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Plankton richness in a eutrophic reservoir (Barra Bonita Reservoir, SP, Brazil)

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Key words: eutrophic reservoir, horizontal heterogeneity, tributaries, plankton richness, cyanophycean blooms, nutrients concentration

Abstract

Species richness of plankton was studied in a eutrophic reservoir (Barra Bonita Reservoir) of the Middle Tietê River, São Paulo State, Brazil, during the period 1985–1986. This reservoir is formed by two rivers: the Tietê and the Piracicaba (the main tributaries), of which the Tiête is more eutrophic, having conductivity and nutrient concentration values twice those of the Piracicaba. In addition, the reservoir is fed by 114 smaller tributaries. Monthly sampling was carried out at three stations representing different environmental conditions: St1 on the Tietê, S2 on the Piracicaba, and St3 at the confluence of the two rivers. For the phytoplankton community, the Piracicaba River (St2) proved the richest site, with a listed 72 species with abundance of Chlorophyta, while St1 and St3 registered 59 and 50 species, respectively, with abundance of Cyanophyta. For the zooplankton community a great difference was not registered in species number at the three stations but the species composition and dominant species of rotifers and copepods were quite different. The occurrence of *Mesocyclops meridianus* and *Metacyclops mendocinus*, specific for St2; *Mesocyclops ogunnus* and *Notodiaptomus iheringi*, specific for St1, and that of these two species plus *Mesocyclops meridianus* at St3 shows that the conditions combining at this station were favorable to *Mesocyclops meridianus* but not to *Metacyclops mendocinus*. Both for phytoplankton and zooplankton, high values found of species richness were compared to species richness of natural lakes, e.g., Dom Helvecio, a monomictic stable lake in eastern Brazil, and another fifteen lakes in the same region.

In conclusion, this work shows that environmental gradients are strong selective factors that enhance plankton richness in eutrophic reservoirs exhibiting environmental instability. This fact could explain the presence of a high number of plankton species associated with a high number of individuals in Barra Bonita Reservoir, supporting the effects of the intermediate disturbance hypothesis.

Introduction

Species richness of plankton in a reservoir is related to its trophic state, spatial heterogeneity in vertical and horizontal structure (thermal, physical, and chemical),and frequency and degree of mixing and stratification of the water column.

Reservoirs are complex systems (Tundisi et al., 1998) with spatial gradients, produced by tributaries that influence local physical, chemical, and biological characteristics of water masses. A reservoir, according to Kimmel & Groeger (1984) presents three very distinct zones: the riverine zone, in the upper reservoir, that is subject to the influence of either the tributaries or river of origin;

the transition zone, downstream from the reservoir, that functions as an intermediate river-lake ecosystem; and the lacustrine zone, located further downstream. These are dynamic zones with interfaces that change periodically, depending on horizontal and vertical forces, and are influenced by wind and the effects of discharge at the dam site (by water spill devices, hydroelectric use, or water supply intakes).

Despite several descriptions, assumptions, theories, and hypotheses regarding spatial heterogeneity in reservoirs (Straskraba et al., 1993; Tundisi & Straskraba, 1999) and demonstrations such as those of Armengol et al. (1999), there is still a lack of data on the effects of these environmental gradients in plankton behavior and distribution affecting species richness in reservoirs.

Barra Bonita is the first of a series of six large reservoirs located in the middle and lower Tietê River, São Paulo State, Brazil. Several studies have been conducted in the last 25 years in order to understand its dynamic features and to provide a basis for its management (Barbosa et al., 1999; Matsumura-Tundisi et al., 1990, 2002; Tundisi & Matsumura-Tundisi, 1990; Tundisi et al., 1998, 2000). These studies show that the system is subject to strong inputs of climatological and hydrological factors that promote mixing processes affecting biogeochemical cycles and primary production. Spatial heterogeneity, resulting from the two main tributaries, the Piracicaba and Tietê rivers, discharging into the main body of the reservoir, has also been demonstrated. Barra Bonita is a eutrophic reservoir due to discharge of non-treated wastewater and agricultural fertilizers. Besides the two main tributaries, this reservoir has many small tributaries draining a vast watershed with diverse hydrogeochemistry and different inputs of chemical substances impacting them (Tundisi & Matsumura-Tundisi, 1990).

In the research reported in this paper, limnetic plankton richness was analyzed at three different limnological stations, each one representing a specific condition of the reservoir. These sites showed a diverse environmental conditions in relation to nutrient concentrations, conductivity, chlorophyll, and suspended matter. In searching for interrelationships between spatial heterogeneity and plankton species richness, the authors attempted to link limnetic zooplankton richness in the reservoir to spatial gradients and heterogeneity.

