issn 0018-8158
coden HYDRB8

hydrobiologia

september 13, 1996 volume 330, no. 3

This issue completes Vol. 330

kluwer academic publishers

hydrobiologia

volume 330, no. 3, september 13, 1996

Hydrobiologia **330:** 163–175, 1996.

Short-term changes in the Barra Bonita reservoir (São Paulo, Brazil): emphasis on the phytoplankton communities

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Received 20 September 1995; in revised form 12 January 1996; accepted 16 February 1996

Key words: phytoplankton, diversity, mixing, stratification, stability, disturbance hypothesis

Abstract

We investigated the biomass, primary productivity, species diversity and their controlling factors in the deeper region of the Barra Bonita reservoir (22°29′S and 48°34′W) in the State of São Paulo, Brazil. To accomplish this, short term changes (days and month) were measured during two periods of the year, winter 1993 and summer 1994. The response of the phytoplankton communities to the variability of the system, taking into account the Intermediate Disturbance Hypothesis (IDH), indicated that the frequency and intensity of the disturbances have a critical influence on the establishment of the communities. In Barra Bonita Reservoir the conditions for mixing in the winter were probably important for maintaining high diversity. On the other hand, in summer, the concentrations of suspended material, the high temperatures, and the greater stability of the water column, were probably responsible for permitting the establishment of *Microcystis aeruginosa*.

Introduction

The ecological factors which determine the structure of the phytoplankton communities has been a subject of debate for years. An explanation of the problem is given in Hutchinson (1961), 'The Paradox of the Plankton', which refers to the coexistence of many species in an apparently homogeneous and isotropic environment. Hutchinson's work (1941, 1953, 1961, 1967) shows that it is impossible to discuss the ecology of phytoplankton communities without examining the theoretical base of ecology in general.

Connell's Intermediate Disturbance Hypothesis (IDH) is close to Hutchinson's famous paradox. According to Connell (1978), disturbance of the intermediate time scale will maintain a high level of species diversity when introduced to the environment before the community reaches steady-state conditions and competitive exclusion. The frequency of disturbances has a critical influence on the diversity of phytoplankton and on the establishment of a state of equilibrium (Sommer et al., 1993).

The recent 'revolution' in thought has brought about new revelations with respect to how organisms interact with their environment. Unless we wholly understand the scales of time and space which dominate the ecology of the organisms we will not be able to correctly interpret the data collected during *in situ* experiments, as well as others. At this point we can see that phytoplankton organisms are sensitive to environmental variability (Calijuri, 1988) and that in the past we have underestimated the importance of small scale rapid processes. For Levins (1968) no organism can instantly obtain perfect behavior. Therefore, it is not possible to combine processes with significantly different time constants.

As such, we can use data analyses in time series to describe the physical and biological variability of the system. These variables of time series analyses have been used to examine the time lags between environmental fluctuations and phytoplankton response (Marra & Heinemann, 1982; Harris, 1983; Septhon & Harris, 1984; Padisák et al., 1993).

In this preliminary study, the objective is to use time scales (days and month) to examine the biomass, primary productivity and species diversity and their controlling factors in the deeper region of the Barra Bonita eutrophic with the goal of evaluating the response of the phytoplankton community to the variability of the system, and to provide further understanding of the processes in stressed environments.

Description of the study site

Barra Bonita Reservoir is the first of a series of six large reservoirs in the middle Tietê river, constructed with the objective of producing hydroelectricity. It is located at latitude 22°29′ S and longitude 48°34′ W, and is at an altitude of 430 meters (Fig. 1).

This reservoir is located in the most populous and developed region of the interior of the State, bounded by the part of the Tietê Valley comprised of the sections between the Pirapora and Barra Bonita dams. The reservoir is formed primarily by the damming of the Tietê and Piracicaba rivers, but also relies on input from innumerable minor and major tributaries. It is located in a transitional region between tropical and subtropical climates, where the seasons are not well defined. The seasonal changes are not very pronounced, the clearest differences being between summer (the rainy season) and winter (the dry season, with little or no rain). During the hottest month (January) the maximum temperature is always above 22 °C (average temperature is 27 °C), and during the coldest month (July) the minimum temperature is below 18 °C (average temperature is 18 °C). The predominant rock in the region is basalt, and the drainage basin of Barra Bonita is predominantly constituted by purple latosoil. The vegetation in the region is made up of monoculture sugar cane (Calijuri, 1988).

The Barra Bonita Reservoir is a polymictic ecosystem with an average depth of 10.2 meters, deeper than most of the reservoirs in the State of São Paulo. It is a eutrophic reservoir where the main external factors are rainfall, wind, flushing rate and retention time of the water. The average retention time 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. During the rainy season input of nutrients occurs, as demonstrated by Henry et al. (1985). According to these authors, limitation of natural light due to large concentrations of suspended matter occurs during the rainy season.

Therefore, this reservoir is a polymictic, eutrophic system with varying retention time producing changing mechanisms of ecological functioning, trophic state and composition of the phytoplankton community.

Materials and methods

The sampling and experiments were carried out during the periods of 30 June to 31 July, 1993, and 11 January to 8 February, 1994, at Station I, in the deepest part of the reservoir. An intensive sampling (every day) was carried out during the periods of 30 June to 10 July, 1993 and 24 January to 2 February, 1994. The other sampled were taken on alternate days. Samples of the entire 5 meters column were collected.

Meteorological data (air temperature, precipitation, solar radiation, wind and data on outflow) were made available by the CESP (Companhia Energética de São Paulo) at the Barra Bonita Reservoir.

