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Temporal changes in the phytoplankton community structure in a tropical and eutrophic reservoir (Barra Bonita, S.P.—Brazil)

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A study of the temporal changes in the phytoplankton community structure in the eutrophic Barra Bonita Reservoir (São Paulo State, Brazil) was carried out during 30 days (samples were taken daily for 10 days and, thereafter, on every other day) in two distinct seasonal periods (dry and rainy seasons). Monthly sampling occurred in the period July 1993 to June 1994. One hundred and thirty-one taxa were registered. A greater diversity (112 taxa) was observed in winter than in summer (79 taxa). In the monthly analysis, 90 taxa were identified. The highest values for species diversity and richness were observed in July 1993 and the lowest in April 1994. The phytoplankton dynamics in this system are apparently dominated by competitive exclusion and disturbance. Within the seasonal cycle, the phytoplankton community structure was determined by underwater light availability, mixing by wind, precipitation and the consequent loss of Cyanophyceae biomass in the upper waters by spillage, and nutrient (principally phosphorus) inputs from anthropogenic sources. The environmental variability in this polymictic system may be favouring a phytoplankton community in equilibrium, with dominance alterations of Bacillariophyceae biomass (Aulacoseira granulata), R-strategists, and Cyanophyceae biomass (Microcystis aeruginosa), S-strategists. Short periods (i.e. 10 days) in non-equilibrium conditions with increased species diversity and coexistence can perhaps be explained by the intermediate disturbance hypothesis.

INTRODUCTION

Temporal variability in the structure and function of a phytoplankton community is of fundamental importance to aquatic system metabolism. Aquatic environments are subject to high temporal variability, with frequent reorganization of relative abundance and phytoplankton species composition, as a result of interaction between physical, chemical and biological variables. The causes of these sequences have been explained not only by the equilibrium approach (which permits the coexistence of species limited by different resources), but also by the non-equilibrium approach (which accepts the frequency of environmental variability, allowing species that share the same resources to coexist). Nowadays, the Intermediate Disturbance Hypothesis (IDH; proposed by Connell (Connell, 1978) and, as applied to phytoplankton, critically discussed by Sommer *et al.* (Sommer *et al.*, 1993)], which tries to explain the 'Paradox of Plankton' (Hutchinson, 1961), has been used because it approaches two aspects of the same theory. Reynolds states that this hypothesis can represent a expression of interactions between the progressive internal movement of the community towards the organization and maintenance of an energetic steady-state, and the stochastic environmental variability imposed on biological systems (Reynolds, 1993).

Most pelagic systems are extremely sensitive to environmental changes, rendering sub-aquatic conditions unstable and advantageous habitat features discontinuous for different species. This is another way of saying that community organization is usually fragile and primitive, because the system is frequently disorganized (Reynolds, 1997).

Changes in phytoplankton community structure (diversity, dominance and biomass) driven by perturbations caused by turbulence and environmental variability, have been emphasized by Harris (Harris, 1978, 1980, 1983, 1986). In general, researchers on phytoplankton community dynamics consider the physical instability of the water column to be the main factor controlling species composition changes.

The species composition of phytoplankton is influenced by several biotic and abiotic factors: water mixing, underwater light, temperature, nutrients, toxic substances, heterotrophic micro-organisms, pathogenic agents, parasites and herbivores (Reynolds, 1987). In reservoirs there are additional factors owing to hydrodynamic differences arising from location, morphometry and the main function of a given system, which may be considered as 'pulses' in the hydrological cycle: precipitation governs dam operation and theoretical water retention times in the system, generating 'pulses' of material and nutrients in suspension, material cycling and biomass losses (Calijuri, 1999).

In the eutrophic Barra Bonita reservoir, where mixing conditions are prevalent and the metabolism is governed by wind, underwater solar radiation, precipitation, outflow and theoretical water retention time, we studied temporal changes in the hydrological cycle and the phytoplankton community structure, in order to characterize them during not only short, well-defined periods but also in the seasonal cycle so as to evaluate the role of 'pulses' on the organisms survival strategy. The study also contributes to our understanding of tropical reservoir biodiversity.

Description of the study site

Barra Bonita Reservoir is the first of a series of six large reservoirs in the middle Tietê River, constructed to produce hydroelectricity. It is located at 22°29′S, 48°34′W, at an altitude of 430 m above sea level (Figure 1).

This reservoir is located in the most populous and developed region of the interior of São Paulo State, within the Tietê Valley in a section between the Pirapora and Barra Bonita dams. The reservoir was formed by damming the Tietê and Piracicaba rivers, and is also fed by several other tributaries. It is located in a transitional region between tropical and subtropical climates where seasonal weather changes are not very pronounced, except for summer (rain) and winter (drought). During January, the hottest month, the average temperature is 27°C. In the coldest month (July), the temperature averages 18°C. The predominant rock in the region is basalt. The Barra Bonita drainage basin is predominantly purple latosoil. Dominant vegetation in the region is a sugar cane monoculture (Calijuri, 1988).

The eutrophic Barra Bonita Reservoir is a polymictic ecosystem with an average depth of about 10 m. The main external factors are rainfall, wind, flushing rate and theoretical water retention time, which on average varies from 30 days to 6 months. The mixing regime is mainly related to the effects of wind, with alternating periods of turbulence and short-term stratification. Most nutrient input occurs during the rainy season, as demonstrated by Calijuri (Calijuri, 1988, 1999).

METHOD

To study temporal changes in the phytoplankton community in Barra Bonita Reservoir, a 30 day period of intensive sampling was undertaken. Samples integrated for the euphotic zone were taken on each of 10 consecutive days and on every other day thereafter in the months of July 1993 and January and February 1994. In addition, monthly samples were collected between July 1993 and June 1994, at Station I, in the deepest part of the reservoir (Figure 1).

Meteorological data at Barra Bonita Reservoir (wind, air temperature and pluviometric precipitation) and outflow data, used to calculate theoretical water retention time during the collection periods, were made available by the CESP (Companhia Energética de São Paulo).

The underwater photosynthetic available radiation (PAR) was measured with a PAR Quantum Radiometer (Licor Instruments) and the water transparency was measured with a Secchi disk. The vertical attenuation coefficient was determined according to Kirk (Kirk, 1986). The thermal structure of the water column was determined by a multisensor (Horiba U-10). The Brunt Väisälä frequency (radians.s^{-1}), used as a measure of water column stability, was calculated from temperature and density profiles, following Reynolds *et al.* (Reynolds *et al.*, 1984).

In the laboratory, the physical and chemical parameters investigated on each sampling day were pH, conductivity, alkalinity and nutrients. Of these, the first three were determined according to Mackereth *et al.* (Mackereth *et al.*, 1978). Ammonium, total dissolved and inorganic phosphate, nitrate, nitrite and reactive silicate, were respectively determined by the following methods (Koroleff, 1976; Strickland and Parsons, 1960; Mackereth *et al.*, 1978; Golterman *et al.*, 1978). Total organic nitrogen was determined according to Golterman *et al.* (Golterman *et al.*, 1978) and total organic phosphorous was measured according to the APHA (American Public Health Association, 1995).

Chlorophyll *a* concentrations were determined according to Nusch (Nusch, 1980). Phytoplankton samples for

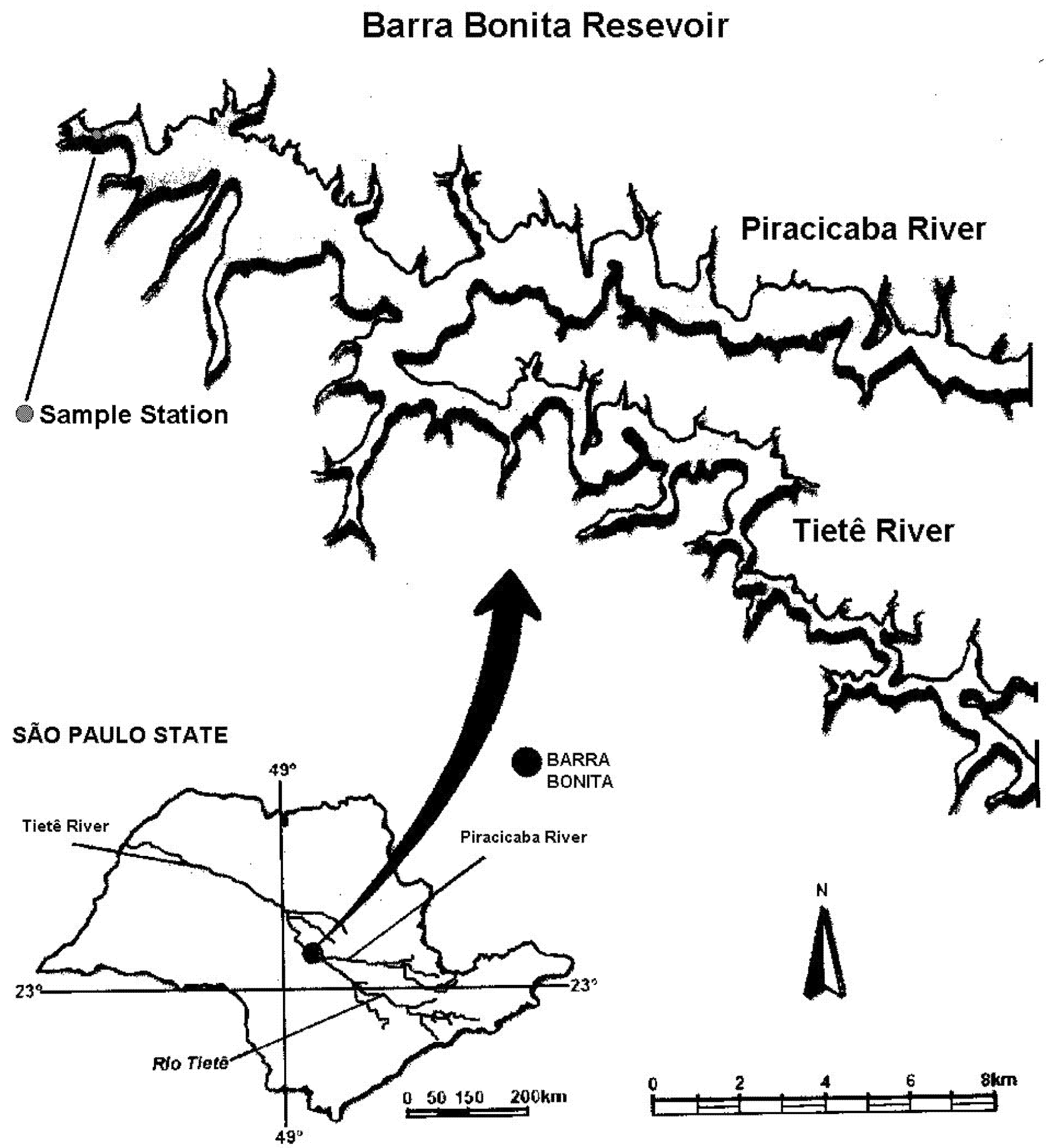

Fig. 1. Localization of sampling station in Barra Bonita Reservoir in São Paulo State, Brazil.