Material and methods

Barra Bonita Reservoir

This reservoir was built in 1963 by the damming of the Tietê and Piracicaba rivers with the aim of establishing a hydropower plant and, later on, a navigation system in the Tietê River. Located between coordinates 23° 31′ 49″ S and 48° 31′ 14″ W, its altitude is 430 m. Climatic characteristics are those of subtropical regions, with a dry period from May to October and a wet period from November to April. The reservoir is inserted into a hydrographic basin having 32 320 km^2 and whose drainage type is open (Tietê/Paraná River Basin). Reservoir area measures 310 km^2; total volume is 3.2 km^3; and dam length is 480 m. The total output of the hydroelectric power plant is 140 MW. During summer (wet season) the flushing rate is approximately 1500 m^3/s; in winter (dry season) it is approximately 200 m^3/s. The maximum depth is about 25 m with an average depth of 10 m. The retention time in summer is 37 days; in winter it is 137 days. The main uses are: hydroelectricity, navigation, recreation, tourism, fisheries, and aquaculture (Tundisi & Matsumura-Tundisi, 1990).

Sampling strategy, data collection, and period of sampling

For the purpose of this research three sampling stations were established: St 1 in the Tietê River, St2 in the Piracicaba River, and St3 at their confluence. Figure 1 shows the location of the reservoir in Brazil and São Paulo State, the satellite image of the reservoir with the Piracicaba and Tietê, location of the sampling stations, and the hydrographic basin with its many tributaries.

Monthly sampling was carried out from July 1985 to June 1986. At each sampling station, a complete vertical temperature profile was obtained, using a Toho Dentan thermistor. For other variables measured, i.e., dissolved oxygen, pH, electrical conductivity, and nutrient concentrations, water samples were collected at the surface

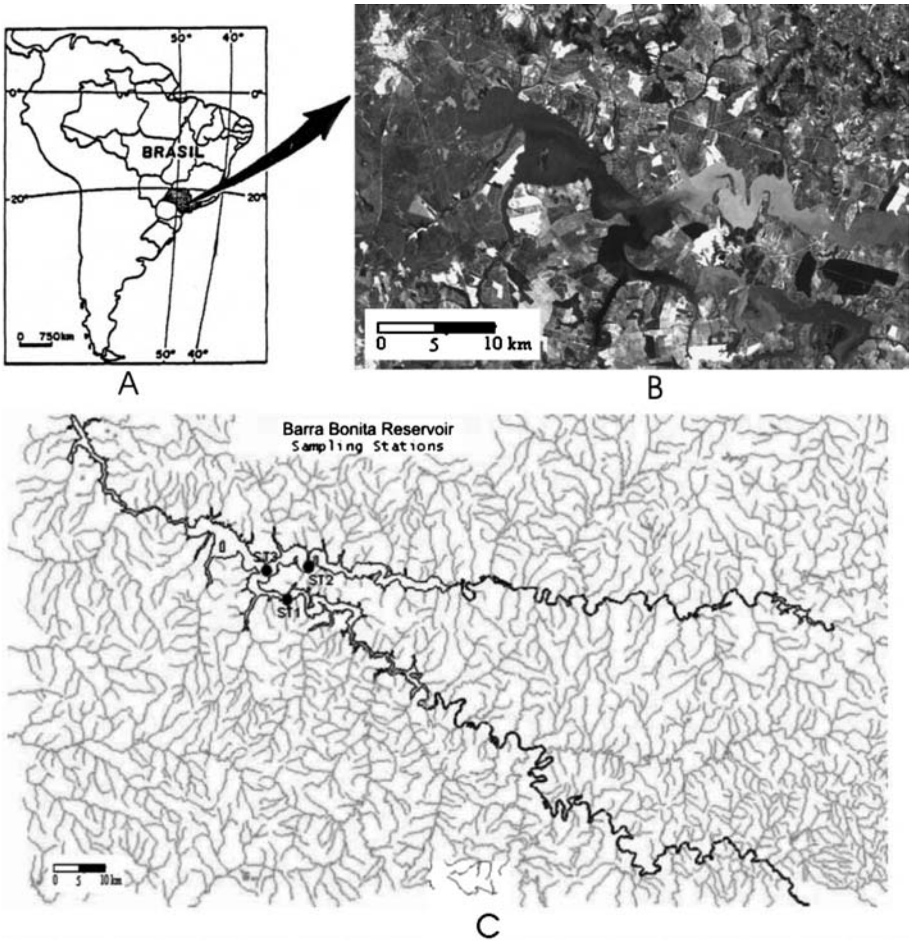

Figure 1. Map showing the location of Barra Bonita Reservoir in São Paulo State, Brazil (A); satellite image of reservoir (B); reservoir with main tributaries (Piracicaba and Tietê River) with the location of sampling stations (St1, St2 and St3) and a rich net work of small tributaries (C).

and bottom layers using a Van Dorn sampler. Chemical analyses were performed in the laboratory using methods described in Mackereth et al. (1978) and Golterman et al. (1978).

