

Spatial and temporal dynamics of phytoplankton functional group in a blocked valley (Brazil).

NABOUT^{1,2}, J.C. & NOGUEIRA¹, I.S.

¹ Departamento de Biologia, Laboratório de Limnologia, ICBI, Universidade Federal de Goiás, C.P. 131, Campus II – Goiânia-GO, Brasil. CEP.74001-970. e-mail: nogueira@icb.ufg.br

² Programa de Doutorado em Ciências Ambientais, Universidade Federal de Goiás, C.P. 131, Campus II – Goiânia-GO, Brasil. CEP.74001-970. e-mail: naboutjc@hotmail.com

ABSTRACT: Spatial and temporal dynamics of phytoplankton functional group in a blocked valley (Brazil).

Lake Tigres is a blocked-valley lake, formed by tributary obstruction from sediment deposition during flooding in the main course of the river. Few studies have treated phytoplankton dynamics in blocked-valley lakes. The aim of this study was to investigate the temporal and spatial patterns of phytoplankton biovolume, to detect and describe the dominant phytoplankton functional groups in Lake Tigres during the dry season and the beginning of the rainy season in 2004. The mean phytoplankton biovolume was $<0.4\text{mm}^3\cdot\text{L}^{-1}$, characterizing Lake Tigres as oligotrophic. During the entire study period, 18 functional groups were found, with a predominance of phytoflagellate functional groups (Y, W1, W2, Lo) and some diatoms (N, P, D). Because of limnological differences in each sampling period, the functional groups were different in each month and principally between the dry and rainy seasons, which was shown by canonical correspondence analysis (CCA). The CCA indicated that in the dry season, the predominant functional groups Y, W1, W2, and Lo were favored by higher nutrient concentrations and high oxygen content. At the beginning of the rainy season, the predominant functional groups P, S1, S, T and N were favored by surface drainage and high water temperature. The dry-season biovolume samples were characterized by nanoplankton species (C-strategists), suggesting that small size is an optimal strategy for nutrient absorption. However, during the early rainy season, biovolume was dominated by microplankton species (SR-strategists).

Key words: Lake Tigres, dry and rainy seasons, tropical environment.

RESUMO: Dinâmica espacial e temporal de grupos funcionais fitoplanctônicos de um vale bloqueado (Brasil). O lago dos Tigres pode ser caracterizado como um vale bloqueado, formado através da obstrução de tributários e pela deposição de sedimentos durante a inundação a partir do curso principal. Poucos trabalhos abordaram a dinâmica fitoplanctônica em vales bloqueados, para tanto, o objetivo desse trabalho foi reconhecer os padrões de distribuição temporal e espacial do biovolume fitoplanctônico e detectar os grupos funcionais fitoplanctônicos dominantes e descritivos do sistema lago dos Tigres durante o período de seca (junho a setembro) e início de chuva (outubro e novembro) de 2004. Os valores de biovolume fitoplanctônico, em média, foram inferiores a $0,4\text{mm}^3\cdot\text{L}^{-1}$, caracterizando o sistema lago dos Tigres como oligotrófico. Durante todo período de estudo foram encontrados 18 grupos funcionais, sendo que o predomínio foi de grupos funcionais de fitoflagelados (Y, W1, W2 e Lo) e de algumas diatomáceas (N, P e D). Devido às diferenças limnológicas em cada período de amostragem os grupos funcionais foram relativamente diferentes em cada mês e principalmente entre os períodos de seca e chuva, o que ficou evidenciado pelos escores derivados da análise de correspondência canônica (ACC). A ACC indicou ainda que, na estiagem os grupos funcionais Y, W1, W2 e Lo foram beneficiados pela maior concentração de nutrientes e elevada saturação de oxigênio, enquanto que durante o período de elevada precipitação os grupos funcionais predominantes foram P, S1, S, T e N, favorecidos pelo escoamento superficial e elevada temperatura da água. Na seca o biovolume dos períodos de amostragem foi caracterizado por espécies nanoplanctônicas, (C-estrategistas), sugerindo que no sistema Lago dos Tigres o pequeno tamanho seja uma estratégia para otimizar a absorção dos nutrientes. Por outro lado durante o período de elevada precipitação o biovolume foi caracterizado por espécies microplanctônicas (SR-estrategistas).

Palavras-chaves: ambiente tropical, Lago dos Tigres, estações chuvosa e seca.

Introduction

Taxonomic groups of phytoplankton are composed of species with very different physiologies, so the analysis of phytoplankton functional groups can better reveal the physiological, morphological, and ecological responses of the phytoplankton community to environmental conditions (Reynolds, 2006). Functional groups of phytoplankton are polyphyletic groups that respond similarly to a determined set of environmental conditions (Reynolds et al., 2002; Reynolds, 2006). Their analysis provides a better understanding of phytoplankton dynamics than describing the dynamics of taxonomic groups (Kruk et al., 2002; Reynolds et al., 2002; Reynolds, 2006). Presently, 31 phytoplankton functional groups are described (Reynolds et al., 2002).

Initially the functional groups were studied in temperate environments; however, this concept appears to be appropriate for tropical environments as well. Currently, phytoplankton functional groups are receiving much attention, and have enhanced descriptions of the dynamics of the community of taxonomic groups (Reynolds, 1997; Kruk et al., 2002; Reynolds et al., 2002; Nabout et al., 2006).

