

Diel responses of phytoplankton of an Amazon floodplain lake at the two main hydrological phases

Respostas diárias do fitoplâncton de um lago da planície de inundação amazônica nas duas principais fases hidrológicas

Kathrin Nere Passarinho¹, Maria Rosélia Marques Lopes¹ and Sueli Train²

¹Postgraduate Program in Ecology and Natural Resource Management,
Federal University of Acre – UFAC, CEP 69920-900, Rio Branco, AC, Brazil
e-mail: kathrinnpschuster@yahoo.com.br; mroselialopes@gmail.com

²Center for Research in Limnology, Ichthyology and Aquaculture – NUPÉLIA,
Department of Biology, State University of Maringá – UEM, CEP 87029-900, Maringá, PR, Brazil
e-mail: train@nupelia.uem.br

Abstract: Aim: This study examines the short-term changes of phytoplankton in an oxbow lake on the floodplain of the Acre River, Amazonia, Brazil. **Methods:** Samples were taken with a Van Dorn bottle, at three depths (surface, middle and bottom), in two periods (low waters and high waters), for seven consecutive days in two schedules, night and morning. **Results:** Phytoplankton was represented by 198 taxa and the Class Euglenophyceae, with 62 taxa, was the best-represented group in both periods. There were abrupt changes in the community during the high waters (potamophase). During this period, in conditions of partial atelomixis, we recorded higher values of phytoplankton biovolume and dominance of *Gonyostomum semen* (Ehr.) Dies. (Raphidophyceae). **Conclusions:** In the low waters (limnophase), conditions in the lake were more stable, the diversity and rate of change in the community were lower, and the frequent periods of stratification and mixing were responsible for the dominance of *Geitlerinema* sp. (Cyanobacteria).

Keywords: phytoplankton biovolume, partial atelomixis, diel variation, low and high waters.

Resumo: Objetivo: O objetivo deste estudo foi avaliar mudanças em curto prazo da comunidade fitoplanctônica em um lago da planície de inundação do Rio Acre, Amazônia, Brasil. **Métodos:** As amostras foram coletadas com garrafa de Van Dorn, em três profundidades (superfície, meio e fundo), durante as estações climáticas (seca e chuvosa), durante sete dias consecutivos, em dois horários, manhã e noite. **Resultados:** A comunidade fitoplanctônica foi representada por 198 táxons e a classe Euglenophyceae foi a mais bem representada em ambos os períodos. Ocorreram mudanças abruptas na comunidade durante a estação chuvosa (potamofase). Durante este período, em condições de atelomixia parcial, foram registrados os mais elevados valores de biovolume do fitoplâncton e dominância de *Gonyostomum semen* (Ehr.) Dies. (Raphidophyceae). **Conclusões:** No período seco (limnophase), as condições do lago foram mais estáveis, a diversidade e a taxa de mudança da comunidade foi mais baixa, e os frequentes períodos de estratificação e mistura foram responsáveis pela dominância de *Geitlerinema* sp. (Cyanobacteria).

Palavras-chave: biovolume do fitoplâncton, atelomixia parcial, variações diárias, águas altas e águas baixas.

1. Introduction

Floodplains are complex, highly dynamic and heterogeneous ecosystems, which contain flooded land areas but also lakes and channels associated with the major rivers and their tributaries. These aquatic habitats differ in their physical and chemical characteristics and are subject to periodic disturbances that promote high spatial and temporal variability, changing the successional processes of their aquatic communities and resulting in high diversity (Ward et al., 1999). This variability also occurs at smaller scales, resulting from stochastic events (such as rain and wind) that outweigh the predictable annual cycles and govern the structure of freshwater aquatic habitats. Thus, variations in the extent of vertical mixing, for example, could be crucial so that successful species must be adapted to the short-term variation, which represents a significant portion of the large-scale variability (Reynolds, 1997).

The river-floodplain concept of Junk et al. (1989) gives emphasis to the interactions and exchanges between the main channel of the river and adjacent water bodies as well as terrestrial environments subject to flooding, so that distinct connectivity among rivers and lentic environments, changing the physical and chemical properties of the environment and is considered as the main structuring force in these environments.

Tropical floodplain lakes pass through two distinct phases, potamophase and limnophase which mainly depend on hydrologic dynamics of tributary-headwaters.

The potamophase, which occurs during the high waters, is characterized by the connectivity of lentic environments to the main channel and includes rising-water, flood, and falling-water periods; whereas in limnophase, which occurs during the low waters, the lentic environments are disconnected from the main channel. Both phases comprise the hydrosedimentological cycle, which is the main factor influencing the different habitats of these ecosystems and is characterized by fluctuations in water level and abiotic variables and changes in aquatic communities (Neiff, 1990).

The dynamics of physical, chemical, and biotic factors in floodplain lakes, however, depends on the degree and type of connectivity of the lakes with the main channel. The connectivity (permanently or temporarily) can be directly to the river or due to infiltration of river water by groundwater of the same watershed or from adjacent watersheds. The high biocomplexity of these ecosystems stems from

the interaction of many processes that operate at different spatial and temporal scales (Amoros and Bornette, 2002).

In the course of the hydrosedimentological cycle, significant fluctuations of abiotic factors determine different patterns of phytoplankton developing condition (García de Emiliani, 1997; Train and Rodrigues, 2004). During the potamophase, biomass values are generally lower and there is an increase in abundance of opportunistic nanoplankton species, especially phytoflagellates (Huszar and Reynolds, 1997; Bovo-Scomparin and Train, 2008). On the other hand, prolonged isolation of a lake during the limnophase can lead to blooms of climax species, especially cyanobacteria (Train and Rodrigues, 2004; Philips et al., 2008).

The Amazon lakes have specific characteristics that make it possible to identify the flood pulse as a forcing function responsible for the changes of abiotic variables and changes in patterns of stratification and mixing, which, according to Tilzer and Goldman (1978), constitute the two major factors controlling the structure of the phytoplankton community. Short-term studies on freshwater phytoplankton communities in these lakes are relatively few. In a diel study in an Amazonian lake, Melo et al. (2000) observed different vertical distributions of phytoplankton in the water column and attributed these to changes in the degree of mixing of the water. Similar observations were reported by Ramírez and Bicudo (2002), who showed that processes of stratification and mixing influenced phytoplankton succession during the year. Lopes et al. (2005) emphasized the importance of temperature as a regulator of lentic aquatic systems in tropical regions, and highlighted its close relationship to the selection and spatial-temporal distribution of phytoplankton species.

The present, short-term study examined the temporal and spatial variations of the phytoplankton community in an Amazonian oxbow lake, in two distinct hydrological phases, high water (potamophase) and low waters (limnophase), aiming to identify the main environmental characteristics responsible for the variability of the phytoplankton community. The study investigated two hypotheses: 1) the phytoplankton community undergoes the most drastic changes during the potamophase and is more stable during the limnophase; and 2) the different mixing regimes in the two periods (partial and total atelomixia) directly influence the composition and temporal and spatial dynamics of the community.

2. Material and Methods

Lake Amapá (10° 02' 36" S; 67° 50' 24" W), a typical whitewater oxbow lake, is located in Amazonia in the Acre-Purus Basin, along the right bank of the Acre River. This river crosses the border of Perú, Bolivia, and Brazil, but its basin is primarily located in the Brazilian states of Acre and Amazonas. Lake Amapá is a typical river meander that was cut off from the main channel (oxbow lake) (Figure 1).

Its high shores and partially preserved riparian vegetation provide good wind protection. The

lake has high sedimentation levels, with direct connection to the main channel only in the high waters, during the potamophase. Its depth ranges from 2.5 m to 7.0 m, and there are no macrophyte banks.