Plankton sampling

Chlorophyll data were obtained from surface water by sampling and filtering 1 l of water through a GF filter; chlorophyll was extracted using acetone 90%. The phytoplankton samples, collected from 250 ml of surface water, were fixed with lugol solution, and analyzed by the Uthermol technique using an inverted microscope. The zooplankton material was obtained by vertical hauls in the water column with a standard plankton net of 64 μm mesh size. The volume of filtered water was calculated using the formula: $V = \pi r^2 d$ where r is the radius of the net opening and d the distance covered by the net within the water column (m). The number of organisms was expressed by m^3.

After withdrawing a 1 ml subsample, small and abundant organisms such as rotifers and copepod nauplii were counted in Sedgewick Rafter cells by optical microscope with 200× of magnification. The microcrustaceans such as cladocerans and copepods were counted by stereo microscope with 80× magnification, withdrawing subsamples of variable volumes until reaching a minimum of 500 organisms for each sample.

Results

Spatial heterogeneity of the limnological conditions of the reservoir

The physical and chemical variables measured at the three stations (St1, St2, and St3) showed that St2, which is influenced by the Piracicaba River, differed widely from the other stations which were affected by the Tietê River. At St3, located at the confluence of both rivers, all data showed greater influence of the Tietê (St1) than was demonstrated for the Piracicaba (St2).

The temperature showed similar values for all three stations, with average minimum values of 17 °C in the dry period (spring/winter) and average maximum values of 28.5 °C in the wet period (autumn/summer). Figure 2 shows the temperature evolution during 1 year (July 1985–June 1986) at each site. In most periods of the year, the water column temperature was homogeneous, showing no thermal stratification. Even in November 1985 at St3, where the greatest difference between surface and bottom temperatures was registered (surface: 29.2 °C; bottom: 20.8 °C), there were no stable stratified layers.

Dissolved oxygen

Low oxygen concentration was registered in the bottom layer of St1, St2,and St3, mainly in the wet period of the year (October–January) (Fig. 3). At St1 in December 1985, high oxygen concentrations at the surface, such as 12.61 mg/l, were registered; these were probably due to the photosynthetic activity of phytoplankton, which showed high chlorophyll *a* concentration.

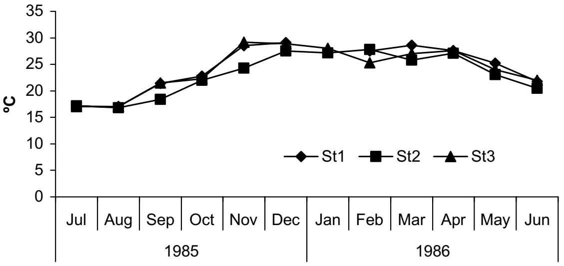

Figure 2. Variation of temperature (average value at the water column) at St1, St2 and, St3 of Barra Bonita Reservoir during the period of 1985–1986.

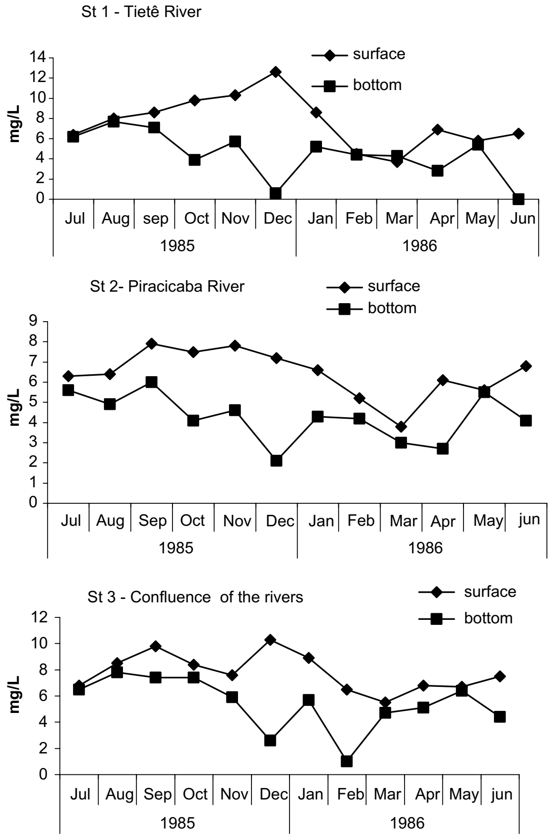

Figure 3. Variation of dissolved oxygen concentration at the surface and at the bottom of St1, St2 and, St3 of Barra Bonita Reservoir.

pH and conductivity

High pH values registered from October to January (wet season) for St1 and St3 (Fig. 4) followed the same distribution pattern presented by oxygen. The average pH values for St1 were 8.1, St2 – 7.1, St3 – 7.8. Conductivity was also high from October to January (Fig. 5).