Analysis of functional groups has been shown to be appropriate for tropical regions. However, no studies have focused on phytoplankton functional groups in blocked-valley lakes. This type of lake is formed by sediment deposition obstructing the tributary during flooding of the main course (Kalff, 2002). This characteristic of Lake Tigres results in different dynamics from other fluvial lake types. An important difference between blocked-valley and other fluvial lakes (oxbow, meander scroll, and others) is their hydrological connectivity. This connectivity has a great impact on dynamics and biodiversity, because it affects the exchange of energy and matter (organisms) between the river and its floodplain (Bini et al., 2003).

The study of spatial and temporal variability is fundamental to understand the structure and function of the phytoplankton community and also to understand the dynamics of aquatic ecosystems. Phytoplankton fluctuations can be predictive and make it possible to recognize changes

in the aquatic environment (Huszar, 2000). The aim of this study was to recognize the temporal and spatial patterns of phytoplankton distribution, and detect the dominant and descriptive phytoplankton functional groups in this blocked valley (Lake Tigres system) during the dry season and the beginning of the rainy season of 2004. We attempted to answer the following questions: (i) Was there any temporal change in functional groups, mainly between the dry season and the beginning of the rainy season? (ii) Was there any spatial change in phytoplankton functional groups, predominantly between the lotic and lentic regions of the Lake Tigres system? (iii) Which limnological variables were associated with these spatial and temporal changes in phytoplankton functional groups? (iv) Do the phytoplankton functional groups provide a good description of the limnological characteristics of the Lake Tigre system?

Material and methods

The source of the Lake Tigres system is the Água Limpa River. It is located in the Britânia district of western Goiás state, central Brazil, in the Tocantins-Araguaia basin, a tributary of the Vermelho River (Fig. 1). Lake Tigres is large, 24.5 km long with a 60.83 km perimeter, and is a popular tourist destination.

There were 11 sampling stations, three in lotic regions (Água Limpa and the Vermelho River) and eight in lentic regions (Lake Tigres), near preserved and deforested areas and a popular tourist region.

Samples were collected in the dry season (June, July, August, and September) and the beginning of the rainy season (October and November) of 2004. Subsurface 100 mL samples were collected for quantitative study; they were placed in dark bottles, fixed with lugol-acetic solution (Vollenweider, 1974), and stored in the dark. The density of the phytoplankton was estimated by the Utermöhl method (Utermöhl, 1958), with a Leitz inverted microscope, at a magnification of 450x. The individuals (cells, colonies, cenobios, and filaments) were counted in random fields; about 100 individuals of the most frequent species were counted, with less than 20% error, at a confidence limit of 95% (Lund et al., 1958).