Samplings were performed during 7 consecutive days during the low waters (September 2004) and high waters (February/March 2005) periods at a single station (maximum depth 2,8 and 4,5-6,0 m, respectively). Abiotic and biotic variables studied were collected with a Van Dorn bottle from the

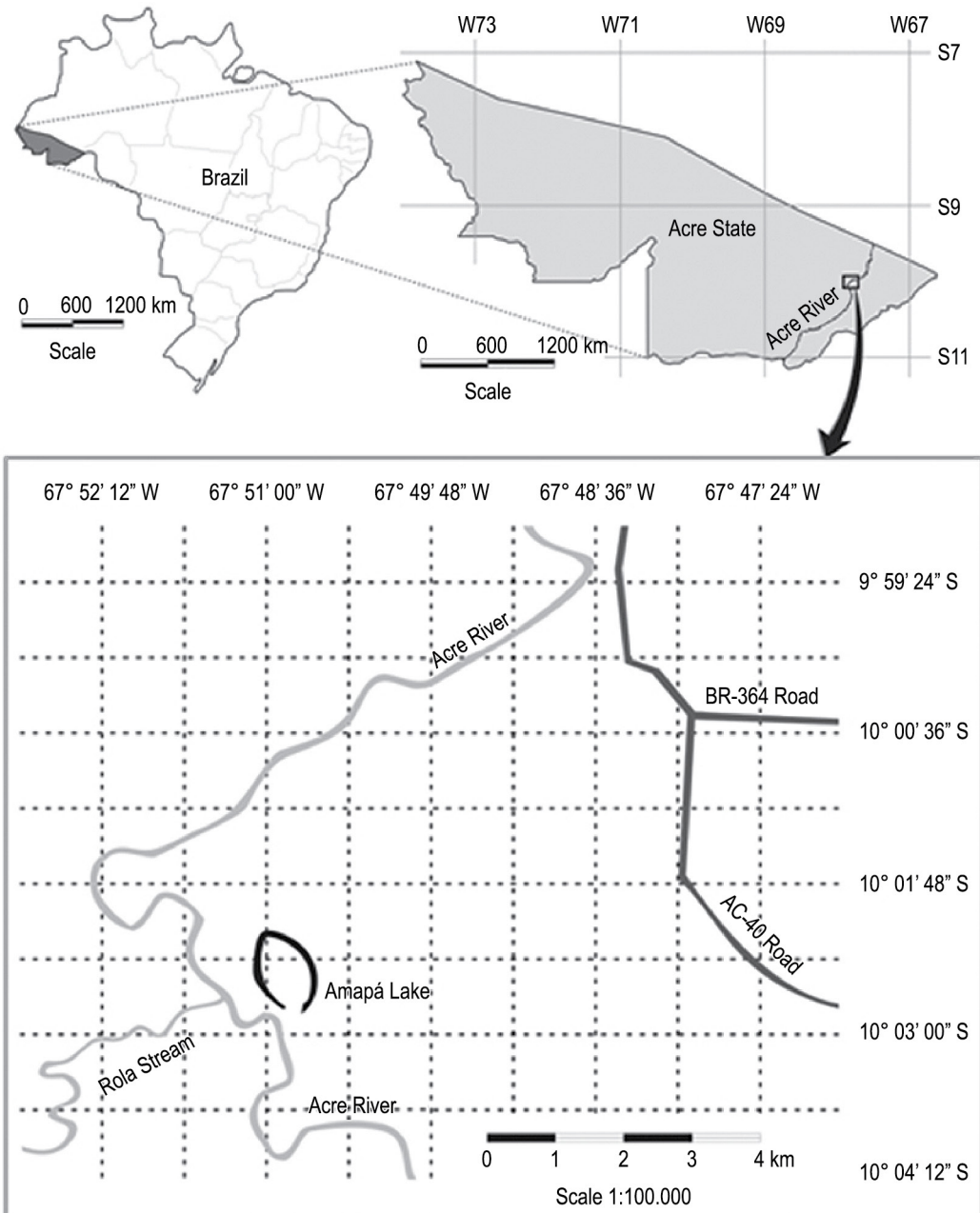


Figure 1. Geographical location of the study area: a map of the River Acre basin in te State of Acre, Brazil, and the Lake Amapá, a typical oxbow floodplain lake.

water column on surface (S = 0,15 m prof.), middle (M = at the midpoint of the water column) and bottom (B = 0,20 m from the sediment), at two different times (7:00 AM and 7:00 PM).

Samples were transported in Styrofoam boxes with ice to the Limnology Laboratory of the Department of Natural Sciences of the Universidade Federal do Acre. Abiotic variables analyzed include water transparency (Secchi disc), water temperature, electrical conductivity, pH, dissolved oxygen (DO) were measured in the field (Hanna Instr.), alkalinity according to (Golterman and Clymo, 1969), total nitrogen (TN) and total phosphorus (TP) according to (Valderrama, 1981), air temperature (mercury thermometer), turbidity (Hach Instr.), mixing zone (Zmix) according to (Reynolds, 1984a), euphotic zone (Zeu) according to Cole (1983) and the attenuation coefficient of the vertical light (k) according to Poole and Atkins (1929).

Samples for phytoplankton quantitative analyses were stored in 300 ml glass vials, fixed and preserved in acetic lugol solution, and immediately stored in darkness at room temperature. Quantification of phytoplankton (ind. mL^{-1}) was done using Utermöhl's (1958) sedimentation chambers and following recommendations in Lund et al. (1958). Countings were performed using a Zeiss Axiovert (400 \times) inverted microscope. Every cell, coenobium, colony, or filament was considered one individual. To define abundant and/or dominant species, Lobo and Leighton (1986) criteria were followed.

The biovolume ($\text{mm}^3 \cdot \text{L}^{-1}$) of each species was obtained by comparing them with the volume of a geometric solid, taken either isolated or combined, that would mostly resemble the cell form (Sun and Liu, 2003). Diversity index (Shannon and Weaver, 1949), evenness index (Lloyd and Ghelardi, 1964), and the change rate of the community (Lewis Junior, 1978, as adapted by Reynolds, 1984a) were calculated using the density data.

To evaluate the significance of the vertical and temporal variations of richness, diversity and evenness of phytoplankton during the low and high waters, we used one-way ANOVA with a significance level of 5%, we used the statistical program BioEstat 5.0.

To determine the key environmental variables that influenced the spatial and temporal variability of the phytoplankton community in the system, we used a Canonical Correspondence Analysis (CCA) to ordinate the sample units, low and high waters, and hours and days of sampling, considering phytoplankton density and abiotic factors. For this

analysis, we used the statistical program PC-ORD for Windows, version 5.0 (McCune and Mefford, 1999), and included species that contributed more than 0.3% of the total density and together made up over 95% of the total density at all hours of sampling. Eight abiotic matrices were used in the CCA. All variables with high correlations with the first two axes of ordination were considered, whereas variables that contained a functional redundancy of information were eliminated to avoid distortions in the analysis. To test the significance of the axes, we applied a Monte Carlo test. Data variability was explained by the canonical coefficient (Ter Braak, 1986).

3. Results

3.1. Thermal structure

It was observed vertical gradients of physical variables in both periods; however the patterns of thermal stratification of the water column and mixing regime were different in the low waters (limnophase) and high waters (potamophase). During the low waters, the mixing zone (Zmix) and euphotic zone (Zeu) were deeper than in the high waters. During the limnophase, there was wide variation in the Zeu:Zmix ratio, and on the fourth day of sampling, the ratio reached 4.8, with Zeu extending to near the bottom (Figure 2).

During the high waters, period of highest turbidity, the Zmix was restricted to the superficial layer, not exceeding 0.5 m, and atelomixia or partial mixing occurred. The Zeu was less than 1.2 m, not exceeding 20% of the maximum depth (Zmax) value (Table 1). Thermal micro-stratifications in the water column were observed during this period (Figure 2).

3.2. Phytoplankton dynamic

Phytoplankton community was represented by 198 taxa, 155 in the high waters, with 95 found only in this period, and 103 during the low waters, with 43 unique to this period. Sixty species were common to both periods.

3.2.1. Low waters

Species richness during low waters was lower than those recorded during the high waters, with variation of richness only between the hours.

