distribution in lotic systems have evidenced an increasing gradient downstream of several community attributes such as biomass, density, diversity, and richness (Hutchinson, 1939; Greenberg, 1964; Drago & Vassalo, 1980; Armengol *et al.*, 1988; Jose de Paggi, 1983; Saunders & Lewis, 1988, 1989; Paggi & Jose de Paggi, 1990; Vasquez & Rey, 1989; Velho *et al.*, 2001). These parameters were mainly related to the increase of phytoplankton densities and primary productivity; to environmental factors like temperature, suspended solids, and current velocity; and to hydrological processes.

Zooplankton community structure in lotic systems may also be affected by interactions between lateral lakes and river and its, especially in the rainy season when connectivity is intense. In rivers, annual fluctuations of water level show a positive relationship with specific richness resulting from the addition of populations coming from lentic water bodies of the floodplain (Paggi & Jose de Paggi, 1990). In floodplain river systems, continuous

interchanges of zooplankton fauna of marginal lakes, channels, and river occurs as a result of the degree of connection between environments which are submitted to highly variable hydrological cycles during the year (Lansac-Tôha *et al.*, 1997).

The aim of this study is to show how the longitudinal distribution of copepod populations varies in the transition zone between the Paranapanema River and the Jurumirim Reservoir, where the water level is lower than in the floodplains. The copepoda populations in two lateral lakes was also studied to compare the structure of lotic and lentic communities. In addition, hydrologic and abiotic factors were examined as potential controlling factors of the copepod community structure.

MATERIAL AND METHODS

Samples were obtained from six stations distributed along 13 km starting from upstream towards the Paranapanema River mouth into Jurumirim Reservoir, in the river-reservoir transition zone-. In this region, there are several lateral lakes, with either temporary or permanent connections with the river system. In January, April, August, and October of 1998, physical and chemical water parameters and zooplankton samples were obtained from surface water of 6 sites along the river channel (P1 to P6) and from the limnetic zone of two lateral lakes (P7, Coqueiral Lake; P8, Camargo Lake) (Fig. 1).

For quantitative analysis of the copepods, three samples of 300 liters were collected at each station using a gasoline-powered water pumping system connected to a hose 38 mm in diameter. The volume was filtered using plankton net with a 55 μm mesh size. All samples were preserved with 4% formalin.

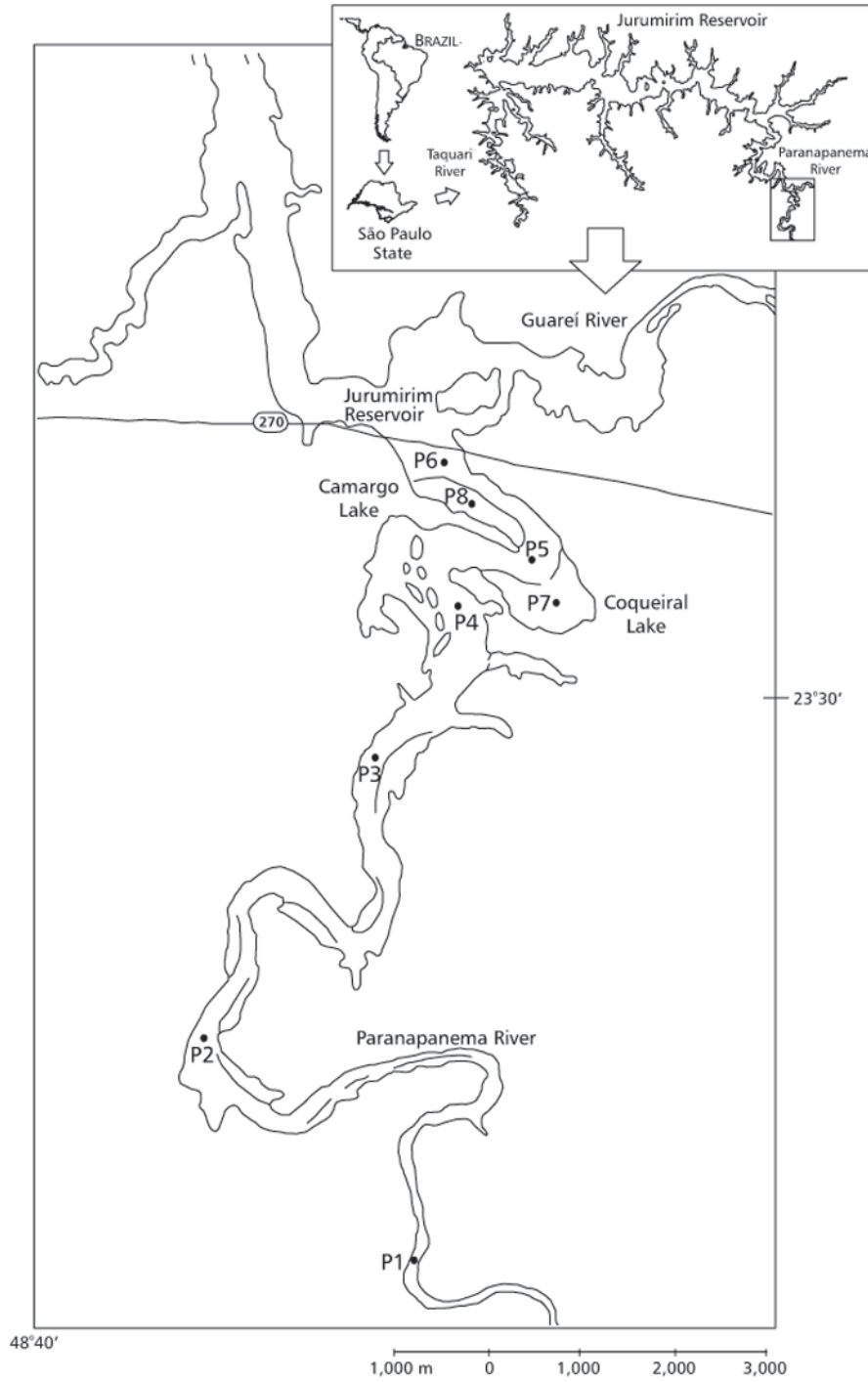


Fig. 1 — Sampling stations in the Paranapanema River mouth into Jurumirim Reservoir (São Paulo State, Brazil).

