Phytoplankton in an Amazonian flood-plain lake (Lago Batata, Brasil): diel variation and species strategies

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Abstract . Phytoplankton diel variations in an Amazonian flood-plain lake (Lago Batata) were studied quarterly for 1 year, according to the hydrometric level fluctuation of the Trombetas river (39.7–47.0 m over sea level), to which the lake is permanently connected. Hydrological and hydrographic conditions determined mixing patterns of the water column and phytoplankton distribution. When the lake is deep (>4.0 m), sparse phytoplankton communities are found at the bottom, by thermal discontinuities, and may remain so for a short duration (days). When the lake is shallow (<4.0 m), mixing of the waters ensures a nearly even distribution of organisms throughout the water column. The weak stability of stratification is a major influence on the distribution of phytoplankton population densities in this shallow flushed lake. The highest phytoplankton densities during the second part of the day, mentioned in the literature, are observed only during decreasing water level. During the other phases of the hydrological cycle (increasing, high and low water levels), no differences in phytoplankton population density were observed throughout the diel cycle. Assemblages, or groups of descriptor species of systems having similar features, have recently been proposed. Assemblages of flushing-tolerant nano-algae (X_1) and of mixing-dependent species (**T, S**) have shown that the physical properties of the environment were often the strongest determinants of the phytoplankton strategies.

Introduction

Minimal seasonal variation in day length and heat income does not prevent remarkable phytoplankton seasonal cycles in the tropics, where the fluctuations in phytoplankton biomass and composition are related mainly to changes in hydrological and hydrographical conditions, including variations in water level in flood-plain lakes (Dias, 1992; Sanchez, 1992; García de Emiliani, 1993; Huszar and Reynolds, 1997; Ibañez, 1998, Train and Rodrigues, 1998). Variations in the dry and rainy seasons, and management of reservoirs, are also important (Calijuri and Tundisi, 1990; Arcifa *et al.*, 1998; Goodwin and Giani, 1998).

The magnitude of diel cycles in limnological processes in tropical waters has been considered to be comparable with the seasonal variations in temperate lakes (Ganf and Horne, 1975; Barbosa *et al.*, 1989; Talling, 1992; Patterson and Wilson, 1995). Different diel patterns of biomass and vertical distribution of tropical and subtropical phytoplankton communities have been documented (Vaas and Sachlan, 1955; Talling, 1957; Ganf, 1974; García de Emiliani, 1976, 1990; Torgan *et al.*, 1981; Reynolds *et al.*, 1986; Toledo *et al.*, 1988; Gavilán, 1990; Huszar *et al.*, 1994; Patterson and Wilson, 1995; Reynolds 1996). Most of these papers reported phytoplankton diel variations in vertical distribution as being dependent on (i)

mixing properties, (ii) occurrence of self-regulating populations by active movement via flagella, or passive movement through pseudovacuoles, and (iii) occurrence of fast-growing species, which are able to change in abundance during a single diel cycle. Another general pattern that has been shown was the occurrence of higher phytoplankton population densities during the second part of the day.

Hydrological and hydrographical properties define the mixing behaviour of water in Amazonian flood-plain lakes. Total mixing of the water column, at least once a day, has been reported when the lakes are shallow (<4–5 m), and persistent stratification when they are deep (>4–5 m) (Tundisi *et al.*, 1984; Camargo and Miyai, 1988; MacIntyre and Melack, 1988; Melack and Fisher, 1990). Co-occurring groups of recurrent phytoplankton species of Lago Batata—hereinafter Batata Lake—are predominantly selected by these hydrological and hydrographical conditions, and not as a consequence of wholly internally-driven processes of the phytoplankton community (Huszar and Reynolds, 1997; Huszar, 1999).