Monthly variation of nutrients, phosphate, nitrate, and ammonium measured at the three stations are presented in Figures 6–8, respectively. The average values presented at the three stations for these nutrients were higher for the Tietê River for phosphate (25 μg/l) and for nitrate (1404 μg/l) than those for the Piracicaba River, where the average value of phosphate concentration was 11.8 μg/l, whereas for nitrate it was 473.5 μg/l. The concentration of ammonium was higher in the Piracicaba River (51.3 μg/l) than in the Tietê

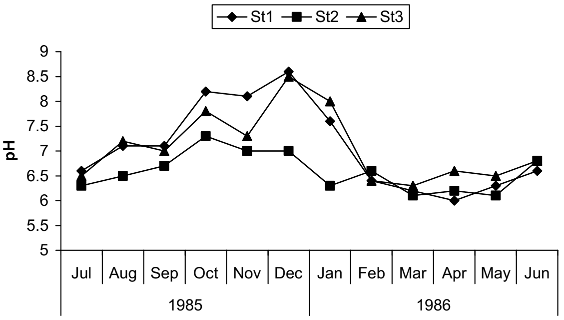

Figure 4. Monthly variation of pH at the St1 St2, and, St3 of Barra Bonita Reservoir.during the period of 1985–1986.

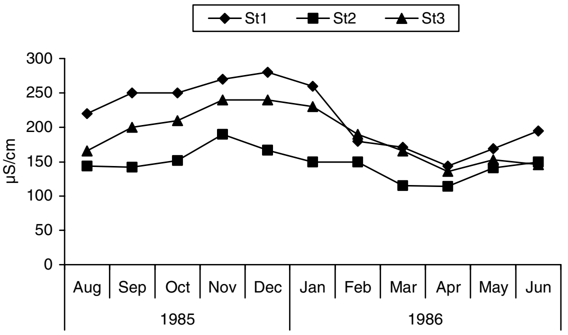

Figure 5. Monthly variation of conductivity at St1, St2, and, St3 of Barra Bonita Reservoir during the period of 1985–1986.

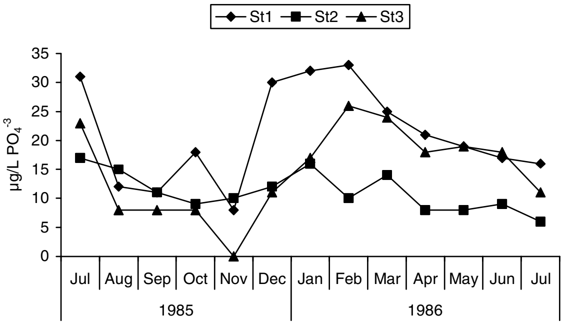

Figure 6. Monthly variation of dissolved phosphorous at St1, St2, and, St3 of Barra Bonita Reservoir during the period of 1985–1986.

(27.5 μg/l). Station 3 presented intermediate values, however it was much more influenced by the Tietê than by the Piracicaba, showing limnological characteristics of the former river (Table 1).

Chlorophyll a and phytoplankton composition

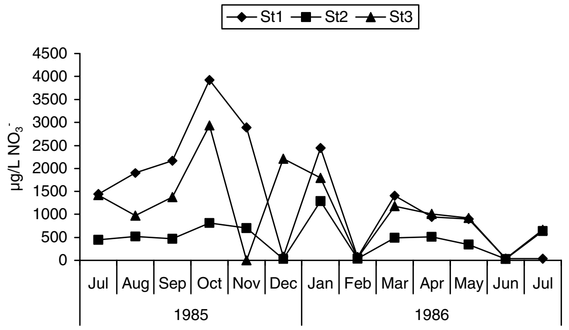

Figure 7. Monthly variation of nitrate at St1, St2 and, St3 of Barra Bonita Reservoir during the period of 1985–1986.

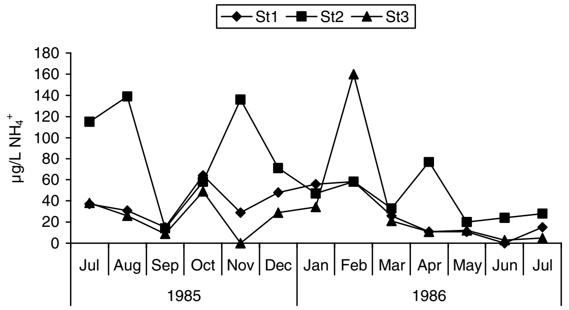

Figure 8. Monthly variation of ammonium at St1, St2, and, St3 of Barra Bonita Reservoir during the period of 1985–1986.

Figure 7 refers to the temporal variation of chlorophyll a at the three stations. At St1, the highest value (41.7 μg/l) was reached in December 1985 owing to the abundance of Cyanophyta, represented mainly by *Aanabaena spiroides* that constituted 99.4% of total phytoplankton. The first of the other two peaks occurred in October 1985 with 20 μg/l due to Chrysophyta (71.8%), represented mainly by *Aulacoseira granulata* and *Aulacoseira italica*; the other peak was reached in April 1986 with 25 μg/l of chlorophyll because of the contribution of Cyanophyta (39.6%), Chlorophyta (43.5%), and Euglenophyta (11.8%) (Table 2).