Calanoida and Cyclopoida (copepodids and adults) were counted on a stereo microscope (Zeiss, Stemi SV6), using sub-samples with at least 150 individuals or the whole sample when the density of organisms was low. Sub-samples were also used to count nauplii in Sedgwick-Rafter chambers, using an optical microscope (Zeiss, Standard 25). Identification of the species was based on Matsumura-Tundisi (1986), Reid (1985, 1988, 1989), Rocha & Matsumura-Tundisi (1976), Reid & Pinto-Coelho (1994), and Sendacz & Kubo (1982).

The following parameters were considered: current velocity (current meter ELE at 0.5 m depth), water temperature (Thermistor Toho Dentan ET-3), transparency (Secchi disk), dissolved oxygen (Winkler method, modified by Golterman *et al.*, 1978), pH (pH meter Micronal B-380), conductivity (Conductivity meter Hach 2511, corrected to 25°C), alkalinity (titration with 0.1 N H₂SO₄, Mackereth *et al.*, 1978), total nitrogen and phosphorus (Valderrama, 1981), total and organic suspended solids (Gravimetry; Teixeira & Kuthner, 1962), and chlorophyll-*a* (water filtration through Millipore AP20 membranes, cold acetone 90% extraction; Golterman *et al.*, 1978).

Statistical analyses were performed to detect significant differences of abiotic factors between

sampling sites and periods (ANOVA), and also to show correlations between abiotic factors and copepod population densities (Canonical correlation analysis; Manly, 1994). These analyses were performed considering total copepod density and also the most abundant taxa (up to 10% of total density, including nauplii and copepodids). For both analyses, the SAS System was used.

RESULTS

Environmental factors

From October 1997 to March 1998, monthly precipitation reached the highest values (Fig. 2). From April to August 1998, precipitation values were lower (15% of the annual precipitation).

Variance analyses revealed temporal ($n = 8$, $p < 0.05$) and spatial ($n = 4$, $p < 0.05$) significant differences for all abiotic factors. Seasonally, two different patterns of environmental factors were observed. Water temperature, current speed, suspended solids (total, organic, and inorganic), and total phosphorus and nitrogen concentrations reached higher values in the rainy season (January and October). Transparency, dissolved oxygen, pH, and conductivity showed higher values during the dry season (April and July) (Table 1).

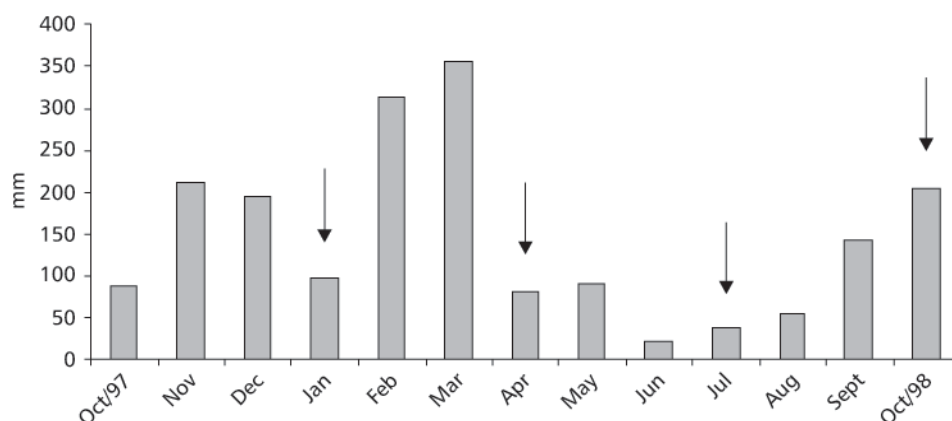


Fig. 2 — Monthly precipitation (mm) in Paranapanema (SP) region, between October 1997 and October 1998 (the arrows indicate the sampling months).

TABLE 1
Mean values of environmental factors in sampling sites (P1 to P6) of Paranapanema River and lateral lakes (P7 – Coqueiral Lake; P8 – Camargo Lake) in 1998.

	Lotic stations						Lentic stations	
	P1	P2	P3	P4	P5	P6	P7	P8
January								
Water transparency (cm)	18	40	43	21	46	25	51	31
Dissolved oxygen (mg.L ⁻¹)	6.96	6.69	6.51	6.31	6.61	6.52	7.13	6.51
pH	6.3	6.2	6.1	6.0	6.3	6.4	6.6	6.4
Water temperature (°C)	22.3	22.1	22.6	22.7	24.5	24.9	26.4	26.0
Chlorophyll- <i>a</i>	5.80	5.18	8.17	5.74	4.80	6.68	15.92	6.93
Alkalinity (mEq.L ⁻¹)	0.351	0.364	0.343	0.328	0.366	0.373	0.417	0.390
Conductivity (μS.cm ⁻¹)	53	50	50	52	54	52	55	55
Organic suspended solids (mg.L ⁻¹)	0.86	0.66	0.55	0.42	0.73	0.82	0.54	0.55
Inorganic suspended solids (mg.L ⁻¹)	5.56	4.29	3.18	3.16	2.66	3.56	0.81	1.40
Total nitrogen (μg.L ⁻¹)	1,188	937	1,034	934	496	332	719	580
Total phosphorus (μg.L ⁻¹)	44	29	28	28	28	22	14	15
April								
Water transparency (cm)	50	50	58	59	64	69	63	75
Dissolved oxygen (mg.L ⁻¹)	7.22	7.17	7.21	7.26	7.25	7.25	6.33	6.73
pH	6.7	6.9	6.9	7.1	7.2	7.2	7.1	7.1
Water temperature (°C)	16.3	16.5	18.7	17.9	18.7	18.3	21.4	20.2
Chlorophyll- <i>a</i>	3.37	4.05	2.81	4.37	3.81	4.93	4.74	5.49
Alkalinity (mEq.L ⁻¹)	0.466	0.459	0.460	0.510	0.512	0.524	0.479	0.505
Conductivity (μS.cm ⁻¹)	64	64	66	62	62	64	59	62
Organic suspended solids (mg.L ⁻¹)	0.44	0.33	0.25	0.21	0.24	0.27	0.23	0.25
Inorganic suspended solids (mg.L ⁻¹)	2.23	1.98	1.18	1.15	1.28	1.30	0.98	1.01
Total nitrogen (μg.L ⁻¹)	281	311	165	166	94	43	86	135
Total phosphorus (μg.L ⁻¹)	15	14	12	9	8	10	8	7
July								
Water transparency (cm)	84	73	89	85	83	73	85	97
Dissolved oxygen (mg.L ⁻¹)	9.12	9.00	9.11	8.75	8.80	8.90	8.39	8.77
pH	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0
Water temperature (°C)	14.7	15.0	14.7	15.1	15.5	14.9	19.0	17.0
Chlorophyll- <i>a</i>	3.93	3.87	2.81	4.43	4.49	5.05	7.80	5.99
Alkalinity (mEq.L ⁻¹)	0.417	0.408	0.412	0.407	0.406	0.418	0.407	0.418
Conductivity (μS.cm ⁻¹)	74	73	72	73	74	72	67	68
Organic suspended solids (mg.L ⁻¹)	0.41	0.48	0.39	0.34	0.38	0.43	0.30	0.21
Inorganic suspended solids (mg.L ⁻¹)	0.72	0.92	0.19	0.18	0.33	0.42	0.06	0.00
Total nitrogen (μg.L ⁻¹)	140	233	353	352	352	343	341	214
Total phosphorus (μg.L ⁻¹)	13	16	9	9	14	16	16	12