counting were fixed with Lugol's preservative. Organism identifications were made under an inverted microscope (Zeiss), and counting was by Utermöhl's method (Utermöhl, 1958). The sedimented sample volume varied from 2 to 10 ml, depending on organism concentration. Sedimentation time was at least 3 h (Wetzel and Likens, 1991). The individuals (cells, colonies, cenobios, filaments) were enumerated in random fields; about 100 individuals of the most frequent species were counted, with less than 20% error, at a confidence limit of 95% (Lund *et al.*, 1958). Phytoplanktonic organism density was calculated using criteria reported previously (American Public Health Association, 1995). Relative abundance was estimated using Lobo and Leighton's criteria (Lobo and Leighton, 1986). The specific diversity calculation was based on Shannon and Weaver (Shannon and Weaver, 1949).

Specific dominance, as defined by Simpson (Simpson, 1949), and richness of species were evaluated based on the number of species found during the study. Biovolume determinations for the predominant species in the sample were made using geometric formulae (Wetzel and Likens, 1991).

RESULTS

Figure 2 presents mean air temperature (°C) and wind force (m.s^{-1}) for the region of Barra Bonita Reservoir from July 1993 to June 1994. During the hottest month (January 1994), the average temperature was 27.5°C; during the coldest month (June 1994) it was below 15°C. According to Calijuri and Dos Santos, July 1993 daily temperatures were between 11°C and 21°C; in summer (January 1994), daily temperature averages varied between 23°C and 31°C (Calijuri and Dos Santos, 1996). High wind intensities occurred during the study year, especially during the second half of 1993.

The longest theoretical water retention times were observed during the dry period. In contrast, during the rainy period, which was characterized by increased outflows and no need to store water, the water retention time varied from approximately 35 to 84 days (Figure 3).

The wind in this system is an important external factor which, together with precipitation, is responsible for the reservoir's polymictic behaviour during most of the year. Figures 4, 5 and 6 illustrate temperature isopleths and Brunt–Väisälä frequency in Barra Bonita Reservoir during the research periods. In the rainy season, when the temperature's gradient splits the system vertically, turbine effects and spill act separately on the stored volume. While spills remove excess volume from the surface, the turbines cause an outflow of deep waters, which are denser and richer in nutrients. This reservoir does not develop persistent thermal stratification. The higher Brunt–Väisälä frequencies occurred during the rainy season.

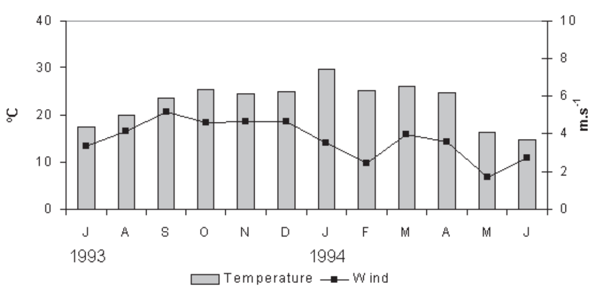

Fig. 2. Mean air temperature (°C) and wind force (m s^{-1}) values for the region of Barra Bonita reservoir, in the period from July 1993 to June 1994.

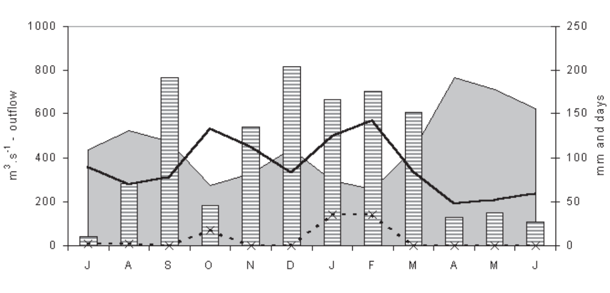

Fig. 3. Monthly values for precipitation (mm), monthly averages for outflow and spillage (m^3 s^{-1}), and theoretical water retention time (days) in Barra Bonita reservoir, in the period from July 1993 to June 1994.

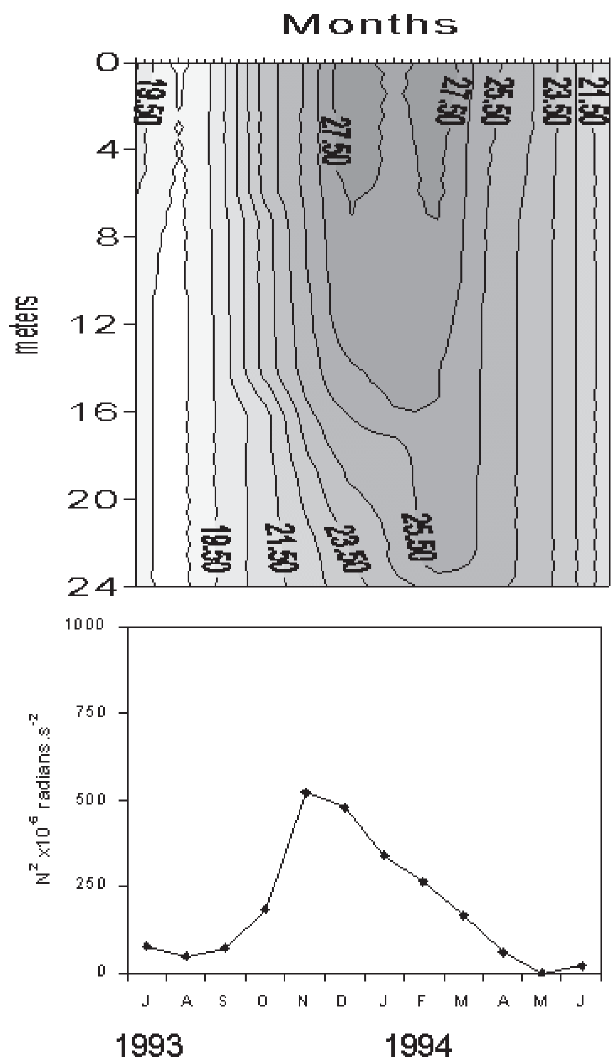

Fig. 4. Temperature (°C) isopleths and Brunt–Väisälä frequency [(radians s^{-1})^2 10^{-6}] in Barra Bonita reservoir in the period of July 1993 from June 1994.

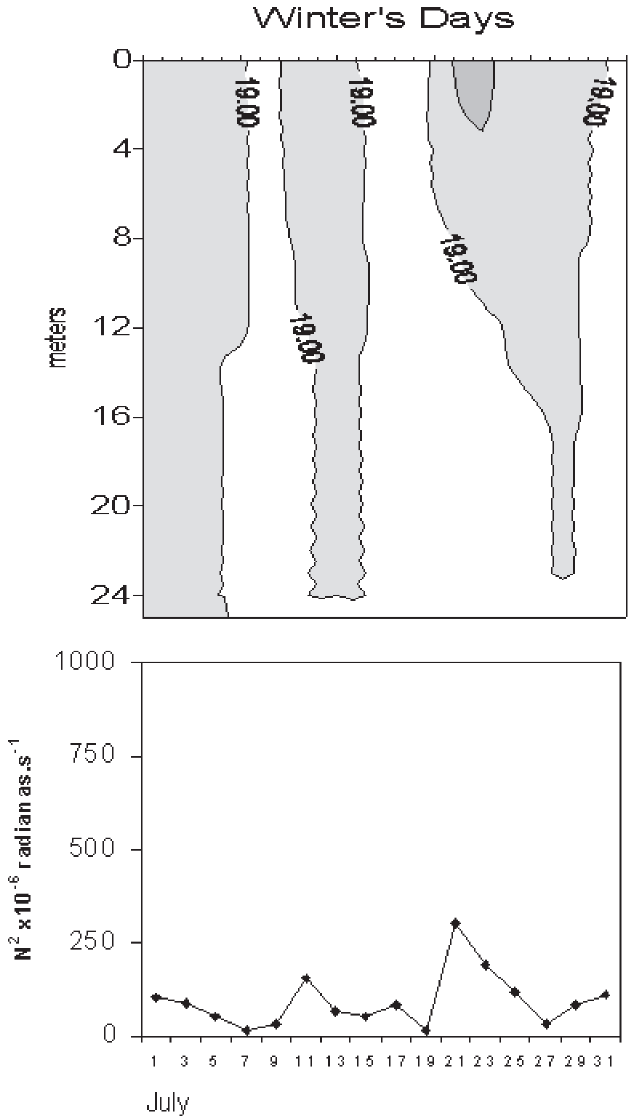

Fig. 5. Temperature (°C) isopleths and Brunt–Väisälä frequency [(radians $s^{-1})^2$ 10^{-6}] in Barra Bonita reservoir in the period from July 1 to 31, 1993 (winter).