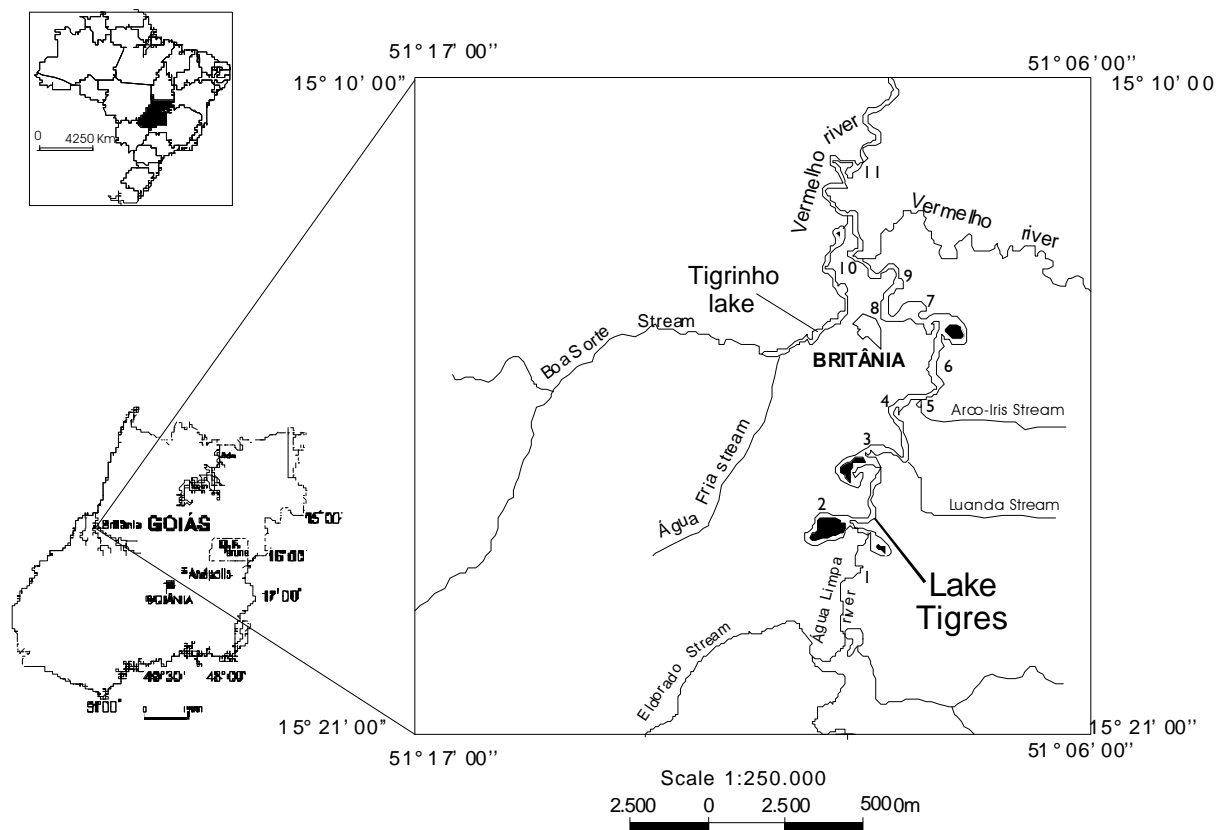


Figure 1: Location of area study, indicating the sampling station

Algae biovolume was approximated according to Hillebrand et al. (1999) and expressed in $\text{mm}^3 \cdot \text{L}^{-1}$. Phytoplankton functional groups were determined from species that represented more than 5% of the biovolume of at least one sample unit (Kruk et al., 2002). The phytoplankton functional groups were defined according to Reynolds (1997) and Reynolds et al. (2002).

Limnological characterization of the lake was based on chemical and physical water information, measured at the same depth as the phytoplankton sampling at each collection station. Variables measured were: water temperature, pH, conductivity, total dissolved solids, and oxygen saturation using a HORIBA U-21 water multianalyzer. Water transparency and depth were measured by Secchi disc. The euphotic zone was calculated as 3 times the depth of Secchi disc disappearance (Cole, 1994).

Water samples were also collected from each site for total nitrogen and phosphorus analysis. They were fixed in the field with 0.5 mL absolute sulfuric acid. Collection procedures and laboratory processing were adopted from Mackereth et al. (1978), Carmouze (1994), and Clesceri et al. (1992).

Floristic dissimilarity between months was measured by the Bray-Curtis index. The functional group data and matrix were used to form the dendrogram, using Bray-Curtis dissimilarity and the UPGMA connection method (Sneath & Sokal, 1973). The cophenetic coefficient of correlation (r) was calculated to evaluate matrix and dendrogram dissimilarity.

Relationships between abiotic and biovolume data were evaluated by canonical correspondence analysis (CCA; Ter Braak, 1986). The null hypothesis of absence of relationship between matrices (biotic and abiotic) was tested with Monte Carlo procedures. The lines of environmental data matrixes were randomly allocated and the CCA was calculated. The entire procedure was repeated 1000 times. Species of algae and environmental data were previously transformed ($\text{Log}(n+1)$). All calculations were done with the PC-ORD program (McCune & Mefford, 1997).

Results

Lake Tigres is a blocked-valley lake, shallow and with low transparency. The limnological variables showed spatial

(between lotic and lentic regions) and temporal differences (between the dry season and the beginning of the rainy season) (Tab. I). In the dry season, the samples revealed higher nutrient concentrations (June, July, and August) and oxygen saturation (September).

At the beginning of the rainy season (November), water temperatures were higher (Nabout & Nogueira, given in publication). These temporal variations demonstrated the strong influence of the hydrological cycle on limnological variables.

Table I: Limnological variables measures registered at the lake Tigres. The mean and standard deviation (SD) are calculated for six samplings in Lake Tigres.

Limnological variables		June	July	August	September	October	November
Depth	SD	1.23	1.06	0.99	1.02	1.21	1.10
	Mean (m)	3.93	3.02	2.75	2.24	2.21	2.70
Transparency	SD	0.13	0.10	0.16	0.06	0.07	0.07
	Mean (m)	0.49	0.52	0.51	0.40	0.45	0.32
Euphotic Zone	SD	0.38	0.31	0.49	0.19	0.22	0.20
	Mean (m)	1.46	1.57	1.52	1.21	1.34	0.96
Water temp.	SD	0.88	0.70	2.05	1.84	1.38	2.23
	Mean (°C)	25.32	25.94	26.19	28.17	30.45	32.01
Conductivity	SD	14.08	7.51	5.84	9.21	13.74	8.86
	Mean (mS.cm ⁻¹)	46.25	31.82	22.62	28.64	46.21	30.91
Ox. Saturation	SD	6.20	6.86	7.98	29.12	9.93	12.19
	Mean (%)	100.88	111.00	131.64	168.91	134.54	155.82
pH	SD	0.46	0.66	0.25	0.40	0.61	0.28
	Mean	7.30	7.51	6.95	6.81	7.61	7.20
Total Nitrogen	SD	99.86	69.97	68.76	68.68	35.08	54.25
	Mean (mg.L ⁻¹)	230	148.18	94.55	68.18	81.36	139.89
Total phosphorus	SD	46.60	57.68	76.66	48.79	53.73	25.19
	Mean (mg.L ⁻¹)	52.50	52.27	58.18	50.00	37.73	29.95

The phytoplankton biovolume showed different horizontal patterns in the lake over six sampling periods, mainly between the dry season and the beginning of the rainy season. During all sampling periods, algae biovolume was low (Fig. 2), from 0.035 mm³.L⁻¹ (Station 1 - November) to 1.64 mm³.L⁻¹ (Station 4 - September). Total biovolume tended towards higher values from September onward.

During the study period, mean biovolume values were less than 0.4 mm³.L⁻¹. Therefore, Lake Tigres is an oligotrophic environment, using Reynolds (1984) biovolume values for trophic state characterization. The highest phytoplankton biovolume values were recorded at Station 4 in September (Fig. 2D; *Euglena* sp.) and Station 10 in November (Fig. 2F; *Aulacoseira granulata* var. *angustissima*).