TABLE 1 (Continued.)

	Lotic stations						Lentic stations	
	P1	P2	P3	P4	P5	P6	P7	P8
October								
Water transparency (cm)	38	39	40	42	37	49	33	43
Dissolved oxygen (mg.L ⁻¹)	6.99	7.07	6.84	7.02	6.97	6.92	7.47	7.17
pH	7.0	7.0	6.9	6.9	6.9	6.9	6.9	7.0
Water temperature (°C)	20.4	20.6	20.7	20.1	20.2	20.1	21.3	21.7
Chlorophyll- <i>a</i>	17.41	17.04	16.86	14.45	9.36	12.29	14.05	12.86
Alkalinity (mEq.L ⁻¹)	0.336	0.337	0.341	0.321	0.321	0.339	0.316	0.360
Conductivity (µS.cm ⁻¹)	54	52	53	50	49	57	50	58
Organic suspended solids (mg.L ⁻¹)	0.82	0.65	0.49	0.55	0.56	0.65	0.29	0.35
Inorganic suspended solids (mg.L ⁻¹)	4.55	4.44	3.90	2.47	3.11	2.69	1.32	1.00
Total nitrogen (µg.L ⁻¹)	319	325	224	224	210	187	188	183
Total phosphorus (µg.L ⁻¹)	48	48	44	57	33	40	37	46

Water temperature and transparency increased towards upstream from station P1 to P6. On the other hand, current velocity, dissolved oxygen, suspended solids, nutrients, and chlorophyll *a* decreased in the opposite direction, reaching minimum values near the reservoir. Current velocity (Fig. 3) and suspended solids (Fig. 4) decreased considerably downstream. No longitudinal pattern for alkalinity, pH, and conductivity was recorded.

Inorganic fraction predominated for suspended solids in river and lakes, except for July, when organic fraction attained 83% and 100% of suspended solids in Coqueiral and Camargo lakes, respectively.

Lateral lakes presented singular features. Water temperature, transparency, and chlorophyll-*a* were higher, whereas suspended solids, dissolved oxygen, and nitrogen and phosphorus concentrations were lower than the values found in the river channel.

COPEPODA

The copepod assemblage in the Paranapanema River and lateral lakes was composed by 9 taxa. The calanoid *Notodiaptomus conifer* (Wright) and the

cyclopoids *Paracyclops* (Claus) and *Thermocyclops decipiens* (Fischer), in addition to *T. minutus* (Lowndes), were common to both systems, i.e., river and lakes. Only in the river, the calanoids *Argyrodiaptomus furcatus* (Sars) and *Notodiaptomus iheringi* (Wright), and the cyclopoids *Eucyclops* (Claus) and *Mesocyclops longisetus* (Thiébaud) were found. Conversely, the cyclopoid *Microcyclops* (Claus) was only found in the lateral lakes. Harpacticoids were recorded in both environments.

Argyrodiaptomus furcatus and *N. iheringi*, observed only in the river, were found in the rainy season (Table 2). *Mesocyclops longisetus* and *Eucyclops* sp. were found in higher densities in the rainy season. However, *Eucyclops* sp. occurred in very low density (1 ind.m⁻³) in July. Among the species common to both systems, higher densities of *N. conifer* were detected in the river channel during the rainy season.

High densities of copepods in the river channel were observed in October (9,913 ind.m⁻³), and low in July (436 ind.m⁻³), while in lateral lakes they occurred in April (151,074 ind.m⁻³) and July (44,788 ind.m⁻³), respectively.