Station 2 showed a more homogeneous distribution of chlorophyll concentration during the year, with slight increases in September 1985, October 1985, and April 1986 (no more than 20 μg/l). In September, Chrysophyta contributed with 95.0% of total phytoplankton, represented mainly by *Aulacoseira italica curvata*, while in October, Chlorophyta contributed with 56.0% represented by *Staurastrum* and *Coelastrum,* and Pyrrhophyta contributed with 26.0% represented by *Peridinium.*

At the confluence of the Tietê and Piracicaba rivers, the bulk of chloropyll at St3 occurred

Table 1. Average values of physical, chemical and biological variables measured during the period of 1 year at the three stations of Barra Bonita Reservoir

	St1	St2	St3
Variables	(Tietê River)	(Piracicaba River)	(Confluence)
Temperature at surface (°C)	24.2	23.1	24.1
Oxygen at surface (mg/l)	7.6	6.5	7.8
Conductivity (μS/cm)	213.5	143.9	183.9
pH	6.8	6.4	6.8
PO_4^{-3} (μg/l)	25.0	11.8	16.1
NO_3^- (μg/l)	1404.0	473.5	1182.0
NH_4^+ (μg/l)	27.5	51.3	26.2
Chlorophyll *a* (μg/l)	14.7	11.7	9.3
No species phytoplankton	59	72	50
No species zooplankton	49	42	40

Table 2. Relative abundance of the phytoplankton taxa at St1, St2 and St3 during the periods of high concentrations of chlorophyll

Phytoplankton taxa	Months			
St1 (Tietê River)	Aug/85	Oct/85	Dec/85	Apr/86
Chrysophyta	90.2%	71.8%	0.4%	5.0%
Cyanophyta	8.3%	35.6%	99.5%	39.6%
Chlorophyta	1.5%	2.6%	0.1%	43.5%
Euglenophyta	–	–	–	11.8%
St 2 (Piracicaba River)	Sep/85	Oct/85	Apr/86	
Chrysophyta	95.0%	3.9%	30.7%	
Cyanophyta	2.1%	11.8%	16.3	
Chlorophyta	1.5%	56.2%	36.3	
Euglenophyta	–	2.0%	16.0%	
Pyrrhophyta	–	26.0%	–	
St3 (Confluence)	Dec/85	Jan/86	Feb/86	
Chrysophyta	51.7%	31.2%	59.2%	
Cyanophyta	44.9%	66.3%	38.7%	
Chlorophyta	2.9%	1.6%	1.8%	
Euglenophyta	–	–	–	
Pyrrhophyta	–	–	–	

between December 1985 and February 1986 (20–25 μg/l) due to the contribution of Cyanophyta (49.9%), represented by *Microcystis* and *Anabaena*, and also the Chrysophyta contribution (47.3%), represented by *Aulacoseira granulata*. The temporal variation of chlorophyll concentration for all three stations was related to phosphate variation but not with nitrate, indicating that phosphorous is a limiting factor for phytoplankton growth, as demonstrated in many papers (Fig. 9).

High phytoplankton diversity was observed for the Piracicaba (St2) with 72 species, the Tietê (St1) with 59 species, and St3 with 50 species (see Table 1).

Zooplankton composition

The zooplankton community of the Tietê River (St1) and that of the Piracicaba (St2) greatly differed both in abundance and composition, as seen

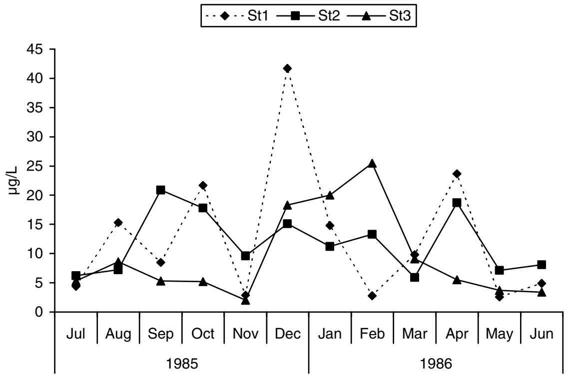

Figure 9. Monthly variation of surface chlorophyll *a* at St1, St2 and St3 of Barra Bonita Reservoir during the period of 1985–1986.

in Tables 3 and 4. The Tietê is richer than the Piracicaba, contributing with 32 species of Rotifera and 17 species of microcrustaceans. The Piracicaba contributed with 25 species of Rotifera and 17 species of microcrustaceans. But at the confluence of both rivers (St3), the number of rotifer species declined to 21 species. However, the microcrustaceans showed a slight increase (18 species).

Another significant difference observed in the three stations refers to the composition of copepods. The Tietê River (St1) was characterized by the presence of two species of Calanoida (*Notodiaptomus iheringi* and *Notodiaptomus conifer*) and four species of Cyclopoida (*Thermocyclops minutus, Thermocyclops decipiens, Mesocyclops ogunnus*, and *Mesocyclops longisetus*). At this site the proportion of Calanoida and Cyclopoida occurrence was similar (44% and 56%, respectively) (Fig. 10). At St2 (Piracicaba River) only Cyclopoida species occurred (*T. minutus, T. decipiens, Mesocyclops meridianus*, and *Metacyclops mendocinus*). At St3, all the species present in St1 and St2 occurred, increasing the richness of Copepoda species. Another special characteristic of this site was the dominance of Calanoida copepods (72%) over Cyclopoida (28%).