Because of limnological differences in each sampling period, the functional groups were relatively heterogeneous in each month. Species that contributed at least 5% of the total biovolume at each sampling station were represented by 18 functional groups over the entire study period. However, there was a general predominance of phytoflagellate functional groups (Y, W1, W2, and Lo) with some diatoms and desmids (N, P, and D) (Fig. 3).

During June, groups P and D were dominant in the lotic region (stations 1, 10, and 11), whereas phytoflagellates (functional groups Y, W2, and Lo) were dominant at all other (lentic) sampling stations.

In July and August, functional group Y was abundant at almost all Lake Tigres sampling stations. Also in these months *Cyclotella* sp.1 (functional group A) was

abundant at Station 11 (lotic region), comprising 23% and 79% of this station's

total biovolume in July and August, respectively.

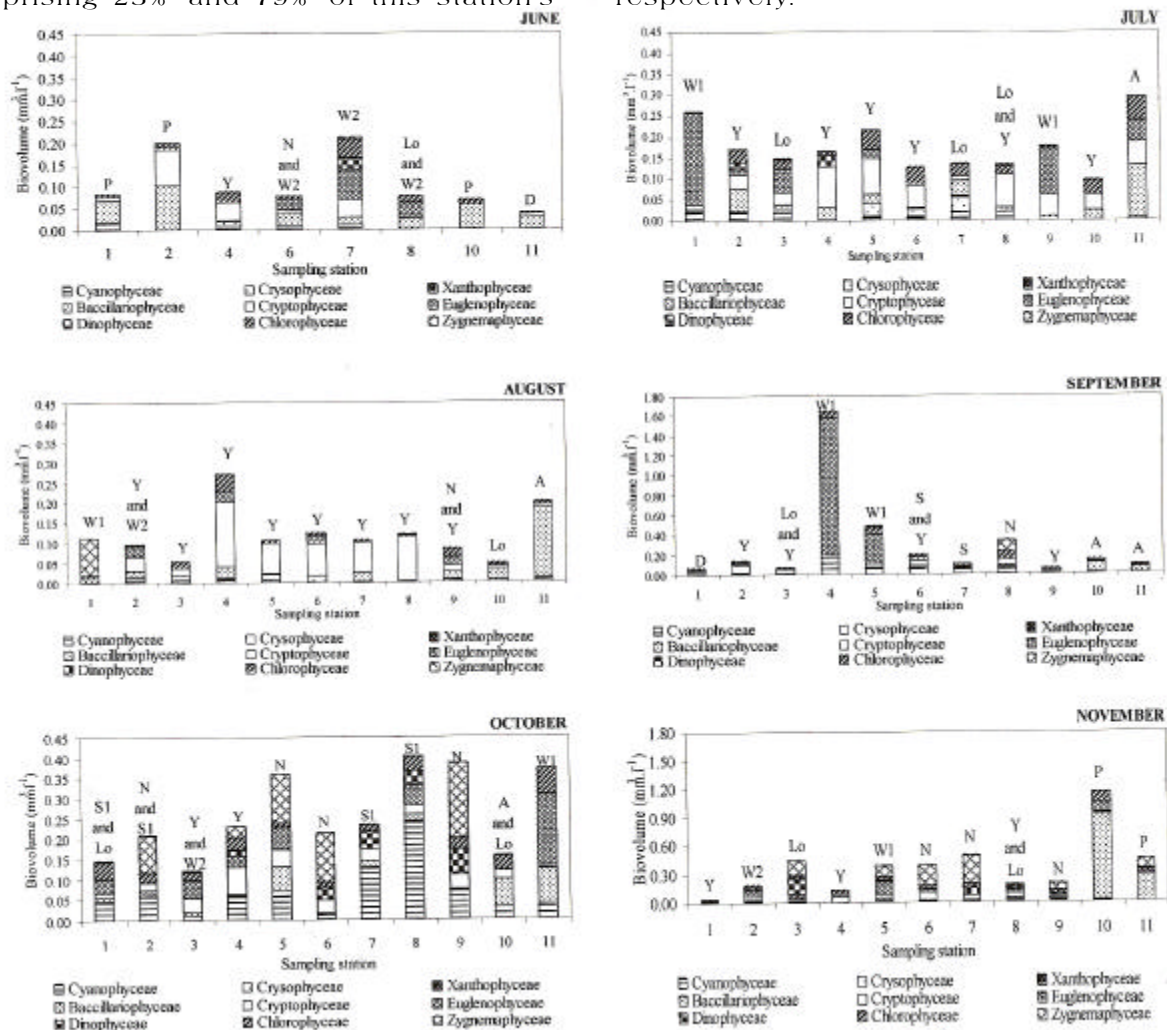


Figure 2: Biovolume of the phytoplankton community ($\text{mm}^3 \cdot \text{l}^{-1}$) of the lake Tiges in always months of sampling station. The letters above the bar indicate the representative functional groups, according to Reynolds et al. (2002).