Lakes can be characterized by groups of phytoplankton species which share common advantageous attributes. Applying a subdivision based on species strategies (C-invasive, S-acquisitive, R-attuning species), Reynolds (Reynolds, 1988, 1997) separated the pelagic vegetation along phytosociological lines, following the precedent set by terrestrial classification (Grime, 1979). C-strategists are small phytoplankton, with a high surface/volume (S/V) ratio, that grow quickly and are selected by conditions of both high light and high nutrients; S-strategists are slow-growing, large unicells or colonies, with a low S/V ratio, which are able to dominate under conditions of high light and low nutrients; R-strategists are generally large, elongated unicells and colonies or filaments, with a high S/V ratio, which are adapted to low light and high nutrient conditions (Reynolds, 1997). According to their growth strategies, the pelagic vegetation was classified in a number of assemblages, each being more likely to occur under particular environmental conditions (Reynolds, 1997; Padisák and Reynolds, 1998, Huszar *et al.*, in press). These groups can be used to indicate recent environmental conditions more accurately than phylogenetic representatives (Reynolds, 1997; Huszar and Caraco, 1998). Flushing-tolerant nano-algae (assemblage X_1 and **Y**; C-strategists), mixing-dependent desmids and diatoms (assemblage **P**), and light-harvesting filamentous cyanoprokaryotes (assemblage **S**; R-strategists), have been noted as the dominant assemblages in Batata Lake during different hydrological cycles (Huszar and Reynolds, 1997).

The dominant role of the river hydrology in determining the seasonality of phytoplankton in Batata Lake has been shown through studies of primary production (Roland *et al.*, 1997). This role has already been recognized in other Amazonian flood-plain systems (Sioli, 1984), and it conforms to the flood-pulse concept of their structure, metabolism and productivity (Junk *et al.*, 1989; Neiff, 1990). Diel variations in physical and chemical conditions, and also in phytoplankton biomass as chlorophyll *a*, have been compared between Batata Lake and another lake on the same flood-plain (Esteves *et al.*, 1994). Despite their close proximity, the metabolism of the lakes differed as a consequence of morphometry, hydrology and position on the flood-plain.

As far as we are aware, phytoplankton diel dynamics in flood-plain lakes have been studied only in a small and shallow system (1.2 m) in the Paraná river (García de Emiliani, 1990). Continuous mixing of the waters here ensured a near even vertical distribution of phytoplankton, and highest population densities were reported during afternoon for that lake.

The aim of this study was to make a detailed investigation of the diel variation in phytoplankton community structure in the high-flushing Amazonian Batata Lake. Differentiation was made between vertical and diel distribution in different seasons. Also, the strategies of the phytoplankton assemblages in relation to the hydrological cycle of Trombetas River are discussed.

Site of study

Batata Lake (56°14′, 56°00′W; 1°28′, 1°33′S) is located on the south bank of the Trombetas River, a north-bank tributary of the Amazon River (Figure 1). The total area and depth of the lake changes considerably during the year as a function of the water level in Trombetas River, which may fluctuate by more than 6 m. From low to high water levels, the area of Batata Lake changes by more than 10 km^2 [18 km^2 at low water level (Panosso *et al.*, 1995) and 30 km^2 at high water level (Roland and Esteves, 1993)]. The Trombetas River and Batata Lake remain interlinked throughout the year. This interlinkage is intensified when the water
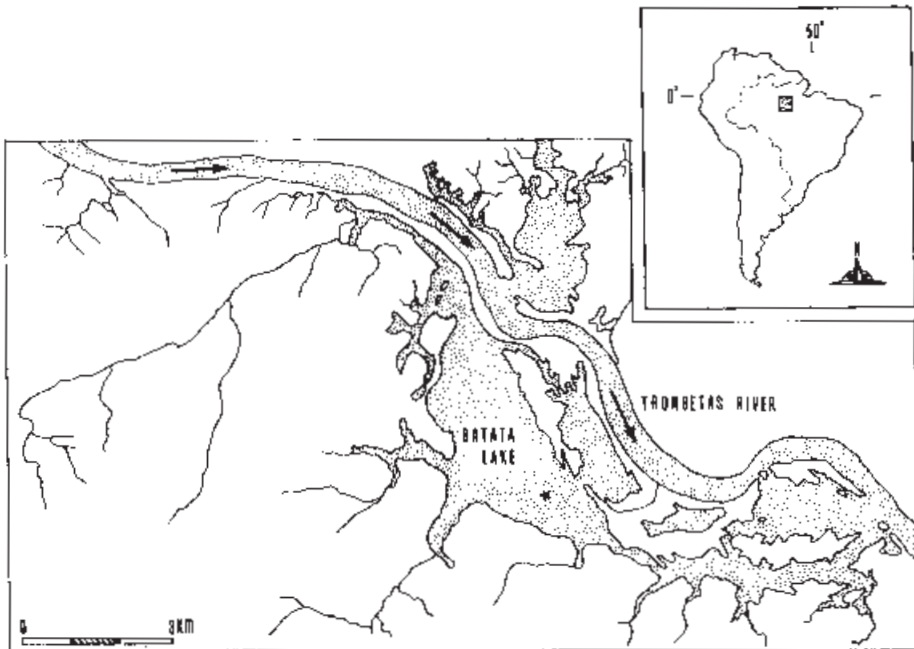
Fig. 1. Map to show the location of Batata Lake and its relation to the Trombetas River and the sampling station (*).

