

Phytoplankton ecological responses to the flood pulse in a Pantanal lake, Central Brazil.

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ABSTRACT: Phytoplankton ecological responses to the flood pulse in a Pantanal lake, Central Brazil.

Phytoplankton distribution patterns and directioner abiotic factors of their temporal variation were analyzed in a floodplain lake (Sá Mariana) of the Pantanal (Mato Grosso State), a huge wetland (140,000 km²) in central Brazil. Samples were collected monthly on the subsurface of a station in the pelagic region from September 1997 to August 1998. Phytoplankton biomass and composition were evaluated using the sedimentation method. Phytoplankton seasonality was strongly related to the flood pulse, with higher biomasses in the low water phase (average= 5.5mg fresh weight L⁻¹), when autochthonous processes lead to the accumulation of biomass. However, maximums also occur in high waters (11.6mg L⁻¹). They are a result of resuspension processes in which sediments containing diatoms are made available in the pelagic environment. Lower phytoplankton diversities (average=1.7 bits mg⁻¹) differentiate Sá Mariana lake from other floodplain lakes like those of the Amazon and Paraná rivers. Association P, represented especially by *Aulacoseira* sp. and *Aulacoseira granulata* and their varieties, dominated the community during the entire hydrological cycle studied. This functional group of the phytoplankton is characteristic of the mixed epilimnia in summers of temperate regions or turbulent shallow tropical lakes. The data indicate that phytoplankton growth in the form of chlorophyll a is more limited by nitrogen than by phosphorus. The availability of light and the mixing regime are also regulator factors of phytoplankton biomass and composition.

Key-words: phytoplankton, assemblages, floodplain lake, seasonality, regulator factors.

RESUMO: Respostas ecológicas do fitoplâncton ao pulso de inundação em uma lagoa do Pantanal, Brasil

Central. Padrões de distribuição do fitoplâncton e fatores abióticos direcionadores de sua variação temporal foram analisados em uma lagoa de inundação (Sá Mariana) do Pantanal de Mato Grosso, uma imensa planície de inundação no Brasil Central. De setembro de 1997 a agosto de 1998, coletaram-se amostras mensalmente na sub-superfície de uma estação na região pelágica. A biomassa e composição fitoplanctônicas foram avaliadas pelo método de sedimentação. A sazonalidade do fitoplâncton esteve relacionada fortemente ao pulso de inundação, com maiores biomassas na fase de águas baixas (média= 5.5 mg peso fresco L⁻¹), quando processos autóctones levam à acumulação de biomassa. No entanto máximos eventuais também ocorrem em águas altas (11.6 mg L⁻¹), resultantes de processos de ressuspensão de sedimentos contendo diatomáceas, disponibilizando-as para o ambiente pelágico. Menores diversidades fitoplanctônicas (média= 1.7 bits mg⁻¹), diferenciam a lagoa Sá Mariana de lagos de outras planícies de inundação como as do Rio Amazonas e Paraná. A associação P, representada, sobretudo por *Aulacoseira* sp. e *Aulacoseira granulata* e suas variedades, dominou a comunidade durante todo o ciclo hidrológico estudado. Este grupo funcional do fitoplâncton é característico do epilimnion mesclado em verões de regiões temperadas ou de lagos rasos tropicais turbulentos. Os dados indicam que o crescimento fitoplanctônico, na forma de clorofila a, está mais limitado por nitrogênio do que por fósforo, sendo a disponibilidade de luz e o regime de mistura também fatores reguladores da composição e biomassa fitoplanctônica.

Palavras-chave: fitoplâncton, associações, lagoa de inundação, sazonalidade, fatores reguladores.

Introduction

In the classical literature, the dominance of diatoms as a large taxonomic group has

been associated with low temperatures (Zhang & Prepas, 1996), low availability of light and deep mixing of the water column (Sommer, 1988). In addition, it is related to

high silica availability and low total phosphorus contents (Tilman et al., 1982). Diatoms generally dominate in lotic environments, including several rivers of the world (Uherkovich & Schmidt, 1974; Garcia de Emiliani, 1990; Rojo et al., 1994; Hötzel & Croome, 1996, O'Farrel et al., 2001; Melo, 2005), as well in deep lakes of temperate regions during the spring and autumn circulations (Huszar & Caraco, 1998) and also in polymictic tropical reservoirs (Marinho & Huszar, 2002; Calijuri et al., 2002) and coastal lagoon in south of Brazil (Torgan, 1998; Salomoni & Schwarzbald, 2004).

The genus *Aulacoseira*, in particular, has been related to turbulent environments (Kilham et al., 1986; Huszar et al., 1998) high flow and low light availability (Sherman et al., 1998). Temperature may be less critical to the occurrence of this genus, than mixing and suspension opportunities (Kilham & Kilham, 1975). Unlike what has been said about diatoms as a large taxonomic group, the genus *Aulacoseira* is related to high contents of total phosphorus and nitrate (Cobelas & Rojo, 1994; Train & Rodrigues, 1998). During periods of stratification, filaments of *Aulacoseira* settle to the bottom and the inocula are then resuspended during the circulation period of the water column (Garcia de Emiliani, 1973; Sommer, 1988; Reynolds, 1994).

It is reasonable to suppose that diatoms might be among the dominant species in the lakes that form the Pantanal complex (Mato Grosso State), an extensive flooded area that belongs to the Paraguay River basin (Central Brazil), whose aquatic systems are shallow and turbulent. Many of these systems have a high degree of connectivity and are submitted to annual fluctuations in water level. These variations promote transformations in the limnological properties and in the structure of the aquatic communities, which respond with adaptations to the flood pulse. There is an influx and outflux of materials, including organisms from lotic systems, through channels that interconnect them to the main rivers of the drainage basin (Junk et al., 1989).