The underwater photosynthetic available radiation (Ph.A.R.) was measured with a Ph.A.R. Quantum Radiometer (Lambda Instruments) and the water transparency was measured with a Secchi Disk. The vertical attenuation coefficient was determined according to Kirk (1986) and the thermal structure of the water was determined using a Toho Dentan thermistor.

The physical and chemical parameters investigated were pH, alkalinity, dissolved oxygen (Strickland & Parsons, 1960) and nutrients (phosphorus and nitrogen) (APHA, 1985). Conductivity was measured *in situ* and corrected to 20 °C, and chlorophyll were determined according to Nusch (1980). The primary production of phytoplankton was determined by the ^{14}C method according to Steemann-Nielsen (1952). After filtration on Millipore filters of 0.45 μm, 25 mm membranes, the filters were placed in scintillation vials with a Bray (1960) solution. Phytoplankton samples for total counting were fixed with Lugol's preservative. The identification of organisms was made under a inverted microscope (Zeiss) and the counting was made using the Uthermöhl (1958) method. The diversity (H′) was calculated on the basis of LN using the Shannon-Weaver Index (Shannon & Weaver, 1949).

Results

Table 1 presents the mean air temperature (°C), solar radiation (μE m^{-2} s^{-1}), precipitation (mm), wind force (m s^{-1}), outflow (m^3 s^{-1}) and water retention time (days) values for the Barra Bonita Reservoir during the intensive collection periods in the winter of 1993

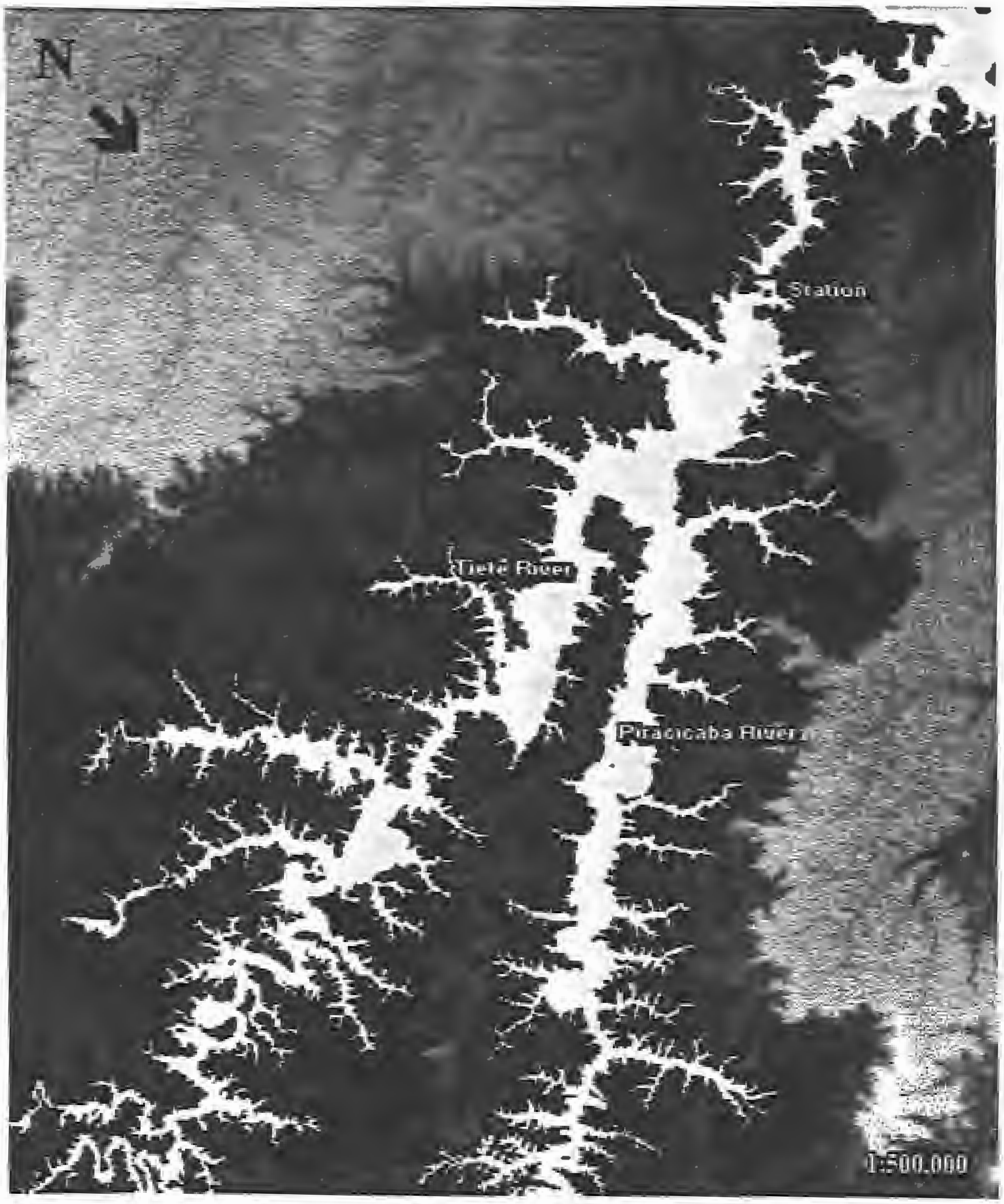

Figure 1. Barra Bonita Reservoir (Calijuri et al., 1995).

and the summer of 1994. The lower temperature values and higher water retention times occurred in July 1993. With the occurrence of rainfall there was an increase in water outflow and a reduction in the water retention time in the reservoir in January–February 1994. The wind in this system is an important external factor, such that together with precipitation they are responsible for the polymictic behavior of the reservoir during the greater part of the year.