level rises above the shoreline dykes which may occur at several places. The regional climate corresponds to the *Am*-type of Köppen (Brasil, 1984), a humid tropical monsoon climate, with high precipitation during some months (February–May) and 1–2 months (August–September) with rather less (<60 mm).

Batata Lake waters are characterized by relatively low values of electrical conductivity, pH, alkalinity and soluble reactive phosphorus (Melo, 1996). By the standards of temperate lakes, the system would be considered to be meso- or eutrophic, but the assemblages of phytoplankton indicate oligo–mesotrophic tendencies (Huszar *et al.*, 1998).

An additional feature of the study site is the bauxite tailings, which cover some 30% of the total lake area at high water level (Roland and Esteves, 1993). These resulted from ore processing by Mineração Rio do Norte S.A. Company.

Method

Sample collections were carried out quarterly over a 1-year period. One sampling station was established in the main body of the lake in an area free of influence by bauxite tailing (Figure 1). The intervals were planned to take into account the different phases of the regional hydrological cycle (Figure 2): September, 1989, with falling water level; December, 1989, minimum water level; March, 1990, when the water level was increasing and June, 1990, with maximum water depth.

The water samples were taken at 10:00, 14:00, 18:00, 24:00 and 06:00 h, at six depths in decreasing water level (0, 1, 2, 3, 4 and 4.5 m), low water level (each 0.5 m) and high water level (0, 1, 2, 3, 5 and 7 m), and at five depths in increasing water level (0, 1, 2, 4 and 6 m). The subsurface samples were collected by filling bottles directly with water and the others with a Van Dorn bottle. The phytoplankton samples were fixed with Lugol's Iodine solution and the phytoplankton were identified and enumerated following the sedimentation and inverted-microscope method of Utermöhl (Utermöhl, 1958). The units (cells, colonies and filaments) were enumerated in random fields (Uhelinger, 1964), at least 100 specimens from the most frequent species [$P < 0.05$; (Lund *et al.*, 1958)]. Species diversity and evenness were estimated according to the Shannon-Wiener index (Shannon and Weaver, 1963) and Pielou (Pielou, 1966), respectively, and species richness by the number of taxa per sample.

Water temperature was taken with a FAC 400 digital thermistor. The maximum mixing zone depth was defined as being the water layer above the persistent thermocline. The euphotic zone (1% of subsurface incident light) was measured with a radiometer LICOR, model B 312, at collection times.

Results

The level of the river fluctuates more through the seasonal variations in the quantity of precipitation in the headwaters and its outfall into the Amazon River than as a result of local precipitation (Table I). The variations in hydrometrical level of the Trombetas River influence the depth of Batata Lake (Figure 2). The mixing behaviour of the water in the lake changes with the river level and associated lake
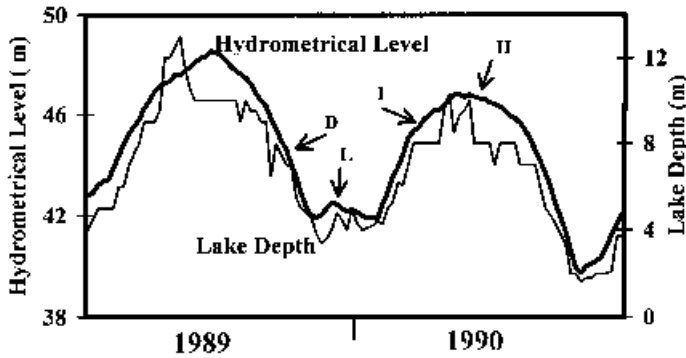
Fig. 2. Hydrometrical level (m) of Trombetas River and Batata Lake depth (m) from January 1989 to December 1990, showing the sampling dates (arrows) for study periods: decreasing water (D), low-water (L), increasing water (I) and high-water (H) levels.

depth. Mixing in Batata Lake is characterized by the reduction in the mixed layer during the periods of most intense solar radiation and by bottomwards expansion at night (Figure 4). During decreasing water level, mixing is restricted only to the first 3.0 m. Total water column mixture conditions were observed during dawn, in low water level. Persistent thermocline, very close to the bottom of the lake, was detected during increasing water level. In high water conditions, the mixing layer extended only about 3.0 m.

