Seasonal mechanisms driving phytoplankton size structure in a tropical deep lake (Dom Helvécio Lake, South-East Brazil).

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ABSTRACT: Seasonal mechanisms driving phytoplankton size structure dynamics in a tropical deep lake (Dom Helvécio Lake, South-East Brazil). Dom Helvécio Lake, located inside Rio Doce State Park (south-east Brazil) is the largest and deepest lake of the middle Rio Doce lacustrine system. Although data on physical, chemical and biological features of some of those lakes have been known since the 70's, the biovolume of phytoplankton species have not yet been studied. In this paper we characterize, for the first time, algae size structure in Dom Helvécio Lake and assess seasonal variations to establish possible associations between algae size structure and the environment, particularly water column stability along stratification changes. Samples were collected in three months during each dry and rainy season from June 2001 to February 2004. Air and water temperature, precipitation, relative humidity and stability of thermal stratification all significantly increased during the rainy (stratified) seasons, while total-P, total-N, DIN and SRSi concentrations were higher during the dry (mixing conditions) seasons. Results suggest a persistent phosphorus limitation to phytoplankton primary production and a variable amount of nitrogen was detected. No significant seasonal variation was verified for total phytoplankton biovolume. Despite this, the distribution of size classes in different stability conditions was distinct: a predominance of nano- and ultraplankton (‹ 20 mm), mainly due to Zygnemaphyceae, during stratification periods and, of micro- and netplankton (› 64 mm), specially Cyanophyceae in mixing ones. This result indicate that the constancy of algae biovolume in Dom Helvécio Lake along 2002 was not a result of a stable phytoplankton community but it occurs as a consequence of significant changes in size structure of phytoplankton.
Key words: Phytoplankton, biovolume, mixing conditions, tropical lake.

RESUMO: Mecanismos sazonais determinando a estrutura de tamanho do fitoplâncton em um lago tropical profundo (Lago Dom Helvécio, sudeste do Brasil). O lago Dom Helvécio situa-se dentro dos limites do Parque Estadual do Rio Doce (sudeste do Brasil) e é o maior e mais profundo do sistema de lagos do Médio Rio Doce. Embora suas características físicas, químicas e biológicas sejam conhecidas desde a década de 70, estudos considerando o biovolume das espécies fitoplanctônicas ainda não haviam sido realizados. Neste trabalho são apresentados dados sobre a estrutura de tamanho das algas planctônicas do Lago Dom Helvécio, procurando estabelecer as possíveis relações entre suas variações e as mudanças ambientais, particularmente as condições de estabilidade da coluna d'água. As amostras foram coletadas em três meses de cada estação seca e chuvosa, entre junho de 2001 e fevereiro de 2004. Temperatura do ar e da água, precipitação, umidade relativa e estabilidade de estratificação térmica aumentaram significativamente no período chuvoso, enquanto as concentrações de P-total, N-total, nitrogênio inorgânico dissolvido e silicato apresentaram-se mais elevadas durante os períodos secos. Limitação permanente por fósforo e variável por nitrogênio foram verificadas, já que suas formas inorgânicas dissolvidas estavam em concentrações abaixo do limite mínimo para produção primária. Nenhuma variação sazonal significativa foi observada no biovolume total do fitoplâncton. No entanto, a distribuição das classes de tamanho entre as diferentes condições de estabilidade foi distinta. Predomínio de nano e ultraplâncton (‹ 20 mm), principalmente devido à presença de Zygnemaphyceae, durante os períodos de estratificação e dominância de microplâncton e plâncton de rede (› 64 mm), especialmente Cyanophyceae, nos períodos de mistura foram registrados. Este resultado indica que a constância sazonal do biovolume do fitoplâncton no lago Dom Helvécio, observada em 2002, não foi um resultado de uma

comunidade fitoplanctônica estável e, pelo contrário, ocorreu em conseqüência de mudanças significativas na estrutura dessa comunidade.

Palavras-chave: Fitoplâncton, biovolume, condições de mistura, lago tropical.

Introduction

The thermal structure of aquatic environments to can determine a water column compartmentalization or a mixing, thus affecting the selection and vertical distribution of species (Barbosa & Padisák, 2002). The thermal conditions can change seasonally within the same lake (Wetzel, 2001; Sterner, 1990) and play an important role on plankton community dynamics, since they affect the availability of essential resources (Weithoff et al., 2000). Moreover, the relative abundance of primary producers in a lake is a result of the competition for light and nutrient sources together with the nature and intensity of zooplankton grazing (Reynolds, 1997).