During the low waters, the class with the largest number of taxa was Euglenophyceae (28), followed by Cyanobacteria (23) and Chlorophyceae (20). The classes less represented were Zygnemaphyceae

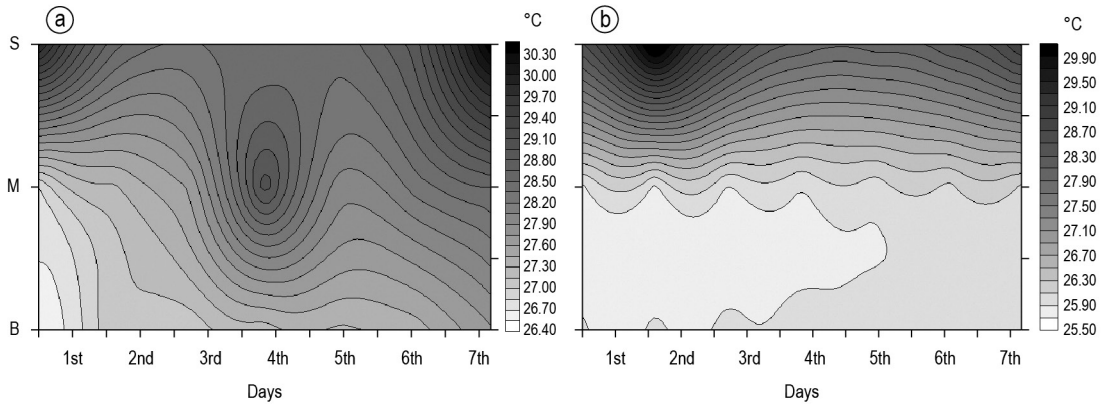


Figure 2. Depth-time diagram of the water temperature in the Lake Amapá during low waters (a) and high waters (b). (S = surface, M = middle, B = bottom).

Table 1. Main variables physical, chemical and phytoplankton attributes of the Lake Amapá during low waters (September 2004) and high waters (February-March 2005). (Zeu = euphotic zone, Zmax = maximum depth, Zmix = mixing zone).

Variable	Low waters			High waters		
	Min.	Max.	CV %	Min.	Max.	CV %
Air temperature (°C)	26.20	33.50	7.85	26.50	33.00	7.63
Water temperature (°C)	26.55	31.80	4.46	25.85	30.42	4.93
Electric conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	65.00	93.00	8.85	44.00	92.00	20.38
Alkalinity ($\text{mEq}\cdot\text{L}^{-1}$)	26.00	32.00	3.27	14.00	28.00	17.28
Dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$)	0.09	11.38	73.55	0.03	10.87	145.30
Turbidity (NTU)	4.00	14.90	35.55	18.80	624.00	89.83
pH	5.99	8.11	8.32	5.69	6.83	4.26
Total nitrogen ($\mu\text{mol}\cdot\text{L}^{-1}$)	6.26	10.77	13.04	9.32	27.30	26.60
Total phosphorus ($\mu\text{mol}\cdot\text{L}^{-1}$)	0.11	0.56	33.55	0.13	1.31	43.49
Secchi disc (m)	0.60	0.80	8.24	0.30	0.40	15.72
Coefficiente k	2.13	2.83	8.43	4.25	5.67	14.9
Zmax (m)	2.80	2.80	0.00	4.50	6.00	15.59
Zeu (m)	1.80	2.40	8.24	0.90	1.20	15.72
Zmix (m)	0.50	2.00	84.85	0.50	1.50	70.71
Zeu:Zmax	0.64	0.85	8.25	0.18	0.22	7.97
Zeu:Zmix	1.8	4.80	24.67	1.80	2.40	15.59
Richness	5	30	34.15	3	47	42.50
Density ($\text{ind}\cdot\text{mL}^{-1}$)	9822	32840	23.34	204	19981	143.17
Biovolume ($\text{mm}^3\cdot\text{L}^{-1}$)	8.92	66.70	47.87	2.15	263.00	191.25
Diversity ($\text{bits}\cdot\text{ind}^{-1}$)	0.34	1.47	35.71	0.19	2.68	40.92
Evenness	0.16	0.47	29.58	0.10	0.98	34.82
Change rate	0.07	0.23	-	0.18	1.63	-

(9), Bacillariophyceae (5), Cryptophyceae (7), Chrysophyceae (3), Raphidophyceae (2), Dinophyceae (3) and Xanthophyceae (3).

This period was characterized by the absence of sharp vertical gradients of phytoplankton density and biovolume distribution, so that low coefficient of variation of these attributes (respectively 23.3% and 47.9%), shows a tendency toward a homogeneous distribution of the community, on both temporal and spatial scales. However, there was a different pattern in the vertical distribution

of these attributes because the highest values were recorded at the bottom, in contrast to the high waters (Figure 3).

Phytoplankton community was dominated by Cyanobacteria, especially *Geitlerinema* sp. (> 78.7% density at all depths and days), in addition to *Planktothrix geitlerii* (Kisselev) Anagnostidis and Komárek and *Merismopedia elegans* A. Braun ex Kützing. *Geitlerinema* sp. showed the same patterns of distribution for density and total biovolume. Considering those species that contributed more

than 0.3% of the total density, in the low waters only five species contributed 95.1% of the total density, and the community was relatively stable. *Geitlerinema* sp. tended toward a homogeneous vertical distribution, with a bloom extending through the entire water column; however, the highest density and biovolume were observed on the surface during the 1st and 2nd days (Figure 3).

Planktothrix geitlerii tended toward a higher concentration near the bottom, although it had high density at the surface on the 6th day. The vertical distribution pattern of *Merismopedia elegans* was similar to that of *Planktothrix geitlerii*, showing higher density in the middle of the water column on the 4th day of sampling and on the bottom on the 6th day (Figure 4). Another abundant species was *Closteriopsis acicularis* (Chodat) J. H. Belcher

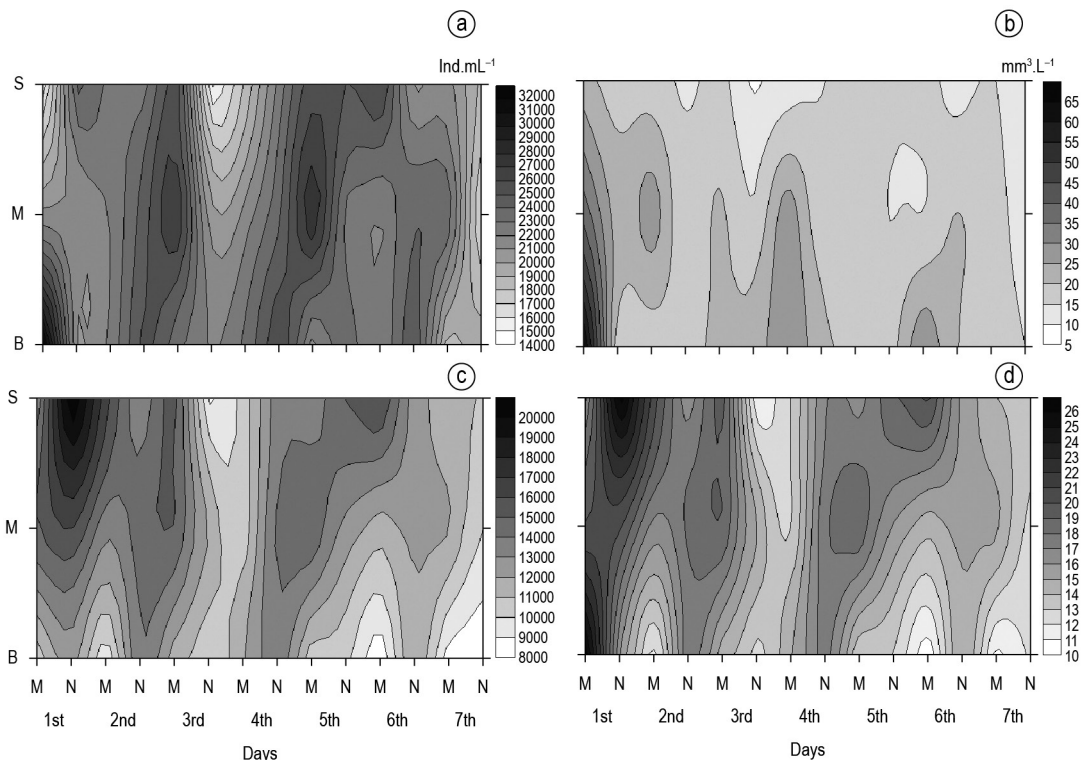


Figure 3. Depth-time diagram of the density and biovolume in the Lake Amapá during low waters: (a) total density, (b) total biovolume, (c) *Geitlerinema* sp. density, (d) *Geitlerinema* sp. biovolume. (S = surface, M = middle, B = bottom, M = morning, N = night).