Figures 2 and 3 show the vertical profiles of the temperature (°C) and dissolved oxygen concentration in the water during the periods of 30 June to 10 July 1993 (winter), and 24 January to 2 February 1994 (summer). These profiles show that during the 10 winter days the

Table 1. Air temperature (°C), solar radiation ($\mu E \times m^{-2} \times s^{-1}$), precipitation (mm), wind ($m.s^{-1}$), outflow ($m^3.s^{-1}$), and retention time (days) values for the water in the Barra Bonita Reservoir for the periods of study (winter 1993 and summer 1994)

Date	Air temperature (°C)	Solar radiation ($\mu E\ m^{-2}\ s^{-1}$)	Precipitation (mm)	Wind ($m\ s^{-1}$)	Outflow (days)	Retention time
1993						
June 30	21.00	150	0.0	–	330	111
July 01	20.15	1150	0.0	1.42	318	115
July 02	19.50	810	0.0	1.22	333	110
July 03	18.75	730	0.0	0.79	328	112
July 04	18.25	1050	0.0	0.82	326	112
July 05	18.05	1350	0.0	1.13	335	109
July 06	20.05	1400	0.0	1.70	309	118
July 07	19.05	450	0.0	2.15	334	110
July 08	18.65	1450	0.0	2.51	412	89
July 09	18.25	430	0.0	2.55	390	91
July 10	19.25	1400	0.0	0.89	412	93
July 11	19.15	1350	0.0	–	403	91
July 13	17.00	125	0.0	–	407	90
July 15	16.50	250	0.0	–	386	95
July 17	18.05	850	0.0	–	416	88
July 19	22.55	720	0.0	–	394	93
July 21	23.25	1050	0.0	–	311	118
July 23	21.40	1000	0.0	–	271	135
July 25	19.40	940	0.0	–	273	134
July 27	18.80	720	0.0	–	258	142
July 29	20.55	950	1.1	–	261	140
July 31	18.15	1100	0.0	–	258	142
1994						
January 11	26.00	570	0.0	–	464	79
January 13	23.60	490	0.0	–	577	63
January 15	25.00	900	0.0	–	557	66
January 17	28.50	1250	0.0	–	444	82
January 19	30.30	1000	3.2	–	436	84
January 21	30.10	1600	0.0	–	444	82
January 23	27.45	900	1.9	–	444	82
January 24	27.45	670	1.3	1.10	444	82
January 25	27.95	860	27.5	1.65	444	82
January 26	28.40	790	7.1	1.84	444	82
January 27	28.50	1300	29.5	1.64	444	82
January 28	29.30	2200	0.3	2.26	554	66
January 29	27.30	1100	0.0	4.93	723	51
January 30	27.20	900	0.6	3.78	892	41
January 31	28.30	1650	0.0	1.46	1022	36
February 01	28.10	1150	0.0	0.85	1028	36
February 02	28.00	1700	0.0	0.61	872	42
February 04	29.60	225	0.0	–	511	72
February 06	28.70	320	0.0	–	444	82
February 08	27.40	240	3.8	–	746	49

reservoir was thermally unstratified, but had lowered concentrations of dissolved oxygen which culminated in hypolimnetic anoxia on 7 July. During the period of 7 July to 9 July it appears that the wind was the external factor responsible for the mixing of the water. When on 10 July the wind diminished, it can be seen that an oxycline was reestablished. In the summer a high degree of environmental stability can be seen during the period of 24 January to 2 February with the presence of a hypolimnetic anoxia or a tendency towards anoxia.

Figures 4 and 5 present the attenuation coefficient (K), euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values for the two periods under study. It can be seen that there were fewer variations of these parameters during the winter than during the summer. With the summer precipitation, there occurred a large inflow of suspended material in large part due to the soil uses in the hydrographic basin. These pulses of suspended material associated with temporary microstratifications are reflected by a more heterogeneous water column, with the Z_{eu} and Z_{eu}/Z_{mix} varying significantly during the period of 11 January to 8 February. These differences which occurred in the Z_{eu}/Z_{mix} ratio during the days studied gives a characterization of the availability of light for the phytoplankton community.

Tables 2 and 3 present the dominant species, abundance, diversity (Shannon-Weaver Index), total number of species, and total nitrogen and phosphorus. Winter (Table 2) was characterized by greater instability with greater species diversity and without the presence of dominant species. In contrast, summer (Table 3) was characterized by a lower diversity of species and the presence of *Microcystis aeruginosa*, which was the dominant organism. It appears that during the summer there is a tendency towards the conditions for equilibrium when compared with the result obtained for winter. Furthermore, it can be seen in Figures 6 and 7 that greater values of phytoplankton primary production are found in the summer and greater values of dark fixation in the winter.

Discussion

The aquatic ecosystem presents a spatial and temporal variety which defines a high degree of uncertainty in relation to the phytoplankton populations. This variability is expressed by physical (light, temperature) and chemical (nutrients, dissolved gasses) characteristics, and results from the high fluctuating structure of the water column in which the phytoplankton develop, and from its interaction with atmospheric factors such as wind, solar radiation and precipitation.

According to Conrad (1986), two important aspects should be considered in the action mechanism of the phytoplankton community in view of a permanent instability: (i) adaptability, that is, the capacity to confront unexpected disturbances, and (ii) the ability or potential to confront internal noise which can be defined as 'reliability' (effective responses). The tendency or potential of the phytoplankton community to confront this problem lies in the processes of diversification of genetic potential, and behavioral and physiological flexibility. According to Harris (1983) environments vary with time, and the fluctuations which occur are highly significant for maintaining diversity.