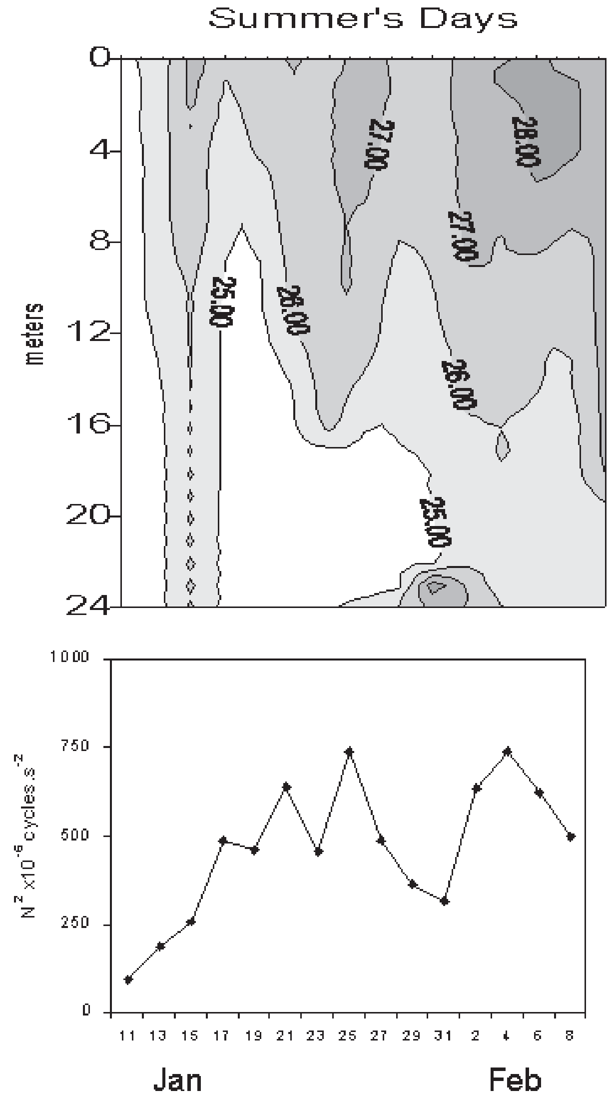

Fig. 6. Temperature (°C) isopleths and Brunt–Väisälä frequency [(radians $s^{-1})^2$ 10^{-6}] in Barra Bonita reservoir in the period from January 11 to February 8, 1994 (summer).

Figures 7 and 8 present the vertical attenuation coefficient (K) as well as euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values for the periods under study. In the monthly variations, in the period from July 1993 to June 1994, the deepest Z_{eu} and the lowest vertical attenuation coefficient were observed in May 1994, and the lowest Z_{eu} was seen in April 1994 (Figure 7). These parameters varied less during winter (Figure 8A) than in summer (Figure 8B). With summer precipitation, a substantial inflow of suspended material occurred, in large part due to soil uses in the hydrographic basin. These pulses of suspended material associated with temporal microstratifications are reflected in a more heterogeneous water column (Calijuri, 1988), with Z_{eu} and Z_{eu}/Z_{mix} varying significantly during the period from January 11 to February 8,1994 (Figure 8B). The differences in the Z_{eu}/Z_{mix} ratio characterize light availability.

Tables I, II and III show total and dissolved nutrient concentrations observed during the research periods. The highest nitrate concentration was observed in January 1994 and the highest nitrite was seen in October 1993. Silicate concentrations found during the rainy season were less than those observed during the study months and those in winter (July 1993). The highest concentration of total phosphorus and total dissolved phosphate was observed in April 1994. Lowest inorganic phosphate

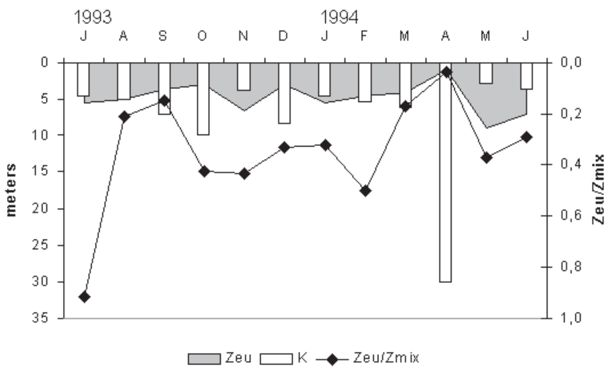

Fig. 7. Vertical attenuation coefficient (*K*), euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values in Barra Bonita reservoir in the period from July 1993 to June 1994.

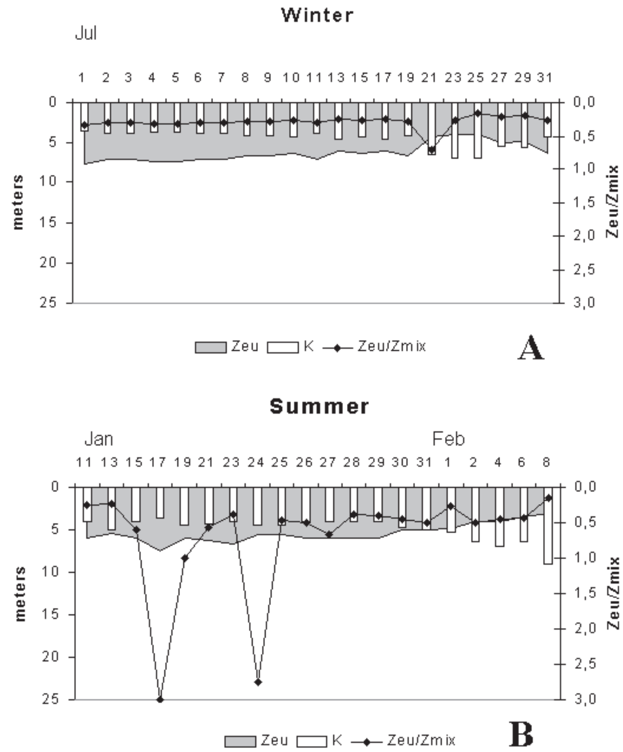

Fig. 8. Vertical attenuation coefficient (*K*), euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values in Barra Bonita reservoir in the periods from July 1 to 31, 1993 (**A**) and January 11 to February 8,1994 (**B**).

concentration was found during the rainy season (January 1994). In the last few years, there has been an abundant nutrient increase in Barra Bonita Reservoir, indicating an accelerating eutrophication process in this system. Phosphorus concentrations in the water are the result of industrial, domestic and agricultural area inputs, in addition to sediment liberation. Water retention time in this reservoir is decisive in nutrient retention and biomass production. The same Tables also show that the highest chlorophyll *a* values occurred in April 1994 and the lowest were seen in March 1994. High chlorophyll *a* concentrations were observed at the end of July 1993.

During the study periods, 131 taxa were identified, distributed in nine taxonomic classes: Cyanophyceae (19), Chlorophyceae (53), Bacillariophyceae (26), Dinophyceae (1), Euglenophyceae (12), Zygnemaphyceae (12), Cryptophyceae (2), Xanthophyceae (2) and Chrysophyceae (4). Figures 9 and 10 (A and B) show the density variation of phytoplankton groups in this reservoir. In the monthly sampling (Figure 9) extending from July 1993 to June 1994, April 1994 presented with the highest organism

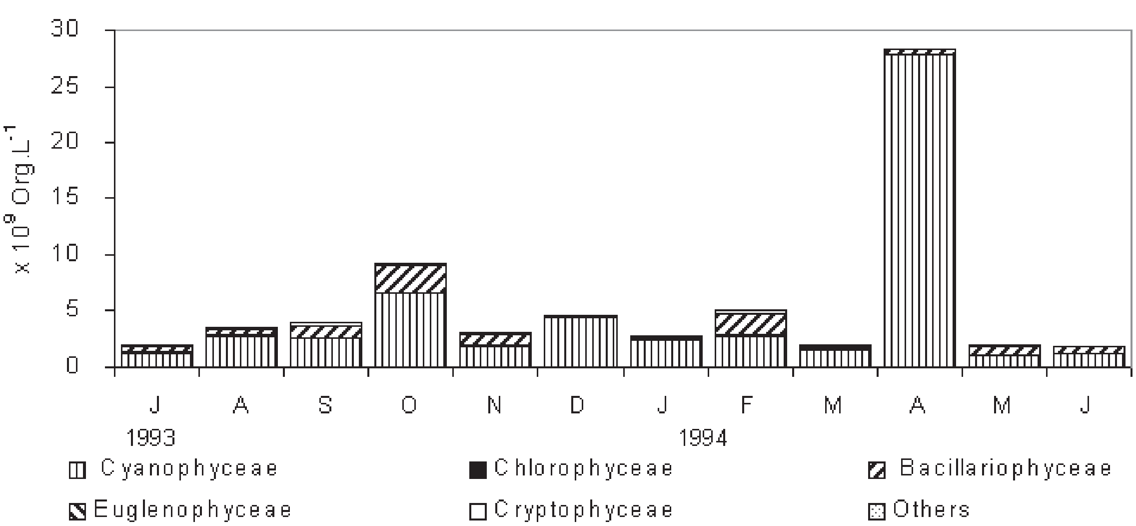

Fig. 9. Density variation of phytoplankton groups ($\times 10^9$ organisms l^{-1}) in Barra Bonita reservoir in the period from July 1993 to June 1994.