Table I. Main features of Batata Lake (climatological, physical, chemical and biological variable averages) during the studied hydrological periods

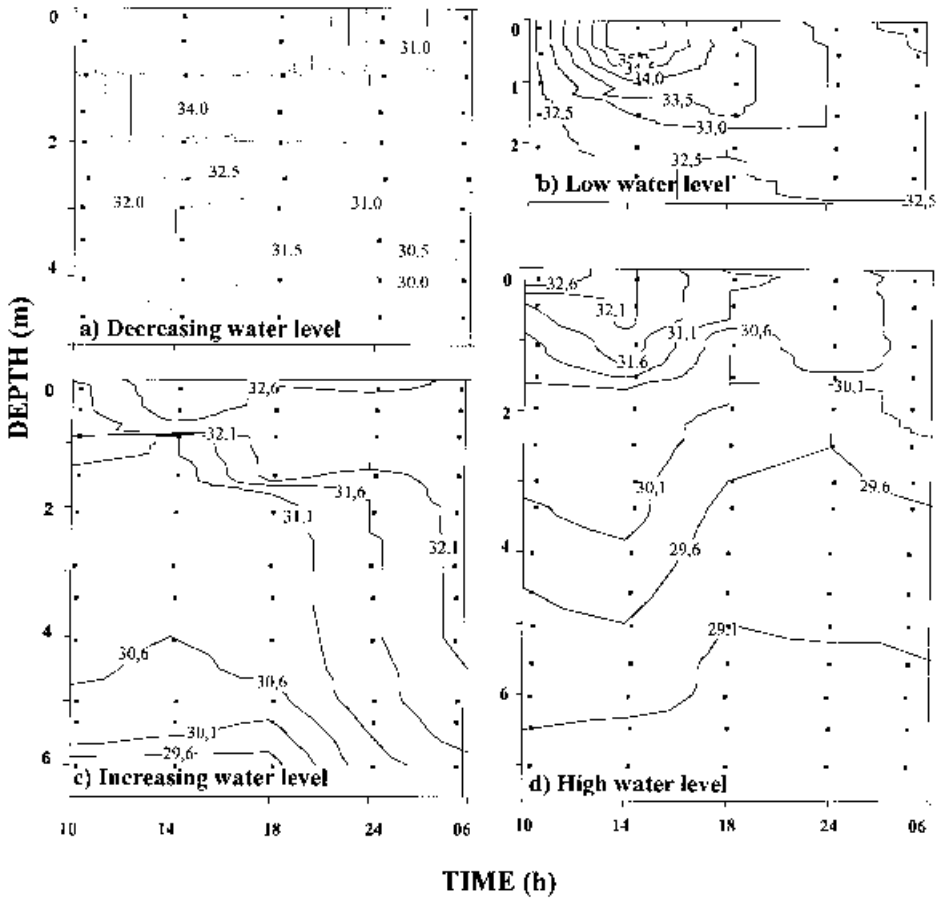|	Decreasing water	Low-water	Increasing water	High-water
Air temperature	33.5	29.1	29.0	33.7
Precipitation (mm)	263	766	804	276
Water temperature (°C)	34.0	32.3	32.0	32.2
Secchi (m)	1.9	1.3	1.6	1.0
Z_{max} (m)	5.0	3.0	6.5	7.5
Z_{eu}/Z_{mix}	1.7	1.0	0.7	1.0
Z_{mix}/Z_{max}	0.6	1.0	0.9	0.4
Dissolved oxigen (%)	96	112	66	64
Conductivity (μS cm^{-1})	13	10	8	10
pH	5.9	5.7	4.7	6.1
Alkalinity (μEq l^{-1})	80	40	20	70
TP (μM)	0.41	1.02	0.51	0.32
TN (μM)	169	202	15	31
TN/TP	412	193	29	97
P.PO$_4$ (μM)	0.08	0.1	*	*
N.NO$_3^-$ (μM)	0.40	0.40	*	0.44
N.NH$_4^+$ (μM)	14.64	10.29	25.60	11.24
Si.SiOH$_4$ (μM)	158	183	160	378
Density (ind. ml^{-1})	5393	11081	2827	1543
Diversity (bits ind^{-1})	4.9	4.7	4.5	4.1
Evenness (%)	89	81	89	90
Species richness (taxa per sample)	51	56	36	26

*Missing data.