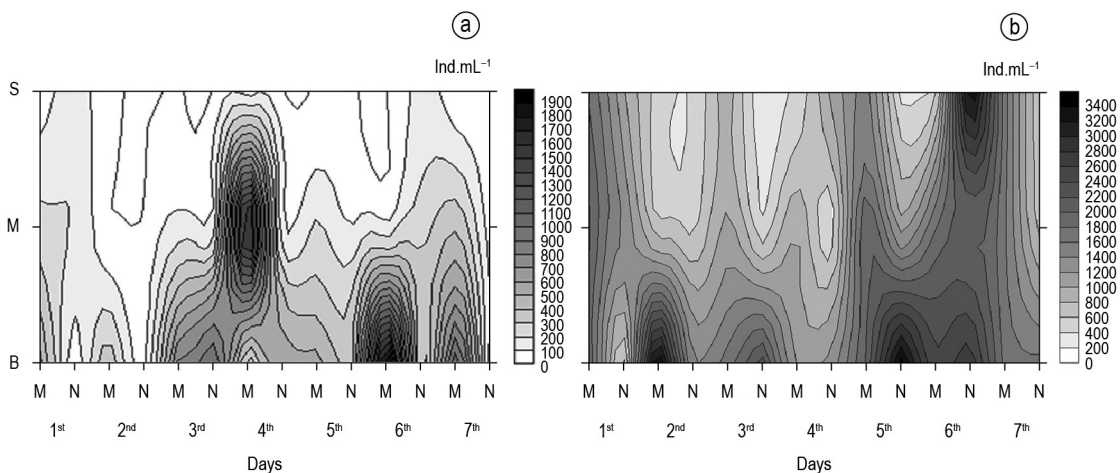


Figure 4. Depth-time diagram of the density of *Merismopedia elegans* (a) and *Planktothrix geitleri* (b) in the Lake Amapá during low waters. (S = surface, M = middle, B = bottom, M = morning, N = night).

and Swale, which occurred almost exclusively at the surface and middle layers.

Evenness remained low, with significant variations only between depths (Table 2), ranging between 0.15 and 0.44 and the lowest values were recorded on the night of the 6th day, and the highest values on the morning of the 7th day (Figure 5). Diversity was low (0.36 to 1.47 bits.ind⁻¹) in relation to the high waters. Significant variations occurred only between depths and sampling hours (Table 2) but not between days. The highest values were recorded at the bottom (maximum on the night of the 6th day), and the lowest at the surface (Figure 5). Daily rate of change remained stable throughout the study period, with values between 0.07 to 0.23 day⁻¹ and from 0.08 to 0.35 per 12 h⁻¹ (Figure 6).

3.2.2. High waters

Species richness varied widely over the sampling days of the high waters. The highest value (47 taxa) was recorded on the night of the 3rd day, and the lowest (3 taxa) on the morning of the 2nd day. Richness only varied significantly among depths (Table 3).

Euglenophyceae (55) was the class with the greatest number of species, followed by Chlorophyceae (30), Zygnemaphyceae (22), and Cyanobacteria (17). The classes with lower species richness were Cryptophyceae (13), Bacillariophyceae (12), Chrysophyceae (2), Dinophyceae (3), and Raphidophyceae (1).

High waters were characterized by pronounced vertical gradients in both the density and distribution of biovolume. Coefficients of variation were high

Table 2. Results of ANOVA performed to establish the significance of the vertical and temporal variations of richness, diversity and evenness of phytoplankton in Lake Amapá during the low waters (September 2004).

Factors	Depth		Hours		Days	
	F	p	F	p	F	p
Richness	18.75	0.000002	3.12	0.080	0.69	0.65
Diversity	15.14	0.000015	9.42	0.004	0.69	0.65
Evenness	2.24	0.120000	22.42	0.000	1.54	0.19

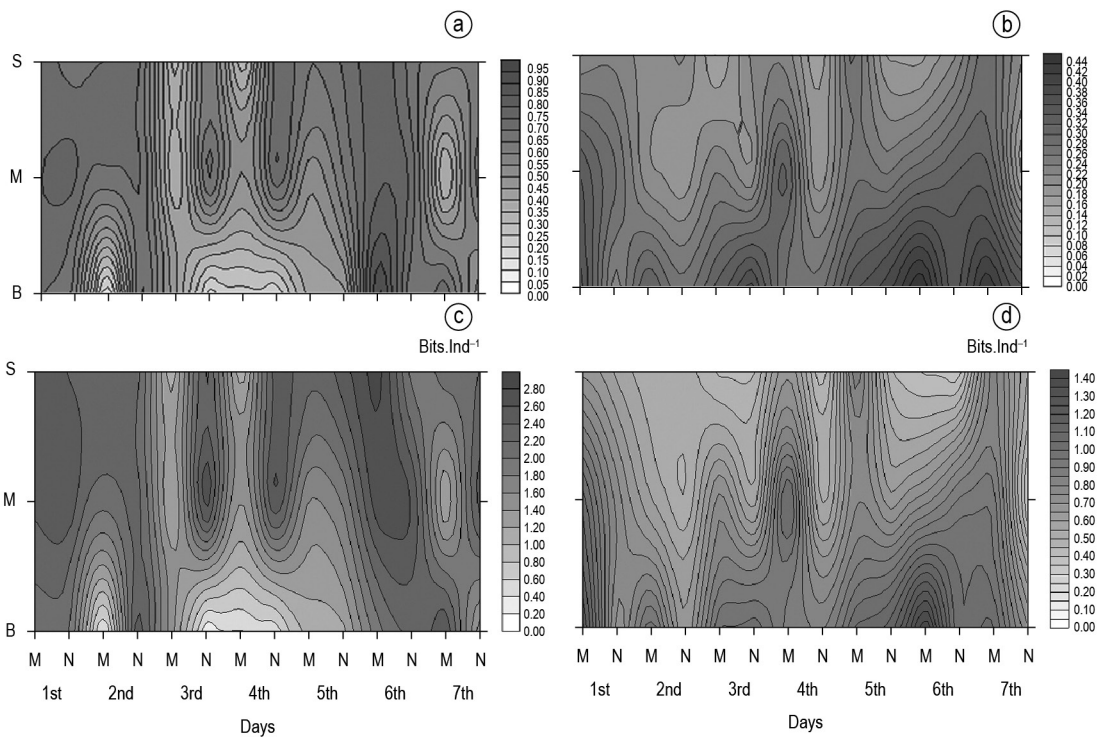


Figure 5. Depth-time diagram of the evenness and diversity in the Lake Amapá during high waters and low waters: (a, b) evenness in high e low waters, respectively, (c, d) diversity in high e low waters, respectively. (S = surface, M = middle, B = botton, M = morning, N = night).

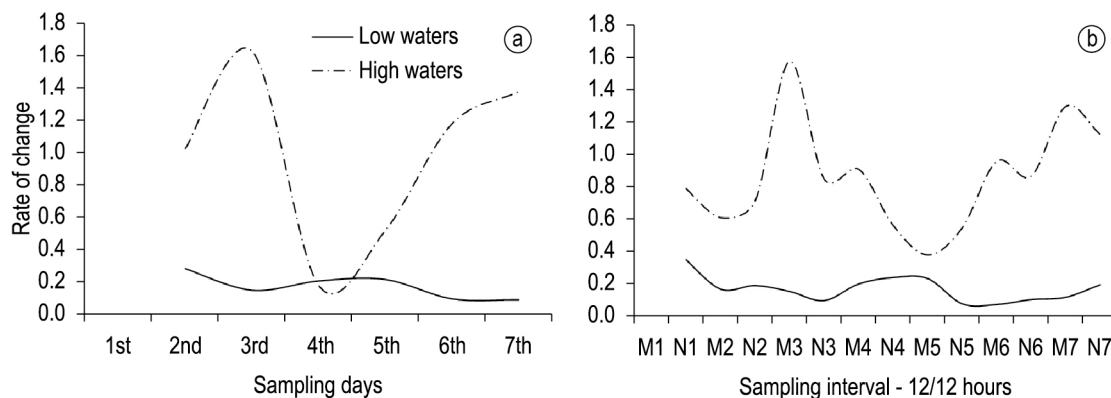


Figure 6. Temporal variation in the rate of change of phytoplankton community among days (a) and times (b) sampling in the Lake Amapá, during low waters and high waters. (M = morning, N = night).