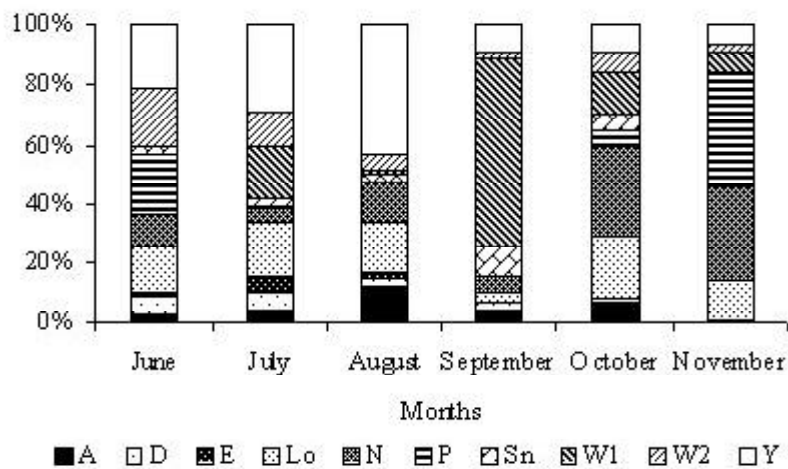


Figure 3: Relative contribution (%) of representative phytoplankton functional groups of Lake Tiges in sampling period of 2004.

During September at Station 1, functional group D (*Cocconeis placentula*) had a total biovolume of 35%. Stations 10 and 11 were abundant in *Cyclotella* sp.1 with 53% and 62% of the total biovolume respectively. Flagellates were always present, with high biovolumes at most stations, with Station 4 having group W1 (*Euglena* sp.) as dominant with 83% of the total biovolume.

In October and November in the beginning of the rainy season, a change in dominant functional groups was observed. In October the functional group S1 had elevated biovolumes, being dominant at Stations 1, 7, and 8 with 25%, 54%, and 57% of the total biovolume, respectively. In November, functional group N (*Haplotaenium minutum*) was dominant at Stations 7 and 9. In the same month, functional group P (*Aulacoseira granulata* var. *angustissima*) was dominant in the lotic region (Stations 10 and 11), with 75% and 48% of the total biovolume, respectively.

Dissimilarity analysis based on phytoplankton functional group data (Fig. 4) showed that the phytoplankton community was formed by similar functional groups in the months of July and August.

Functional groups Y and Lo predominated in these two months (Fig. 3). October and November were distinguished from the other months by the presence of functional groups N, P, and Lo. September showed a more distinct phytoplankton community than other months, probably because of elevated biovolumes and a predominance of functional group W1.

The first two axes of the canonical correlation analysis (CCA – Fig. 5) explained only 20.5% (12.1% axis 1; 8.3% axis 2) of total data variability. The Monte Carlo Test (Table II) indicated that the first three canonical correlations were significant ($p < 0.05$).

Environmental variables positively correlated with the first axis were transparency, total phosphorus, and oxygen saturation; whereas those negatively correlating with the second axis were oxygen saturation and electrical conductivity. CCA ordination of phytoplankton functional groups suggested that groups Y, W2, Lo, N, and D were correlated with low nutrient concentrations at most stations in June, July, and August. These functional groups (or at least one of them) were always abundant in at least one sampling station.