Despite the importance of the Pantanal as a World Biosphere Reserve (www.mma.gov.br), due to the impressive amount of lotic and lentic ecosystems found in this biome, and activities such as fishing and ecotourism, the region has only recently

been studied from an ecological point of view. Knowledge of the aquatic community ecology of this large flooded area is of fundamental importance because the economic practices in the region should be guided by the diversity of the controlling factors of the dynamics of these environments, including their biological communities (e.g. phytoplankton). In relation to the phytoplankton community ecology, the aquatic systems of the Pantanal are among the least known in Brazil (Huszar & Silva, 1999) - only three quantitative studies exist. These studies point to the dominance of diatoms (including the genus *Aulacoseira*) in systems with less lotic influence and Cryptophyceae (especially *Cryptomonas* spp.) in environments with a more prolonged connection to the rivers, all with fluctuation in populations densities linked to the hydrological cycle (Lima, 1996; Espíndola et al., 1996; Oliveira & Calheiros, 2000).

The study of phytoplankton follows the most modern trends in ecology in the use of different biological features to include species in coherent functional groups, whose performance reflects important processes such as growth, loss and the acquisition of nutrients. They allow the prediction of characteristics of different environments (Statzner et al., 1997; Huszar & Caraco, 1998; Willby et al., 2000; Weithoff, 2003). Considering these aspects, the habitat model concept has been applied to phytoplankton, taking into account a certain number of diagnostic environmental axes, which differentiate attributes and adaptations of species that compose the pelagic vegetation (Reynolds, 1997; Kruk et al., 2002). The latest version of the scheme morphological-functional (Reynolds et al., 2002), still under construction, grouped species of phytoplankton into 31 (thirty one) assemblages, identified by an alphanumeric code and descriptions of different environmental conditions. Six of these assemblages include diatoms, all from well-mixed environments going from oligotrophic (assemblage A) to mesotrophic (assemblages B and N) and eutrophic (assemblages C, D and P) systems.

In this work, we looked at the temporal distribution patterns of the phytoplankton of a Pantanal floodplain lake (Mato Grosso State) and investigated the physical (light and mixing) and chemical (nutrients) factors that regulate dominance. We also used the

functional approach based on dominant species to examine phytoplankton dynamics. Biological regulation by grazing or parasitism, which may be important in controlling species composition and abundance, was not considered in this study.

Material and methods

Sá Mariana lake (Fig. 1) is located in the northern region of the Pantanal (16°14'S, 55°58'W, Mato Grosso State, Central Brazil) and situated on the left bank of the Cuiabá River, a tributary of the Paraguay River which is a large tributary of the Paraná River. The Pantanal is an extensive flood area of about

140,000 km², whose hydraulic gradient varies from 0.7 to 6.5 cm km⁻¹ (Ponce, 1995). Its complex hydrography, together with edaphic and geomorphological heterogeneity, determines a mosaic of landscapes with different hydrological conditions. This is due to the different positions they occupy on the floodplain. The climate of the region corresponds to type Aw of Köppen (Savannah Tropical) - hot and humid with rains in the summer and drought in the winter. Historical data show that annual total precipitation varies from 800 to 1600mm and annual average temperature fluctuates between a maximum of 29 to 32°C and a minimum of 17 to 20°C (PCBAP, 1997).

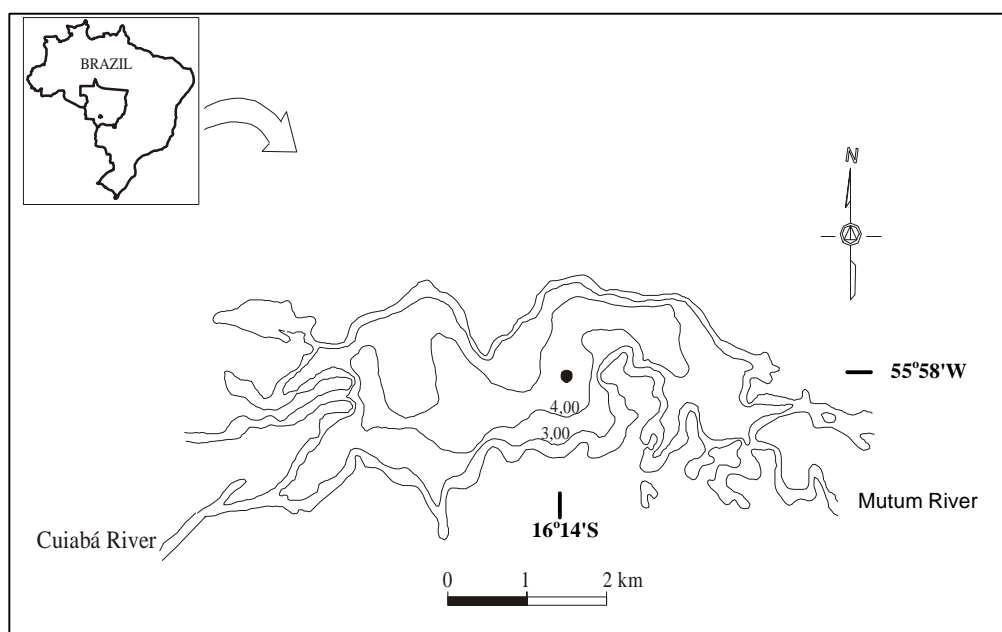


Figure 1: Location and map of Sá Mariana lake (Pantanal, Mato Grosso State) showing the sampling station (black dot).