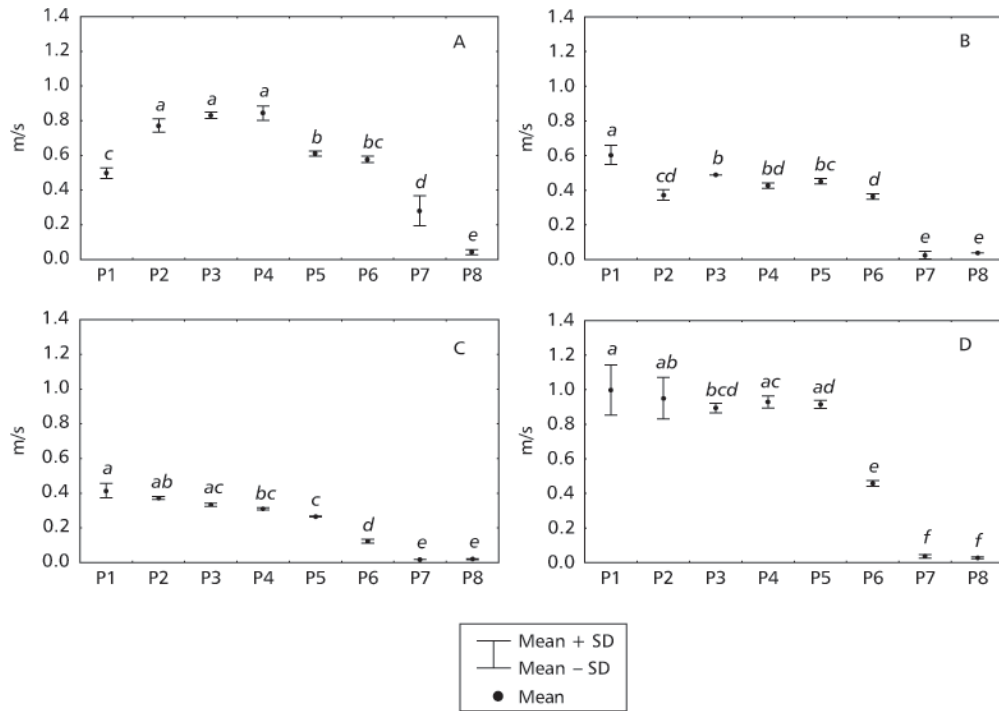


Fig. 3 — Current velocity in January (A), April (B), July (C), and October (D) of 1998, in Paranapanema River (P1 to P6) and in lateral lakes (P7 – Coqueiral Lake; P8 – Camargo Lake). Statistically significant differences are represented by different letters ($p < 0.05$).

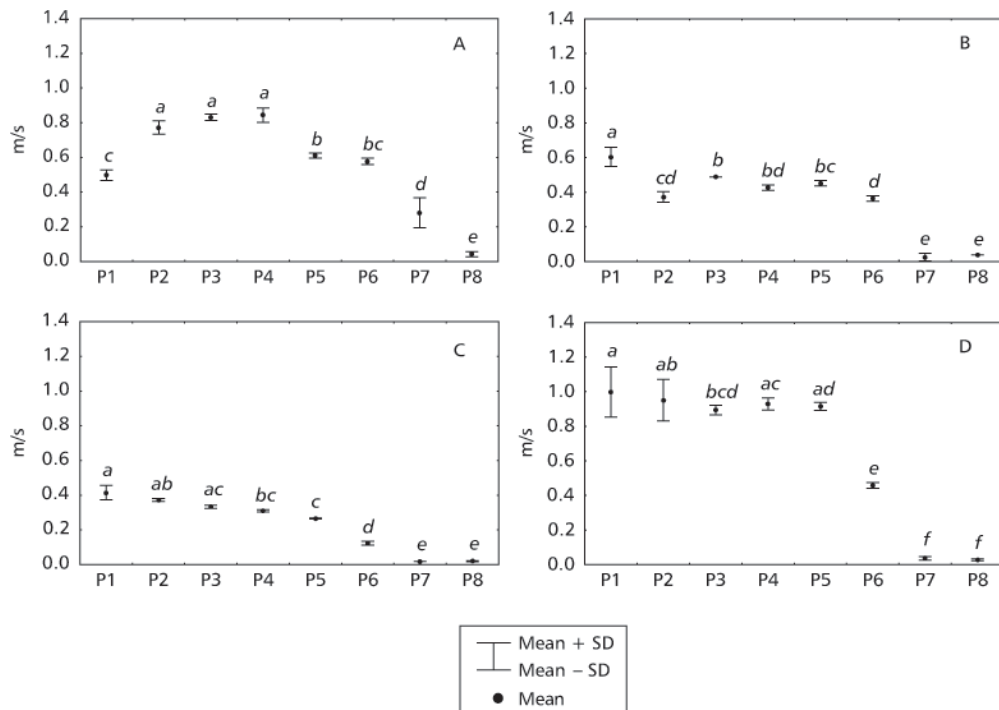


Fig. 4 — Suspended solids in January (A), April (B), July (C), and October (D) of 1998, in Paranapanema River (P1 to P6) and in lateral lakes (P7 – Coqueiral Lake; P8 – Camargo Lake). Statistically significant differences are represented by different letters ($p < 0.05$).

TABLE 2
Copepods abundance (ind.m⁻³) in Paranapanema River (P1 a P6) and lateral lakes
(P7 – Coqueiral Lake; P8 – Camargo Lake) in 1998.

	Lotic stations						Lentic stations	
	P1	P2	P3	P4	P5	P6	P7	P8
January								
<i>Eucyclops</i> sp.	3	0	9	3	94	4	0	0
<i>Mesocyclops longisetus</i>	0	0	0	3	98	0	0	0
<i>Microcyclops</i> sp.	0	0	0	0	0	0	8	0
<i>Notodiaptomus conifer</i>	9	0	3	46	94	4	0	0
<i>Notodiaptomus iheringi</i>	0	0	0	6	3	4	0	0
<i>Paracyclops</i> sp.	0	0	0	0	3	0	16	0
<i>Thermocyclops minutus</i>	4	7	11	40	0	18	110	355
<i>Thermocyclops decipiens</i>	6	4	9	10	94	21	546	539
April								
<i>Eucyclops</i> sp.	0	0	0	4	0	3	0	0
<i>Mesocyclops longisetus</i>	0	1	0	0	4	0	0	0
<i>Microcyclops</i> sp.	0	0	0	0	0	0	237	113
<i>Notodiaptomus conifer</i>	0	0	2	0	9	4	60	0
<i>Paracyclops</i> sp.	148	1	0	1	0	0	116	87
<i>Thermocyclops decipiens</i>	8	2	8	3	5	12	1,590	398
<i>Thermocyclops minutus</i>	3	6	5	2	0	13	373	155
July								
<i>Eucyclops</i> sp.	0	0	0	0	0	1	0	0
<i>Paracyclops</i> sp.	0	1	0	0	1	0	0	0
<i>Thermocyclops decipiens</i>	3	2	1	2	1	6	2,167	224
<i>Thermocyclops minutus</i>	0	0	3	0	4	4	1,511	326
October								
<i>Argyrodiaptomus furcatus</i>	0	0	0	0	5	0	0	0
<i>Ergasilus</i> sp.	0	6	0	0	0	0	0	74
<i>Eucyclops</i> sp.	0	0	0	6	5	4	0	0
<i>Mesocyclops longisetus</i>	4	11	26	3	33	4	0	0
<i>Notodiaptomus conifer</i>	0	0	6	8	0	0	0	0
<i>Paracyclops</i> sp.	9	25	14	6	0	4	0	0
<i>Thermocyclops decipiens</i>	15	24	20	25	34	39	1,081	545
<i>Thermocyclops minutus</i>	79	44	44	56	59	46	722	455

A copepod density decrease was observed in the river toward the reservoir (specially between P1 and P5 stations). However, in July and October an increase was observed in P6, located in front of Camargo Lake. In the lentic habitats, copepod density was always higher than that in the river system (Fig. 5A, C, E, and G).