Table 3. Results of ANOVA performed to establish the significance of the vertical and temporal variations of richness, evenness and diversity of phytoplankton in Lake Amapá during the high waters (February/March 2005).

Factors	Depth		Hours		Days	
	F	P	F	p	F	p
Richness	10.65	0.00	0.84	0.36	0.76	0.60
Evenness	2.30	0.11	1.56	0.21	2.52	0.03
Diversity	5.35	0.01	2.47	0.12	1.53	0.19

(143.17% and 191.2%, respectively), showing a heterogeneous distribution of the community on temporal and spatial scales (Figure 7). Considering the number of species that contributed more than 0.3% of the total density, eight species accounted for 83.6% of the total density for this period.

The highest values of phytoplankton density were recorded in the surface layer on the 3rd and 4th days and in the middle of the water column on the 7th day, periods when *Gonyostomum semen* (Ehrenberg) Diesing (Raphidophyceae) was dominant. Other abundant species in the surface layer were *Closterium diana* Ehrenberg ex Ralfs, *Closterium tortum* B. M. Griffiths (Zygnemaphyceae), and *Trachelomonas volvocinopsis* Swirenko (Euglenophyceae). *Cuspidothrix tropicalis* (Horecká and Komárek) P. Rajaniem, J. Komárek, R. Willame, P. Hrouzek, K. Kastovská, L. Hoffmann and K. Sivonen (Cyanobacteria), *Aulacoseira granulata* (Ehrenberg) Simonsen (Bacillariophyceae), *Cryptomonas erosa* Ehrenberg, and *Cryptomonas marsonii* Skuja (Cryptophyceae) were frequent in the middle layer, but not abundant.

During the first two days of sampling, when it was found the lowest density, Cyanobacteria (*Cuspidothrix tropicalis*), Zygnemaphyceae (*Closterium tortum*, *C. diana*), Bacillariophyceae (*Aulacoseira granulata*), and Cryptophyceae (*Cryptomonas erosa*) were more abundant.

In the first two days of sampling, the most abundant species was *Aulacoseira granulata*, which was dominant in the morning of the 1st day, at the bottom of the water column, and *Cuspidothrix tropicalis*, which was dominant on the morning of the 2nd day, also at the bottom. From the 3rd day there was a dominance of *Gonyostomum semen*, with the highest density recorded at the surface in the mornings of the 3rd and 4th days.

The total biovolume values were high (2.15 to 263 mm³.L⁻¹), and the highest values were recorded at the surface. Lower values were observed during the first two sampling days, and increased from the 3rd day, following the increase in density. The vertical distribution patterns of density and total biovolume corresponded to those of *Gonyostomum semen*, a large-sized species (Figure 7).

Evenness showed significant variation between sampling days, with values between 0.27 and 0.79. The lowest values occurred on the morning of the fourth day, while the highest values were found on the morning of 6th day (Figure 5). Wide variation in species diversity was noted (0.19 and 2.61 bits. ind⁻¹), showing significant variation only between depths (Table 3). The highest values were observed on the night of the 3rd day, while the lowest was recorded on the same morning (Figure 5).

The rate of change in the community was high, and the daily change values ranged from

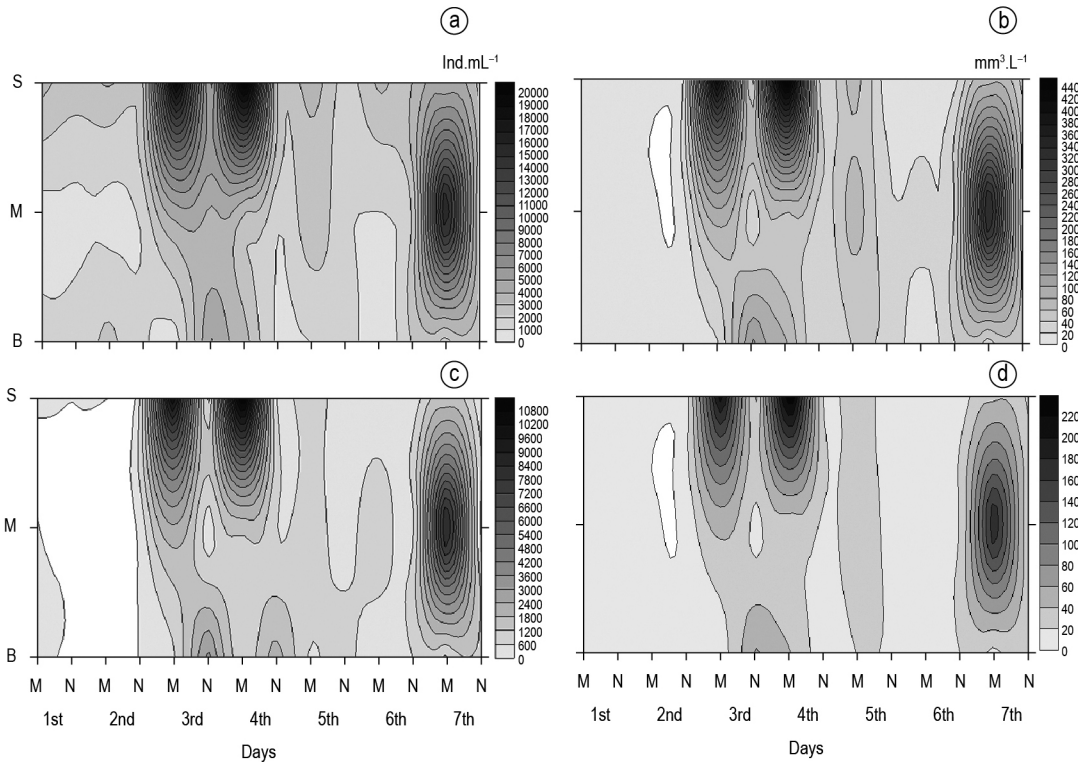


Figure 7. Depth-time diagram of the density and biovolume in the Lake Amapá during high waters: (a) total density, (b) total biovolume, (c) *Gonyostomum semen* density, (d) *Gonyostomum semen* biovolume. (S = surface, M = middle, B = bottom, M = morning, N = night).

0.18 to 1.63 day⁻¹. Greater variation was observed in the period between the 2nd and 3rd day, and stable values between the 3rd and 4th day, with more significant changes between the morning and night, which ranged from 0.37 to 1.58 per 12 h⁻¹ (Figure 6).

3.2.3. Integrated analysis of both climatic periods: low waters and high waters

The analysis of both climate periods ordered by the CCA showed a significant percentage of the total variance (37.8%, $\lambda=0,666$). The Monte Carlo test ($p = 0,001$) used to test the significance of the two first canonical axes showed statistically significant differences indicating that there were significant relationships among the sampling units, abiotic variables, and phytoplankton species (Table 4). The canonical coefficients for Axis 1 showed that the Zeu:Zmax ratio was the variable with the greatest weight in the ordination. ‘Intra-set’ correlations indicated that in addition to the Zeu:Zmax ratio, alkalinity, TN, TP, and turbidity contributed effectively to the species-environment relationship (Table 5).

Table 4. Results of Canonical Correspondence Analysis (CCA) using eight abiotic variables and 12 biotic variables (species) held the Lake Amapá including the two climatic periods studied: low waters (September 2004) and high waters (February/March 2005).

	Axis 1	Axis 2
Eigenvalue (λ)	0.666	0.094
Percents of explained variability	37.80	5.30
Pearson’s Correlation (specie -environment)	0.967	0.773
Monte Carlo Test (Eigenvalue) - ρ	0.001	0.001
Monte Carlo Test (corr. specie-environment)	0.001	0.001

As seen in the diagram, *Geitlerinema* sp. and *Closteriopsis acicularis*, predominant in the low waters, were more associated with the surface and middle sampling units while *Merismopedia elegans* and *Planktothrix geitlerii* were related to the bottom sampling units (Figure 8).

The species that discriminates the high waters, *Closterium diana*, *Closterium tortum*, and *Aulacoseira granulata* were related to sampling units from the surface, *Cryptomonas erosa* and *Trachelomonas*

Table 5. Canonical coefficient and ‘intra-set’ correlation of environmental variables with ordination axes for 12 biological variables of the Lake Amapá during the low waters and the high waters. (Zeu = euphotic zone, Zmax = maximum depth).