In recent years, a number of studies has been published which show that fluctuations in the stability of surface water in scales of time of about 10 days are responsible for changes in algae composition and diversity, and that the biomass and taxonomic composition of the phytoplankton can be controlled by changes in the mixing layer over a few days (Harris, 1986; Reynolds et al., 1987; Capblancq & Catalan, 1994).

As such, in order to evaluate the frequency and amplitude with which the external forcing events disturb an ecosystem removing it from a state of equilibrium it is necessary to take a holistic view of it. The Barra Bonita Reservoir is a eutrhopic, polymictic system which is frequently stressed by physical forces such as wind, precipitation, and outflow. Furthermore, this reservoir receives high levels of nutrients which come from large urban areas and agroindustrial activities in the entire hydrographic basin. Wind is responsible for frequent episodes of mixing in the reservoir, and precipitation for the pulses of material in suspension. The outflow gives a variation over time in water retention over the course of the year.

The ratio Z_{eu}/Z_{mix} appears to have smaller variation during the winter than during summer. The fluctuations in the day to day availability of light in the winter were most likely due to the phytoplankton biomass and to the pulses of material in suspension during summer. Following Calijuri (1988), the introduction of material in suspension into the reservoir in the period of greater precipitation causes changes in the optical quality of the water, the diminishment of the euphotic zone, and an increased influence of light as a limiting factor in the primary production of phytoplankton.

In winter, the water column remained unstratified during the ten days of the study. Variations occurred in

Table 2. Dominant species, abundance (%), chlorophyll concentrations ($\mu g\ l^{-1}$), diversity (Shannon-Weaver Index), total number of species, total nitrogen ($mg\ l^{-1}$) and total phosphorus ($\mu g\ l^{-1}$), during the period of 30 June to 10 July (winter 1993)

Date 1993	Dominant species	Abundance (%)	Chlorophyll ($\mu g\ l^{-1}$)	Diversity (bits)	Total of species	Total nitrogen ($mg\ l^{-1}$)	Total phosphorus ($\mu g\ l^{-1}$)
June 30	*Pseudoanabaena mucicola*	22	2.23	1.00	19	0.62	34.10
	Gloeothece sp.	17					
	Cryptomonas pseudopirenoidifera	17					
	Monoraphidium tortile	13					
July 01	*Cryptomonas pseudopirenoidifera*	19	1.05	1.26	32	0.87	42.99
	Ankistrodesmus falcatus	11					
	Pseudoanabaena mucicola	8					
	Monoraphidium tortile	8					
July 02	*Cryptomonas pseudopirenoidifera*	17	3.35	1.22	29	1.14	34.49
	Monoraphidium tortile	17					
	Pseudoanabaena mucicola	14					
	Cyclotella stelligera	6					
July 03	*Pseudoanabaena mucicola*	29	1.40	1.03	29	0.87	69.24
	Monoraphidium tortile	17					
	Cryptomonas pseudopirenoidifera	14					
	Cyclotella stelligera	8					
July 04	*Cryptomonas pseudopirenoidifera*	17	2.51	1.06	20	1.05	34.10
	Monoraphidium tortile	15					
	Phacus longicauda	13					
	Oocystis lacustris	11					
July 05	*Cryptomonas pseudopirenoidifera*	23	1.12	1.00	19	1.28	29.47
	Euglena sp.	21					
	Cyclotella stelligera	12					
	Gloeothece sp.	9					
July 06	*Cryptomonas pseudopirenoidifera*	32	1.67	0.96	20	1.10	26.00
	Cyclotella stelligera	20					
	Monoraphidium tortile	11					
July 07	*Cryptomonas pseudopirenoidifera*	35	1.40	0.80	17	0.91	29.45
	Euglena sp.	20					
	Cyclotella stelligera	13					
July 08	*Euglena* sp.	16	1.40	1.11	22	0.91	65.38
	Cryptomonas pseudopirenoidifera	13					
	Cyclotella stelligera	11					
	Monoraphidium tortile	9					
July 09	*Cryptomonas pseudopirenoidifera*	18	3.07	0.83	14	0.82	32.26
	Microcystis aeruginosa	13					
	Pseudoanabaena mucicola	12					
	Euglena sp.	10					
July 10	*Euglena* sp.	24	6.42	0.98	22	1.55	34.10
	Microcystis aeruginosa	23					
	Cryptomonas pseudopirenoidifera	15					