As for the cladocerans, all stations were characterized by dominance of *Diaphanosoma birgei, Ceriodaphnia cornuta + C. silvestrii, Bosmina longirostris*, and *Daphnia gessneri. Other species*, such as *Diaphanosoma brevireme, Daphnia ambigua, Moina minuta, Moina micrura, Bosmina hagmanni, and Bosmina tubicen* were represented.

In relation to the rotifer populations whose assemblage and temporal variation at these sites were studied (Matsumura-Tundisi et al., 1990), the Tietê River (St1) presented more richness of species than was found for the Piracicaba River (St2) (see Table 3). Eleven species were specific to the Tietê River (St1): *Brachionus angularis, Brachionus caudatus, Euchlanis dilatata, Euchlanis* sp., *Lecane cornuta, Lecane dorysa, Synchaeta patina, Trichocerca bicristata, Trichocerca elongata, Trichocerca mus*, and *Trichocerca pusilla*. For St2, only three species were specific: *Brachionus* sp., *Gastropus* sp., and *Synchaeta pectinata*. At the confluence of the two rivers (St3), the number of species fell, owing to the elimination of specific species.

Discussion

Plankton composition, species richness, and abundance of organisms in natural lakes are dependent on various factors such as lake origin, trophic state, colonization processes, and presence or absence of toxic substances or pollutants. Besides these factors, in man-made lakes, among them reservoirs, the contribution of tributaries can be a factor of considerable weight. In natural lakes, a patent difference exists in plankton richness between small and large lakes, as demonstrated by Patalas, 1975, with higher richness found in very large lakes. Both in temperate and tropical lakes the mean numbers per lake of rotifers, cladoceran, and copepods species have been recorded as 7, 4, and 2 for Lake Lanao (the Philippines) by Lewis, 1979. In addition, for comparing plankton richness of lakes, it is important to separate limnetic and littoral plankton because samplings at both spatial and temporal scales could affect the composite number of species. In relation to trophic states, according to Maitland (1978) oligotrophic lakes support a high number of phytoplankton and zooplankton species but represented only by a small number of individuals, while eutrophic lakes support small numbers of plankton species, but large numbers of individuals for each species.

The example given in this paper on Barra Bonita Reservoir could be considered as part of a more general picture on spatial heterogeneity in reservoirs and their influence on plankton richness

Table 3. Composition and abundance of Rotifera species at the three localities (St1, St2 and St3) of Barra Bonita Reservoir

	Tietê River (St1)	Piracaba River (St2)	Confluence (St3)
Ascomorpha ovalis	+	+	+
Asplanchna sieboldi	+	+	
Brachionus angularis	+		
Brachionus calyciflorus	+ + +	+	+ + + +
Brachionus caudatus	+		
Brachionus falcatus	+	+	+ + +
Brachionus sp.		+	
Conochiloides coenobasis	+ + +	+	+
Conochilus unicornis	+ + + +	+ + +	+ + + +
Euchlanis dilatata	+		+
Euchlanis sp.	+		
Filinia terminalis	+	+	+
Filinia sp.	+	+	
Gastropus sp.		+	
Hexarthra mira	+	+	+ + +
Keratella americana	+ + +	+	+ + +
Keratella cochlearis	+ + + +	+ + +	+ + +
Keratella lenzi	+	+	+
Keratella tropica	+ + +	+ + +	+ + +
Lecane cornuta	+		
Lecane dorysa	+		
Lecane sp.	+	+	+
Lepadella patella			+
Platyias patulus	+	+	+
Polyarthra vulgaris	+ + +	+ + + +	+ + +
Pompholyx complanata		+	+
Ptygura libera	+	+	+
Synchaeta pectinata		+	+
Synchaeta stylata	+	+ + +	+
Testudinella patina	+		
Trichocerca bicristata	+		
Trichocerca capucina	+	+ + +	+
Trichocerca elongata	+		
Trichocerca mus	+		
Trichocerca pusilla	+		
Trichocerca similis	+	+	+
Trichocerca sp.	+	+	
No. of species	32	25	21

+ – <1000 ind/m^3; + + + – 1000–10 000 ind/m^3; + + + + – >10 000 ind/m^3.

and diversity. Reservoirs are generally more complex than natural lakes, because of their interaction with the watershed and the influx of tributaries (Straskraba, 1997; Straskraba and Tundisi, 1999). Moreover, these reservoirs in southern Brazil are relatively shallow and, being polymictic, are subject to permanent mixing (Tundisi et al., 2004).