67
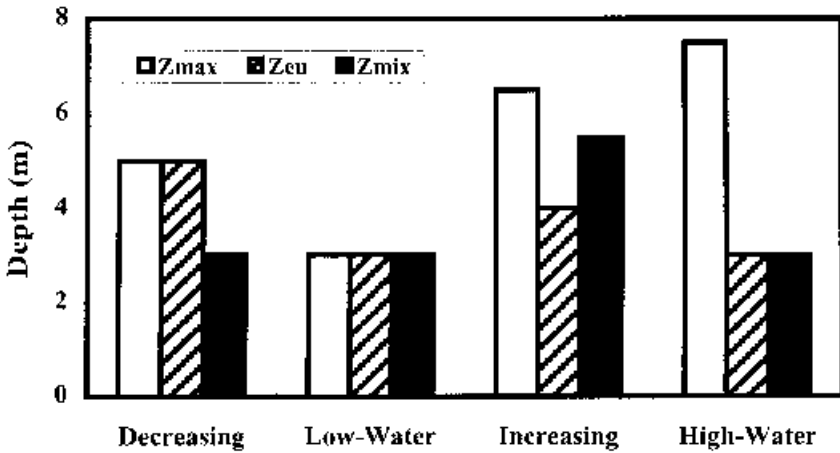
Fig. 3. Maximum depth (Z_{max}), euphotic zone (Z_{eu}) and mixing zone (Z_{mix}) in Batata Lake recorded for study periods: (**a**) decreasing water, (**b**) low-water, (**c**) increasing water and (**d**) high-water levels.

Except for the decreasing water depth period, the euphotic zone was always equal to, or shallower than, the mixed zone ($Z_{eu}/Z_{mix} = 0.7$–1.0). During the decreasing water period, the euphotic zone reached to the bottom of the lake, whereas during increasing and high water periods, it extended only through 60 and 40% of the depth profile, respectively (Figure 3).

A total of 203 algal taxa were noted during the present study (20 Cyanophyceae, 74 Chlorophyceae, 47 Zygnemaphyceae, five Euglenophyceae, two Raphidophyceae, 14 Bacillariophyceae, four Xanthophyceae, 22 Chrysophyceae, eight Cryptophyceae, seven Dinophyceae). The Batata Lake phytoplankton was found to be quite diverse (4.4–4.9 bits ind^{-1}), with an average of between 26 (high water) and 56 taxa (low water) occurring per sample. The high specific diversities and evenness which characterize the lake (Table I) imply that there is no sustained period of dominance by specific algae. At different phases of the hydrological cycle, some 5–10 species comprised most of the phytoplankton population density, but none with a contribution exceeding 15% of the total.