The importance of temporal and spatial variations of the environment upon the availability of resources and, consequently, over the structure of aquatic communities was first noticed by Hutchinson (1961). Since then, several studies searching for a better understanding of environment–community relations were developed. The model proposed by Sommer et al. (1986), which describes a combination of physical and chemical factors with trophy effects controlling the producer–herbivorous chain in Lake Constance (Central Europe), is among the best known examples. Judgmental (Huisman & Weising, 1995; Diehl, 2002) and empirical studies (Diehl et al., 2002; Kunz & Diehl, 2003) were conducted focusing specifically on the combined effects of light availability and nutrients on freshwater planktonic systems. However, the majority of the studies were conducted in temperate environments. In order to allow for comparative studies on phytoplankton responses to environmental changes (Reynolds, 1984) and to develop models for tropical systems of fundamental importance for the improvement of water quality management strategies, data in the tropics are necessary.

In this paper we characterize, for the first time, the phytoplankton biomass, as biovolume, in Dom Helvécio Lake (Rio Doce valley, Southeastern Brazil). Considering that phytoplankton size structure is clearly important to determine the plankton food web and nutrients fate (Bergquist et al., 1985), since that species of the same fraction tend to respond similarly to environmental changes (Becker & Motta-Marques, 2004), we also aimed to measure the lake's seasonal variations in order to assess associations between biovolume and environmental features, in particular, the water column stability along stratification changes.

Study Area

The Rio Doce State Park is the largest remnant of Atlantic Forest (36,113 ha) in the state of Minas Gerais, Brazil. It is located in the middle part of the Doce River basin (19º29'24" – 19º48'18" S; 42º28'18" – 42º38'30" W) surrounded mostly by Eucalyptus plantations and 29 municipalities. One third of the middle Doce River lacustrine system is protected within the Park (Barbosa, 1997). The local climate is tropical semi-humid, the average temperature is around 25 ºC, and there is a 4–5 month period displaying dry season characteristics (Barbosa & Moreno, 2002). Dom Helvécio is the largest (6.87 km^2) and deepest lake of the system (32.5 m) characterized as dendritic and oligotrophic (de Meis & Tundisi, 1997). Dom Helvécio is identified as a warm-monomictic lake, stratifying between September and April and exhibiting an almost isothermal condition from May to August (Henry & Barbosa, 1989).

Material and methods

Samples were collected with a van Dorn bottle at a limnetic station in three months of each dry (June/July/August) and rainy (December/January/February/March) season, from 2001 to 2004. In each sampling, three depths corresponding to 100, 10 and 1 % of incident light at the surface within the euphotic zone were determined according to Secchi disk estimations (Cole, 1983). Vertical profiles of water temperature and electric conductivity were measured with a Horiba multi probe and the mixing zone extension (Z_{mix}) was identified. Calculations of the stability stratification were also performed for each month (Cole, 1983) using water density tables from Hutchinson (1957). Daily measurements (ten days before each sampling) of air temperature, precipitation and relative humidity data were provided by a climatic station c. 50 km distant from the park.

The concentrations of total phosphorus (TP), soluble reactive phosphorus (SRP: PO_4^{3-}-P), total nitrogen (TN), dissolved inorganic nitrogen (DIN: NO_3^--N, NO_2^--N and NH_4^+-N) and soluble reactive silicate (SRSi) were estimated (Golterman et al., 1978; Koroleff, 1976; Mackereth et al., 1978). The trophy status of the lake was defined according to Salas & Martino (1991).

Phytoplankton samples were preserved with lugol's iodine solution and at least 400 specimens of the most frequent species were enumerated (Lund et al., 1958) using the settling technique (Utermöhl, 1958). The algal biovolume was determined with formulae for geometric shapes of the cells (Edler, 1979) using ALGAMICA software (Gosselain & Hamilton, 2000). For size fractions, the determination of the Greatest Axial Linear Dimension (GALD) was used and the organisms' size classification done according to ALGAMICA software. Specific biovolume was estimated from the product of the population and the mean unit (cells, colonies and filaments) volume. Total algae biovolume/total density ratio was used to estimate the mean cellular biovolume (Buzzi, 2002). For the zooplankton analysis, samples were taken with a pump and concentrated (200 L) with a net (60 mm). The organisms were colored with Bengal rose, fixed with 4% formaline and then counted in Sedgwick-Rafter chamber (Bottrell et al., 1976).

Results

Taking into account the variability in climatic and stability variables, periods of dry/mixing and rainy/stratified conditions were recognized. Air and water temperature, precipitation, relative humidity and stability of thermal stratification all significantly increased during the rainy seasons comparing with dry periods. No variation on Secchi disk extinction depth was detected (Tab. I). The mixing zone extension was restricted to the epilimnion from (6 to 8 m) during the rainy periods and deepened (from 14 to 28 m) during the dry ones (Fig. 1). Unusual values were recorded during March/2002 (14 m) and February/2004 (9 m), both considered rainy months, because precipitation occurred right before the sampling days which, in turn, most likely disturbed water column stability. Therefore, the Z_{eu}/Z_{mix} ratio (Fig. 1) accompanied the seasonal variation on stability of stratification being › 1 during the rainy and ‹ 1 during the dry periods.