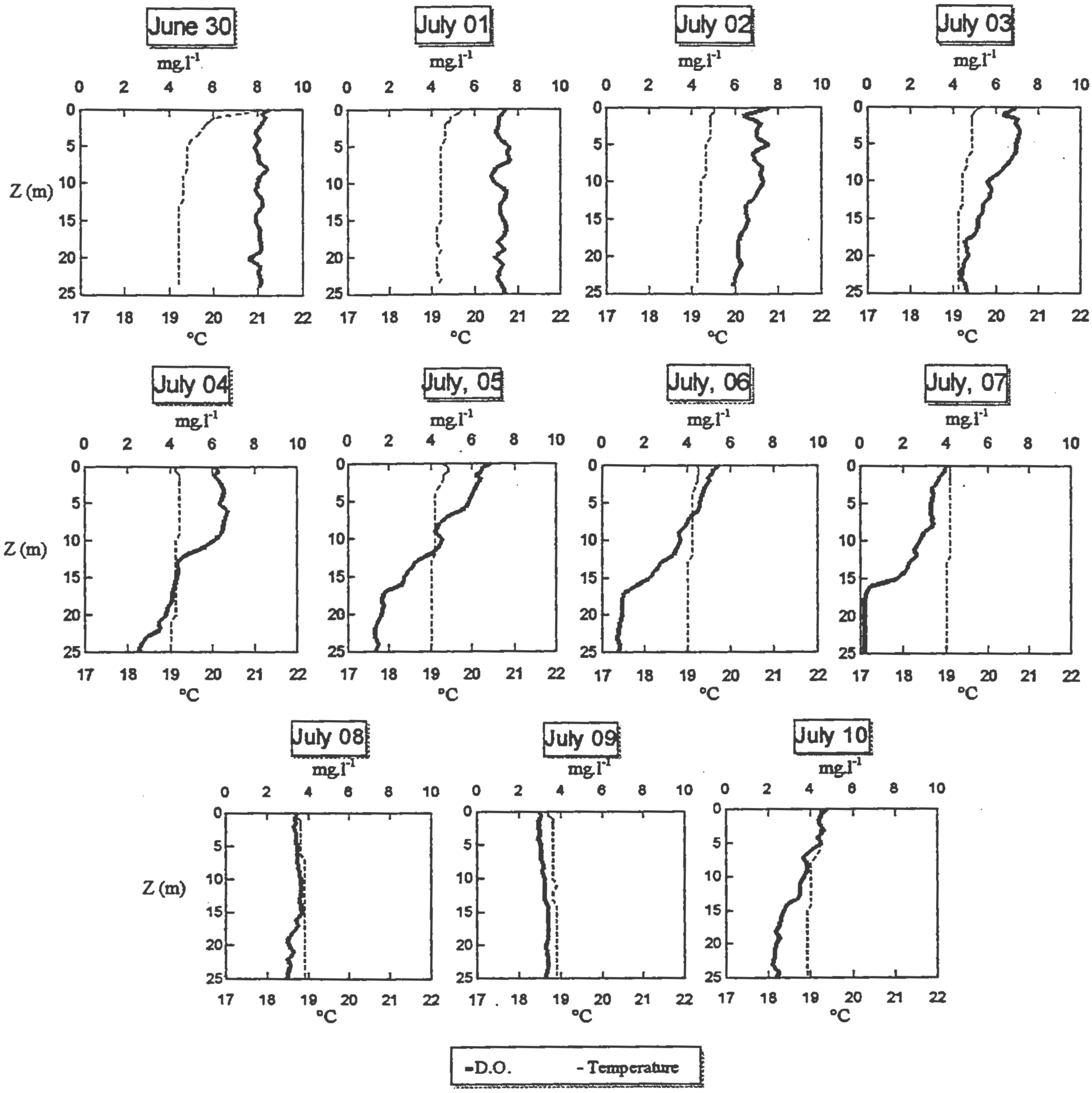

Figure 2. Vertical profiles of water temperature (°C) and dissolved oxygen (mg l^{-1}) in the Barra Bonita Reservoir during the period of 30 June to 10 July, 1993 (winter).

the concentrations of dissolved oxygen which culminated with hypolimnetic anoxia on 7 July, and homogenization of the water column shortly thereafter. In this period there did not appear to be any dominant species, and the total concentrations of chlorophyll and phosphorus in the water column varied greatly, confirming the relationship of the hypolimnetic oxygen deficit to the increase in phytoplankton biomass.

Esteves (1983) showed that the mean phosphate content in the sediment of Barra Bonita reservoir (513.6 ppm) was the highest of the 13 Brazilian reservoirs. According to Esteves et al. (1981), the iron content of