With regard to vertical distribution, two phytoplankton density patterns were noted (Figure 5). First, there were homogeneous vertical profiles during low and increasing water levels (Figure 5b and c). Secondly, the vertical profiles of algal distribution during high and decreasing water levels exhibited differences with depth (Figure 5a and d).
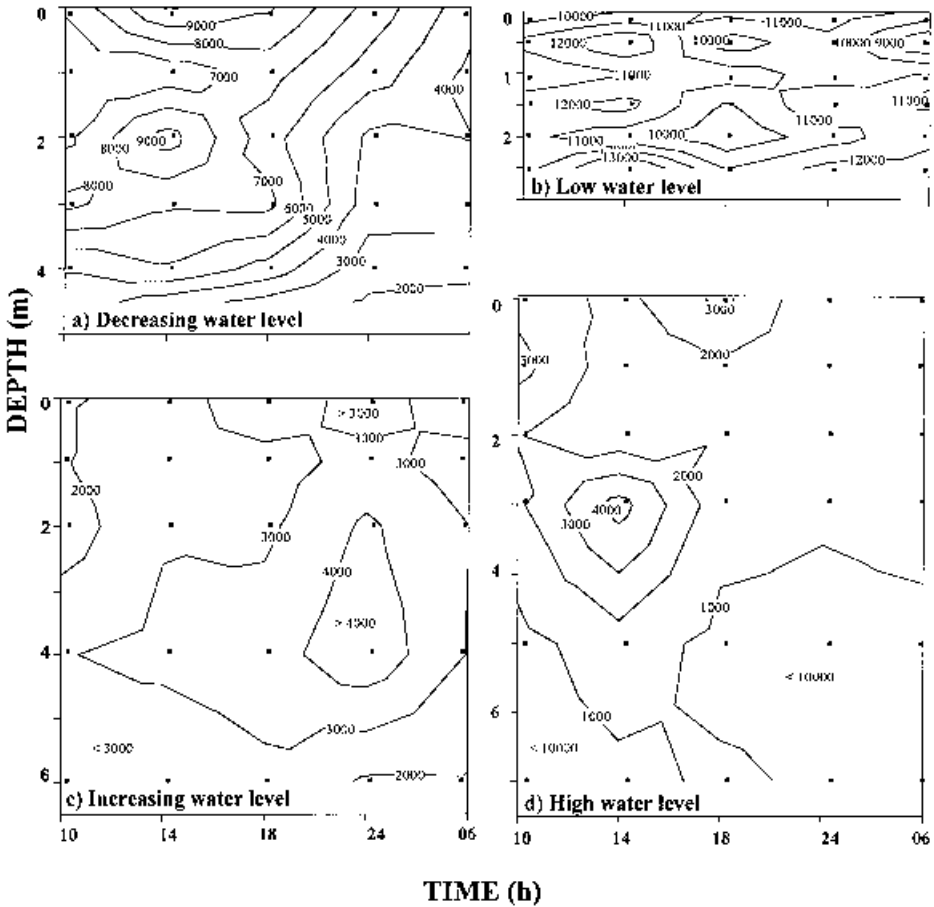
The phytoplankton during decreasing water level in September was characterized by small chroococcales (*Synechococcus elongatus* Nägeli, *S.elegans* (Wolosyznska) Komárek, *Aphanothece chlatrata* West and West, *Eucapsis alpina* Clementz and Shantz), chlorococcales (*Chlorella homosphaera* Skuja) and diatoms (*Brachysira vitrea* [Grunow] R.Ross). During low-water level, *Mougeotia* cf. *delicata* Beck, *Mesotaenium chlamydosporum* De Bary and *Mesotaenium* sp. were the dominant algal species, together with colonial microplanktonic (*Ankistrodesmus fusiformis* Corda) and nanoplanktonic chlorophyceans

Fig. 4. Depth–time diagrams of water temperature (°C) recorded for study periods: decreasing water, low-water, increasing water and high-water levels.

(*Chlorella homosphaera*), and pennate diatoms (*Brachysira vitrea* and *Pinnulari*a sp.). When the water level was rising in March, *Oscillatoria quadripunctulata* Brühl and Biswas and *O.limnetica* Lemmermann, in addition to *Chlorella homosphaera*, and together with other small chroococcales, characterized the phytoplankton of the lake. During high-water level in June, small greens and blue-greens were dominant (*Chlorella homosphaera, S.elongatus, Choricystis cylindracea* Hindák), together with the flagellate *Cryptomonas pyrenoidifera* Geitler and diatoms, particularly *Urosolenia eriensis* H.L.Smith var. *morsa* [West and West] Torgan (Table II).

Differences were found in the phytoplankton distribution and population density during the diel cycle, in the period of decreasing water level, especially between sunrise (06:00 h), mid-morning (10:00 h) and afternoon (14:00 h).

69

Fig. 5. Depth–time diagrams of phytoplankton density (ind. ml^{-1}) recorded for study periods: (**a**) decreasing water, (**b**) low-water, (**c**) increasing water and (**d**) high-water levels.

Discussion

An important effect of fluctuating water levels in Batata Lake is the imposition of an annual cycle of alternation between stratified and effectively unstratified water conditions, with important transitional characteristics in the water column between these periods. This imparts a strong seasonality to environmental conditions in the water column of the lake, independent of the annual cycle of temperature and solar irradiance that regulate the thermal structure of lakes at high latitudes. This seasonality is marked by the occurrence of sparser phytoplankton communities during periods of high water level. This may result from dilution processes. The gradual changes in the hydrological regime of the Trombetas River, and the irregularity of water circulation in Batata Lake, act upon the phytoplankton community and lead to continuous processes of reorganization