Table I: Mean and standard deviation of environmental variables of the Rio Doce State Park region and in Dom Helvécio Lake.

Variable	Dry 2001	Rainy 2002	Dry 2002	Rainy 2003	Dry 2003	Rainy 2004
Air temperature (°C)	21 ±1.1	25 ±0.8	22 ±0.6	25 ±0.4	-	25 ±1.2
Maximum air temperature (°C)	28 ±0.7	32 ±0.7	29 ±1.3	33 ± 0.0	-	32 ±1.8
Minimum air temperature (°C)	15 ±1.4	21 ±0.3	16 ±0.6	22± 0.2	-	21 ±1.1
Precipitation (mm)	1 ±0.9	8 ±7.8	1 ±0.9	12 ±1.8	-	21 ±13.3
Minimum relative humidity (%)	48 ±2.0	61 ±10.0	52 ±7.5	68 ±4.0	-	76 ±4.4
Maximum relative humidity (%)	76 ±3.2	84 ±5.1	80 ±6.3	88 ±1.4	-	91 ±1.9
Water temperature (°C)	24 ±1.1	28 ±2.0	25 ±0.5	29 ±2.1	25 ±1.0	29 ±1.3
Stability of stratification (g-cm.cm^{-2})	87 ±78.4	517 ±64.1	115 ±41.4	508 ±73.1	66 ±59.4	423 ±49.3
Secchi disk extinction depth (m)	3 ±1.1	3 ±0.2	3 ±0.1	3 ±0.3	2 ±1.0	3 ±0.3
Trophy (Total P; mg/l)	23 ±14.3	15 ±7.0	58 ±2.0	17 ±9.6	16 ±3.9	15 ±7.7