In a comparative study carried out in Barra Bonita Reservoir and Lake Dom Helvécio, a nat-

Table 4. Composition and abundance of microcrustacean species at the three localities (St1, St2 and St3) of Barra Bonita Reservoir

	Tietê River (St1)	Piracicaba River (St2)	Confluence (St3)
Cladocera			
Bosmina hagmanni	+	+ +	+ +
Bosmina tubicen		+ +	
Bosmina longirostris	+ + +	+ + + +	+ + +
Bosminopsis deitersi	+ +	+ + +	+ +
Ceriodaphnia cornuta	+ + +	+ + +	+ + + +
Ceriodaphnia silvestrii	+ + +	+ + +	+ + + +
Daphnia ambigua	+	+ +	+
Daphnia gessneri	+ + +	+ + +	+ +
Diaphanosoma birgei	+ + + +	+ + + +	+ + +
Diaphanosoma brevireme	+	+ +	+
Moina minuta	+ +	+ +	+ +
Moina micrura	+ +	+ +	+ +
Copepoda			
Notodiaptomus conifer	+ +		+ +
Notodiaptomus iheringi	+ + +	+	+ + + +
Thermocyclops minutus	+ +	+ + +	+ +
Thermocyclops decipiens	+ +	+ + + +	+ +
Mesocyclops ogunnus	+ +		+ + +
Mesocyclops longisetus	+		+
Mesocyclops meridianus		+ + +	+
Metacyclops mendocinus		+ + +	+
No. of species	17	17	19

+ – <100 ind/m^3; + + – 100–1000 ind/m^3; + + + – 1000–10 000 ind/m^3; + + + + – >10 000 ind/m^3.

ural warm monomictic lake in eastern Brazil, Tundisi and Matsumura-Tundisi (1994) showed that Barra Bonita has a greater number of limnetic zooplankton species (37 species: 20 Rotifera, 8 Cladocera, and 9 Copepoda) than does Lake Dom Helvécio (16 species: 6 Rotifera, 5 Cladocera, and 5 Copepoda). Despite the strong vertical gradients in water temperature and in the other physical and chemical variables, Dom Helvécio shows a less diverse community, probably because of its stability (8 months of thermal and chemical stratification). In another fifteen lakes of the same region, Tundisi et al. (1997) registered low plankton richness and, principally, low species numbers as well as a few abundance of rotifers in relation to microcrustaceans. In only a few lakes of this region a large abundance of rotifers (80–90% of total zooplankton) occurred. Barra Bonita, being a polymictic reservoir, is subject to permanent vertical mixing, and its 114 tributaries, both small (2–3 m^3/s discharge) and large (10–15 m^3/s), probably account for its higher diversity and species richness.

Changes in the plankton composition and diversity are observed frequently in reservoirs as eutrophication proceeds and planktonic species are substituted by other species adapted to the new conditions. Such changes in the last 20 years in the zooplankton in Barra Bonita Reservoir were demonstrated in a recent paper by Matsumura-Tundisi & Tundisi (2003). Despite these changes, species richness remained high. But it must also be taken into account that the sediment can contain a strong diversity component produced by resting zooplankton eggs. Thus, species richness at each station may also be influenced by resting egg development during periods of favorable water quality for each species. Development of and recruitment from resting eggs has been pointed out by Matsumura-Tundisi & Tundisi (2003) as a cause of shifts in species composition but not in

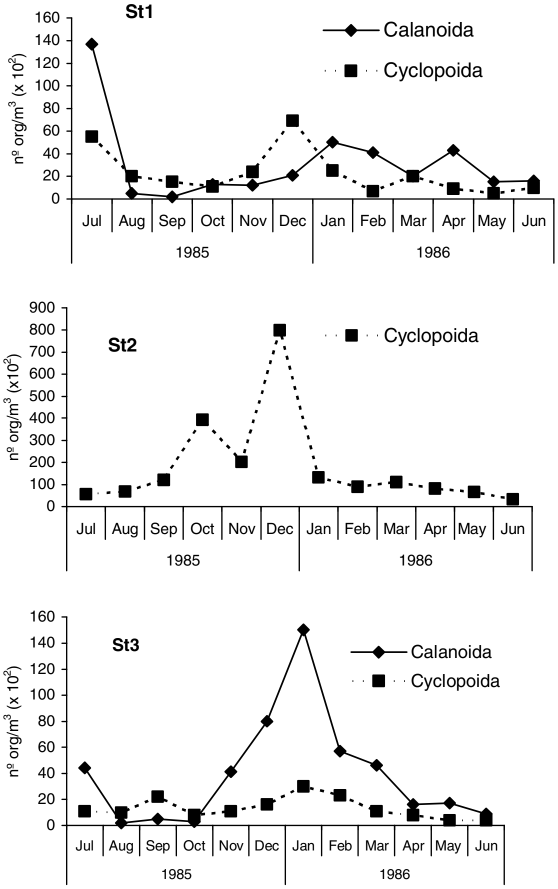

Figure 10. Abundance of Calanoida and Cyclopoida copepods at the three stations of Barra Bonita Reservoir.

species richness, as has been verified in a shallow reservoir (Lobo/Broa Reservoir) by Rietzler et al. (2002).