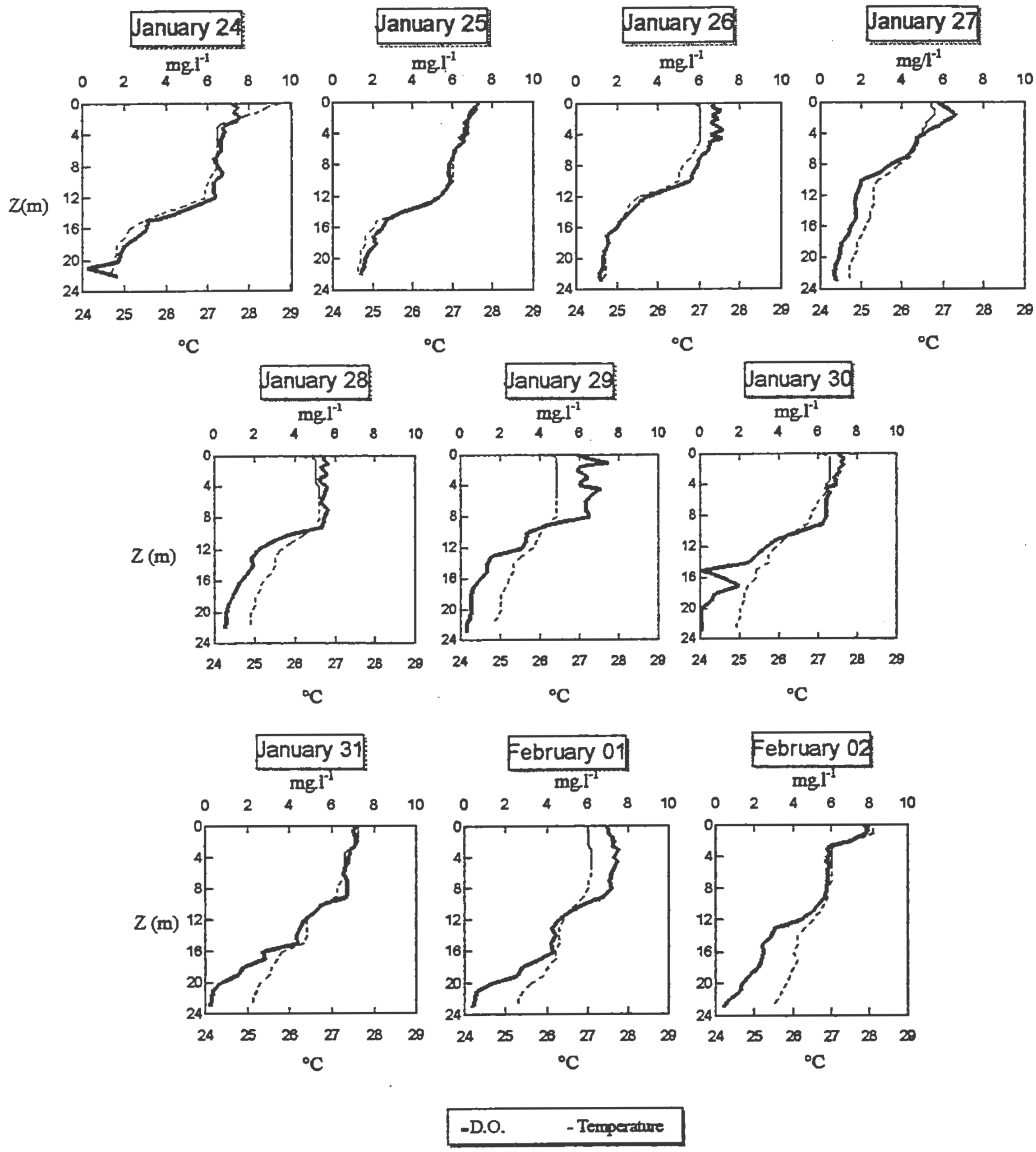

Figure 3. Vertical profiles of water temperature (°C) and dissolved oxygen (mg l^{-1}) in the Barra Bonita Reservoir during the period of 24 January to 2 February, 1994 (summer).

the sediment (27,866.7 ppm) is another indication of phosphorous accumulation by precipitation in the sediment in this reservoir. However, in this ecosystem, the limiting effect of light penetration on photosynthetic activity is stronger than that of nutrients (Henry et al., 1985; Calijuri, 1988).

Following Tundisi et al. (1993), the seasonal cycle of phytoplankton and the primary production in Barra Bonita Reservoir is strongly related to the water reten-

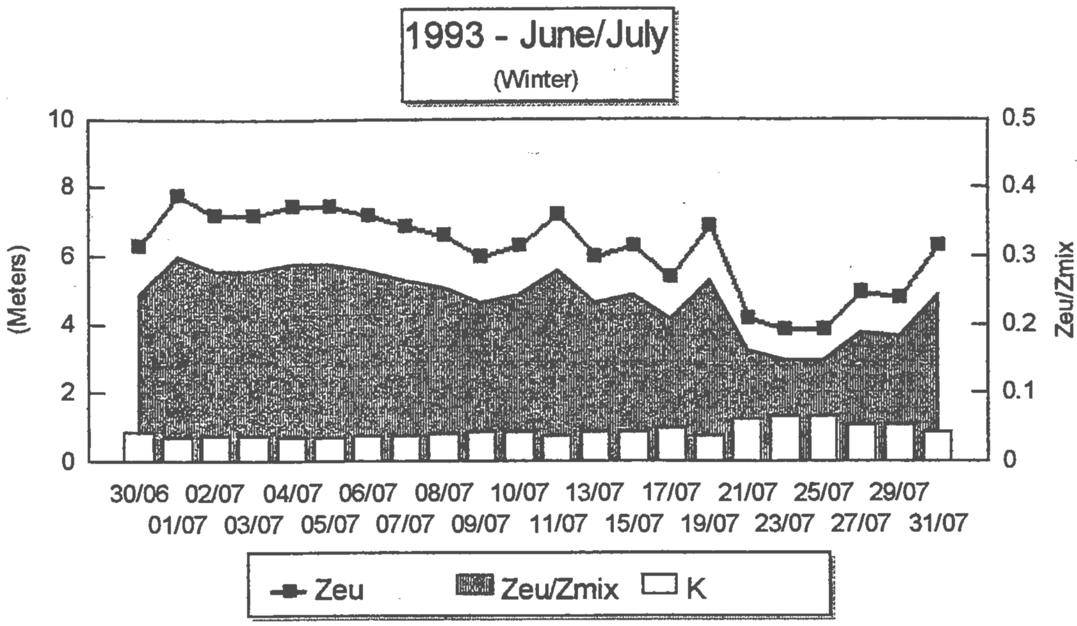

Figure 4. Attenuation coefficient (K), euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values for the Barra Bonita Reservoir in winter 1993.