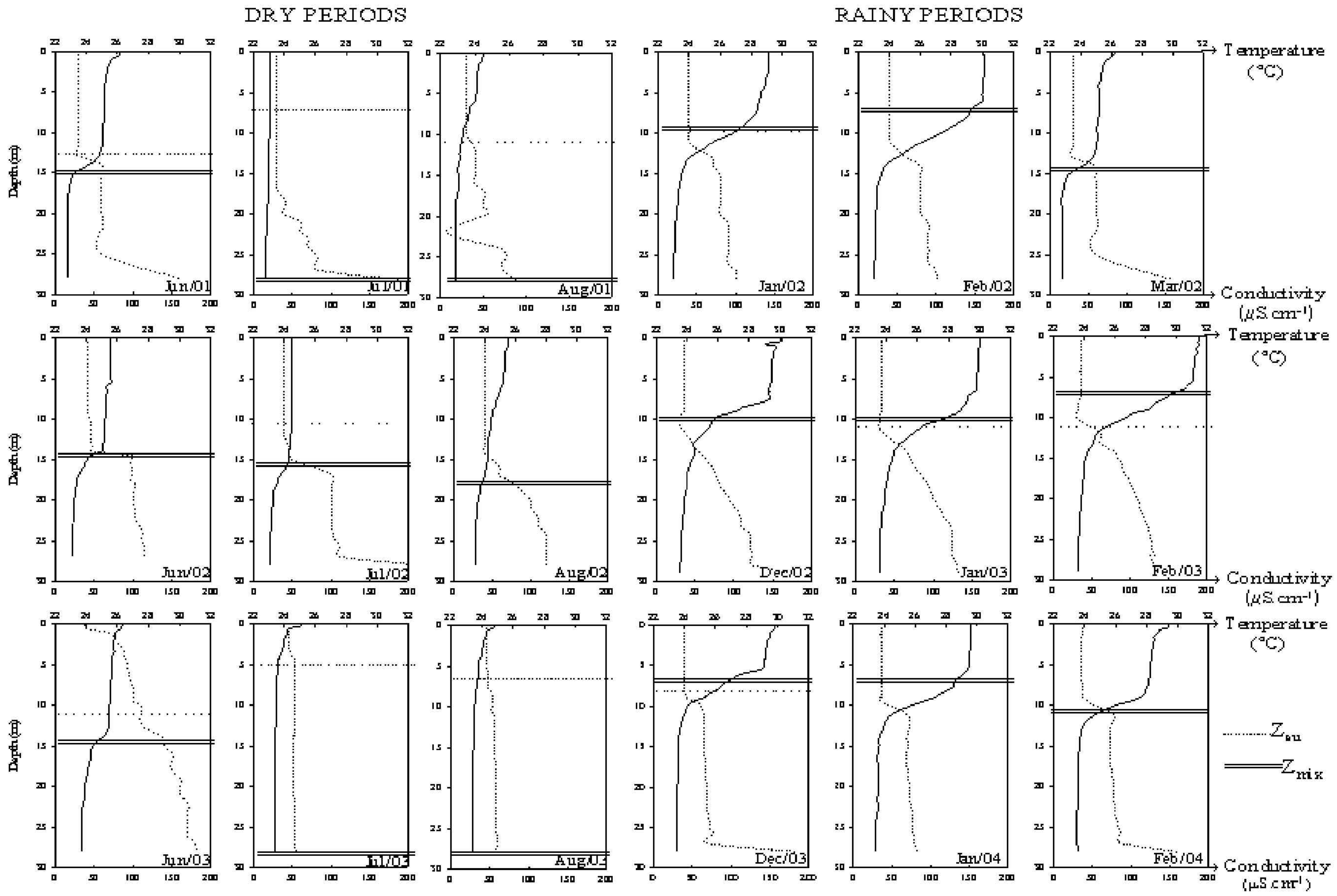

Figure 1: Water temperature (solid line) and electric conductivity (dotted line) vertical profiles in Dom Helvécio Lake during the mixing and stratified periods from 2001 to 2004. The euphotic (discontinuous line) and mixing zone (doubled line) depths are shown.

Both total phosphorus and nitrogen presented the highest concentrations during the mixing conditions. In these periods the greatest DIN was also recorded. SRP values became greater in stratified months, especially at lower depths, while soluble reactive silicate mean concentration was relatively low throughout the years and without no difference in dry and rainy seasons. During two dry periods (2001 and 2002) the lake exhibited mesotrophic features while during all the rainy periods it was characteristically oligotrophic (Tab. II).

Table II: Mean and standard deviation of total and dissolved nutrient concentrations in Dom Helvécio Lake.

Light*	Nutrients	Dry	Rainy	Dry	Rainy	Dry	Rainy
		2001	**2002**	**2002**	**2003**	**2003**	**2004**
	Total P (mg.L^{-1})	23 ±15.0	12 ±5.6	51 ±3.7	15 ±9.9	20 ±7.0	13 ±6.2
	PO_4^{3-} -P (mg.L^{-1})	3 ±1.8	3 ±1.3	2 ±1.9	5 ±3.2	0.5 ±0.2	3 ±1.1
100%	Total N (mg.L^{-1})	249 ±171.0	389 ±184.2	536 ±114.9	240 ±117.5	441 ±165.6	289 ±71.8
	DIN (mg.L^{-1})	104 ±22.5	78 ±35.3	78 ±42.2	21 ±9.0	238 ±139.3	94 ±98.1
	SRSi (mg.L^{-1})	2 ±0.2	2 ±0.3	4 ±2.1	3 ±0.2	2 ±0.5	2 ±1.2
	Total P (mg.L^{-1})	23 ±15.3	17 ±9.3	55 ±1.6	16 ±11.6	14 ±5.6	14 ±8.9
	PO_4^{3-} -P (mg.L^{-1})	3 ±2.2	3 ±2.4	4 ±1.7	5 ±4.3	0.5 ±0.3	3 ±2.6
10%	Total N (mg.L^{-1})	204 ±134.6	379 ±197.7	575 ±110.9	269 ±158.0	433 ±171.9	292 ±84.2
	DIN (mg.L^{-1})	125 ±38.8	50 ±31.1	73 ±39.8	22 ±5.4	221 ±120.0	43 ±19.5
	SRSi (mg.L^{-1})	2 ±0.1	2 ±0.9	4 ±2.1	3 ±0.2	3 ±0.9	2 ±1.3
	Total P (mg.L^{-1})	18 ±10.6	19 ±6.9	69 ±5.9	20 ±6.7	17 ±6.4	17 ±8.3
	PO_4^{3-} -P (mg.L^{-1})	3 ±1.6	3 ±1.6	6 ±0.3	5 ±3.6	2 ±0.8	3 ±2.0
1%	Total N (mg.L^{-1})	525 ±269.6	402 ±103.9	607 ±86.1	274 ±106.6	478 ±167.9	307 ±113.1
	DIN (mg.L^{-1})	378 ±202.3	183 ±262.0	101 ±32.7	39 ±24.2	265 ±149.4	91 ±69.2
	SRSi (mg.L^{-1})	2 ±0.7	3 ±0.3	5 ±1.4	3 ±0.3	3 ±0.8	2 ±0.5

* Depths corresponding to superficial light incidence.