Table I: Total and dissolved nutrients, and chlorophyll a concentrations, in Barra Bonita reservoir in the period from July 1993 to June 1994

Months	Chl *a* ($\mu g\ L^{-1}$)	Reactive silicate ($mg\ L^{-1}$)	Total P ($\mu g\ L^{-1}$)	Total diss. PO_4 ($\mu g\ L^{-1}$)	Inorganic PO_4 ($\mu g\ L^{-1}$)	Total Organic N ($\mu g\ L^{-1}$)	Nitrite ($\mu g\ L^{-1}$)	Nitrate ($\mu g\ L^{-1}$)	NH_4 ($\mu g\ L^{-1}$)
July	26.9	4.4	47.1	13.4	6.5	8402.5	5.1	1210.4	2.2
Aug.	12.2	4.1	22.6	4.1	2.5	2724.8	19.9	1224.7	7.4
Set.	73.9	2.7	131.3	13.0	1.3	2761.8	82.5	848.7	201.8
Oct	148.6	3.7	58.5	14.2	5.6	9799.2	160.3	1550.7	72.3
Nov.	15.4	2.7	83.7	12.7	6.3	7558.0	56.2	642.1	57.7
Dec.	108.8	3.3	138.4	6.7	3.2	7602.0	82.0	650.1	28.7
Jan.	34.2	1.2	59.9	6.0	5.2	3662.0	33.6	2243.6	10.1
Feb.	24.9	4.1	66.8	15.6	1.2	860.0	16.5	735.5	24.4
Mar.	7.4	6.7	64.0	22.4	11.2	644.0	0.6	704.2	19.9
Apr.	438.0	7.8	307.1	36.4	19.4	8478.0	10.0	604.6	38.5
May.	14.3	5.2	21.8	11.8	6.1	670.0	2.0	748.0	7.5
June.	9.8	6.9	31.4	15.7	10.2	564.0	2.7	745.8	6.7

Chl *a*, chlorophyll *a*; P, phosphorus; diss. PO_4, dissolved phosphate; N, nitrogen; NH_4, ammonium.

Table II: Total and dissolved nutrients, and chlorophyll a concentrations, in Barra Bonita reservoir in the period from July 1 to 31, 1993

Months	Chl *a* ($\mu g\ L^{-1}$)	Reactive silicate ($mg\ L^{-1}$)	Total P ($\mu g\ L^{-1}$)	Total diss. PO_4 ($\mu g\ L^{-1}$)	Inorganic PO_4 ($\mu g\ L^{-1}$)	Total Organic N ($\mu g\ L^{-1}$)	Nitrite ($\mu g\ L^{-1}$)	Nitrate ($\mu g\ L^{-1}$)	NH_4 ($\mu g\ L^{-1}$)
July 1	12.2	3.6	43.0	25.2	15.2	868.0	3.3	1072.0	9.8
July 2		4.2	34.5	22.1	15.9	1143.0	2.7	1093.8	2.3
July 3	13.9	4.0	69.2	19.9	15.9	868.0	2.0	1220.2	7.9
July 4		3.8	34.1	18.8	13.1	1051.0	1.7	902.3	11.7
July 5	17.5	4.9	29.5	17.8	13.8	1280.0	1.7	730.5	1.2
July 6		4.6	26.0	20.2	13.8	1097.0	2.9	1030.8	3.0
July 7	7.0	4.4	29.5	21.7	12.9	914.0	3.3	732.3	4.2
July 8		3.8	65.4	24.8	16.0	914.0	9.5	1423.2	34.2
July 9	13.9	4.3	35.3	23.0	20.7	823.0	25.8	1290.8	76.7
July 10		3.2	34.1	20.8	18.5	1554.0	41.2	897.3	56.1
July 11	49.4	4.2	43.9	18.4	9.2	3998.0	49.6	1650.8	32.4
July 13	48.4	4.6	64.1	17.9	10.1	4630.0	49.6	1471.7	7.9
July 15	11.1	4.8	44.2	21.5	15.1	2047.5	5.6	2022.6	3.3
July 17	8.3	4.1	33.6	16.2	11.6	4010.0	2.1	1675.5	0.7
July 19	26.9	4.0	37.0	14.1	6.4	4670.0	3.4	1482.7	1.2
July 21	72.5	4.4	47.1	13.4	6.5	8402.5	5.1	1210.4	2.2
July 23	161.9	4.0	41.1	11.0	3.8	16,642.5	5.3	1141.7	0.8
July 25	138.2	4.1	30.9	8.7	4.0	8987.5	6.9	1378.6	5.1
July 27	77.9	4.2	32.5	20.9	4.8	3857.5	5.2	1331.6	5.9
July 29	187.3	4.3	89.3	9.5	4.0	6543.3	4.1	1328.3	7.0
July 31	47.4	3.9	29.3	10.4	1.9	4,764.0	4.1	1314.3	10.0

Chl *a*, chlorophyll *a*; P, phosphorus; diss. PO_4, dissolved phosphate; N, nitrogen; NH_4, ammonium.

Table III: Total and dissolved nutrients, and chlorophyll a concentrations, in Barra Bonita reservoir in the period from January 11 to February 8, 1994

Months	Chl *a* (µg L^{-1})	Reactive silicate (mg L^{-1})	Total P (µg L^{-1})	Total diss. PO_4 (µg L^{-1})	Inorganic PO_4 (µg L^{-1})	Total Organic N (µg L^{-1})	Nitrite (µg L^{-1})	Nitrate (µg L^{-1})	NH_4 (µg L^{-1})
Jan 11	43.7	1.1	101.0	11.0	3.6	2926.4	34.5	1894.5	10.4
Jan 13	43.5	1.2	59.9	6.0	5.2	2212.8	33.6	2243.6	10.1
Jan 15	36.4	0.8	75.9	12.9	4.1	2459.8	32.5	654.1	18.4
Jan 17	27.9	0.8	80.6	11.0	4.1	3667.2	34.1	656.1	10.1
Jan 19	34.2	1.3	73.3	7.2	4.1	2212.8	36.8	652.1	14.6
Jan 21	41.4	0.5	162.8	10.3	3.1	3191.8	51.0	657.7	19.8
Jan 23	21.5	0.5	49.6	9.5	2.4	1600.2	45.6	648.8	24.7
Jan 24		1.2	67.8	6.5	0.0	640.0	40.0	657.4	12.0
Jan 25	30.5	1.2	66.1	4.9	0.0	2240.0	33.4	658.1	6.9
Jan 26		1.1	64.5	5.2	0.0	1509.0	42.2	657.1	19.3
Jan 27	16.2	1.1	123.9	5.4	0.0	1554.0	33.6	656.2	15.3
Jan 28		1.2	183.3	5.5	1.2	2835.0	25.1	655.4	11.4
Jan 29	16.9	1.1	101.9	5.0	0.5	1646.0	20.1	650.9	7.5
Jan 30		1.0	20.6	4.4	0.0	1208.0	15.2	646.4	3.7
Jan 31	38.5	1.1	12.8	3.1	0.0	1463.0	23.9	651.4	4.4
Feb 1		1.1	64.1	6.4	0.0	1143.0	26.1	650.1	6.2
Feb 2	58.2	0.9	73.7	3.3	0.0	1326.0	37.6	649.4	22.9
Feb 4	75.5	0.8	150.0	10.7	1.8	2368.4	31.8	656.3	10.3
Feb 6	75.7	0.9	133.9	9.6	1.1	2505.6	39.2	656.0	14.8
Feb 8	74.8	1.0	80.8	9.1	1.4	4892.2	42.5	650.4	27.6

Chl *a*, chlorophyll *a*; P, phosphorus; diss. PO_4, dissolved phosphate; N, nitrogen; NH_4, ammonium.

density, followed by October 1993; the lowest was observed in July 1993. In winter 1993 (Figure 10A), density values were between 1.8×10^9 organisms l^{-1} (19 July) and 13.8×10^9 organisms l^{-1} (5 July); in summer 1994 (Figure 10B), values varied from 2.8×10^9 organisms l^{-1} (19 January) to 14.2×10^9 organisms l^{-1} (25 January).

The variations in relative abundance of the most frequent species in the reservoir are presented in Figures 11 and 12 (A and B). The greatest relative abundance, both seasonally and daily, was of *Microcystis aeruginosa* free cells.

Winter 1993 showed greater species richness (112 taxa) than summer (79 taxa). During the intensive winter study, all taxonomic classes presented a higher number of species, taking into account that, during the first 11 days, the relative abundances of Chlorophyceae, Cryptophyceae, Bacillariophyceae and Cyanophyceae changed. On July 1, the species that presented the greatest relative abundance was *Microcystis aeruginosa* free cells. On July 2, *Microcystis aeruginosa* free cells were substituted by *Monoraphidium tortile*. On July 3, 4 and 5 Chlorophyceae still predominated, but on July 3 *Chlorella vulgaris* was the most frequent. *Cryptomonas tetrapyrenoidosa* and *Aulacoseira granulata granulata* predominated on July 6 and 7. *Chlamydomonas* spp predominated on July 8, and *Cyclotella stelligera* on July 9. From July 13 to July 31, *Microcystis aeruginosa* free cells dominated (Figure 12A) and throughout the summer period (Figure 12B), they were again dominant.

Although Cyanophyceae (*Microcystis aeruginosa* free cells) was the taxonomic class presenting greater relative abundance, the Bacillariophyceae (*Aulacoseira granulata granulata*) was the taxonomic class contributing most to biovolume values (mm^3 l^{-1}), in Barra Bonita Reservoir, during our temporal series (Figures 13, 14A,B).