Variable	Canonical coefficient		Correlation coefficient (‘intra-set’)	
	Axis 1	AAxis 2	Axis 1	Axis 2
Water temperature	0.322	0.405	0.312	0.297
Turbity	-0.572	-0.487	-0.553	-0.357
pH	0.388	0.168	0.375	0.123
Electric conductivity	0.479	-0.522	0.464	-0.383
Alkalinity	0.887	-0.112	0.858	-0.082
Total nitrogen	-0.676	-0.564	-0.654	-0.413
Total phosphorus	-0.612	-0.722	-0.591	-0.529
Zeu:Zmax	0.997	0.018	0.964	0.013

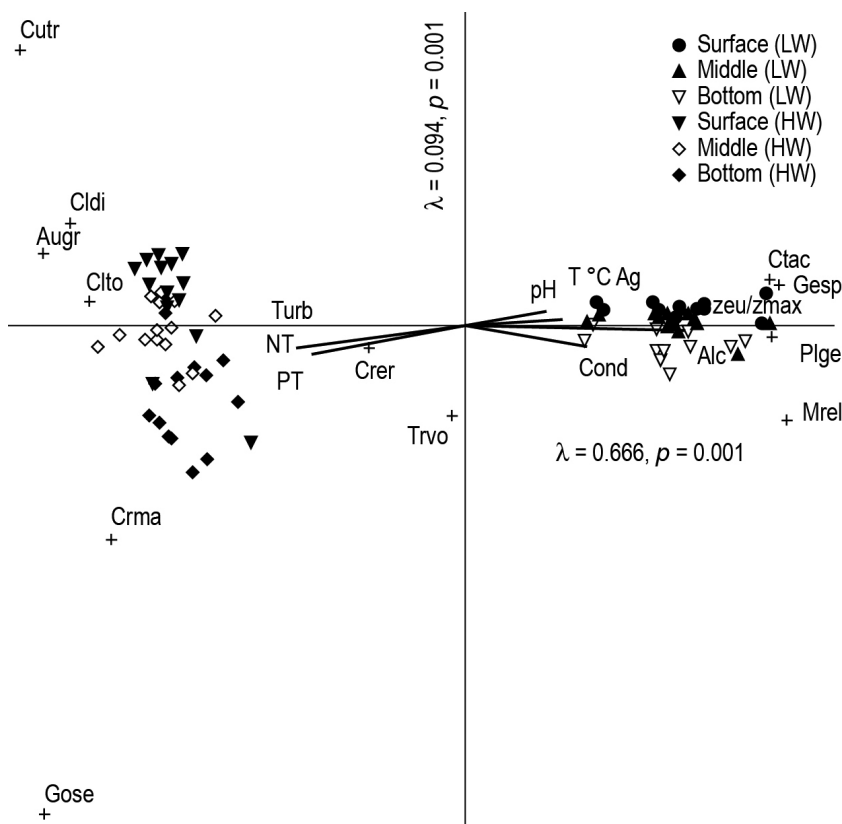


Figure 8. Ordination of sample units by the CCA in the Lake Amapá generated from eight environmental variables and 12 phytoplankton species: °C (Water temperature), Turb (turbidity), Alc (alkalinity), Zeu / Zmax (ratio of euphotic zone of maximum depth), PT (total phosphorus), NT (total nitrogen), pH and Cond (conductivity). Species: Gose (*Gonyostomum semen*), Cutr (*Cuspidothrix tropicalis*) Cldi (*Closterium diana*) Clto (*Closterium tortum*) Augr (*Aulacoseira granulata*), Crer (*Cryptomonas erosa*) Trvo (*Trachelomonas volvocinopsis*), Ctac (*Closteriopsis acicularis*), Gesp (*Geitlerinema* sp) Plge (*Planktothrix geitlerii*) and Mrel (*Merismopedia elegans*). (LW = low waters, HW = high waters).

volvocinopsis to the middle and bottom, and *Cryptomonas marsonii* only to the sampling units from the bottom. There was a clear spatial separation for these species, whereas *Cuspidothrix tropicalis* and *Gonyostomum semen* showed no clear relationships with the sampling units and locations distant from both axes (Figure 8).

4. Discussion

The greater species richness detected during the potamophase was possibly related to the prolonged thermal stratification and greater availability of nutrients from the influx of allochthonous material into the lake, caused by the flood pulse. These results agree with those reported by other studies focusing

on the phytoplankton of Brazilian floodplain lakes (Ibañez, 1998; Train and Rodrigues, 2004; Melo et al., 2005; Bovo-Scomparin and Train, 2008; Phlips et al., 2008).

In the low waters, the rate of change was lower, indicating a community with greater temporal stability with respect to the composition and relative abundance of species. The observed diversity, richness, and evenness possibly indicate more stable environmental conditions during this period. However, significant changes in biovolume and density were observed during the study, and therefore the low waters, by the criteria of Rojo and Álvarez-Cobelas (2003), cannot be considered stable.

No visible shift was detected, but the richness and density of species varied, without, however, resulting in sudden changes in the phytoplankton. The CCA revealed that the correlation between species and sampling units was related to the occupation of different niches, indicating that the more closely related species require similar environmental conditions.

Most cyanobacteria reach optimum growth under shaded environmental conditions, protected from intense solar radiation and high temperature (Shapiro, 1990). For *Planktothrix geitlerii* and *Merismopedia elegans*, this condition, as well as the increased availability of nutrients in the water column during the low waters, conferred a competitive advantage. *Geitlerinema* sp. showed less sensitivity to high light incidence, tolerating a wide spectrum of radiation. The results of this study are similar to those found by Huszar et al. (2000) for a lake in southeastern Brazil, where *Geitlerinema* sp. contributed 81% of the total density, and environmental conditions, such as transparency, were close to those in the Lake Amapá. These authors observed the dominance of *Geitlerinema* under high light attenuation and mixing regime in an enriched environment, characterizing this species with similar requirements to *Cylindrospermopsis* sp. In this study, the lower values of diversity found during the low waters, possibly indicated a more advanced stage of succession, due to the increased stability of the environment. Thus *Geitlerinema* sp., an R-strategist, would have established its dominance in this period through a competitive advantage.

Phlips et al. (2008) and García de Emiliani (1997) reinforced this idea by reporting high values of phytoplankton diversity in floodplain lakes during connection phases with the river, and lower values in periods of isolation. The latter author described the dominance of heterocytous cyanobacteria during the isolation period and diatoms during the flood,

relating the phases of connection and disconnection of the lake to the river successional patterns, and identifying the pulse as a reset factor of successional processes. Similar patterns were observed by Train and Rodrigues (2004) in the floodplain of the Paraná River. Therefore, it is possible to conclude that the lack of connectivity favors development toward advanced stages of succession in temporarily isolated lakes, such as Lake Amapá.

During the high waters, the occurrence in low densities of *Cuspidothrix tropicalis*, a typical, provides evidence that the disturbance generated by the flood pulse caused this species to decline from day 3, allowing the establishment of new niches. According to Reynolds et al. (2002), this species is adapted to a stable water column, resistant to light limitations, although it is sensitive to the conditions of flushing and mixing processes, which explains because it is not favored during the potamophase.

Short-term disturbance events can be measured by the rate of change of the community, where values less than 0.20 characterize a relatively stable community and values greater than 0.20 indicate abrupt changes in the community, in which several species decline and are quickly replaced by others (Huszar and Reynolds, 1997). Therefore, the rate of change allows the identification of transition in community organization, generated by the critical changes of the environment (Lopes et al., 2005).

Melack (1979) described three events that could lead to abrupt community changes: 1) periodically, such as changes in the hydrological pattern, flood pulse, or mixing; 2) absence of periodicity, expressed by encouraging competition; and 3) changes of an assemblage to another by internal factors. In the Lake Amapá, periodicity, especially in regard to connectivity with the river during the flood pulse, was likely related to the high rates of change recorded during the high waters.

Cardoso and Marques (2003) considered the action of wind as a disturbance factor for freshwater phytoplankton, observing a change rate up to 0.38 h^{-1} ; while Lewis Junior (1978) reported values between 0.02 to 0.13 d^{-1} . In this study, the rate of change during the high waters varied significantly, indicating marked changes in the community. The values found in this study ($0.07\text{-}1.63 \text{ dia}^{-1}$) extend the range of variation previously reported in the literature (Lewis Junior, 1978; Reynolds, 1984a, b).