A total of 119 phytoplankton taxa were found in Dom Helvécio lake among which 64 contributed to 96% of the total density and were considered in our analysis (Tab. III). Fourteen species were identified as ultraplankton, with major contributions from Zygnemaphyceae, Chlorophyceae, and Cyanobacteria; nanoplankon was composed of 20 Zygnemaphyceae and Chlorophyceae species; microplankton was the most heterogeneous size class presenting 24 taxa from all taxonomic groups; and netplankton (7 species) was mainly formed by filamentous Cyanobacteria. Considering the taxonomic classes, Zygnemaphyceae (desmids) and Chlorophyceae (green algae) contributed with the highest number of species (21 and 18, respectively) followed by Cyanobacteria (11), Bacillariophyceae (5), Dinophyceae, 3), Euglenophyceae (3), Chrysophyceae (2) and Cryptophyceae (2). The GALD (mm) and biovolumes (mm^3) of Dom Helvécio taxa are compiled in Tab. III. The highest GALD was recorded for Oscillatoria limosa (C. Agardhi) Gomont (571.5 mm) and colonies of Botryococcus braunii Kützing presented the highest biovolume (71,622.8 mm^3). Merismopedia sp. cells presented the lowest values (1.1 mm and 0.7 mm^3, respectively).

The total biovolume varied widely during the study, temporally and vertically (Fig. 2).

Table III: Greatest axial linear dimension (GALD) and cell volume of phytoplankton taxa in Dom Helvécio Lake.

Taxa	GALD (µm)	Cell volume (µm³)	Taxa	GALD (µm)	Cell volume (µm³)
Ultraplankton (2.1–10.0 µm)			**Microplankton (20.1–64.0 µm)**		
Chlamydomonas sp.	9.0	169.6	*Navicula* sp.	20.1	101.9
Chlorella sp.	6.1	118.8	*Nitzschia* sp.	29.3	191.8
Crucigenia rectangularis Nägeli	5.0*	9.2*	Pennales 1	30.0	589.0
Oocystis pusilla Hansgirg	9.0	169.6	*Urosolenia longiseta* Zacharias	63.4	1147.3
Tetraedron caudatum (Corda) Hansgirg	9.0	63.0	*Ankistrodesmus falcatus* (Corda) Ralfs	40.5	392.6
Aphanocapsa sp.	2.5	8.2	*Ankistrodesmus tortus* Komárek et Comas	35.6	58.2
Chroococcales 1	3.0*	14.1*	*Botryococcus braunii* Kützing	61.4*	71622.8*
Chroococcus sp.	8.8	356.8	*Closteriopsis* sp. 1	57.2	113.0
Merismopedia sp.	1.1	0.7	*Closteriopsis* sp. 2	53.7	106.8
Radiocystis fernandoi Komárek et Komárková - Legnerová	6.0	65.4	*Coelastrum reticulatum* (Dangeard) Senn	23.1	6464.1
Cosmarium asphaerosporum Nordstedt	5.9	72.5	*Monoraphidium* sp.	37.1	60.9
Cosmarium bioculatum Brébisson	9.0	95.4	*Mallomonas* sp.	35.0	8418.5
Sphaerozosma sp.	8.1	155.5	*Synura* sp.	30.4	3925.1
Spondylosium panduriforme (W. et G.S. West) Teiling	9.0	508.1	*Cryptomonas* spp.	20.4	905.3
Nanoplankton (10.1–20.0 µm)			*Pseudanabaena* sp.	20.5	20.1
Achanthosphaera sp.	14.3	1531.1	*Gymnodinium* sp.	28.6	7716.4
Elakatothrix sp.	13.5	19.6	*Peridinium inconspicuum* Lemmermann	49.4	63121.8
Kirchneriella obesa (Turpin) Kützing	10.2	77.0	Euglenales 1	31.5	6185.0
Nephrocytium sp.	17.9	284.7	*Phacus* sp.	27.0	10306.0
Scenedesmus bijugus (W. West) Schmidle	15.8	573.8	*Staurastrum rotula* Nordstedt	39.7	3275.4
Schroederia sp.	13.0	21.7	*Staurastrum smithii* (G.M. Smith) Teiling	29.5	356.8
Rhodomonas sp.	10.5	176.1	*Staurastrum tetracerum* (Kützing) Ralfs	23.9	224.7
Peridinium pusillum (Penard) Lemmermann	16.8	1330.8	*Staurodesmus dejectus* (Brébisson ex Ralfs) Teiling	25.0	1098.5
Trachelomonas volvocina Ehrenberg	17.0	2572.4	*Staurodesmus jaculiferus* (W. West) Teiling	20.3	678.6
Cosmarium contractum Kirchner	13.2	301.1	**Netplankton (> 64.0 µm)**		
Cosmarium sp.	13.4	577.1	*Synedra* sp.	66.6	967.2
Staurastrum forficulatum Lundell	20.0	2094.4	*Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju	147.4	612.4
Staurastrum gemelliparum Nordstedt	14.7	234.1	*Lyngbya hieronymusii* Lemmermann	460.0	692721
Staurastrum laeve Ralfs	10.8	229.0	*Oscillatoria limosa* (C. Agardh) Gomont	571.5	52354.5
Staurastrum subungulatum	15.8	518.3	*Planktolyngbya limnetica* (Lemmermann) Komárkova-Legnerová et Cronberg	252.7	793.9
Staurodesmus crassus (West) Florin	13.0	490.1	*Spirulina* sp.	76.5	290.8
Staurodesmus cuspidatus (Brébisson) Teiling	16.5	675.1	*Closterium moniliferum* (Bory) Ehrenberg	121.0	19837.0
Staurodesmus incus (Brébisson) Teiling	13.2	301.1			
Teilingia sp.	10.9	422.0			