Figures 15 and 16A,B present the richness, diversity and dominant species variation in the phytoplankton community. In the monthly analysis (Figure 15), 90 taxa were identified, the highest richness and species diversity values being observed in July 1993 and the lowest, in April 1994. February 1994 presented the lowest dominance

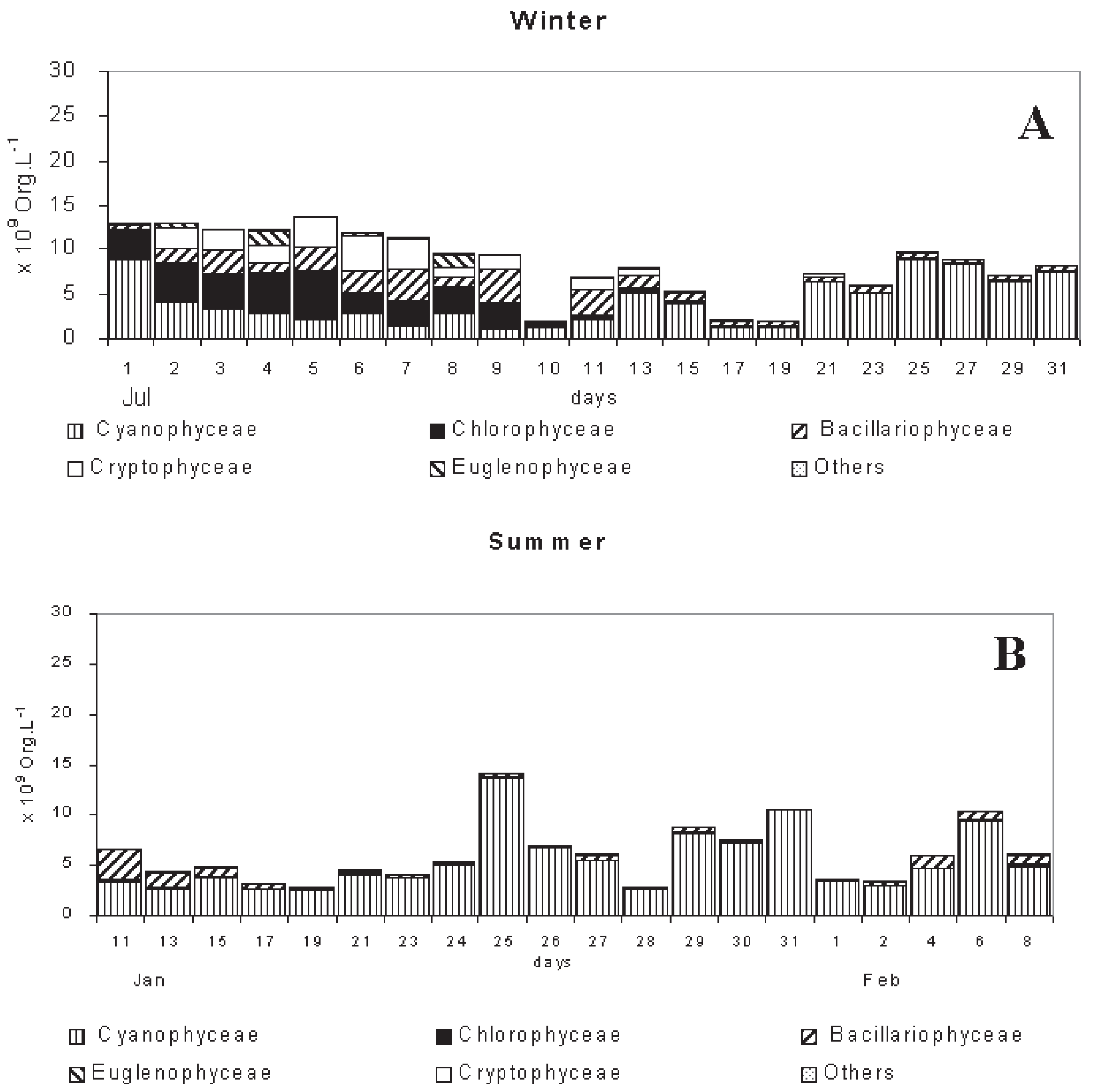

Fig. 10. Density variation of phytoplankton groups ($\times 10^9$ organisms l^{-1}) in Barra Bonita reservoir in the periods from July 1 to 31, 1993 (**A**) and January 11 to February 8, 1994 (**B**).

value. Winter (Figure 16A) was characterized by greater instability with greater species diversity. In contrast, summer (Figure 16B) was characterized by a lower species diversity and the presence of *Microcystis aeruginosa*, the dominant organism.

DISCUSSION

Recent papers have summarized information on phytoplankton composition and environmental factors and proposed general patterns for lakes and reservoirs of different trophic status (Reynolds *et al.*, 2000). High phytoplankton diversity in many eutrophic freshwater systems contradicts the competitive exclusion principle (Hardin, 1960). This dilemma, known as the 'paradox of the plankton' (Hutchinson, 1961) has been explained by non-equilibrium fluctuation of the environment. The intermediate disturbance hypothesis (Connell, 1978), adapted to phytoplankton ecology by Reynolds (Reynolds, 1988a), has suggested interpreting seasonal succession as the

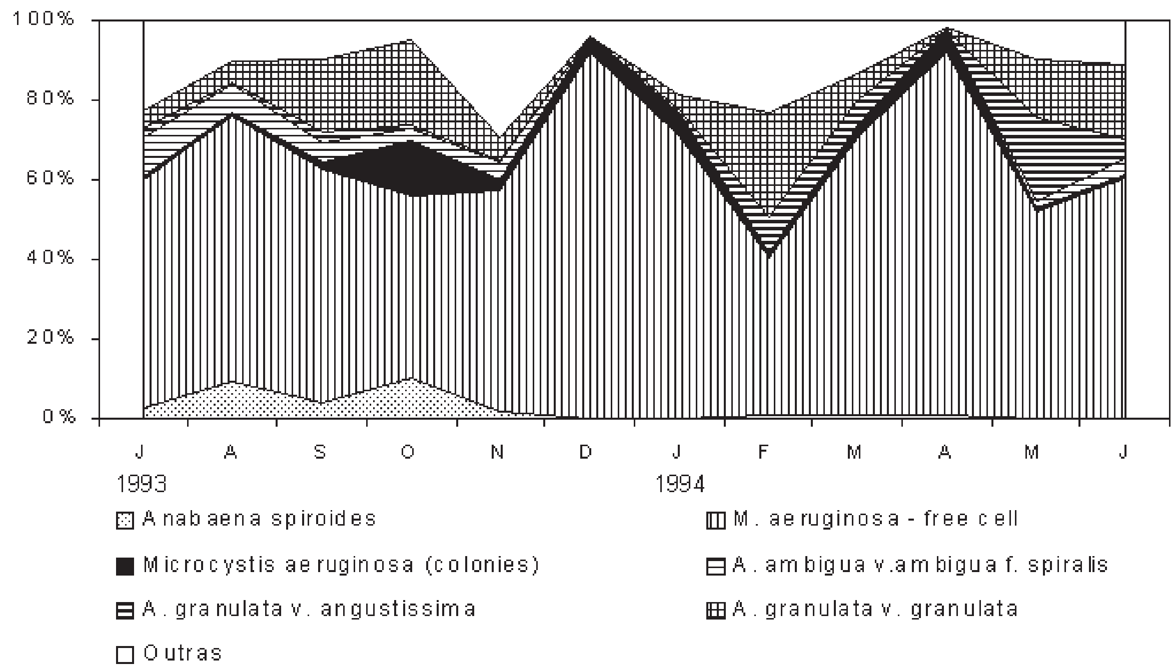

Fig. 11. Relative abundance variation (%) of the most frequent phytoplankton species in Barra Bonita reservoir in the period from July 1993 to June 1994.

interaction between true successional development and intermediate disturbance.

Aquatic ecosystems are subject to spatial and temporal variability which results in a high degree of uncertainty in relation to phytoplankton assemblages. On a smaller scale, a successful species, for Reynolds (Reynolds, 1998), has the physiological flexibility to accommodate the range of environmental variability to which it is exposed or to survive those phases when physiological tolerance limits are temporarily exceeded. Hence, the evolution of organisms has favored developmental strategies promoting prospects for growth and survival. Such strategies can be considered as groupings of similar morphological, physiological, reproductive and behavioural characteristics, evolved among species or populations and allowing better adaptation under a series of environmental conditions (Grime, 1979).

Macarthur and Wilson were the first to recognize ordinary strategies among organisms, dividing them on a single scale between two extremes: r-strategists (with high reproductive potential) and k-strategists (those having lower reproductive potential than r-strategists but more adapted to competition for resources) (Macarthur and Wilson, 1967). Later, these concepts were applied to the phytoplankton community. According to Reynolds (Reynolds, 1988a), phytoplankton can be divided into three groups with distinct, not mutually exclusive, strategies: C-strategists (competitors: small, high area to volume ratio, and metabolic activity; susceptible to removal by grazers, and explore environments saturated by light and nutrients); R-strategists (ruderal: sizes vary from intermediary to large; high metabolic activity and area to volume ratio; fast growth rate; specialized in tolerating turbulent transport and light gradients); S-strategists (stress tolerant: large; low area to volume ratio; low metabolic activity, and low growth rate *in situ*; high nutrient-storage capacity; enhanced resistance to sinking and grazing losses).

In reservoirs, the factors involved in structuring a phytoplankton community arise from the relationship generated by chemical (nutrients, particularly phosphorus, in regulating phytoplankton primary production), physical (temperature, underwater light climate), and biological (composition and abundance of zooplankton) conditions that are strongly regulated by hydraulic exchanges and resultant surface level fluctuations. Nevertheless, the morphometry of a reservoir and its rate of hydrological flushing may strongly interfere with normal environmental variability patterns and, consequently, in the phytoplankton community structure.