Sá Mariana lake is an elongated permanent body of water with an area of 11 km² in the low water phase, a maximum depth of 4.7 m and an average depth of 3.6 m (Pinto-Silva, 1980). It constitutes an enlargement of a black water river, rich in dissolved organic matter and linked to the turbid Cuiabá River even during low waters. This determines the occurrence of two distinct regions. In the rainy season, it is also connected to an adjacent turbid-water lake, forming a wide flooded area of 450 km². It is located in an open area under constant wind action and has a coastal region covered by aquatic macrophytes, predominantly *Eichhornia azurea* Swartz and *E. crassipes* Martens.

Samples were collected monthly from September 1997 to August 1998 for the purpose of analyzing phytoplankton and the physical, chemical and physical-chemical variables of the water. This was carried out by passing a flask on the subsurface of a pelagic area heavily influenced by a dark-water river. The annual cycle covered the four phases of the hydrological cycle characteristic of floodplain lakes (rising, high water, falling, low water).

Phytoplankton samples were fixed with Lugol's solution and populations were enumerated in random fields (Uehlinger, 1964) using the inverted microscope technique (Utermöhl, 1958) at 200x magnification for the *Aulacoseira*

populations and 400x magnification for other populations. The units (cells, colonies and filaments) were enumerated to at least 100 specimens of the most abundant species (Lund et al., 1958). Specific biomass (mg fresh weight L⁻¹) was estimated from the product of the population density and mean unit volume of each species (Edler, 1979), assuming a specific density of phytoplankton cells of 1 g.cm⁻³. When it was possible, the determination of average cell size was based on measurements of at least thirty cells. Mean unit volume of diatoms was calculated from biovolume minus 35%, which corresponds to the vacuoles in pennate forms, and minus 65% in centric forms (Round et al., 1990). Phytoplankton assemblages were established according to Reynolds et al. (Reynolds et al., 2002) from species that contributed more than 5% to total biomass. Species richness was evaluated considering the total number of species in each sample (taxa per sample) and diversity by the Shannon and Wiener index (Shannon & Weaver, 1963).

Meteorological data were provided by Padre Ricardo Remetter Meteorological Station, about 40 km in a straight line from the lagoon. Temperature, electrical conductivity of the water and pH were measured using a WTW portable meter; alkalinity through the method of Golterman et al. (1978); water transparency by the depth of disappearance of the Secchi disc (SD); turbidity using a HACH 2100P turbidimeter; and suspended material according to Teixeira et al. (1965). The euphotic depth (Z_{eup}) was estimated as 3.0 times the extinction depth of SD (Cole, 1994). The depth ratio of the euphotic depth/maximum depth ($Z_{\text{eup}}/Z_{\text{max}}$) was used as a measure of the availability of light in the water column (Jensen et al., 1994). Dissolved oxygen was analyzed using the Winkler method modified by Golterman et al. (Golterman et al., 1978); total nitrogen (TN), ammonia nitrogen (N NH₄⁺) and nitrate (N NO₃⁻) by diazonic complex; total phosphorus (TP) and reactive soluble phosphorus (P-PO₄³⁻) by molybdate blue (Golterman et al., 1978; Mackereth et al., 1978).

Total light extinction (K_{total}) was calculated from SD as $K_{\text{total}} = -1 \times \ln(\text{SD}_{\text{light}})/\text{SD}$, where SD_{light} is the fraction of surface light penetration at SD depth, generally reported as 10% (Wetzel & Likens, 1991). Total light extinction (K_{total}) is the sum of extinction from the phytoplankton themselves (K_{phyto}), as well as extinction from colored organic

matter and inorganic turbidity (residual K , K_{res}). K_{phyto} was calculated as $\text{EP} \times \text{Chl-a}$, where EP is the biomass specific extinction (in m² mg Chl⁻¹) of phytoplankton, which generally varies between 0.01 and 0.02 for different phytoplankton (McBride et al., 1993). Here we use a value of 0.016.

Least square regressions were done on logarithmic (base 10) transformed data. Differences between data sets were calculated using non-paired T-tests. The biomasses of the main large taxonomic groups and the phytoplankton assemblages were related to the abiotic variables using Spearman Rank correlations (significant at $p < 0.05$). The reduced number of samples could have been the reason why significant correlations was not reached with the abiotic variables.

Results

The results consider three periods, according to the variation in phytoplankton composition and biomass: period I (September to November 1997), phases of low waters and the beginning of the rising; period II (December 1997 to June 1998), phases of rising, high waters and falling; period III (July and August 1998), covering a second low water phase (Fig. 2).

The monthly precipitation presented marked variability (Fig. 2a), being relatively high during the rising (end of period I and beginning of period II) and practically absent at the end of falling to the beginning of low waters in 1998 (end of period II to the beginning of period III). If compared to historical averages the period studied had very little rain (700 mm). This corresponds to El Niño event (1997-98), which in this region results in a more conspicuous dry period with significant reduction in hydrometric level ($p < 0.001$) in relation to previous years. The annual average of air temperature was 27°C, fluctuating in a range of 7.3°C between the coldest and the hottest month of the year. The surface water temperature varied between 19 and 40°C during the study (Fig. 2a and 2b). The falling period coincided with the months in which the temperatures were lower. The wide variation in the maximum depth of the lake (0.5 to 3.0 m, Fig. 2b) was not significantly related ($p = 0.42$) to the local pluviometric precipitation, but it was significantly related to the hydrometric level (HL) of the Cuiabá river ($p < 0.0001$), which explained 95% of