70

Table II. Average percentage of phytoplankton assemblages (Ass.), as dominant groups of species, during the studied hydrological periods in Batata Lake

Decreasing water	Ass.	Low-water	Ass.
8% *Synechococcus elongatus*	**X₁**	15% *Mougeotia delicata*	**T**
6% *S.elegans*	**X₁**	7% *Mesotaenium chlamydosporum*	**T**
5% *Chlorella homosphaera*	**X₁**	6% *Mesotaenium* sp.	**T**
3% *Chroococcus minor*	**X₁**	6% *Ankistrodemus fusiformis*	**J**
3% *Scenedesmus ellipticus*	**X₁**	4% *C.homosphaera*	**X₁**
3% *Merismopedia tenuissima*	**Lo**	8% *Pinnularia* sp.	**?**
5% *Aphanothece chlatrata*	**Lm**	9% *Brachysira vitrea*	**A**
5% *B.vitrea*	**A**		
5% *Eucapsis alpina*	**?**		
3% *Pinnularia* sp.	**?**		

Increasing water		High-water	
10% *Oscillatoria quadripunctulata*	**S**	14% *C.homosphaera*	**X₁**
6% *Oscillatoria limnetica*	**S**	8% *S.elongatus*	**X₁**
8% *C.homosphaera*	**X₁**	5% *Choricystis cylindracea*	**X₁**
4% *S.elegans*	**X₁**	4% *Cryptomonas pyrenoidifera*	**Y**
4% *E.alpina*	**?**	3% *Urosolenia eriensis var. morsa*	**A**

Labels according to Reynolds (1997).
?, no information about the species.

(Huszar and Reynolds, 1997; Huszar, 1999). The seasonal phytoplankton patterns noted by Huszar and Reynolds (Huszar and Reynolds, 1997) for another hydrological cycle (1988–9) were similar to those analysed here, suggesting regular variation in phytoplankton in Batata Lake on an annual basis. Moreover, the specific density, species richness and diversity of phytoplankton within the different phases of the hydrological cycle described here have shown similar patterns to other flood-plain lakes of the Solimões (Ibañez, 1998), Paraná (García de Emiliani, 1993) and Orinoco (Sanchez, 1992) rivers.

When the lake is deep, mixing does not reach the bottom, contributing to the formation of a metalimnetic layer over periods of several consecutive days. In conditions of low water level in the lake, mixing reaches the bottom and turns over the entire water column on most days, sometimes continuously (Huszar and Reynolds, 1997). The precise point has been resolved (Huszar, 1994) by reference to calculations involving the Wedderburn Number (Imberger and Hamblin, 1982). When the density gradient of the water between a depth of 4 and 5 m beneath the surface remains between 0.1 and 0.4 kg m³ m⁻¹ (corresponding to a temperature gradient of 1–2°C m⁻¹ within the range 27–30°C), the structure is resistant to windspeeds of <4.2 m s⁻¹; such windspeed is surpassed in the region at 3–7 days intervals (Huszar, 1994). Persistent thermoclines, at between 3 and 5 m depth beneath the water surface, have been recorded in other flood-plain lakes of the Amazon basin (Tundisi *et al.*, 1984; Camargo and Miyai, 1988; MacIntyre and Melack, 1988).

With decreasing water level, despite penetration of light to the bottom of the lake, mixing is restricted to only the first 3 m (60% of the water column). This

imposes differentiated distribution of the phytoplankton, with lower phyto-plankton population densities below the mixing layer during the diel cycle. The small and stout species of chroococcales (*Synechococcus elongatus, S.elegans*), chlorococcales (*Chlorella homosphaera*) and diatoms (*Brachysira vitrea*), which can grow rapidly, were found in this region with accessible nutrients. They are some of the morphological types which are successful in this kind of environment with a high rate of flushing. Most of these plants are thought to be invasive species (C-strategists), making up assemblage X_1 (Reynolds, 1997), typical of environments with good light conditions and accessible resources. *Synechococcus* and *Synechocystis* sp., as picoplankton representatives of large, clear and oligotrophic lakes, were originally included in the **Z** assemblage by Reynolds (Reynolds, 1997). However, according to their invasive and fast-growing characteristics, some species of these genera, common in hypertrophic Brazilian coastal lagoons, were considered as X_1 assemblage by Huszar *et al.* (Huszar *et al.*, in press).