Barra Bonita Reservoir, besides being a dynamic system, has strong gradients in the limnological conditions and longitudinal processes along its two main tributaries: the Tietê and Piracicaba rivers. Spatially and temporally changing states promote gradients of conditions that are reflected in phytoplankton and zooplankton composition. In addition, physical and chemical changes interfere strongly with the dynamics of planktonic communities.

In this paper, it was shown that a very distinct pattern of planktonic community composition followed horizontal gradients. In reservoirs, these gradients are relatively common, as has already been shown extensively for other artificial aquatic ecosystems (Armengol et al., 1999; Straskraba, 1997; Straskraba & Tundisi, 1999).

The differing physical and chemical conditions in Barra Bonita Reservoir at each of the sampling stations is due to differential patterns of river circulation and flow. The gradients in this reservoir are typically controlled by mesoscale structures of 1.0–20.0 km (Tundisi et al., unpublished results). The existence of patches of phyto- and zooplankton, each with differing composition and properties, reflects an input of external energy consistent with the contemporaneous disequilibrium hypothesis set forth by Margalef (1967) and Reynolds (1997). According to this hypothesis the 'pelagic environment resembles a mosaic of microhabitats' (Legendre & Demers, 1984) where different species have distinct requirements resulting from environmental condition gradients. Margalef (1991) considers that the input of external energy breaks the regularity of the systems, leading them to decompose into horizontally heterogeneous units. The distribution of each 'cell' is related to the external energy input. In the Piracicaba and Tietê rivers, this external energy depends on the climatological and hydrological cycle, and on the input of nutrient and toxic substances promoting horizontal gradients. The many tributaries at Barra Bonita Reservoir promote a strong horizontal heterogeneity, increasing the horizontal discontinuities. Each tributary discharging into the reservoir produces a frontier of water masses which increases discontinuities and, therefore, high diversity of planktonic organisms. Thus, horizontal mixing and vertical instability augment diversity, which therefore boosts planktonic community responses over short periods and relatively small spatial scales.

The dominance of rotifers at all stations shows a pattern characteristic of reservoirs as has also been pointed out by Armengol et al. (1999). The rotifer dominance at Barra Bonita Reservoir has already been demonstrated by Matsumura-Tundisi et al. (1990) and is a consequence of an unstable and dynamic environment favoring the growth of *r*-strategists such as rotifers. As for rotifer diversity, it was higher for the Tietê River (St1) than for the Piracicaba (St2). However, for other groups such as cladocerans and copepods, there was no difference in number of limnectic species at the three stations. Station 2 is also characterized by the absence of Calanoida copepods and the presence of large-size species of Cyclopoida, e.g., *Metacyclops mendocinus* and *Mesocyclops meridi-*

anus. On the other hand, St1 (the Tietê) was characterized by the presence of *Notodiaptomus iheringi*, the smallest Calanoida species, and *Mesocyclops ogunnus*, smaller than any species of Cyclopoida present in the Piracicaba River (St2). The Tietê River is more eutrophic than the Piracicaba and the occurrence of Cyanophyta is more frequent and abundant. In this kind of environment, the zooplankton structure is composed of small-size organisms such as rotifers and small species of cladocerans and copepods that present a short-life cycle with energy spent on reproduction rather than growth. As shown by Rietzler et al. (2002), Notodiaptomus *iheringi* is an indicator of eutrophic systems, being a substitute of *Argyrodiaptomus furcatus*, a large species occurring in environments without Cyanophyta growth. *Notodiaptomus iheringi* feeds upon bacteria and free-floating small particles of detritus and phytoplankton < 20 μm size. Matsumura-Tundisi et al. (2002) related the zooplankton diversity in two localities of Billings Reservoir, a very eutrophic reservoir in the City of São Paulo, with periodic occurrence of Cyanophyta blooms. In the locality with frequent occurrence of Cyanophyta blooms the zooplankton structure was composed of small-size organisms and showed low diversity. In the other locality, without Cyanophyta blooms but presenting several species of Chlorophyta, zooplankton was composed by large species and showed high species richness. Thus, the zooplankton composition depends largely on phytoplankton composition.

In conclusion it seems clear from these results that, superimposed upon the eutrophication processes, horizontal gradients and vertical instability are strong factors enhancing plankton richness at Barra Bonita Reservoir, which can be an example of a more general pattern in other reservoirs showing the same characteristics. The high richness of planktonic species shown by this reservoir was probably due to its strong horizontal gradients which are promoted by the many tributaries flowing into the reservoir. Thus, horizontal mixing probably favors exploitation of new ecological niches by phytoplankton and zooplankton. In addition, vertical instability and horizontal variability may promote diversity, therefore enhancing responses of the planktonic community over short periods and at relatively small spatial scales. As stated by Tundisi & Matsumura-Tundisi (1994), changing temporal patterns of turbulence and intermediate disturbance factors are probably the forcing functions that provide Barra Bonita Reservoir with high richness of species in the pelagic environment.

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