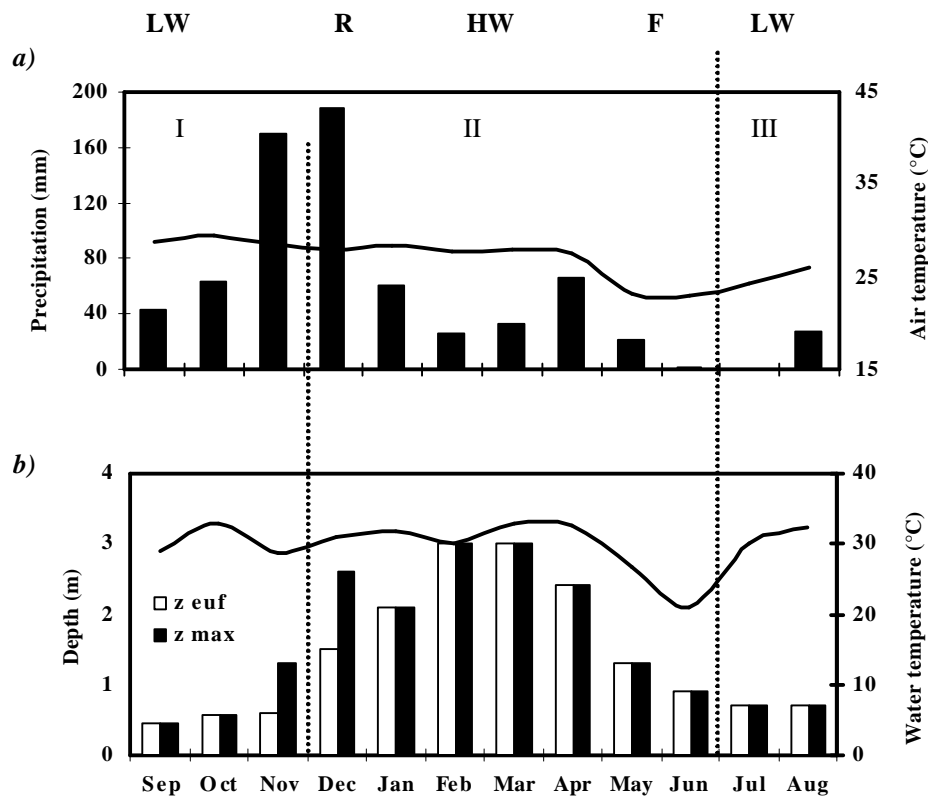


Figure 2: Variation in a) precipitation (columns) and air temperature (line); b) maximum depth (z_{\max}), euphotic zone (z_{eup}) and temperature in surface waters in Sá Mariana lake (LW= low water, R= rising, HW= high water, F= falling).

the maximum depth variability of the lake ($z_{\max} = -0.96 + 0.744 \text{ HL}$). The wide ratio between the area of the lake and its average depth, as well as the wind regime of the region (Tab. 1), allied to its shallowness, impose a daily circulation regime of the water mass on the lake. Maximum winds of $4 \text{ m}\cdot\text{s}^{-1}$, which blow most of the year in the direction of the transversal axis of the lake (2.7 km), were recorded during most of the sampling dates.

The high coefficient of light extinction in Sá Mariana lake (average = 4.649 m^{-1}) and the high proportion of extinction by non-phytoplankton particulate material and/or by dissolved organic matter (average $K_{\text{res}} = 4.548 \text{ m}^{-1}$) suggests that the limitation by light may be an important factor acting on the phytoplankton. However, no significant correlation was found between total biomass or taxonomic groups and the coefficient of extinction by non-phytoplankton material. It should be emphasized that the ratio z_{eup}/z_{\max} (euphotic depth/maximum depth), as an expression of light availability, was high, indicating a

totally illuminated water column during most of the study. November and December were exceptions due to the more intense rains during the rising, when the euphotic zone reached 50 and 60% of the water column, respectively (Fig. 2b). If the averages of turbidity and suspended material are considered (Tab. 1), the waters of the lake may be evaluated as more turbid during the second low water period (period III) than in the other periods.

On average, the waters of the lake were slightly acidic, with low alkalinity values and, consequently, high CO_2 concentrations (Tab. 1). The punctual data of pH revealed a tendency for lower values (5.3 - 6.5) in the first low water phase and during the rising (period I and the beginning of period II) and higher values (5.6 - 8.0) starting from this phase until the end of the study (Fig. 3a). The waters of Sá Mariana were, on average, supersaturated in dissolved oxygen in the first low water phase and subsaturated in the other phases (Tab. 1). The electrical conductivity of the water was relatively low during the entire study, with 83% of the

Table I: Average and standard deviation of climatological and limnological variables, and phytoplankton in surface waters of Sá Mariana lake during the study period (Z_{\max} = maximum depth; Z_{eup} = euphotic zone).