In Barra Bonita Reservoir, variations in mixing conditions, as well as wind and available underwater light

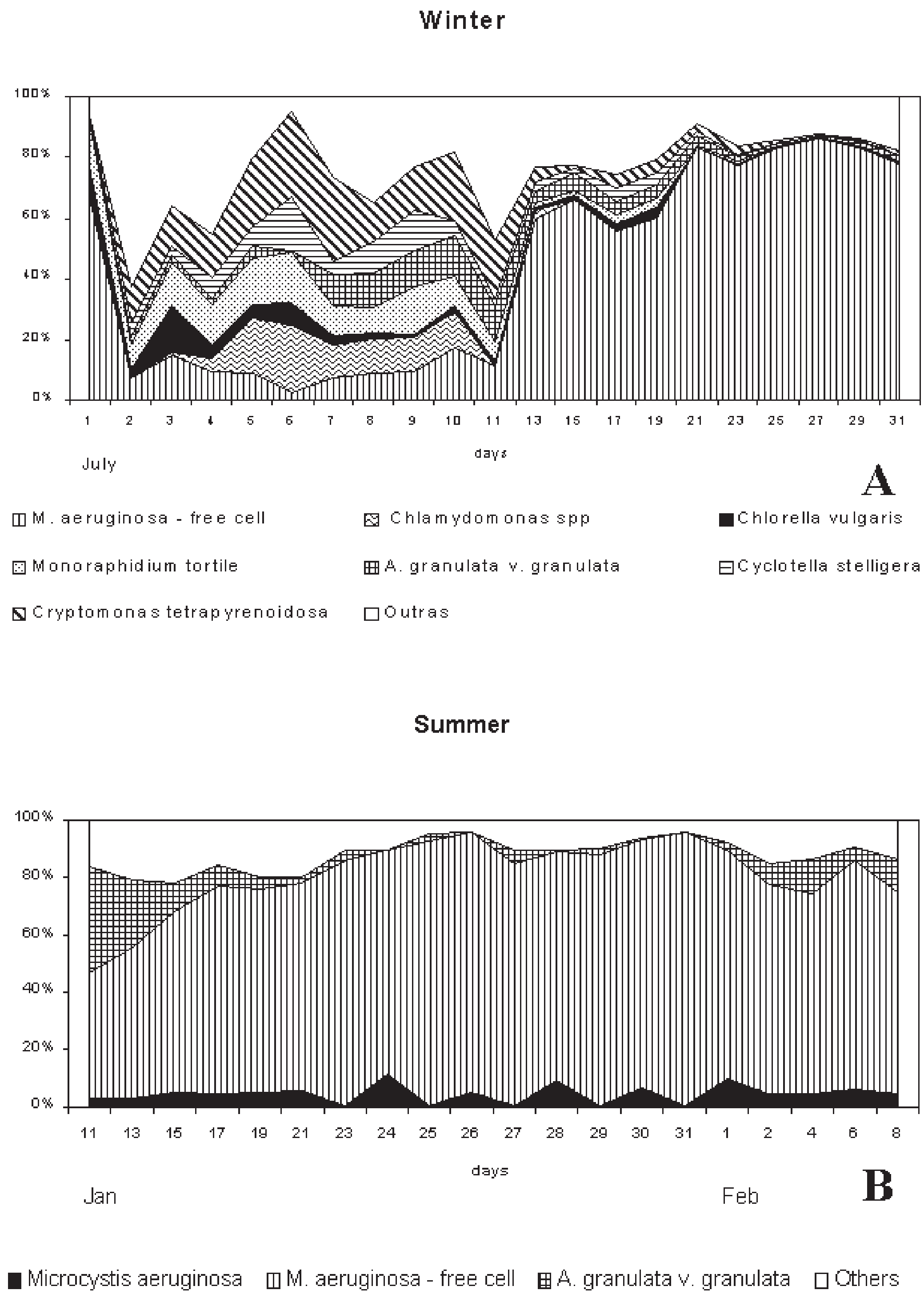

Fig. 12. Relative abundance variation (%) of the most frequent phytoplankton species in Barra Bonita reservoir in the periods from July 1 to 31, 1993 (**A**) and January 11 to February 8, 1994 (**B**).

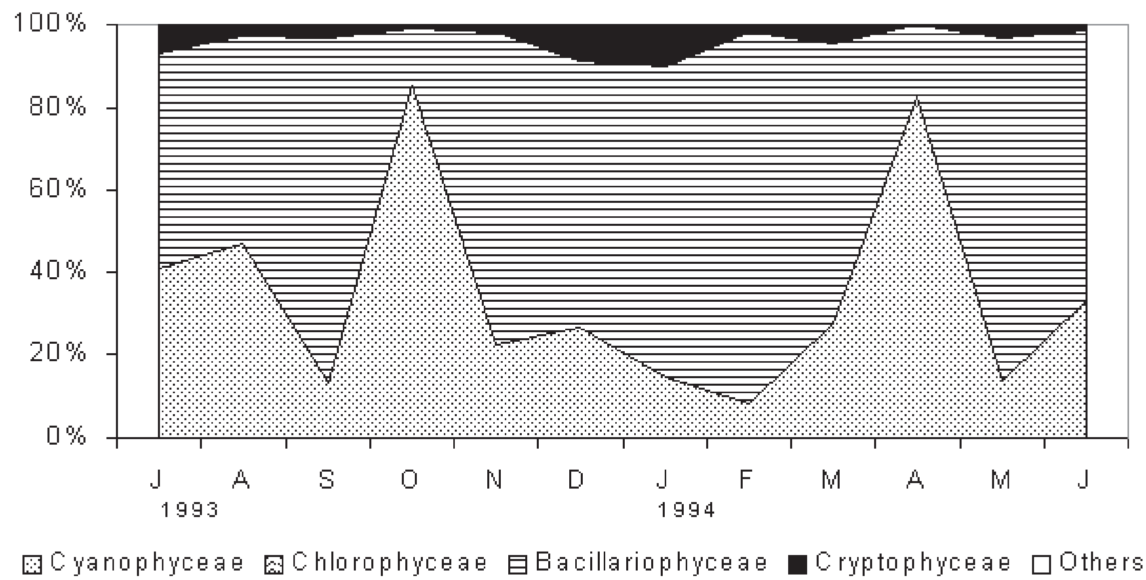

Fig. 13. Relative abundance (%) variation of taxonomic classes by biovolume ($mm^3\ l^{-1}$) in Barra Bonita reservoir in the period from July 1993 to June 1994.

were important for maintaining high diversity. The appearance of green algae, *Monoraphidium tortile*, *Chlamydomonas* spp, *Chlorella vulgaris* and diatoms (*Cyclotella stelligera*), all C-strategists, on the first days of July may be related to sufficient nutrient availability, comparatively good light conditions, high organism growth rates, and the mixing. Regression analyses (Figures 17 and 18) show how relative Chlorophyceae abundance is positively related to water transparency (Z_{DS}) and inorganic phosphate concentration. In this period, the water column remained unstratified, with a deeper euphotic zone. According to Calijuri and Dos Santos, variations occurred in dissolved oxygen concentrations which culminated in hypolimnetic anoxia on July 7, and homogenization of the water column shortly thereafter (Calijuri and Dos Santos, 1996). In the same period, no dominant species appeared, and phosphorus and chlorophyll *a* concentrations in the water varied greatly, confirming the relationship between hypolimnetic oxygen deficit and phytoplankton biomass increase.

The development of *Microcystis aeruginosa* at the end of July may have been favoured by greater water column stability. For Reynolds (Reynolds, 1986), daily alterations in thermal stratification and mixing represent an environmental constancy level which can favour *Microcystis* dominance in tropical lakes.

Winter in Barra Bonita was characterized by greater physical instability of the water column and predominant environmental conditions favoured more disturbance-tolerant species. The rapid species succession with increased diversity observed in the first days of July, and the later establishment of *Microcystis* dominance may be explained by the intermediate disturbance hypothesis (IDH).

In summer, characterized by reduced species diversity, on most days the water column was thermally and chemically stratified and, according to Calijuri and Dos Santos (Calijuri and Dos Santos, 1996), the hypolimnion remained anoxic. In this period, higher temperatures and greater water column stability probably permitted establishment and dominance of *Microcystis aeruginosa*.

The primary production rate in Barra Bonita is strongly regulated by the underwater light regime whose limiting effect on photosynthetic activity is stronger than that of nutrients (Calijuri and Dos Santos, 2001). According to Reynolds and Walsby, under conditions of light deprivation, algae capable of adjusting their position in the water column can develop a competitive advantage over species relying solely on water movements to overcome gravitational force (Reynolds and Walsby, 1975).

Regression analysis (Figure 19) shows how Cyanophyceae abundance is significantly and positively related to the attenuation coefficient (K), in the reservoir. In April 1994 the highest density and relative abundance values of *Microcystis aeruginosa* in the seasonal study were observed. That month the lowest precipitation and outflow values were recorded and, consequently, the