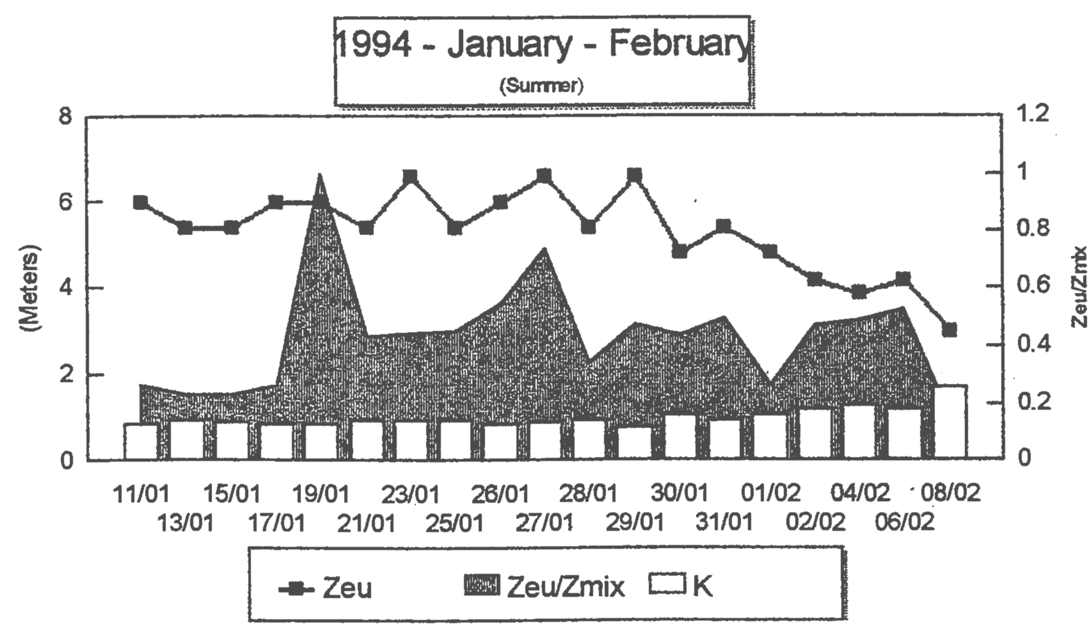

Figure 5. Attenuation coefficient (K), euphotic zone (Z_{eu}) and euphotic zone/mixing zone (Z_{eu}/Z_{mix}) values for the Barra Bonita Reservoir in summer 1994.

Table 3. Dominant species, abundance (%), chlorophyll concentrations ($\mu g\ l^{-1}$), diversity (Shannon-Weaver Index), total number of species, total nitrogen ($mg\ l^{-1}$) and total phosphorus ($\mu g\ l^{-1}$), during the period of 24 January to 2 February (summer 1994)

Date 1994	Dominant species	Abundance (%)	Chlorophyll ($\mu g\ l^{-1}$)	Diversity (bits)	Total of species	Total nitrogen ($mg\ l^{-1}$)	Total phosphorus ($\mu g\ l^{-1}$)
January 24	*Microcystis aeruginosa*	58	3.07	0.75	28	0.64	43.09
	Merismopedia spp.	9					
	Oscillatoria moeugotia	6					
January 25	*Microcystis aeruginosa*	61	2.23	0.71	18	2.24	54.89
	Microcystis elachista	7					
	Oscillatoria moeugotia	5					
January 26	*Microcystis aeruginosa*	96	2.51	0.12	19	1.51	67.81
January 27	*Microcystis aeruginosa*	95	2.51	0.15	21	1.55	30.54
January 28	*Microcystis aeruginosa*	57	4.19	0.80	24	2.84	40.50
	Coelastum microporum	8					
	Microcystis elachista	5					
January 29	*Microcystis aeruginosa*	54	2.23	0.77	17	1.65	31.65
	Microcystis elachista	9					
	Oscillatoria moeugotia	8					
January 30	*Microcystis aeruginosa*	93	4.46	0.19	23	1.21	22.79
January 31	*Microcystis aeruginosa*	71	5.58	0.55	19	1.46	15.04
	Microcystis elachista	8					
	Merismopedia spp.	5					
February 01	*Microcystis aeruginosa*	57	5.58	0.72	17	1.14	23.90
	Aulocoseira granulata	10					
	Aphanocapsa roseana	9					
February 02	*Microcystis aeruginosa*	72	8.37	0.51	16	1.33	36.44
	Oscillatoria moeugotia	8					
	Microcystis elachista	6					

tion time, the nutrient cycle and climatological factors. The functioning of this reservoir is a basic external factor in the phytoplankton community structure and primary production cycle.

During the intensive summer sampling (from 24 January to 2 February) the water column was thermally and chemically stratified. During the majority of the days, the hypolimnion remained anoxic. As the temperatures rose there was an increase in the concentrations of chlorophyll and in water outflow, and *Microcystis aeruginosa* was the dominant species. The diversity indices obtained during the summer were much lower to those from the winter. Following 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.'

In the Barra Bonita Reservoir the conditions for mixing in the winter were probably important for maintaining high diversity. As Margalet (1978, 1980) pointed out, the development of phytoplankton goes from an initial peak in diatoms and flagellates to dinoflagellates and blue green algae in the last stages. In this work, the appearance of non-motile green algae *(Monoraphidium tortile)* and diatoms *(Cyclotella stelligera)* in win-