Cyclopoids were usually more abundant in all stations and throughout the year (< 50%). Cyclopoids and harpacticoids were more abundant in the river compared to lakes, in which cyclopoids reached more than 90% of the total density in January and October (Fig. 5B and H). In the river, harpacticoids predominated only in April in upstream stations, reaching 78% of the total density in P1 (Fig. 5D). In lateral lakes, harpacticoid density was never more than 0.2%. Calanoid density was always lower than 22% of Copepoda total density in the river, and reached a maximum of 36% in April, in Camargo Lake (Fig. 5D).

Calanoid and cyclopoid nauplii and copepodids, and harpacticoids were the most abundant copepods, while adults always represented lower densities (Table 2). Concerning calanoids, nauplii and copepodids were scarcely represented in the river channel. In the lakes, the densities were always higher than in the river (Fig. 6). Longitudinal increase in nauplii density occurred in January, July, and October (Fig. 6A, B and D). For copepodids, density increased only in April (Fig. 6B). In July, copepodid density in the river was near to zero (Fig. 6C). In January and October, no significant longitudinal variations were found (Fig. 6A and D).

A longitudinal decrease in cyclopoid nauplii and copepodid density occurred from P1 to P4 stations. However, an increase was recorded near lateral lakes, specially in front of Camargo Lake (P6) (Fig. 7). Higher densities were observed inside the lakes.

In the river channel, harpacticoid density decreased from P1 to P6 stations. In lateral lakes, nauplii were absent while copepodids and adults occurred only in January (Coqueiral Lake) and in July (Camargo Lake) (Fig. 8).

Correlation between species and environmental variables

The correlation coefficient corresponding to the first three pairs of canonical variables was

significant ($p < 0.05$). Nauplii and adult harpacticoids were positively correlated with chlorophyll-*a*, total phosphorus, suspended solids (total and organic), temperature, and current velocity. However, they were negatively correlated with alkalinity, conductivity, dissolved oxygen, and water transparency ($Ra = 0.974$; $p < 0.0001$) (Table 3). The second pair of canonical variables ($Ra = 0.957$; $p < 0.0001$) showed a negative correlation of copepoda (total) with current velocity and suspended solids. Other correlations of these variables were also obtained, being positive in relation to harpacticoid nauplii, copepodids, and adults, and negative to calanoid and cyclopoid nauplii and copepodids (Table 3). The third pair of canonical variables ($Ra = 0.8285$; $p < 0.0001$) showed a positive correlation of Copepoda (total), calanoid and cyclopoid nauplii and copepodids with water temperature, and negative with dissolved oxygen (Table 3).

DISCUSSION

Rivers are systems in which water movement is horizontal. In these systems, water, nutrients, sediments, and organisms move according to the water speed. This flow is permanent and is a controlling factor in the distribution and abundance of organisms (Neiff, 1996). Since rivers present a strong relationship with lateral lakes and terrestrial habitats, to determine if the zooplankton community shows a similarity with that in the lentic environments, laterally associated with the river system, is important.

Among the species collected, four of nine were sampled only in the Paranapanema River, while just one was limited to the lakes. For these species, distribution is probably related to the season, since some of them were observed in higher densities in the rainy season while others were found exclusively in this period. The high biotic exchange between these different systems, when the water level is high, can explain this observation. According to Paggi & Jose de Paggi (1990), the annual fluctuations of water level show a positive relationship with specific richness, as a consequence of the added population coming from lentic water bodies to the lotic environment.

Concerning the nonoccurrence of adult instars of these species in the lakes, Martins (2000) observed high densities of *Notodiaptomus* spp. in the littoral habitats of Camargo Lake.