	Period I Sep-Nov 1997	Period II Dec-Jun 1998	Period III Jul-Aug 1998
Air temperature (°C)	30.9±4	29.4±5.4	37.2±4.4
Precipitation (mm)	92±67.8	56±62.2	14±19.5
Monthly maximum wind (m s ⁻¹) *	3.8±0.74	2.9±1.35	2.0±0
Hydrometric level of the Cuiabá River (m)	2.5±0.4	4±1.1	2±0.1
Water temperature (°C)	30.2±2.4	29.4±4.3	31.1±1.6
Z_{\max} (m)	0.77±0.5	2.19±0.8	0.70±0
Z_{eu} (m)	0.54±0.1	2.03±0.8	0.70±0
Z_{eu}/Z_{\max}	0.9±0.3	1.0±0.2	1.0±0
Suspended material (mg L ⁻¹)	10±0	10±0	20±2
Turbidity (NTU)	6.7±2.4	8.8±5.6	18.6±4.3
Conductivity (µS cm ⁻¹)	11±10.3	16±8	7±1.7
pH	6±0.4	6.8±1.2	6.75±0.8
Alkalinity (meq L ⁻¹)	180±7	234±16	65±85
CO ₂ (mg L ⁻¹)	5.6±3.8	5.8±8.3	0.6±0.8
Dissolved oxygen (%)	125±20.9	75±16.6	87±2.2
N NH ₄ ⁺ (µM)	3.14±1.1	2.57±2.3	1.49±0.3
N NO ₃ ⁻ (µM)	1±0.8	0.85±0.8	0.5±0
P PO ₄ ³⁻ (µM)	1.3±0.5	1.3±1.3	0.8±0.1
Total nitrogen (µM)	11±6.2	22±8.8	12±0.5
Total phosphorus (µM)	6.3±4.9	6.7±4.8	1.9±0.2
Total nitrogen/Total phosphorus (atomic)	3±3.4	9±13.3	6±0.3
Biomass (mg fresh weight L ⁻¹)	3.5±1	2.5±4.1	7.5±4
Richness (taxa/sample)	19±5.1	18± 4.2	24 ±4.2
Diversity (bits mg ⁻¹)	1.4±0.6	1.8±0.8	1.6±0.3

*Maximum wind in the 24 hours before the collection.

data below 20 mS cm⁻¹. Monthly values increase during the rising (5-31 mS cm⁻¹) and declined (6-20 mS cm⁻¹) from high waters until the second low water phase (Fig. 3a).

Sá Mariana lake is characterized by low concentrations of both dissolved inorganic nitrogen (average DIN= 3.35 mM) and total nitrogen (average TN= 17.70 mM), with 74% of the DIN as N NH₄⁺. On the other hand, relatively high contents of total phosphorus (average TP= 5.8 mM) and reactive soluble phosphorus (average P PO₄³⁻= 1.1 mM, Tab. I) were recorded. The dissolved forms of N and P tended to decline from the first low water phase until the beginning of the rising (periods I and II). The wide data variability, with two maxima in the dissolved inorganic forms in the high water phase (N in March and P in February, Fig. 3b) should be emphasized. In addition, N NH₄⁺ values near zero and greatly reduced N NO₃⁻ values were recorded in January 1998. TN was characterized by higher average

concentrations in period II (rising, high water and falling) and TP in periods I and II (Tab. I). A clear increase in the TN concentrations was observed from the low waters of 1997 until the end of the falling phase (periods I and II), decreasing markedly again in the second low water phase (period III, Fig. 3c). Fluctuations in TP were more conspicuous and presented values below The atomic ratio average TN/TP was low during the entire study (<7), with higher values (>16) only in April and May (falling).

During the study, 80 taxa of planktonic algae were recorded in Sá Mariana lake: 26 Chlorophyceae, 24 Bacillariophyceae, 14 Cyanobacteria, 12 Zygnemaphyceae, 02 Cryptophyceae, 01 Dinophyceae and 01 Chrysophyceae. However, on average, only five species and their varieties contributed more than 5% each to total biomass in each period (Tab. II).