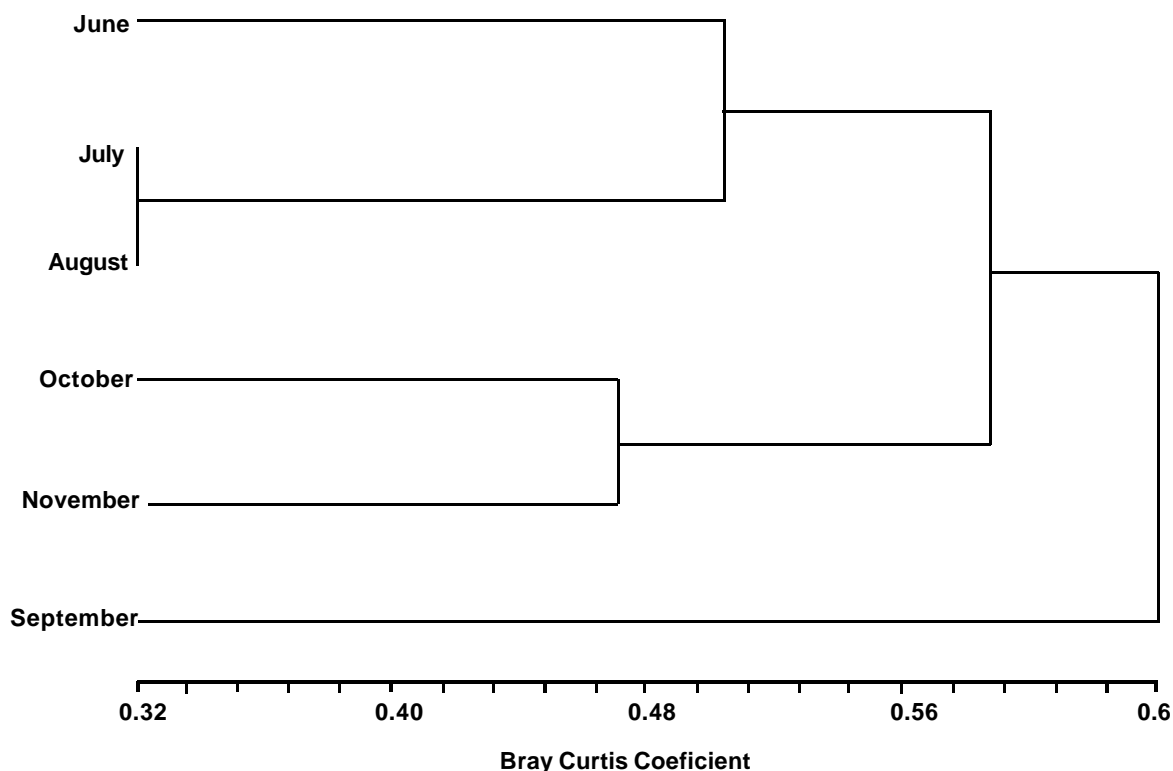


Figure 4: Dendrogram of the dissimilarity coefficient, when phytoplankton of the lake Tigres was obtained on basis of the functional groups with more than 5% of the total biovolume of each sampling station. ($r=0.78$).

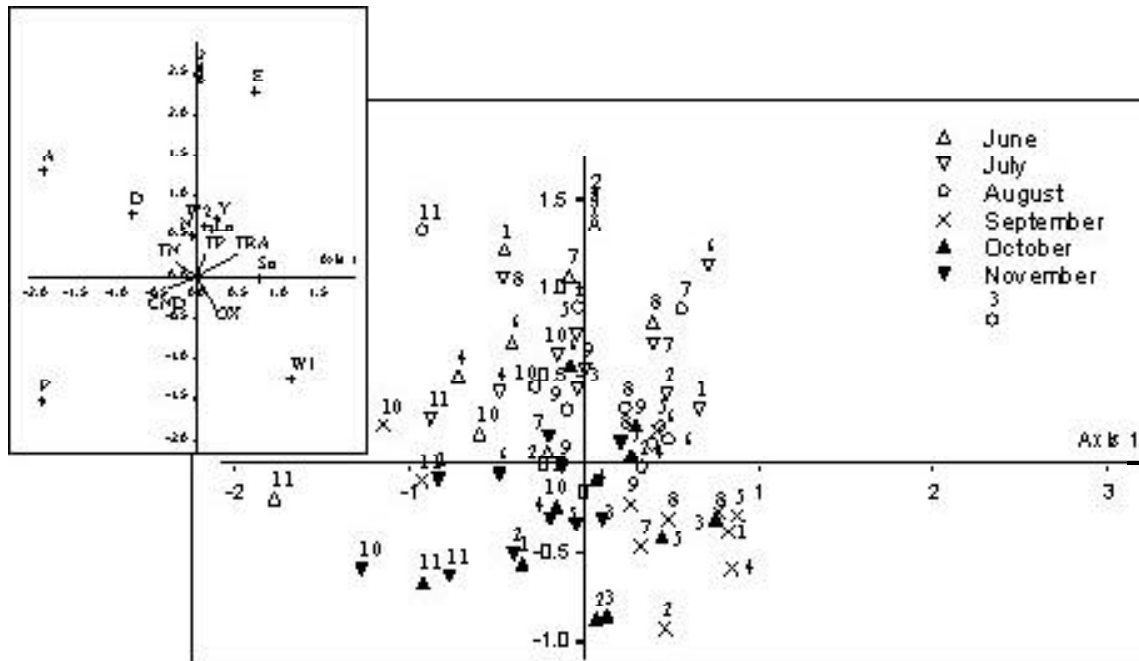


Figure 5: Scores derived from the canonical correspondence analysis (CCA) applied to the biovolume dominant phytoplankton species and environmental variables. The numbers represent the station sampling and the letter the phytoplankton functional groups according Reynolds et al. (2002). Codes for the environmental variables are CND, electrical conductivity; OX, oxygen saturation; TRA, water transparency; TN, total nitrogen and TP, total phosphorous.

Table II: Statistical data of Monte Carlo test—species—environment correlations for Lake Tigres. Species—environment correlation, canonical correlation; Mean, canonical correlation average obtained with the aleatory data; Minimum, minimum value of the canonical correlation obtained with the aleatory data; Maximum, maximum value of the canonical correlation obtained with the aleatory data; P, significance level.

Axes	Species – environment	Mean	Minimum	Maximum	P
1	0.798	0.615	0.355	0.854	0.012
2	0.662	0.467	0.243	0.710	0.007
3	0.495	0.370	0.179	0.685	0.032

Discussion

In floodplain lakes, flooding is a factor regulating phytoplankton species biovolume in tropical regions, e.g., in the Paraná River (Thomaz et al., 1997; Train & Rodrigues, 1997), the Amazon floodplain (Melo & Huszar, 2000), and the Pantanal floodplain (Oliveira & Calheiros, 2000; Junk et al. 2006). However, in blocked-valley lakes, the climate regime and consequent increase in water column are also important factors. The Lake Tigres system showed changes in the biovolume and phytoplankton composition during the beginning of the rainy season (Fig. 2).

Functional group Y was important in terms of biovolume in June, July, and August (dry season). These small organisms are found in practically all aquatic environments, principally tropical lakes. According to Klaveness (1988) and Sommer (1981), they prefer mixing of the water column by wind, because they have greater adaptability to turbulent water column mixing and low transparency conditions. The ideal environment for this group is moderately nutrient-rich water, because they are well adapted to low light levels (Reynolds et al., 2002).