Later, the intermittently-stratified lake changes into a continuously mixed shallow water column. During low water level, the lake is shallow with mixing throughout its depth and the euphotic zone reaches throughout the water column. This feature results in a uniform vertical distribution of the algae during the 24 h cycle, which has also been described in a shallow flood-plain lake of the Paraná river (García de Emiliani, 1990). At this time, the phytoplankton was dominated by filamentous and elongated species (R-strategists) with high surface/volume ratio (Reynolds, 1997), able to live in mixed-water environments (Happey-Wood, 1988). *Mougeotia* cf. *delicata, Mesotaenium chlamydosporum* and *Mesotaenium* sp. may be regarded as belonging to the **T**-assemblage, provisionally proposed by Reynolds (Reynolds, 1997) for a spectrum of algae covering a range between the desmids–*Aulacoseira* assemblage **P**, to the *Limnothrix/Planktotothirx agardhii* assemblage **S**. All these intermediate organisms are filaments (*Tribonema, Geminella, Mougeotia*) and reflect an increasing tolerance of reducing light and increasing mixing depth (Happey-Wood, 1988).

During increasing water level, the thermal structure in the diel cycle results in a persistent thermocline very close to the bottom of the lake. This leads to a near even distribution of organisms throughout the water column. These conditions allow the phytoplankton access to the entire depth of the euphotic zone, a depth of about 60% of the water column. At this point, the phytoplankton tend towards homogeneity throughout the water column during the 24 h period. In these well mixed conditions, *Oscillatoria quadripunctulata* and *O.limnetica* were the dominant organisms. These species (R-strategists) have been described as having efficient light antennae and are typical representatives of assemblage **S**, selected in turbulent water environments (Olrik, 1994; Reynolds, 1997).

When the lake is deeper during high water conditions, the euphotic zone coincides with the mixing depth, both extending 3 m, only to about 40% of the water column. The greatest development of the phytoplankton community during the diel cycle at this time was restricted to about a 3 m layer, showing stratified patterns during the entire diel cycle. During flood conditions, accumulation of phytoplankton population densities is restricted, and the rate of basin flushing restricts the flora to small, fast-growing and invasive (C-strategists, assemblage

$\mathbf{X_1}$) species (*Chlorella homosphaera, Synechoccocus elongatus, Choricystis cylindracea*), with the potential rate of growth to be able to resist dilution from the lake (Reynolds and Lund, 1988).

The most remarkable variation in the diel cycle was the increase in phytoplankton between 10:00 and 14:00 h during decreasing water level. In the other hydrological phases, no differences in phytoplankton concentrations, during the 24 h cycle, were observed. Greater population densities during the second half of the day have been documented both for natural lakes (García de Emiliani, 1990; Huszar *et al.,* 1994) and tropical reservoirs (García de Emiliani, 1976; Toledo *et al.*, 1988), and for temperate regions (Ilmavirta, 1975; Pick and Bérubé, 1992). No process, however, has been clearly identified to drive this pattern, probably because of the difficulty in appraising all community growth and loss processes of the microalgal time scale.

Finally, despite the short-term nature of the thermal structure in Batata Lake and the absence of migrating organisms such as pseudovacuolates, cyanoprokaryotes and/or flagellates, a relative vertical structuring in the phytoplankton over 24 h was maintained during periods when the lake was relatively deep. Hydrological and hydrographic conditions, however, result in frequent dissipation of the physical structure, so the mechanical forces of mixing prevent greater opportunities for interaction among the algal populations, either for rarification and competition, or for a greater community maturity (Reynolds, 1992). The lack of dominance by S-strategist species, which are capable of surviving in a chronic deficiency of nutrients and good light conditions typical of advanced succession stages (Reynolds, 1997), the remarkable dominance of flushing-tolerant invasive nano-algae (C-strategists; $\mathbf{X_1}$, $\mathbf{Y}$ assemblages) and of mixing-dependent species (R-strategists; $\mathbf{T}$, $\mathbf{S}$ assemblages) have shown that the environmental physical properties are often the strongest determinants of the phytoplankton dynamics in this shallow and high flushing Amazonian lake. Moreover, despite some differences in composition at species level, the assemblages represented are broadly the same as those previously documented by Huszar and Reynolds (Huszar and Reynolds, 1997) for Batata Lake. This suggests that phytoplankton groups, according to their strategies, can be used to indicate recent environmental conditions more reliably than can phylogenetic representatives.

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