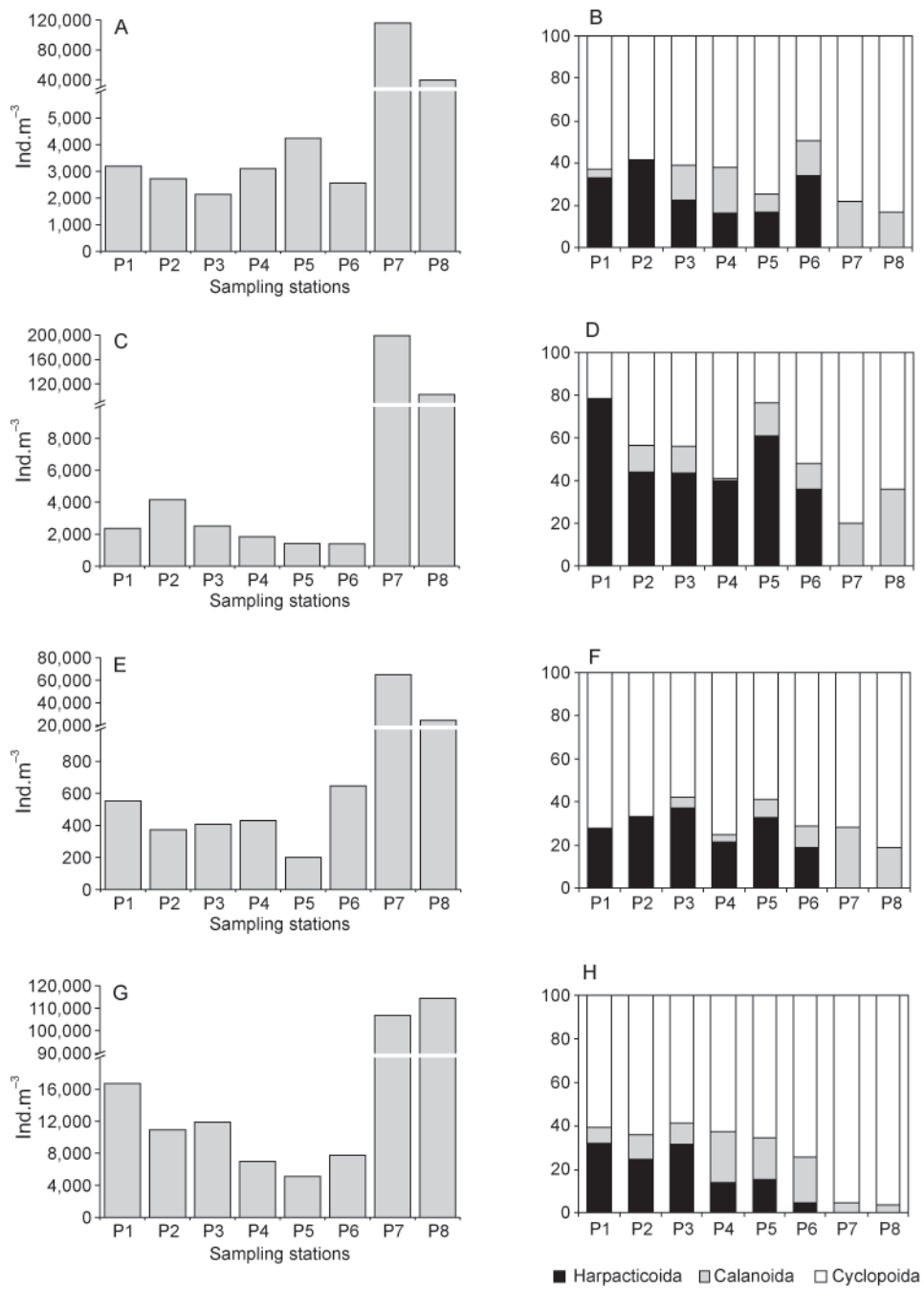


Fig. 5 — Total of Copepods (ind.m⁻³) and relative abundance (%) of Calanoida, Cyclopoida, and Harpacticoida in Paranapanema River (P1 to P6) and in lateral lakes (P7 – Coqueiral Lake; P8 – Camargo Lake), in January (A, B), April (C, D), July (E, F), and October (G, H) 1998.

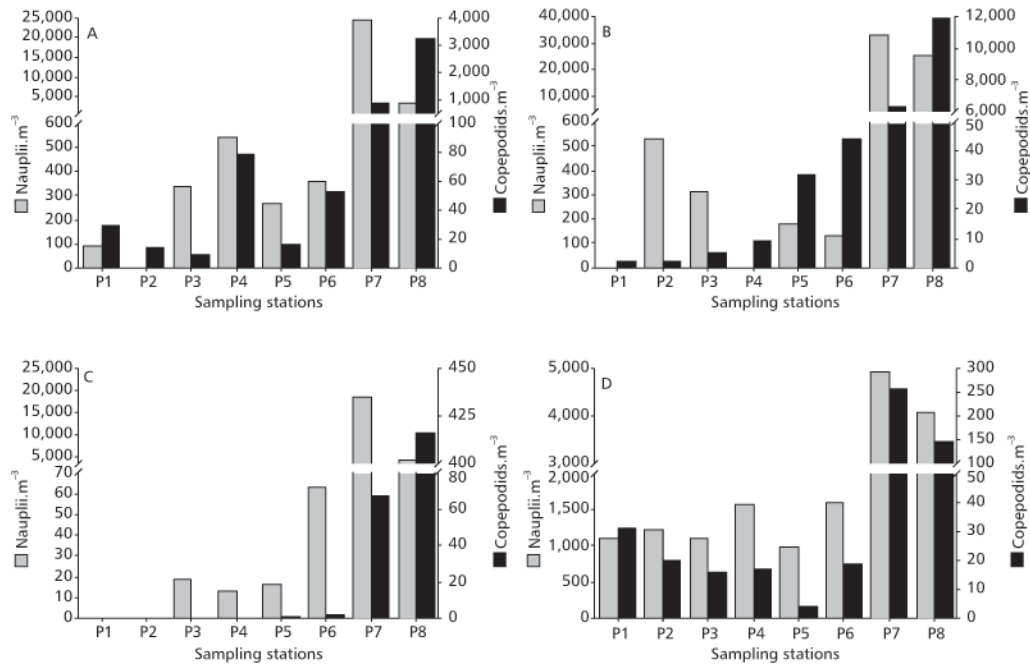


Fig. 6 — Mean density of calanoid nauplii (□) and copepodids (■) in Paranapanema River (P1 to P6) and lateral lakes (P7 – Coqueiral Lake and P8 – Camargo Lake), in January (A), April (B), July (C), and October (D) 1998.