* Colony

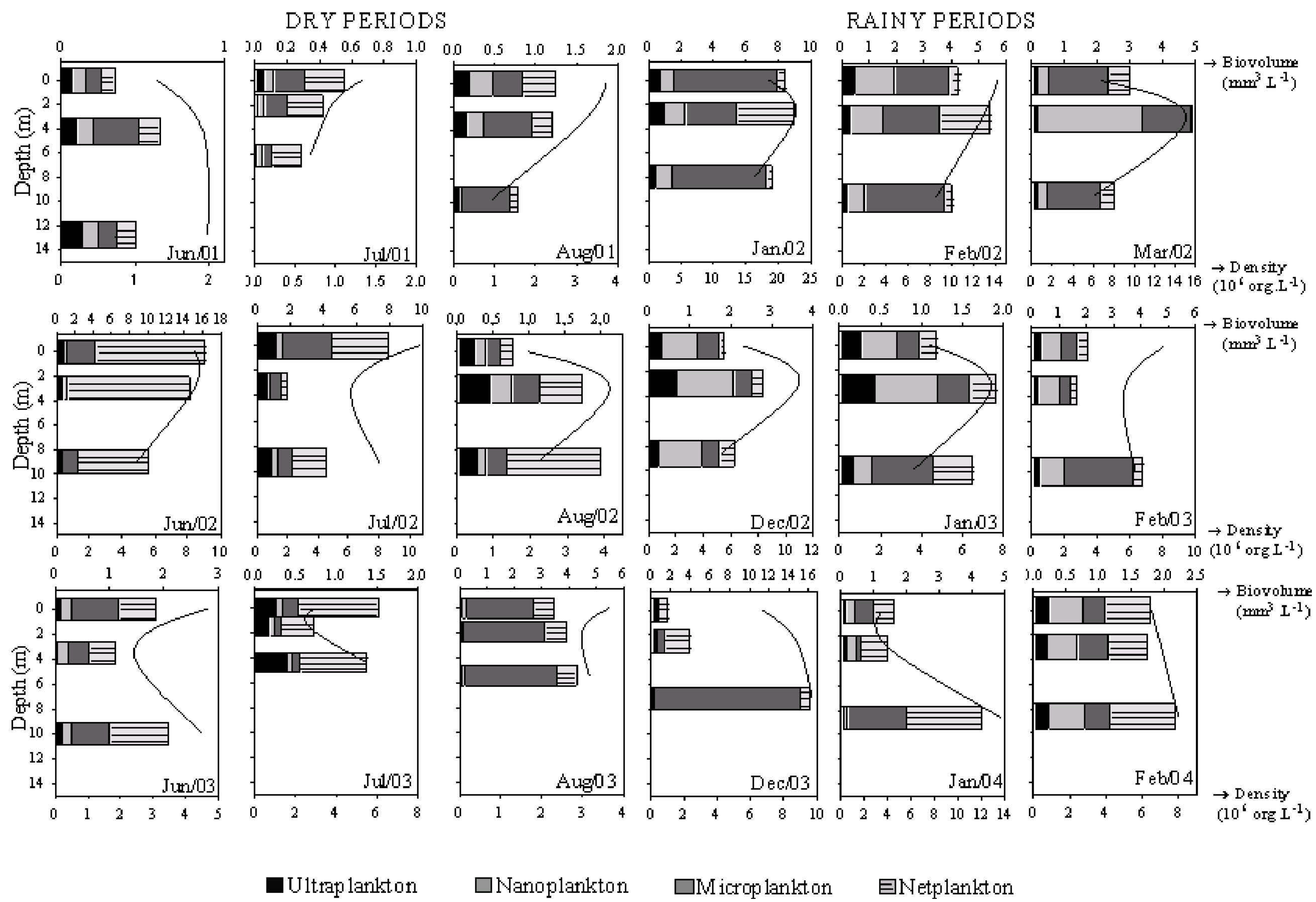

Figure 2: Variation of phytoplankton size classes biovolume (columns) and total density (solid lines) in Dom Helvécio Lake. (Note the expressive change in scale values).