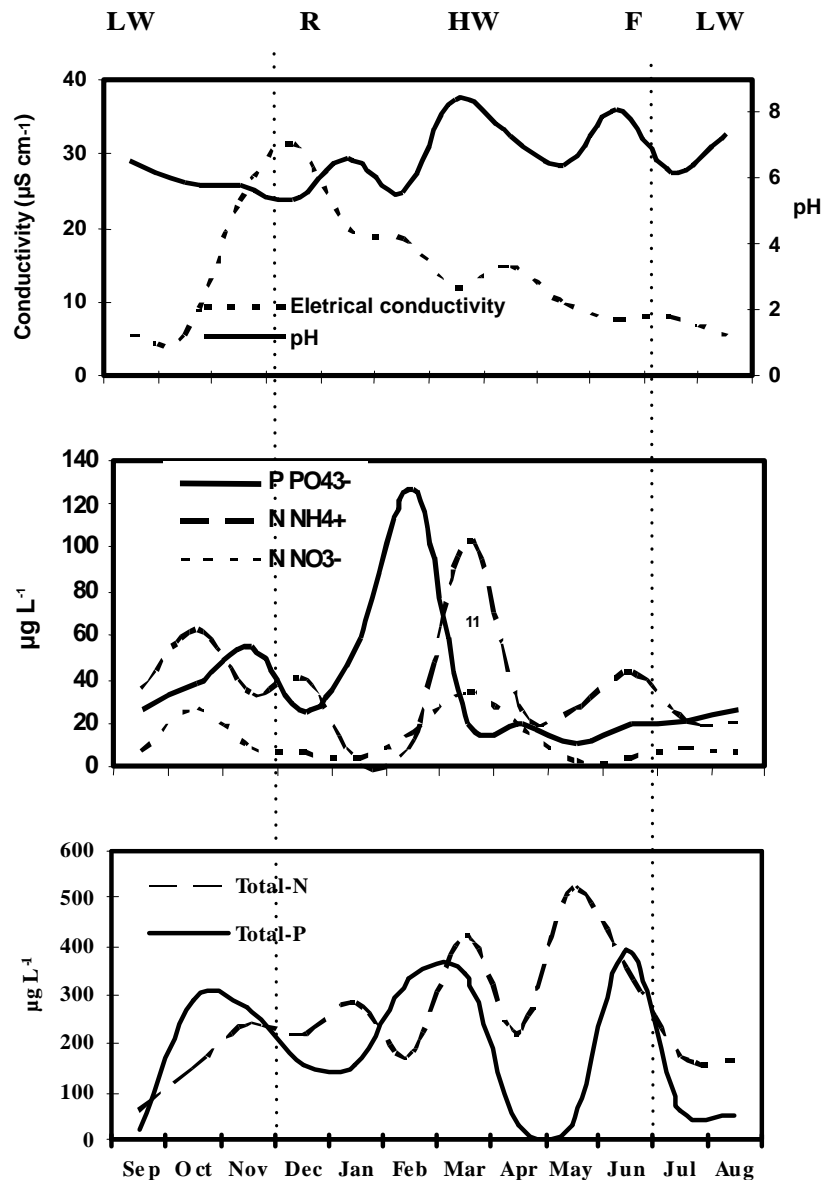


Figure 3: Variation in a) electrical conductivity and pH; b) SRP, ammonium and nitrate concentrations; and c) total nitrogen (Total-N) and total phosphorus (Total-P) concentrations in surface waters of Sá Mariana lake (LW= low water, R= rising, HW= high water, F= falling).

The total biomass of the phytoplankton, expressed in the form of fresh weight, varied from 0.2 to 11.6 mg L^{-1} , with maximums in March (high waters) and July (low waters), which were about 2.5 times greater than the average biomass of the entire study. No significant correlation was found between total biomass, as fresh weight, and its predicted driving factors like temperature, light, hydrometric level and nutrients. However, if the phytoplankton

biomass expressed in the form of chlorophyll a is considered, the variability was significantly explained ($p=0.009$) by DIN concentrations, Z_{max} and coefficient of extinction of the non-phytoplankton light, K_{res} ($\log\text{-Chl}=0.266 + 0.496 \log\text{-DIN} - 0.884 \log\text{-}Z_{\text{max}} - 0.406 \log\text{-}E_{\text{res}}$; $r^2=0.83$).

Three periods were recognized, taking into account the variability in the phytoplankton composition and biomass (Fig. 4).

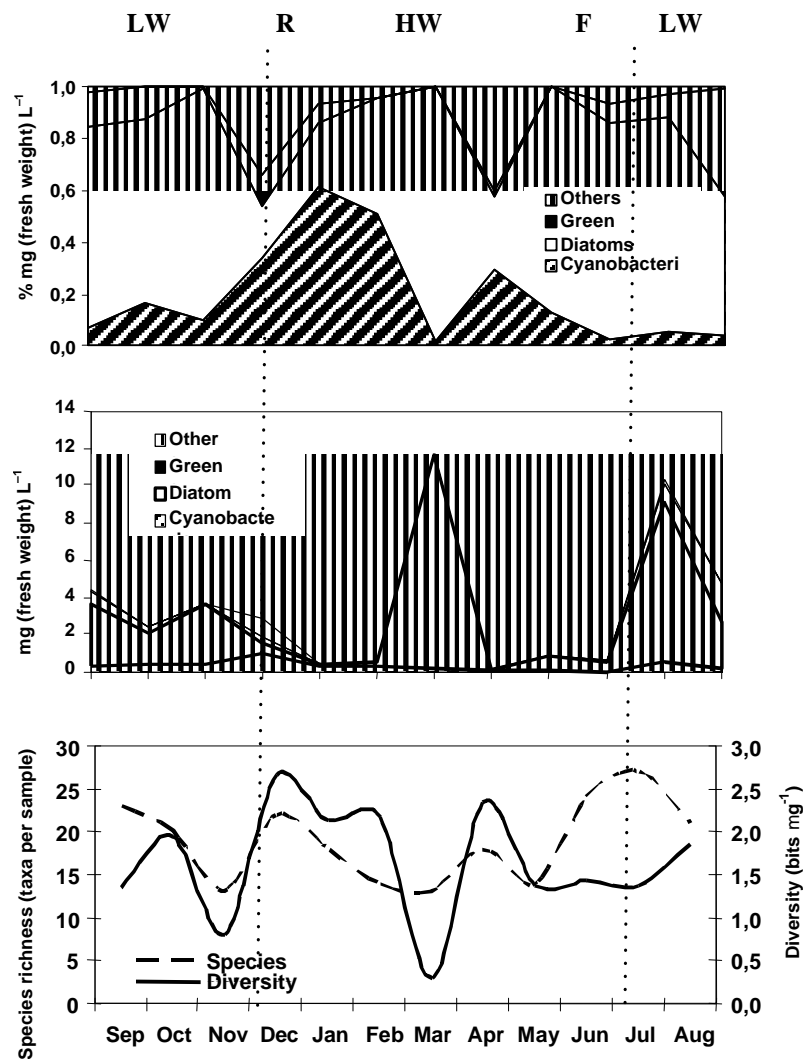


Figure 4: Variation in a) relative and b) absolute phytoplankton biomass per taxonomic group; and c) species diversity and richness in surface waters of Sá Mariana lake (LW= low water, R= rising, HW= high water, F= falling).