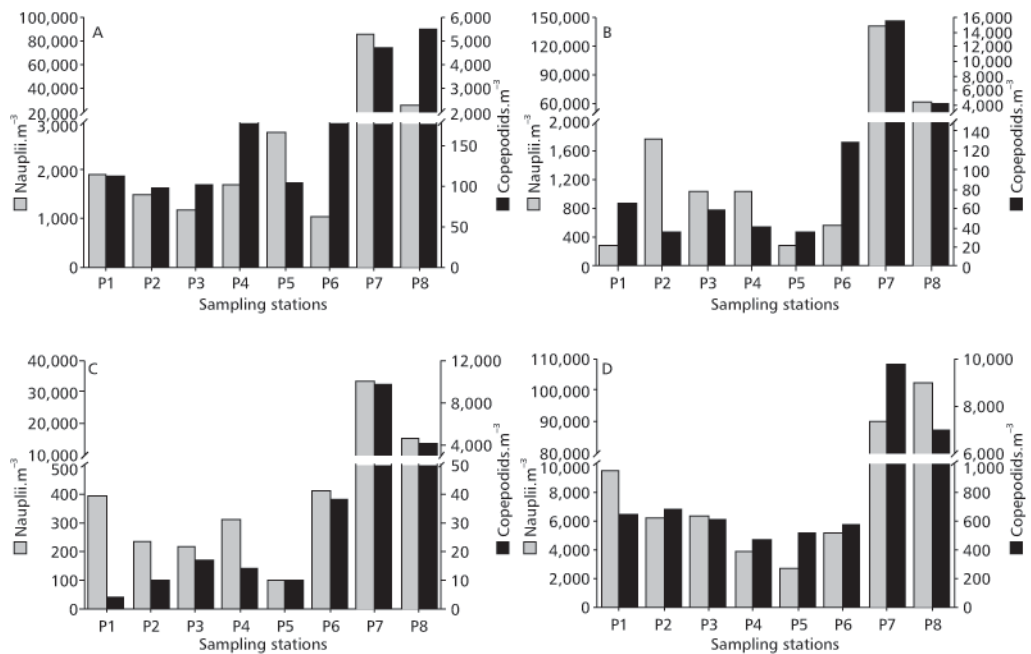


Fig. 7 — Mean density of cyclopoid nauplii (□) and copepodids (■) in Paranapanema River (P1 to P6) and lateral lakes (P7 – Coqueiral Lake and P8 – Camargo Lake), in January (A), April (B), July (C), and October (D) 1998.

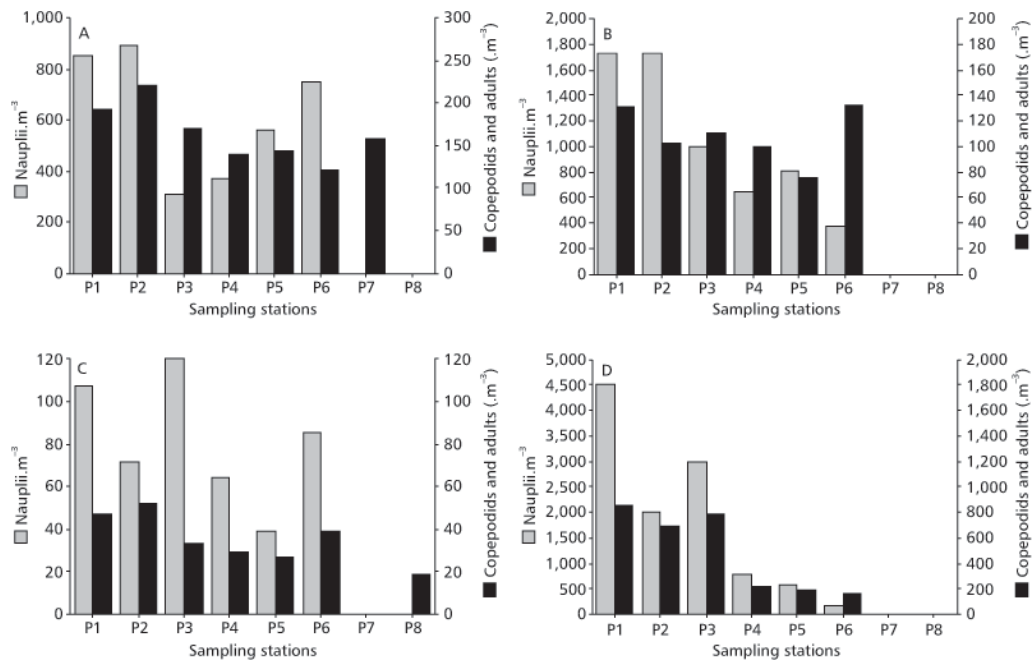


Fig. 8 — Mean density of harpacticoid nauplii (□) and copepodids and adults (■) in Paranapanema River (P1 to P6) and lateral lakes (P7 – Coqueiral Lake and P8 – Camargo Lake), in January (A), April (B), July (C), and October (D) 1998.

Copepod richness in the river (6 taxa) and in the lakes (5 taxa) was similar due to the influence of high precipitations, rising of water level, and consequent water exchange between river and lakes and, thus, of the number of taxa. Lansac-Tôha *et al.* (1997) obtained similar patterns in lotic, semi-lotic, and lentic environments in the Upper Paraná floodplain. There are permanent interchanges between microcrustacean fauna of lakes, channels, and rivers in the limnetic and littoral zones, due to interconnections between systems and to the water level variation pattern.

Though the number of cyclopoid species is relatively low (6), a similar observation was obtained by Sendacz (1993, 2001) in the Upper Paraná River and in 7 lateral lakes (4 and 2 species, respectively) and Velho *et al.* (2001) in the Corumbá River and Reservoir (3 species). On the other hand, Paggi & Jose de Paggi (1990) found

25 species in lentic and lotic environments in the middle Paraná River, of which 9 species were common to rivers and ponds.

In this study, Calanoida was scarcely represented (3 species) compared to other studies in the Upper Paraná River and its lateral lakes (7 species; Sendacz, 1993, 2001), the Orinoco River and its floodplain lakes (13 species; Dussart, 1984), and in the southern Pantanal (4 species, Reid & Moreno, 1990). In the other hand, Velho *et al.* (2001) found only one calanoid (*Notodiaptomus iheringi*) in 21 sampling stations along the Corumbá Reservoir, including the river (upstream and downstream from the dam), tributaries, and lateral arms. In this study, *Notodiaptomus iheringi* reached small densities although it was frequent and, attained high densities in the lacustrine zone of Jurumirim Reservoir (Nogueira & Panarelli, 1997; Panarelli *et al.*, 2001; Nogueira, 2001).

TABLE 3
Correlation between copepod abundance and canonical variables (V_1 , V_2 and V_3) and correlation between environmental factors and canonical variables (W_1 , W_2 and W_3).