Despite the great fluctuation (see the expressive change in scale values), no seasonal pattern for total biovolume was identified; however, the phytoplankton biovolume to density mean ratio showed significant variation from 4 ±0.7 x $10^{-7}mm^3.org^{-1}$ in rainy months to 6 ±2 x $10^{-7}mm^3.org^{-1}$ during dry ones, indicating that the mean cellular biovolume increases when the water column is mixed. The dry period of 2002 presented the highest values reaching 21 x $10^{-7}mm^3.org^{-1}$ in June. The highest values of total biovolume and total density were also recorded during the year 2002. The maximum phytoplankton biovolume was estimated during the mixing period (mean value 13 ± 3 $mm^3.L^{-1}$, in June, mainly due to Lyngbya hieronymusii Lemmermann), while phytoplankton total density peaked during the stratified one (mean value 19 ± 3 x 10^6 $org.L^{-1}$ in January, mainly due to Staurastrum smithii (G. M. Smithi) Teiling, Cosmarium asphaerosporum Nordstedt, and Chlorella sp.). Both were low during June and July 2001 (< 0.6 $mm^3.L^{-1}$ and 2 x 10^6 $org.L^{-1}$ in each month). Differently to the biovolume, the mean phytoplankton density was significantly higher during the rainy seasons (Fig. 2).

The zooplankton total density showed high variation among years and periods (Fig. 3A). Two peaks were registered: one in the dry period of 2002 mainly due to copepods and the other in the rainy season of 2004, when rotifers were more abundant. Cladocerans were always rare.

As for the size fractions and major phytoplankton taxonomic groups (Fig. 3B) mixing periods were marked by largest netplankton and Cyanobacteria biovolume represented mainly by Cylindrospermopsis raciborskii (Woloszynska) Seenaya et Subba Raju, Lyngbya hyeronymusii, and Planktolyngbya limnetica (Lemmermann) Komárkova-Legnerová et Cronberg.

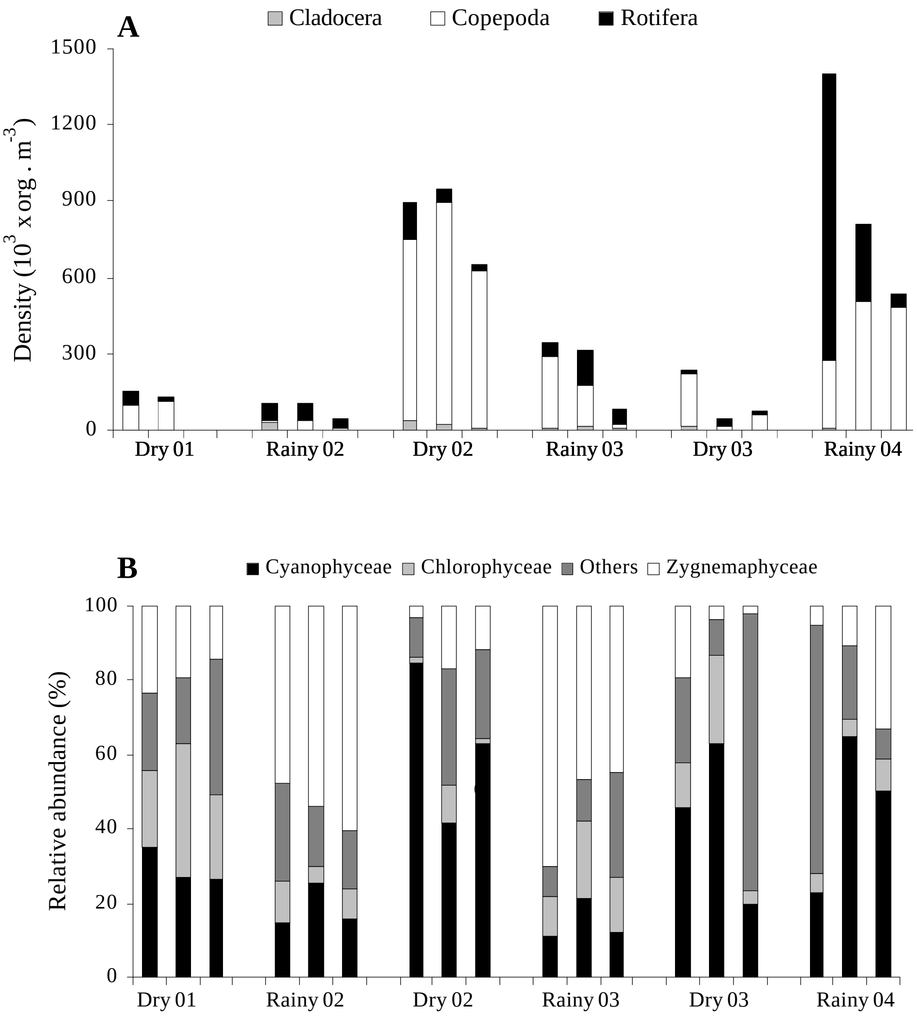

Figure 3: Changes in (A) total zooplankton density (10^3 x $org.m^{-3}$) and (B) mean phytoplankton relative abundance based on biovolume of the major taxonomic groups in Dom Helvécio Lake during dry and rainy periods from 2001 to 2004.