CCA for Lake Tigres (Fig. 5) demonstrated that functional group Y was

correlated with stations that showed higher nutrient contents (phosphorus) and lower transparency. In functional group Y, *Cryptomonas erosa*, *C. marsonii*, and *C. obovata* were responsible for the highest biovolume values. These species were characterized by Olrik (1994) as C-strategists, with high surface/volume ratios, facilitating rapid growth by rapid nutrient absorption. Functional group Y was also abundant in Lake Castelo in the Paraguay River (Oliveira & Calheiros, 2000), in lakes of the Upper Paraná River during the dry season (Train & Rodrigues, 2004), and in floodplain lakes of the Middle Araguaia River, mainly during low-water periods (Nabout et al. 2006), where sampling characteristics were similar to those found in Lake Tigres during June, July, and August. In the Araguaia River lakes, as well as a predominance of Cryptophyceae, biovolume values also tended to be oligotrophic, as observed in this study. Lakes Dumbazinho, Landi, and Japonês (Nabout et al., 2006) were also classified as blocked valleys by Morais et al. (2005); when information from Lake Tigres was compared with these lakes, there were some similarities in phytoplankton functional groups, such as dominant group Y in the 2000 dry season and dominant group W1 in Lake Japonês in the 2000 rainy season.

Phytoplankton functional groups W2 (*Trachelomonas* sp.4 and *Strombomonas verrucosa*) and Lo (*Peridinium umbonatum* and *P. corillionii*) were also abundant in June, July, and August. All these groups were cited by Reynolds et al. (2002) as being adapted to moderately nutrient-rich waters. In this study, the CCA demonstrated that these functional groups were correlated with more-concentrated nutrient environments. Functional group Lo was also abundant in the Middle Paraná River (Garcia de Emiliani, 1993). Functional group W2 was also abundant during low-water periods in some Araguaia River lakes (Nabout et al. 2006).

In June, July, and August, the Bacillariophyceae comprised functional groups A (*Cyclotella* sp.1) and D (*Gomphonema parvulum* and *Cocconeis placentula*). Functional groups A and D (Bacillariophyceae) require turbulence and low light levels, and have a tendency to grow in eutrophic environments (Sommer, 1988). Both functional groups, according to the CCA (Fig. 5), were correlated with

locations where total nitrogen was higher and water transparency lower than in other areas in Lake Tigres. These species mainly occurred at Stations 1 (Água Limpa River), 10, and 11 (both in the Vermelho River). Because these were lotic region stations, they showed high turbulence and probably high silica availability, since the sediment was sand or clay.

Analysis of dissimilarity (Fig. 4) demonstrated that the beginning of the rainy season provoked differentiation in phytoplankton functional group composition. Physical and chemical analysis of Lake Tigres water (Nabout & Nogueira, given in publication) indicated high temperatures and low transparency in October and November. Detailed analysis of phytoplankton functional groups in these months showed a predominance of different phytoflagellate and diatom groups.

During October and November, functional groups S and N were abundant at some stations. These groups are to be found in turbid and mesotrophic environments (Reynolds et al., 2002). The class functional group S has been reported as being at home in environments with elevated temperatures (Shapiro, 1990) and high turbulence (Ganf, 1983). Functional group N was reported as being quite well adapted to low-light and high-turbulence environments (Happety-Wood, 1988). Groups S and N are SR-strategists, which can minimize grazing (Olrik, 1994), mainly because of their size or cell shape.

Analysis of dissimilarity (Fig. 4) and CCA (Fig. 5) demonstrated that September differed from all the other months. CCA showed that sampling stations in this month showed correlations between high oxygen saturation values and a dominance of functional group W1 (Euglenophyceae). In the Araguaia River floodplain lakes, functional group W1 was co-dominant with group P during the high-water period (Nabout et al., 2006). According to Reynolds et al. (2002), this functional group can be found in shallow environments, with vegetation or other sources of organic matter, and requires high dissolved oxygen contents.

In summary, phytoplankton biovolume responded to the climate rhythm, being different in each period. The dry and early rainy seasons showed different phytoplankton dynamics; CCA highlighted the importance of the hydrological cycle for

phytoplankton dynamics. There was spatial differentiation between lotic and lentic environments. The predominant functional groups at the lotic stations were P, A, and D; and at the lentic stations were Y, W1, W2, and Lo. Therefore, analysis of the phytoplankton functional groups provided a good description of the Lake Tigres system, better representing the spatial and temporal phytoplankton dynamics and the influence of limnological variables.