Abiotic variables	Canonical variable	Biotic variables	Canonical variable
	V_1		W_1
Alkalinity	-0.751	Harpacticoid nauplii	0.525
Conductivity	-0.789	Harpacticoid (copepodids and adults)	0.748
Dissolved oxygen	-0.528		
Transparency	-0.696		
Chlorophyll- <i>a</i>	0.814		
Total phosphorus	0.877		
Suspended solids	0.756		
Organic suspended solids	0.554		
Water temperature	0.529		
Current velocity	0.644		
	V_2		W_2
Current velocity	-0.622	Copepod (total)	0.658
Suspended solids	-0.425	Cyclopoid copepodid	0.704
		Cyclopoid nauplii	0.692
		Calanoid nauplii	0.433
	V_3		W_3
Dissolved oxygen	0.686	Copepod (total)	-0.537
Water temperature	-0.423	Calanoid copepodids	-0.695
		Cyclopoid copepodids	-0.425
		Calanoid nauplii	-0.539
		Cyclopoid nauplii	-0.491

Cyclopoids were represented by *Mesocyclops* and *Thermocyclops*, the latter genus being the most abundant. *Thermocyclops* was represented by two species, *T. minutus* and *T. decipiens*. These species are the most abundant cyclopoids in Jurumirim Reservoir (Nogueira, 2001). *T. decipiens* presents a dominance in the crustacean zooplankton from mesotrophic to eutrophic reservoirs, while *T. minutus*, though present in large populations in some eutrophic systems, tends to be more numerous in oligotrophic to mesotrophic reservoirs (Reid, 1989). This pattern was not observed in the Paranapanema River mouth since both species occurred in similar densities.

The average density of copepods in Paranapanema River was high (3,911 ind.m⁻³). Similar data were reported by Lansac-Tôha *et al.* (1997) for lotic environments of the Upper Paraná River floodplain (1,500-2,000 ind.m⁻³), and by Vasquez & Rey (1989) in the Orinoco River and its delta (Venezuela) (1,500-3,400 ind.m⁻³). High abundance was due to high densities of young instars (nauplii and copepodids). Similar observations were reported by Saunders & Lewis (1988) for the Caura River (Venezuela), by Sendacz (1993) and Lansac-Tôha *et al.* (1997) for the Upper Paraná River; and by Carvalho (1983) and Hardy *et al.* (1984) for the Amazon River Floodplain.

Sendacz (1993) pointed out that in the Upper Paraná systems, especially in Lake Jota, copepodids reached higher densities than did nauplii. Copepod ontogeny involves great modifications in body size, behavior, and feeding; thus, suitable conditions for one instar of the life cycle of a species are frequently inappropriate for another instar. Hardy (1980) and Carvalho (1983) found that nauplii correspond to from 60% to 98% of the total zooplankton in Amazonian lakes. Carvalho (1983) observed that in the Grande Lake (AM), except for *T. minutus*, adult instars always had densities below 1% of total copepod abundance.

In the Caura River (Venezuela), Saunders & Lewis (1988) found cyclopoid nauplii accounting for 85% of the copepods. According to the authors, the prevalence of their early life history stages without adults suggest that young copepods in the river come from adjacent source areas and do not grow rapidly in the river.

Immature copepods appear particularly susceptible to downstream washout. Although at later developmental stages they exhibit progressively greater resistance to water flow, at immature stages they would have poor swimming ability, since these instars have poorly developed swimming appendages (Richardson, 1992). Thus, these immature instars often dominate densities of animals in drift in lotic environments (Saunders & Lewis, 1989).

High concentration of suspended solids, resulting from high water turbulence in lotic environments directly affects zooplankton by obstructing filter and respiratory appendages, and indirectly affect it by reducing light penetration, thus decreasing primary productivity. Notwithstanding, the suspended solids could constitute alimentary sources, like detritus and bacterium. According to Carvalho (1983), the direct influence of suspended solid particles on zooplankton seems to affect only determinate populations, changing only species composition.

Current velocity has been considered one of the main environmental factors affecting abundance and even the existence of lotic zooplankton (Hynes, 1970). The majority of copepods showed negative correlation with current velocity, suspended solids, and dissolved oxygen, and positive correlation with water temperature. Similar results were obtained by Frutos (1998) in the Salado and Negro rivers

(Argentina), in which copepod nauplii were negatively correlated with suspended solids and positively correlated with temperature.

Increase of some copepods, specially calanoid nauplii and copepodids, toward the reservoir is probably due to lower current velocity and higher water temperature and transparency. This trend probably results in increased growth and reproduction rates of these organisms. Moreover, higher densities may also be related with zooplankton exportation from lateral lakes.

Studies on the effects of current velocities on distribution of copepods in lotic environments have shown that cyclopoids can exhibit relatively large populations due to their ability to resist and avoid flowing water. Moreover, organisms able to climb substrates should occur in greater densities than those that are strictly planktonic (Richardson, 1992). This could explain the higher densities of cyclopoids and harpacticoids in the Paranapanema River. Harpacticoids commonly found on stream beds are less likely to be exposed to flowing water since they inhabit the hyporheic zone, and their entry into the water column appears to be the result of complex interactions in which water velocity may be a controlling factor.

Longitudinal variations in composition, density, and distribution of communities are also affected by seasonal changes in environmental factors, due mainly to the hydrological regime. Variations of the hydrologic regime are undoubtedly of great importance, and responsible for main changes in a great number of environmental factors related to each other and to the zooplankton, such as flow, current velocity, turbidity, and suspended solids. Precipitation not only modifies the physical and chemical features of the environment, but also causes an increase in water level, increasing communication between the river system and the lateral associated environments.

According to Saunders & Lewis (1988), changes in water level that cause lateral inundation tend to increase zooplankton abundance in the main channel. In the mouth of the Paranapanema River, copepods reached higher abundances in October (rainy season) when the connection between river and lakes is well established. High densities of copepods in high waters were also recorded by Lansac-Tôha *et al.* (1997) in lotic environments of

the Upper Paraná River floodplain, and by Vasquez & Rey (1989) in the Orinoco River and its delta (Venezuela).

In these upstream reaches of reservoirs, the interconnection between lateral lakes and the river system is strongly influenced by the hydrological level. Depending on the connection, these areas can act like reproduction or exportation areas. The copepod downstream transport toward the reservoir is mainly represented by young instars. Since these animals cannot develop in the river channel, downstream transport is an important factor in maintaining copepod community in the reservoir.

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