The low water and beginning of the rising phases of 1997 (period I) were characterized by intermediate-value average biomass (3.5 mg L⁻¹) and little temporal variability. The diatom *Aulacoseira* sp. was the dominant species and contributed, on average, 76% to total biomass. Populations of *Aulacoseira* (*A. granulata* (Ehrenberg) Simonsen var. *granulata*, *A. granulata* var. *angustissima* (O. Müller) Simonsen, *A. distans* (Ehrenberg) Simonsen, *A. italica* (Ehrenberg) Simonsen and *A. herzogii* (Lemmermann) Simonsen) also contributed. Accompanying populations of chlorophyceae *Eutetramorus* sp. and cyanobacteria *Microcystis aeruginosa* Kützing, with average contributions of 6 and 7%, respectively, were recorded in this

period. The end of the rising, high waters and falling phases (period II) were marked by relatively low average biomass (2.5 mg L⁻¹) and by dominance of *Aulacoseira* sp. (46%) and *A. granulata* and their varieties. This dominance was followed by *Microcystis aeruginosa* (16%) and desmid *Closterium setaceum* Ehrenberg ex Ralfs (10%). Differently from period I, however, conspicuous fluctuation in biomass due to a maximum value occurred in March (11.6 mg L⁻¹) was observed, with the almost total dominance (99%) of *Aulacoseira* sp. The second low water phase (period III) was marked by high average biomass (7.5 mg L⁻¹) and the dominance of *Aulacoseira* sp. and *A. granulata* and their varieties (64%), followed by *Botryococcus* sp. (16%) and

Eutetramorus sp. (8%). A second conspicuous increase in biomass occurred in this period, with populations of Aulacoseira contributing, on average, 64% to a total of 10.4 mg L⁻¹.

In Sá Mariana lake, diversity was, on average, relatively low during the entire study (Tab. I; Fig. 4c) and was lower (1.4 and 1.6 bits.mg⁻¹, respectively) in both low water phases (periods I and III), if compared to the rising, high water and falling phases (period II; 1.8 bits mg⁻¹ and 43%, respectively). Assemblages of dominant algae were aggregated, to which five species together contributed, on average, 83% of the total biomass during the study (Tab. II). Assemblage P, formed by filamentous diatoms (Aulacoseira spp.) and

elongated unicellular desmids (Closterium setaceum), was the main describer assemblage of the system, contributing, on average, 64% to total biomass. It was followed by assemblage F (8%), formed by immobile algal colonies embedded in mucilage (Eutetramorus sp. and Botryococcus sp.), and assemblage M (12%), comprising cyanobacteria colonies (Microcystis sp.). P assemblages, is common in mesotrophic lakes in low latitudes; F assemblages, characteristic for clear epilimnia, tolerant to low nutrient and sensitive to high turbidity; and M assemblage, may dominate in shallow lakes with daily mixing in low latitudes, according to Reynolds (1997).

Table II: Percentage of biomass (means) of phytoplankton assemblages (Ass.) as dominant groups of species, per period in Sá Mariana lake. Labels according to Reynolds et al. (2002).

Period I	Ass	Period II	Ass	Period III	Ass
Sep-Nov 1997		Dec-Jun 1998		Jul-Aug 1998	
76% Aulacoseira sp.	P	52% Aulacoseira sp.	P	64% Aulacoseira sp.	P
7% Eutetramorus sp.	F	16% Microcystis aeruginosa	M	16% Botryococcus sp.	F
6% M. aeruginosa	M	10% Closterium setaceum	P	8% Eutetramorus sp.	F

Discussion

The influence of the variation in water level in structuring aquatic communities generally in floodplain lakes has been widely recognized in the literature (Junk et al., 1989; Neiff, 1990). The phytoplankton in these systems, for example, has temporal distribution patterns driven by a group of forces produced by the flood pulse, which interact with climatic and biotic factors (Train & Rodrigues, 1997; Ibanez, 1998; Huszar, 2000). In Sá Mariana lake, some attributes of the phytoplankton community could be associated with the seasonal variability of the environmental conditions, even if significant correlations between the regulating factors and plankton composition/biomass have not been found. Peaks of total biomass occurred in both low and high waters but the highest average biomass occurred in the two low water phases. The absence of causal relationships between the bottom up control (light and nutrients) and the phytoplankton biomass may be thought as a reflection of the intense hydrodynamism of the system.

In addition, the great diversity of habitats in systems such as the Pantanal probably allows the co-occurrence of many species with differing strategies and levels of adaptation as a result of cyclical changes caused by the flood pulse (Junk et al., 1989). However, contrary to what has been recorded for floodplain lakes in the Amazon (Huszar & Reynolds, 1997), and the upper (Train & Rodrigues, 1998) and middle (Garcia de Emiliani, 1993) Paraná River, phytoplankton diversity in Sá Mariana lake was low (average= 1.7 bits mg⁻¹), owing to the dominance of diatom Aulacoseira sp. Typical species of well-mixed environments persist in Sá Mariana throughout the year. The high species abundance of this group of algae and of the associated chlorophyceae was also observed in other water bodies in the Pantanal (Lima, 1996; Oliveira & Calheiros, 2000). Indeed, when dominant in freshwater systems, diatom species generally occur in small number usually varying from 1 to 4 species (Cobelas & Rojo, 1994). The persistent dominance of Aulacoseira throughout the year is clearly associated with the continual mixing of the

system, which promotes its maintenance in the pelagic environment and still allow frequent access to layers with greater availability of light (Kilham & Kilham, 1975; Reynolds, 1994; Hötzel & Croome, 1996; Sherman et al., 1998). Daily periods of stratification and mixing recorded in previous 24-hours study in Sá Mariana lake (Pinto-Silva, 1980) and homogeneous thermal profiles observed during the present study permit its inclusion in continuous warm polymictic systems according to the classification of Lewis (1983).