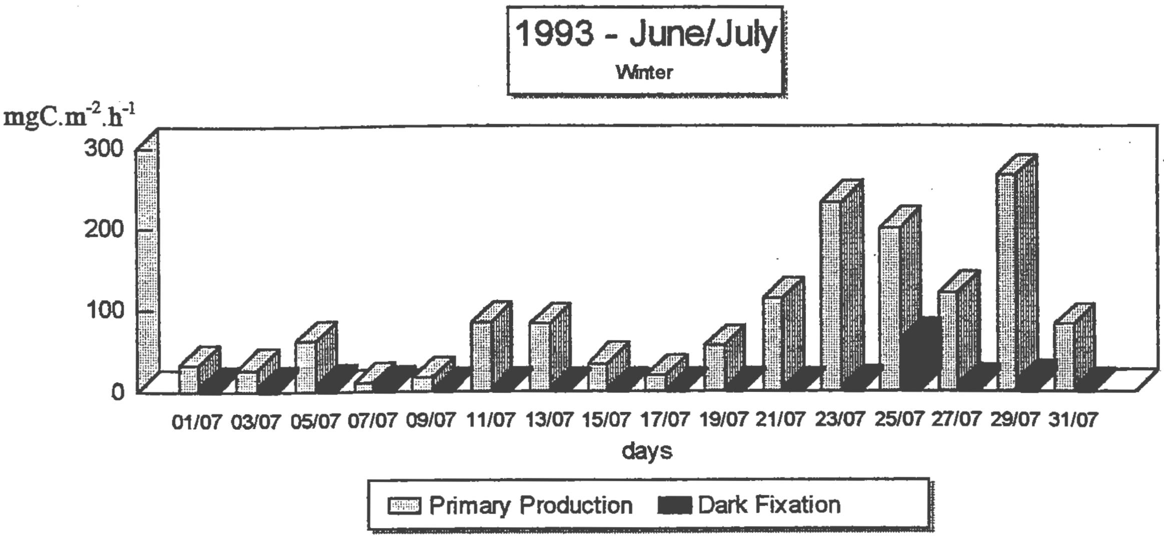

Figure 6. Phytoplankton primary production and dark fixation values for the Barra Bonita Reservoir in winter 1993.

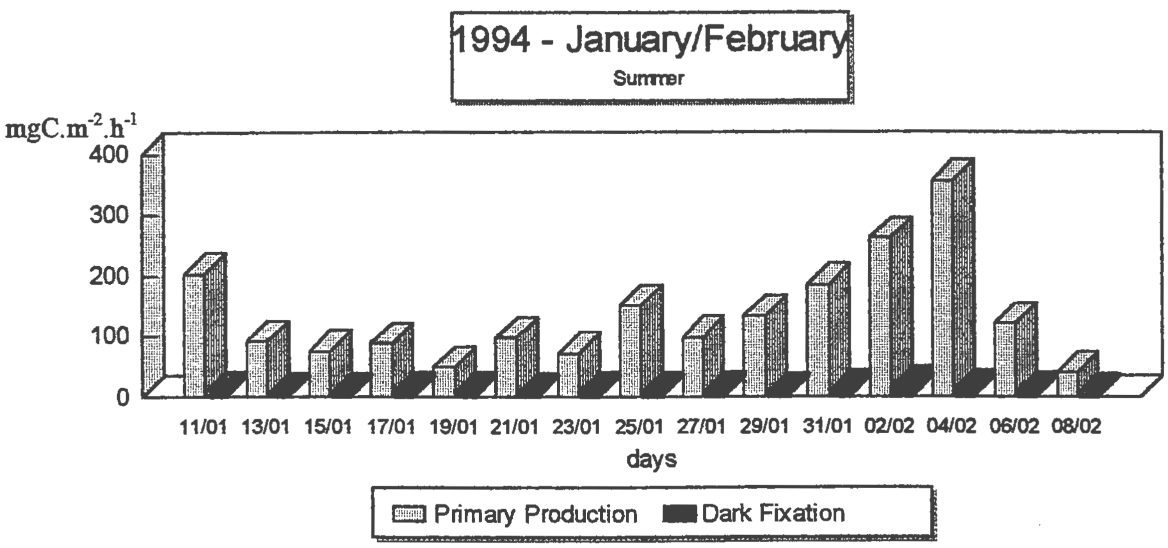

Figure 7. Phytoplankton primary production and dark fixation values for the Barra Bonita Reservoir in summer 1994.

ter, is probably related to sufficient nutrient availability, relativity good light conditions, high growth rates of these organisms and the mixing period. The appearance of the blue green algae *Microcystis aeruginosa* as of 9 July may have been favored by the beginning of a stagnation period, a low N/P ratio which occurred on 8 July and luxury uptake of P with the consequent increase in the chlorophyll concentrations.

On the other hand, in summer, higher temperatures and greater stability of the water column, were probably responsible for permitting the establishment of *Microcystis aeruginosa*.

For Reynolds (1984), the colonies of *Microcystis* establish themselves in the epilimnion after growth has been initiated in deep, anoxic waters. In many stratified lakes which support populations of *Microcystis*, this stimulus occurs only after the lake becomes thermally and chemically stratified (Reynolds, op. cit.). *Microcystis* will grow in unstratified water but it may still need anoxic sediments for its survival.

In more ecologically stable environments, such as that of the Barra Bonita Reservoir in the summer, the presence of the K-strategist, *Microcystis*, as an extreme K-selected phytoplankton was expected. In Lake George, Ganf (1974) attributed the presence of *Microcystis*, one of the strongest K-strategists to the frequency of the daily alterations between microstratification and holomixes. For Reynolds et al. (1987), in tropical lakes the daily alterations in thermal stratification and mixing represent a level of environmental constancy which could favor the dominance of *Microcystis*. The opposite was true during the ten days of winter, during which the environmental conditions favored the species which are more disturbance tolerant, that is, the r-strategists.

Conclusion

Although it appears to be difficult and problematic to identify disturbances in a highly mixed reservoir, with the presence of occasional stratifications and subject to external factors such as wind, precipitation, outflow, and the input of large loads of nutrients, the results show that the frequency and intensity of the disturbances have a critical influence on the establishment of the phytoplankton communities. Through the study of time scales carried out, it was possible to show that during summer (10 days) a state of equilibrium is established, with greater stability in the water column and lower diversity of species, and that situations of non-equilibrium occur during winter (10 days), with greater instability of the water column and greater diversity of species.

Acknowledgements

The authors wish to express their thanks to Dr. Colin Reynolds for the review and suggestions, to the FAPESP (Process number 91/0612-5), CNPq (Process number 300214/90-1), and CESP (Companhia Energética de São Paulo). The authors also thank Misha Klein for English translations and assistance.

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