During the high waters, it was observed the replacement of *Cuspidothrix tropicalis* by *Gonyostomum semen* from day 3 of sampling, onward. *G. semen* is an opportunistic species with a high reproductive rate (1.5 to 3.0 days) and low surface-volume ratio (Figueroa and

Rengefors, 2006). Le Cohu et al. (1989) mentioned that *G. semen* goes through a cycle of sudden population increase and decrease, rarely showing mass deployment for a longer period. The present study confirmed this behavior, since we observed sudden increases and decreases in its abundance.

The large number (up to 20%) of encysted cells of *G. semen*, beginning on day 5 of sampling, indicated the existence of adverse environmental conditions. Factors that may trigger this behavior are poorly known. Low pH, eutrophication, and limitation of light are mentioned as favoring the development of *Gonyostomum* (Eloranta and Palomaki, 1986; Pithart et al., 1997).

Phytoplankton communities are considered stable when there are no marked changes in community composition for a minimum of 15 days, and also when dominant species represent at least 50% of the total biomass (Rojo and Álvarez-Cobelas, 2003; Komárková and Tavera, 2003). During the high waters, there was no stable pattern apparent for the community.

Some studies have reported the coexistence of *G. semen* with other species, for example *Aulacoseira granulata*, which could indicate similar environmental requirements, as well as *Gonyostomum* blooms during the summer under conditions of stratification (Korneva, 2001). In the Lake Amapá, the presence of *G. semen* was possibly related to several factors, including thermal stratification, increased turbidity, and nutrient concentrations.

The vertical gradient of phytoplankton distribution, as evidenced by the CCA during the high waters, was related to the long-lasting thermal stratification of the lake in that period. In contrast, in the low waters, when daily circulation occurred, vertical gradients were inconspicuous.

The cryptomonas (*C. erosa*, *C. marsonii*, and *C. brasiliensis*), although less abundant, were more frequent during the high waters, when there was greater availability of nutrients and less light in the water column. The high surface:volume ratio and high metabolic activity indicate a high degree of adaptability and efficiency of these species in the opportunistic exploitation of nutrients under adverse conditions, favoring their development under such conditions (Klaveness, 1988).

Phlips et al. (2008) found a predominance of small phytoflagellates in Lake Amapá and an abundance of *Aulacoseira granulata* in the high waters, as observed in this study. Hamilton and Lewis Junior (1987) made similar observations in a floodplain lake of the Orinoco river, where they attributed the predominance of small phytoflagellates to the high sediment load and a limited euphotic

zone. Similar patterns were observed for this species by Bovo-Scomparim and Train (2008), Borges et al. (2008), O'Farrell (1994), and Unrein (2002), who also emphasized the adaptation of this potamoplanktonic species, common in large, highly turbid rivers, to flushing and its strategies for nutrient uptake. The observations in the present study agreed with this pattern, in which turbidity and TP were the main factors affecting the species.

The phytoplankton community proved to be adapted to prolonged stratification during the wet period, when it was represented by phytoflagellates. The results also showed that the influence of partial atelomixia with a mixture in the surface layer, was a key event for resuspension and maintenance of larger, non-flagellated species including *Aulacoseira granulata* and several species of *Closterium* in the water column, emphasizing the ecological importance of this event in floodplain lakes.

In this study, during the stage of the flood pulse, biomass decline due to the dilution effect. The higher rates of change and diversity indices recorded during the potamophase disturbance can be attributed to the flood, which caused system instability. It was unclear, however, whether this disturbance was strong enough to cause permanent changes. The short-term sampling scale, does not allow conclusive inferences about the persistence and resilience of the community. On the other hand, the observed lower rates of change and diversity indices indicate trends in the low waters toward community stability and likely a succession process.

Acknowledgements

We are grateful to Graduate Program in Ecology and Environmental Management of the UFAC of the Federal University of Acre; to CNPq for the M.Sc. scholarship and for financial support; to Limnology Group at the NUPELIA of the State University of Maringá for helpful discussions during the CAPES's PROCAD Program; to Rosano Ramos Marcelino for making the abiotic data available and to Amy Duchelle, Post Doctoral Associate for the University of Florida's Amazon Conservation Leadership Initiative based at the Federal University of Acre, for the revision of the English text.

References

- AMOROS, C. and BORNETTE, G. 2002. Connectivity and biocomplexity in riverine floodplains. *Freshwater Biology*, vol. 47, p. 761-776. <http://dx.doi.org/10.1046/j.1365-2427.2002.00905.x>
- BORGES, PAF, TRAIN, S. and RODRIGUES, LC. 2008. Estrutura do fitoplâncton, em curto período de tempo, em um braço do reservatório de Rosana

- (Ribeirão do Corvo, Paraná, Brasil). *Acta Scientiarum*, vol. 30, p. 57-65.
- BOVO-SCOMPARI, VM. and TRAIN, S. 2008. Long-term variability of phytoplankton community in an isolated lake of Ivinhema River State Park, Brazil. *Hydrobiologia*, vol. 610, p. 331-344. <http://dx.doi.org/10.1007/s10750-008-9448-3>
- CARDOSO, LS. and MARQUES, DM. 2003. Rate of change of the phytoplankton community in Itapeva Lake (North Coast of Rio Grande do Sul, Brazil), based on a wind driven hydrodynamic regime. *Hydrobiologia*, vol. 497, p. 1-12. <http://dx.doi.org/10.1023/A:1025449202083>
- COLE, G. 1983. *Textbook of Limnology*. 3rd ed. London: The C.V. Mosby Co. 401 p.
- ELORANTA, P. and PALOMAKI, A. 1986. Phytoplankton in Lake Konnevesi with special reference to eutrophication of the lake by fish farming. *Aqua Fennica*, vol. 16, p. 37-45.
- FIGUEROA, RI. and RENGEFORS, K. 2006. Life cycle and sexuality of the freshwater raphidophyte *Gonyostomum semen* (Raphidophyceae). *Journal of Phycology*, vol. 42, p. 859-871. <http://dx.doi.org/10.1111/j.1529-8817.2006.00240.x>
- GARCÍA DE EMILIANI, MO. 1997. Effects of water level fluctuations on phytoplankton in a river-floodplain lake system (Paraná River, Argentina). - *Hydrobiologia*, vol. 357, p. 1-15.
- GOLTERMAN, HL. and CLYMO, RS. 1969. *Methods for chemical analysis of freshwaters*. Oxford: Blackwell Scientific Publications. (International Biological Program Handbook n° 8). 171 p.
- HAMILTON, SK. and LEWIS JUNIOR, WM. 1987. Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. *Limnology and Oceanography*, vol. 32, p. 1277-1290. <http://dx.doi.org/10.4319/lo.1987.32.6.1277>
- HUSZAR, VLM. and REYNOLDS, CS. 1997. Phytoplankton periodicity and sequences of dominance in an Amazonian floodplain lake (Lago Batata, Pará, Brazil): responses to gradual environmental change. *Hydrobiologia*, vol. 346, p. 169-181. <http://dx.doi.org/10.1023/A:1002926318409>
- HUSZAR, VLM., SILVA, LHS., MARINHO, M., DOMINGOS, P. and SANT'ANNA, CL. 2000. Cyanoprokaryote assemblages in eight productive tropical Brazilian waters. *Hydrobiologia*, vol. 424, p. 67-77. <http://dx.doi.org/10.1023/A:1003996710416>
- IBAÑEZ, MSR. 1998. Phytoplankton composition and abundance of a central Amazonian floodplain lake. *Hydrobiologia*, vol. 362, p. 79-83.
- JUNK, WJ., BAYLEY, PB. and SPARKS, RE. 1989. The Flood Pulse Concept in River-Floodplain Systems. In DODGE, DP. (Org.). *Proceedings of the International Large River Symposium (LARS)*. Canadian Special Publication of Fisheries and Aquatic Sciences, vol. 106, p. 110-127.
- KLAVENESS, CD. 1988. Ecology of Cryptomonadida: a first review. In SANDGREN, C., org. *Growth and reproductive strategies of freshwater phytoplankton*. New York: Cambridge University Press. p. 105-133.
- KOMÁRKOVÁ, J. and TAVERA, R. 2003. Steady state of phytoplankton assemblage in the tropical Lake Catemaco (Mexico). *Hydrobiologia*, vol. 502, p. 187-196. <http://dx.doi.org/10.1023/B:HYDR.0000004281.11917.7a>
- KORNEVA, LG. 2001. Ecological aspects of mass development of *Gonyostomum semen* (Ehr.) Dies. (Raphidophyta). *International Journal of Algae*, vol. 3, p. 40-54.
- LE COHU, R., GUITHARD, J., COMOY, N. and BRABET, S. 1989. *Gonyostomum semen* (Raphidophyceae) nuisance potentielle de grands reservoirs français du lac de Pareloup. *Archiv für Hydrobiologie*, vol. 117, p. 223-246.
- LEWIS JUNIOR, WM. 1978. Analysis of succession in a tropical plankton community and a new measure of succession rate. *The American Naturalist*, vol. 112, p. 401-414. <http://dx.doi.org/10.1086/283282>
- LLOYD, M. and GHELARDI, RJ. 1964. A table for calculating the equitability component of species diversity. *Journal of Ecology*, vol. 33, p. 217-225. <http://dx.doi.org/10.2307/2628>
- LOBO, E. and LEIGHTON, G. 1986. Estruturas de las fitocenosis planctónicas de los sistemas de desembocaduras de rios y esteros de la zona central de Chile. *Revista de Biología Marina*, vol. 22, p. 143-170.
- LOPES, MRM., BICUDO, CEM. and FERRAGUT, C. 2005. Short-term spatial and temporal variation of phytoplankton in a shallow tropical oligotrophic reservoir, southeast Brazil. *Hydrobiologia*, vol. 542, p. 235-247. <http://dx.doi.org/10.1007/s10750-004-8332-z>
- LUND, JWG., KIPLING, C. and LE CREN, ED. 1958. The inverted microscope method of estimating algal numbers and statistical basis of estimation by counting. *Hydrobiologia*, vol. 11, p. 143-170. <http://dx.doi.org/10.1007/BF00007865>
- MCCUNE, B. and MEFFORD, MJ. 1999. *PC-Ord. Multivariate analysis of ecological data, version 4.0*. Oregon: MjM Software Design, Gleneden Beach. 237 p.
- MELACK, JM. 1979. Temporal variability of phytoplankton in tropical lakes. *Oecologia*, vol. 44, p. 1-7. <http://dx.doi.org/10.1007/BF00346388>
- MELO, SV., REBELO, SRM., SOUZA, KF, MENEZES, M. and TORGAN, LC. 2005. Fitoplâncton. In SILVA, ENS., APRILE, FM., SCUDELLER, VV. and MELO, S., orgs. *Bio Tupé. Meio físico, diversidade biológica e sociocultural do Baixo Rio Negro, Amazônia Central*. Manaus: INPA. p. 87-98.