The diatoms constituted two maxima, independent of lake depth: one in high waters and the other in the second phase of low waters. It should be emphasized that even in high waters, the lake was only three meters deep, which keeps it in the shallow system category and subject to daily total mixing. In fact, assuming the considerations of Reynolds (1997) on page 47 and the intensity of the winds at the sampling time (generally about 4 m s^{-1}), a three-meter thick layer could, on average, be submitted to a mixing time of only nine minutes. Everything indicates that suspended maintenance, more than access to light, was the key factor in the massive dominance of *Aulacoseira* sp. in Sá Mariana lake, since the high z_{eu}/z_{eup} ratio showed the availability of light in the entire water column during most of the study.

In addition to the physical regime, the bottom up control by nutrients is of fundamental importance to the understanding of phytoplankton assemblage dynamics, which are strongly related to the trophic state of the systems. The identification of the trophic state of shallow tropical aquatic environments is complex (Esteves, 1988; Huszar et al., 1998). If the criteria widely accepted by the Organization for Economic Cooperation and Development (OECD) are considered (Vollenweider & Kerekes, 1980), as well as the annual average of TP (5.77 mM), Sá Mariana lake could be classified as an eutrophic system. However, if the chlorophyll content is considered (7.6 mg.L^{-1}) the system would be included in the mesotrophic range. It may be supposed, therefore, that other factors than phosphorus could be influencing phytoplankton growth. Indeed, if the average concentrations of TN (17.7 mM) are considered, the system is clearly oligotrophic. Thus, the classic, significant

and strong correlation between P-total and chlorophyll a verified for temperate regions, where P is the main limiting factor for phytoplankton growth (Smith, 1982; Mazumder, 1994; Nürnberg, 1996), was not verified for Sá Mariana lake. There was no significant correlation between TP and chlorophyll a, but the chlorophyll a concentrations were strong ($r^2=0.83$) and significantly ($p=0.0093$) predicted by the combination of the variability in dissolved inorganic nitrogen concentrations, maximum depth of the lake and coefficient of extinction of light by non-phytoplankton contribution. This is indicative that N can be thought as limiting to phytoplankton growth in the lake, which has been argued by other authors writing about tropical regions (Lewis, 1996).

Analyses of changes in the phytoplankton community have been traditionally focused on the main taxonomic groups and/or dominant species. Adequate filters to cover the occurrence of most species are difficult to establish while the conditions that favor large taxonomic groups are ambiguous and overlap. The functional group (phytoplankton assemblages) approach, using tolerances and sensitivities, can better define the conditions of the system and contribute to a better understanding of the habitat where these assemblages live (Reynolds et al., 2002). Given the physical and chemical conditions of Sá Mariana lake, assemblages C, D and P, typical of enriched turbulent environments, should be the most likely dominants. In fact, assemblage P, typical of the mixed epilimnion in summers of temperate regions or low-latitude shallow lakes, sensitive to stratification and to depletion of silica and tolerant of carbon and light deficiency, was the main functional group present in Sá Mariana lake. The dominant genus *Aulacoseira* includes species widely recognized as characteristic mainly of turbulent periods in eutrophic lakes (Kilham & Kilham, 1975; Lima et al., 1979; Cobelas & Rojo, 1994; Reynolds et al., 2002). The growth limitation levels of diatoms may be estimated from the half-saturation constants for population growth (K_s), in relation to the main nutrients (Reynolds, 1997) such as reactive soluble phosphorus ($0.10\text{-}0.16 \text{ mM}$) and dissolved inorganic nitrogen ($6\text{-}8 \text{ mM}$), and reactive soluble silica (average= 1.5 mM) as shown for 10 ten diatom species from thirty 30 data

in the literature (Tilman & Kilham, 1976; Kilham et al., 1977; Tilman et al., 1982; Sommer, 1988). Assuming these levels, it is unlikely that the phosphorus concentrations (average SRP= 0.67 mM) could limit phytoplankton growth in Sá Mariana lake. Low concentrations of dissolved inorganic forms of nitrogen (average= 3.2 mM), which are below those required to half-saturate the growth of most algal species, indicate that this nutrient may restrict phytoplankton growth. In fact, ammonium was the only nutrient that was significantly related ($p=0.03$) to diatom biomass, explaining 33% of biomass variability. Low TN/TP ratios (by atom), almost always below 16 (Redfield et al., 1963), also suggest that nitrogen may be the nutrient more likely to limit phytoplankton growth, while silica is probably not a limiting nutrient. Although there are no silica data for the present study, previous information indicated high silica concentrations in Sá Mariana lake (96 mM) (Pinto-Silva, 1980). These values are about 65 times higher than the half-saturation constant for diatom growth.

Considering that N probably limits phytoplankton growth in Sá Mariana lake and both the absolute concentrations of N and P (Reynolds, 1999) and their ratios in the definition of the freshwater phytoplankton composition, an ample development of cyanobacteria was expected (Bulgakov & Levich, 1999; Smith & Bennett, 1999). However, the relative environmental constancy that favors the dominance of cyanobacteria (Paerl, 1988) was not verified, at least in the sampling region with great river-influenced hydrodynamism. In fact, during the low water period of 1997 (September/October), the development of *Anabaena cf. spiroides* was observed in areas less influenced by the river (not sampled in detail in this study).

In short, the seasonality of the phytoplankton of Sá Mariana lake was strongly related to the flood pulse, with high biomass in the low water phase and peaks occurring in high waters. Low phytoplankton diversities differentiate this lake from others of the Amazon and Paraná floodplains. Assemblage P (*Aulacoseira* sp. and *Aulacoseira granulata* and their varieties), formed by species typical of turbulent environments, dominated the community during the entire hydrological cycle. In addition, phytoplankton growth

limitation, expressed in the form of chlorophyll a, is more related to N than P. Light availability and the mixing regime are

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