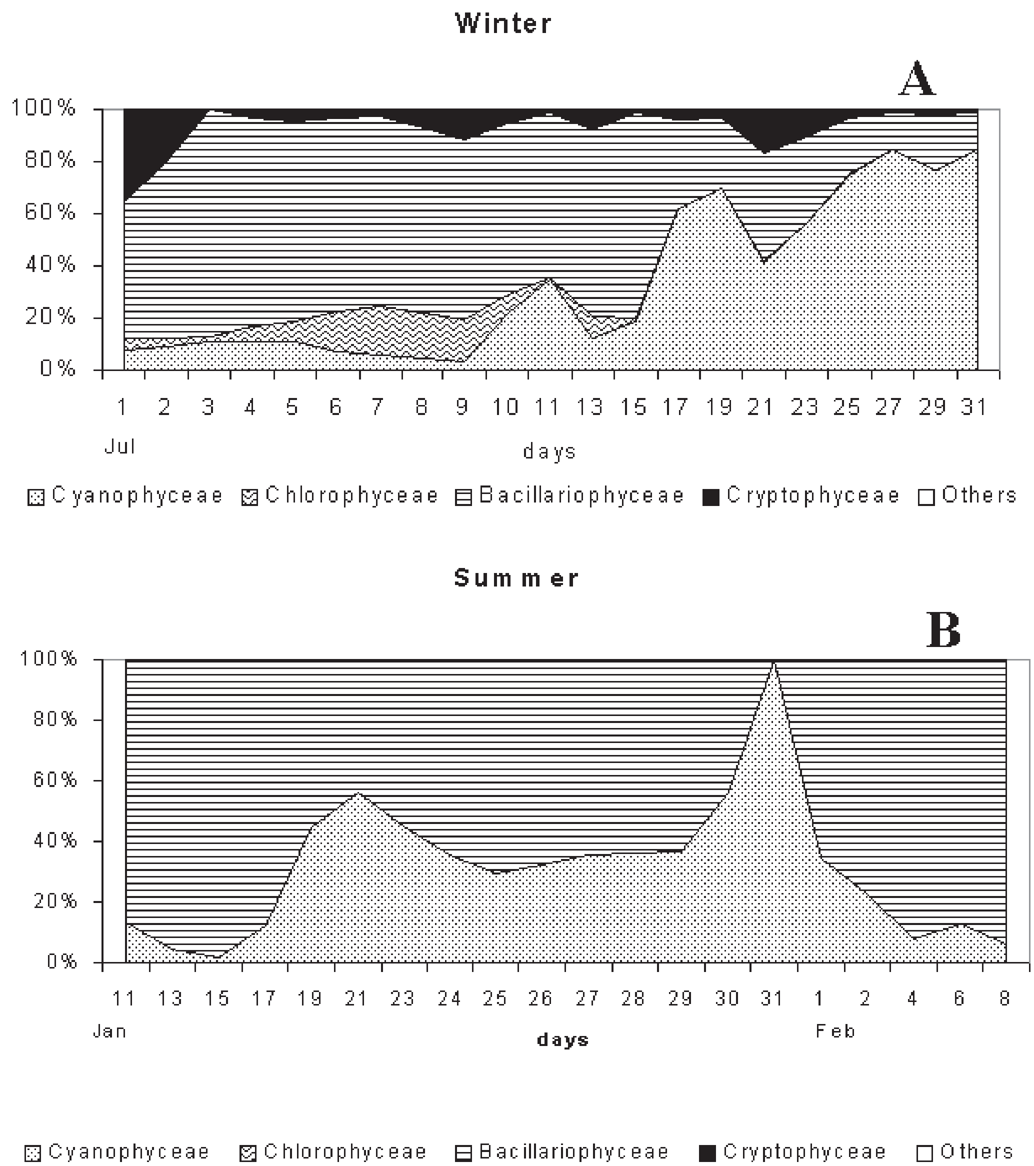

Fig. 14. Relative abundance (%) variation of taxonomic classes by biovolume ($mm^3\ l^{-1}$) in Barra Bonita reservoir in the periods from July 1 to 31, 1993 (**A**) and January 11 to February 8, 1994 (**B**).

longest theoretical water retention time in the system was found, besides the greatest total phosphorus and total dissolved phosphate concentration. It was also one of the months of study showing reduced wind intensity in addition to the higher chlorophyll concentration and primary production (Calijuri and Dos Santos, 2001). Organism density made it practically impossible to determine Z_{eu} with precision. In this system, algal chlorophyll concentration was the major factor determining underwater light attenuation from July 1993 to June 1994.

According to Hambright and Zohary (Hambright and Zohary, 2000), at the onset of winter in Hartbeespoort Dam (South Africa), as solar radiation and temperature declined, dense surface accumulations of *Microcystis* maintained control of the underwater light climate, thus excluding other taxa. For Robarts and Zohary (Robarts and Zohary, 1984), the double ecological advantage of buoyancy and increasing colony size with increasing abundance made *Microcystis* a formidable and successful competitor in Hartbeespoort Dam.

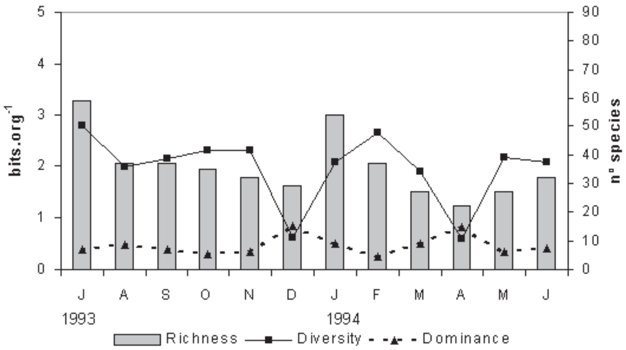

Fig. 15. Richness (species number), diversity (bits.organism^{-1}) and dominant species variation in the phytoplankton community in Barra Bonita reservoir in the period from July 1993 to June 1994.

Microcystis aeruginosa, an S-strategist, and apparently characteristic of waters with phosphate oscillations, is a specialist in phosphate storage and efficient in regulating its density (ability to float). Requiring high temperatures, it tolerates low light intensity, and is not subject to predation by herbivores (Kilham and Hecky, 1988; Kromkamp *et al.*, 1989).

Henry and Simão (Henry and Simão, 1988), in artificial enrichment experiments and measurement of their effects on surface phytoplankton during 1 year in Barra Bonita Reservoir, demonstrated that phosphate was the stimulating nutrient of phytoplankton growth. Our results show (Figure 20) that in this system, relative Cyanophyceae abundance related positively to total phosphorus concentrations, although Watson *et al.* (Watson *et al.*, 1992) demonstrated the sigmoidal nature of the phosphorus–biomass relationship. Increased phosphorus concentration due to the longer theoretical water-retention time in the system was also responsible for bloom occurrence in April 1994. In the summer months (high precipitation period), the combined effect of phosphorus originating in desorption of phosphate from suspended solid matter (Calijuri, 1999), decreased light penetration due to inorganic particles in suspension, and greater physical stability of the water column made *Microcystis aeruginosa* establishment possible.

Watson *et al.* (Watson *et al.*, 1997), attribute the development of Cyanobacteria blooms in eutrophic lakes to their ability to accommodate environmental changes such as reduced N : P and light associated with enrichment, and to their low edibility, coupled with lack of herbivore regulation by other taxa. The relative importance of these mechanisms varies among blue-green taxa and none of the associated environmental factors is as well correlated with blue-green biomass as is total phosphorus.

Water turbulence, in different degrees, magnitudes and durations, is a determining factor in phytoplankton growth, especially in Cyanophyceae dominance (Reynolds and Walsby, 1975; Pearl, 1995). In Hartbeesport hypereutrophic reservoir, low turbulence was observed to be the main factor leading to *Microcystis aeruginosa* dominance (Zohary and Robarts, 1989). The crucial factor in *Microcystis* dominance for Reynolds is its ability to regulate its buoyancy to accommodate severe daily changes in mixing intensity (Reynolds, 1999).

During this research, apart from *Microcystis aeruginosa* free cells, small colonies (up to 20 cells) were also observed. Medium and large colonies were few or absent. Colony size can be modified by the systemic turbulence (Reynolds *et al.*, 1981). For Watson *et al.*, the mixing regime strongly influences the predominant cyanobacterial life-form (Watson *et al.*, 1997). In fact, our regression analysis (Figure 21) shows that colony size in Barra Bonita Reservoir correlates positively with Brunt–Väisälä frequency, or water column stability. The polymictic behaviour of the system was responsible for the occurrence of *Microcystis aeruginosa* free cells.

Temperature isopleths in Barra Bonita Reservoir show that, in general, thermal stratification did not occur (except in summer) rather, microstratification prevailed as is the case in tropical regions where small differences in water density are extremely important in spatial distribution and determination of phytoplankton community temporal changes. During the study periods, aside from the lack of distinct thermal stratification, dissolved oxygen stratification with anoxic hypolimnion was frequently observed (Calijuri and Dos Santos, 1996; Calijuri, 1999). For Reynolds (Reynolds, 1984), *Microcystis* colonies establish themselves in the epilimnion following growth initiation in deep anoxic waters and after water becomes thermally and chemically stratified. This observation is supported by the results obtained in the Salto Grande Reservoir [SP, Brazil; (Calijuri *et al.*, 1999)] and in the Barra Bonita Reservoir (Calijuri and Dos Santos, 1996) as well as those obtained in this research.

Annual phytoplankton biovolume evolution and phytoplankton groups densities were different in Barra Bonita Reservoir. In later winter and early spring (August–September 1993) Cyanophyceae biomass declined, probably due to water mixing resulting from increased wind intensity and precipitation occurrence. In this period, mixing conditions increase and Z_{eu}/Z_{mix} decrease may have been responsible for Bacillariophyceae biomass dominance. In contrast, in October 1993 Cyanophyceae biomass (principally *Anabaena spiroides*) established dominance due to the return of favourable conditions: lower wind intensity and precipitation; high temperature; and increased Z_{eu}/Z_{mix}. In the summer months (November and December 1993; January, February and March 1994)