- MELO, S., HUSZAR, VLM., ESTEVES FA. and BOZELLI, R. 2000. Phytoplankton diel variation and vertical distribution in two Amazonian floodplain lakes (Batata Lake and Mussurá Lake, Pará-Brasil) with different mixing regimes. *Amazoniana*, vol. 18, p. 1-10.
- NEIFF, JJ. 1990. Ideas para la interpretación ecológica del Paraná. *Interciencia*, vol. 156, p. 424-441.
- O'FARRELL, I. 1994. Comparative analysis of the phytoplankton of fifteen lowland river systems of the River Plate Basin (Argentina). *Hydrobiologia*, vol. 289, p. 109-117. <http://dx.doi.org/10.1007/BF00007413>
- PHILIPS, EJ., HAVENS, KE. and LOPES, MRM. 2008. Seasonal dynamics of phytoplankton in two Amazon floodplain lakes of varying hydrologic connectivity to the main river channel. *Archiv für Hydrobiologie*, vol. 172, no. 2, p. 99-109. <http://dx.doi.org/10.1127/1863-9135/2008/0172-0099>
- PITHART, D., PECHAR, L. and MATTSON, G. 1997. Summer blooms of raphidophyte *Gonyostomum semen*, and its diurnal vertical migration in a floodplain pool. *Algological Studies*, vol. 119, p. 119-133.
- POOLE, HH. and ATKINS, WRG. 1929. Photo-electric measurement of submarine illumination throughout the year. *Journal of the Marine Biological Association*, vol. 16, p. 297-324. <http://dx.doi.org/10.1017/S0025315400029829>
- RAMÍREZ, JJ. and BICUDO, CMR. 2002. Variation of climatic and physical co-determinants of phytoplankton community in four nictemeral sampling days in a shallow tropical reservoir, Southeastern. *Brazilian Journal of Biology*, vol. 62, p. 1-14. PMID:12185909.
- REYNOLDS, CS. 1984a. *The ecology of freshwater phytoplankton*. Cambridge: University Press. 384 p.
- REYNOLDS, CS. 1984b. Phytoplankton periodicity: the interactions of form, function and environmental variability. *Freshwater Biology*, vol. 14, no 2, p. 111-142. <http://dx.doi.org/10.1111/j.1365-2427.1984.tb00027.x>
- REYNOLDS, CS. 1997. Vegetation processes in the pelagic: a model for ecosystem theory. In KINNE, O., org. *Excellence in Ecology*. Oldendorf Luke Germany: Ecology Institute. 371 p.
- REYNOLDS, CS., HUSZAR, VLM., KRUK, C., NASELLI-FLORES, L. and MELO, S. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, vol. 24, p. 417-428. <http://dx.doi.org/10.1093/plankt/24.5.417>
- ROJO, C. and ÁLVAREZ-COBELAS, M. 2003. Are there steady-state phytoplankton assemblages in the field? *Hydrobiologia*, vol. 502, p. 3-12. <http://dx.doi.org/10.1023/B:HYDR.0000004266.79941.cc>
- SHANNON, CE. and WEAVER, W. 1949. *The Mathematical Theory of Communication*. Urbana: University of Illinois Press. 132 p.
- SHAPIRO, J. 1990. Current beliefs regarding dominance by blue green: the case for the importance of CO₂ and pH. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, vol. 24, p. 38-54.
- SUN, J. and LIU, D. 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. *Journal of Plankton Research*, vol. 25, p. 1331-1346. <http://dx.doi.org/10.1093/plankt/fbg096>
- TER BRAAK, CJF. 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, vol. 67, p. 1167-1179. <http://dx.doi.org/10.2307/1938672>
- TILZER, MM. and GOLDMAN, CR. 1978. Importance of mixing, thermal stratification and light adaptation for phytoplankton productivity in Lake Tahoe (California-Nevada). *Ecology*, vol. 59, p. 810-821. <http://dx.doi.org/10.2307/1938785>
- TRAIN, S. and RODRIGUES, LC. 2004. Phytoplanktonic Assemblages. In THOMAZ, SM., AGOSTINHO, AA. and HAHN, NS., orgs. *The Upper Paraná River and its Floodplain: Physical aspects, Ecology and Conservation*. Leiden: Backhuys. p. 103-124.
- UNREIN, F. 2002. Changes in phytoplankton community along a transversal section of the Lower Paraná floodplain, Argentina. *Hydrobiologia*, vol. 468, p. 123-134. <http://dx.doi.org/10.1023/A:1015254320940>
- UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitativen Phytoplanktonmethodik. *Mitteilungen Internationale Vereinnigung für Theoretische und Angewandte. Limnologie*, vol. 9, p.1-38.
- VALDERRAMA, JC. 1981. The simultaneous analysis of total nitrogen e total phosphorus in natural waters. *Marine Chemistry*, vol. 10, p.109-122. [http://dx.doi.org/10.1016/0304-4203\(81\)90027-X](http://dx.doi.org/10.1016/0304-4203(81)90027-X)
- WARD, JV., TOCKNER, K. and SCHIEMER, F. 1999. Biodiversity of floodplain river ecosystems: ecotones and sustentability. *Regulated Rivers: Research and Management*, vol. 15, p. 125-139. [http://dx.doi.org/10.1002/\(SICI\)1099-1646\(199901/06\)15:1/3<125::AID-RRR523>3.0.CO;2-E](http://dx.doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E)