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References

- Bini, L.M., Velho, L.F.M. & Lansaç-Tôha, F.A. 2003. The effect of connectivity on the relationship between local and regional species richness of testate amoebae (Protozoa rhizopoda) in floodplain lagoons of the upper Parana River, Brazil. *Acta Oecol.*, 24:145-151.
- Carmouze, J.P. 1994. O metabolismo dos ecossistemas aquáticos: fundamentos teóricos, métodos de estudo e análises químicas. Edgard Blucher, São Paulo. 253p.
- Clesceri, L.S., Greenberg, A.E. & Trussell, R.R. 1992. Métodos normalizados para el analisis de águas potables y residuales. 17^a ed. Ediciones Diaz de Santos, Madrid. IV.
- Cole, G. 1994. Textbook of limnology. 4th ed. Waveland Press, Illinois. 412p.
- Ganf, G.G. 1983. An ecological relationship between Aphanizomenon and Daphnia pulex. *Aust. J. Mar. Freshwater Res.*, 34:755-773.
- Garcia de Emiliani, M.O. 1993. Seasonal succession of phytoplankton in a lake of the Paraná River floodplain, Argentina. *Hydrobiologia*, 264:101-114.
- Happety-Wood, C.M. 1988. Ecology of freshwater planktonic green algae. In: Sandgren, C.D. (ed.) Growth and survival strategies of freshwater Phytoplanktonic. Cambridge University Press, Cambridge. p.175-226.
- Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U. & Zohary, T. 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.*, 35:403-424.
- Huszar, V.L.M. 2000. Fitoplâncton. In: Bozelli, R.L., Esteves, F.A. & Roland, F. (eds). Lago Batata: impacto e recuperação de um ecossistema amazônico. IB-UFRJ/SBL, Rio de Janeiro. p.91-104.
- Junk, W.J., Cunha, C.N., Wantzen, K. M., Petermann, P., Strüssmann, C., Marques, M.I. & Adis, J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat. Sci.*, 68:278-309.
- Kalff, J. 2002. Limnology: inland water ecosystems. Prentice-Hall, Upper Saddle River. 574p.
- Klaveness, D. 1988. Ecology of the Cryptomonadida: a first review. In: Sangren, C.D. (ed). Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge. p.103-133.
- Kruk, C., Mazzeo, N., Lacerot, G. & Reynolds, C.S. 2002. Classification schemes for phytoplankton: a local validation of a functional approach to the analysis of species temporal replacement. *J. Plankton Res.*, 24:901-912.
- Lund, J.W.G., Kipling, C. & Le Cren, E.D. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia*, 11:143-170.
- Mackereth, F.J.H., Heron, J. & Talling, F.J. 1978. Water analysis: some revised methods for limnologists. Titus Wilson & Sons, Kendall. 117p. (Freshwater Biological Association Scientific Publication, 36).
- McCune, B. & Mefford, M.J. 1997. Multivariate analysis of ecological data version 3.0. MjM Software. Gleneden Beach.
- Melo, S. & Huszar, V.L.M. 2000. Phytoplankton in a Amazonian flood-plain lake (Lago Batata, Brasil): diel variation and species strategies. *J. Plankton Res.*, 22:63-76.
- Morais, R.P., Oliveira, L.G., Latrubesse, E.M. & Pinheiro, R.C.D. 2005. Morfometria de

- sistemas lacustres da planície aluvial do médio rio Araguaia. *Acta Sci.*, 27:203-213.
- Nabout, J.C., Nogueira, I.S. & Oliveira, L.G. 2006. Phytoplankton community of floodplain lakes of the Araguaia River, Brazil, in the rainy and dry seasons. *J. Plankton Res.*, 28:181-193.
- Oliveira, M.D. & Calheiros, D.F. 2000. Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. *Hydrobiologia*, 427:101-112.
- Olrik, K. 1994. Phytoplankton ecology: determining factors for the distribution of phytoplankton in freshwater and the sea. Ministry of Environment, Denmark. 183p.
- Reynolds, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge. 384p.
- Reynolds, C.S. 1997. Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Germany. 378p.
- Reynolds, C.S. 2006. Ecology of phytoplankton. Cambridge University Press, Cambridge. 535p.
- Reynolds, C.S., Huszar, V.L.M., Kruk, C., Naselli-Flores, L. & Melo, S. 2002. Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.*, 24:417-428.
- Shapiro, J. 1990. Currents beliefs regarding dominance by blue-greens: the case for the importance of CO₂ and pH. *Verh. Int. Ver. Limnol.*, 24:38-54.
- Sneath, P.H. & Sokal, R.R. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman and Co., San Francisco. 573p.
- Sommer, U. 1981. The role of r and K selection in succession of phytoplankton in Lake Constance. *Acta Oecol. Gen.*, 2:327-343.
- Sommer, U. 1988. Growth and survival strategies of planktonic diatoms. In: Sandgreen, C.D. (eds.) Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge. p.227-260.
- Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67:1167-1179.
- Thomaz, S.M., Roberto, M.C. & Bini, L.M. 1997. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. In: Vazzoler, A.E.A.M., Agostinho, A.A. & Hahn, N.S. (eds.) A planície de inundação do Alto Rio Paraná: aspectos físicos, biológicos e socioeconômicos. EDUEM, UEM-NUPELIA, Maringá. 460p.
- Train, S. & Rodrigues, L.C. 1997. Distribuição espaço temporal da comunidade fitoplanctônica. In: Vazzoler, A.E.A.M., Agostinho, A.A. & Hahn, N.S. (eds.) A planície de inundação do Alto Rio Paraná: aspectos físicos, biológicos e socioeconômicos. EDUEM, UEM-NUPELIA, Maringá. 460p.
- Train, S. & Rodrigues, L.C. 2004. Phytoplanktonic assemblages. In: Thomaz, S.M., Agostinho, A.A. & Hahn, N.S. (eds.) The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. Backhuys, Leiden. p.103-124.
- Utermöhl, H. 1958. Zur vervollkommung der quantitativen phytoplankton-methodik. *Mitt. Int. Ver. Limnol.*, 9:1-38.
- Vollenweider, R.A. 1974. A manual on methods for measuring primary production in aquatic environments. 2nd ed. Blackwell Scientific Publications, Oxford. 225p. (IBP, 12).

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