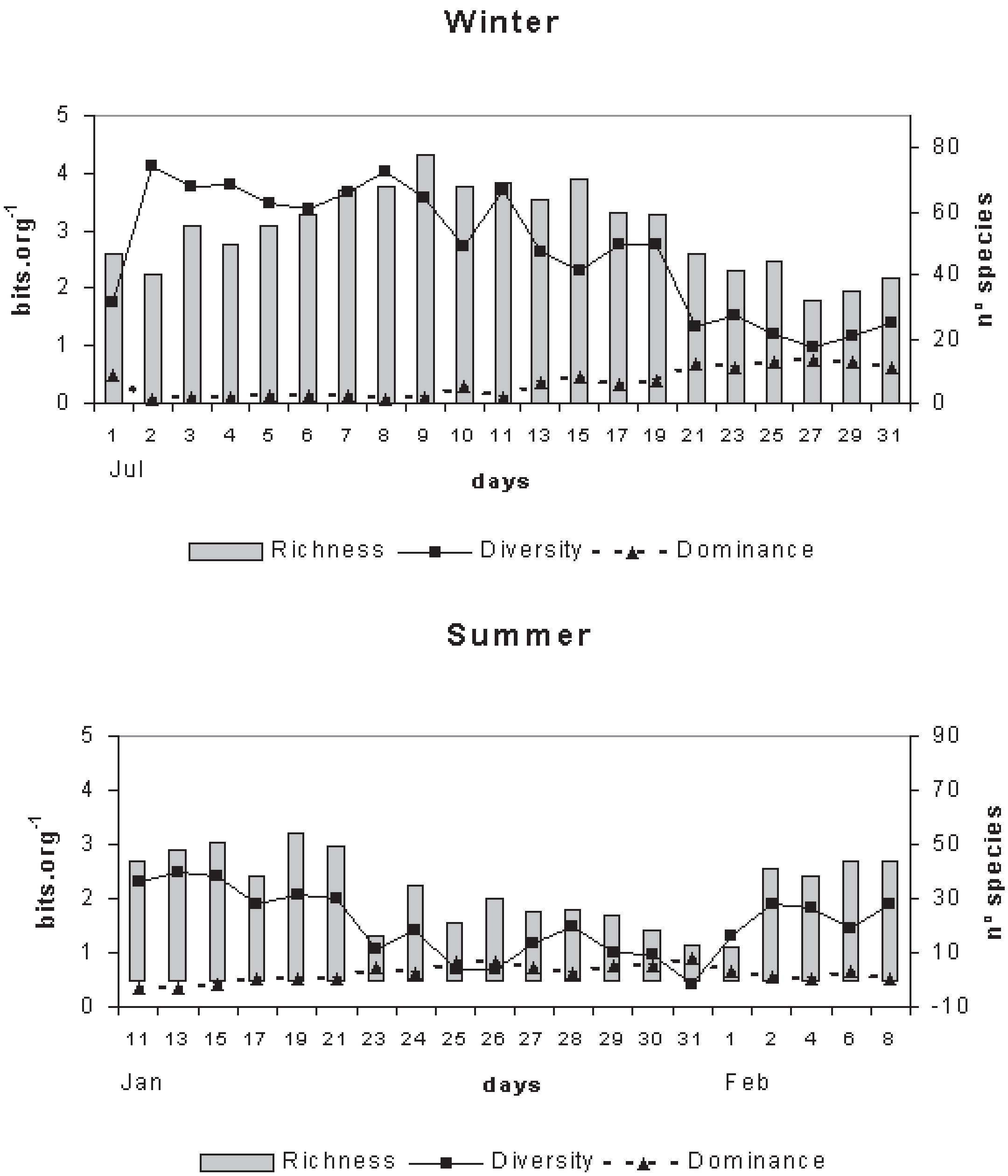

Fig. 16. Richness (species number), diversity (bits.organism^{-1}) and dominant species variation in the phytoplankton community in Barra Bonita reservoir in the periods from July 1 to 31, 1993 (**A**) and January 11 to February 8, 1994 (**B**).

disturbance to the Cyanophyceae biomass (principally *Microcystis*) through high precipitation and spillage (which cannot be considered an intermediate disturbance) may have allowed Bacillariophyceae biomass increase. In April 1994, *Microcystis* developed in the upper waters, due to a return of the favourable conditions just discussed, becoming a light limitation for other taxa. In May 1994, June 1994, and the first days of July 1993, besides mixing conditions, increased light penetration (deeper Z_{eu}) allowed the proliferation of other taxa and Bacillariophyceae biomass dominated.

According to Reynolds (Reynolds, 1998), in frequently and well-mixed systems, the impact of eutrophication amplifies opportunities that favour the more

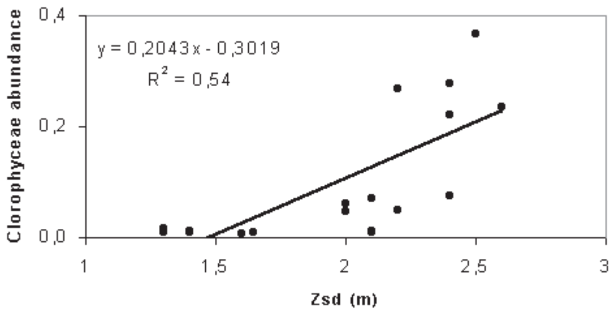

Fig. 17. Relationship between Chlorophyceae relative abundance and Secchi disk depth, in Barra Bonita Reservoir in July 1993 (winter).

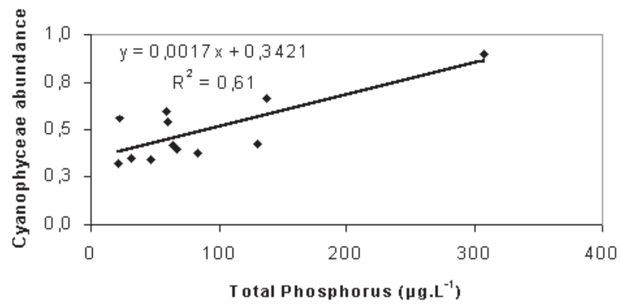

Fig. 20. Relationship between Cyanophyceae relative abundance and total phosphorus concentrations in Barra Bonita Reservoir from July 1993 to June 1994.

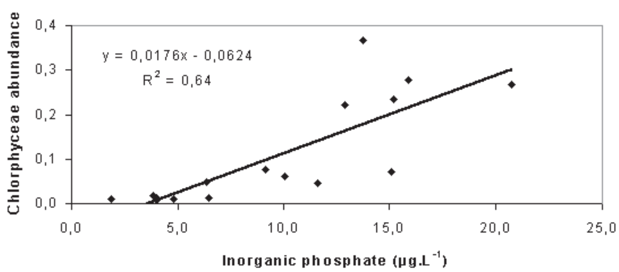

Fig. 18. Relationship between Chlorophyceae relative abundance and inorganic phosphate concentrations in Barra Bonita Reservoir in July 1993 (winter).

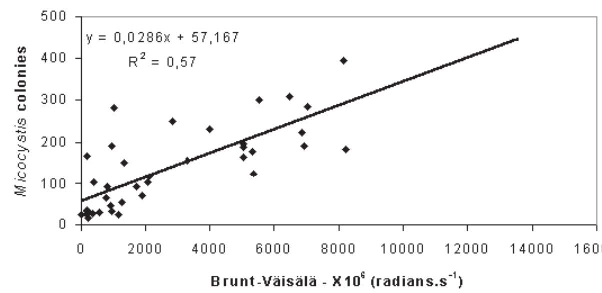

Fig. 21. Relationship between Brunt–Väisälä frequency and *Microcystis aeruginosa* colony predominance in Barra Bonita Reservoir from July 1993 to June 1994.

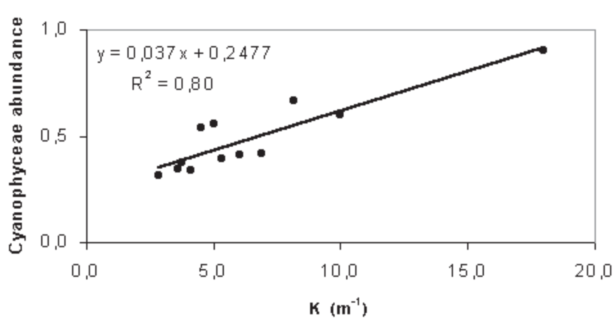

Fig. 19. Relationship between Cyanophyceae relative abundance and attenuation coefficient (*K*) in Barra Bonita Reservoir from July 1993 to June 1994.

photosynthetically-efficient species and those which are more photoadaptable (slender, filamentous species capable of enhancing their chlorophyll content and accessory pigments). High water transparency not only compensates optically for increased mixing depth, but also permits longer residence within the euphotic zone for a sinking alga under mixing conditions (Sommer, 1988). Because water transparency and Si : P or Si : N ratios tend to decrease with eutrophication, decreasing importance of diatoms is expected. But, since water transparency and nutrient availability are seasonal in eutrophic system, this periodicity favours the relative importance of diatoms (Sommer, 1988).

Most communities are organized by mixing forces and competition/disturbance, whose relative importance depends on a combination of factors that can render the system, alternately either closer to or far from their equilibrium. In natural phytoplankton communities, it is difficult to determine if a certain phase of succession sequence can be considered to be in a state of equilibrium or not, because of frequently insufficient data or samples. Following Sommer *et al.* (Sommer *et al.*, 1993), in practice a given 'phase in a seasonal sequence can be considered to be in a state of equilibrium when: (i) 1, 2, or 3 species of algae contribute more than 80% of total biomass; (ii) their existence or coexistence persists for more than 1–2 weeks; and (iii) during that period the total biomass does not increase significantly'.

Apparently, considering organism density and biomass, Cyanophyceae (*Microcystis aeruginosa*) have competed with Bacillariophyceae (*Aulacoseira granulata*) in Barra Bonita Reservoir. Probably, the prevailing environmental conditions in this system, with alternations between microstratification and holomixes, and phosphorus availability, provided a sufficient environmental constancy for the development of equilibrium conditions with *Microcystis aeruginosa* dominance. For Reynolds (Reynolds, 1988b), few researchers have found natural phytoplankton populations living in equilibrium. Long periods of *Microcystis* dominance were observed in some equatorial lakes subject to minor seasonal variations (Reynolds, 1988b). Seasonal events in the phytoplankton community, probably due to mixing by wind, loss of Cyanophyceae biomass from the upper water surface by spillage in periods of precipitation, and underwater light availability allowed dominance of Bacillariophyceae (*Aulacoseira granulata*) biomass.

In Brazil, large reservoirs have been constructed to generate power. In them, water spill and outlet placement cause spatial complexity during operation, thus establishing temporal complexity in the phytoplankton seasonal cycle. The natural seasonal cycle is disturbed by water-level fluctuations and flow modifications imposed by dam operation which, in general, is irregular on both annual and daily scales. Phytoplankton dynamics in the tropical and eutrophic Barra Bonita Reservoir is apparently dominated by competitive exclusion and disturbance. In this system, the seasonal sequence can be considered to be in a state of equilibrium with alternation of R- and S-strategists. In the short term (10 days), non-equilibrium conditions resulting from physical disturbance (mixing by wind), with increase of species diversity and coexistence can perhaps be explained by intermediate disturbance hypothesis (IDH).

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