Furthermore, the importance of nanoplankton and Zygnemaphyceae, especially Staurastrum smithii, Staurodesmus incus (Brébisson) Teiling, and Cosmarium sp. for the community biovolume increased significantly during the stratified/rainy seasons, particularly at 100% and 10% of surface incident light corresponding depths. The relative abundance of other phytoplankton classes did not show significant variation between seasons or depths, only among years (Fig. 3) and on account of the following taxa: an important contribution of green algae was observed in June and August 2001 (with dominance of Chlorella sp. and B. braunii), diatoms in January 2002 (Urosolenia longiseta Zacharias), whereas cryptomonads (Cryptomonas spp. and Rhodomonas sp.) were dominant in July 2001 and January 2004, and dinoflagellates (Peridinium pusillum (Penard) Lemmermann and Gymnodinium sp.) in August 2001, July 2002, and most months (February, June, July, August and December) of 2003.

Discussion

The lacustrine system of the middle Rio Doce valley has been studied for almost six years through a Long Term Ecological Research project (Brazil-LTER, site # 4) and Dom Helvécio Lake is one of the monthly monitored lakes within the park. Physical, chemical and biological features of some lakes of this system have been known since the 70's (Barbosa, 1979; Pontes 1980; Aleixo, 1981). The seasonal phytoplankton composition, with an expressive Zygnemaphyceae contribution in species number followed by Chlorophyceae and Cyanobacteria corroborates data of other studies (Barbosa & Pádisak, 2002; Barros et al., 2003). Furthermore, the desmids predominance as nanoplankton corroborates Dom Helvécio's oligotrophic status, whith well-mixed condition and geographical isolation (Reynolds, 1997).

Climatic variables are considered active factors involved in thermal regulation of lakes (Timms, 1975). During the dry periods, when isothermal profiles were recorded in Dom Helvécio Lake the weather was characterized by lower precipitation, relative humidity and temperature, which can cause a significant reduction of the lake's heat content and stability (Henry et al., 1997a). Therefore, the recorded seasonal variation on temperature and stability of thermal stratification were similar to data of Henry & Barbosa (1989) and Henry et al. (1989).

Considering the inverse relation between mixing conditions and phytoplankton population densities observed in Dom Helvécio Lake, the decrease on algae abundance can be attributed to light limitation. Mixing prolongs the time of permanence of these organisms in depths with lower light, increasing respiratory losses and biovolume degradation, having a direct influence upon the algae growth rate (Erikson, 1998). Although most part of the studies showing this relation have been developed in temperate and shallow lakes (Danilov & Ekelund, 2001; Diehl, 2002; Diehl et al., 2002; Huisman, 1999), the reduced values of phytoplankton population densities during the period of decreased stability in Dom Helvécio Lake indicate that the ability of community maintenance on euphotic layers might also play a primary role on algae growth in deep tropical environments.

Higher total-N, DIN, total-P, and soluble reactive silicate concentrations in the mixing period are probably a result of sediment re-suspension. As nutrient availability frequently governs the distribution and fluctuation in biovolume of different groups of planktonic algae (Marinho & Huszar, 2002; Weithoff et al., 2000), mean phytoplankton total biovolume can be significantly increased during these conditions. However, no variation on biovolume in wet and dry seasons was obtained, corroborating previous study in this lake Henry et al. (1997a), which showed no differences between phytoplankton primary productivity in different stability conditions.

According to Reynolds (1999) the minimal SRP concentration needed to sustain phytoplankton growth rates is 3-6 $mg.L^{-1}$ and very likely phosphorus concentrations could be acting as an important factor limiting phytoplankton biovolume development as observed by Henry et al. (1997b) from enrichment experiments conducted in this lake. Phytoplankton production in Dom Helvécio's euphotic zone, and particularly at lower depths, seems to be constrained by this nutrient during mixing conditions. Furthermore, in the rainy/stratified periods and lower depths, a nitrogen limitation occurred since dissolved inorganic forms concentrations are below the minimum limits necessary for primary production (‹100 mg.L^{-1}, as also indicated by Reynolds, 1999). Even in oligo- or mesotrophic conditions, phytoplankton growth is chronically limited to phosphorus in Dom Helvécio Lake while nitrogen availability also restricted algae development.

The contribution of each phytoplankton size fraction to the total biovolume changed seasonally and might have compensated the seasonal difference in population densities, explaining why the mean total phytoplankton biovolume, along all sampled seasons, showed no variation. There was a predominance of nano- and ultraplankton (‹20 mm) with higher population densities during stratification periods, and a dominance of micro- and netplankton (›64 mm) in terms of biovolume in mixing ones despite lower population densities. Therefore, the small algae, especially Zygnemaphyceae, which have higher growth rates (Agrawal, 1998), could have played a major role on total density increase during the rainy months, when phosphorus exhibited higher levels. According to Reynolds (1989) and Barbosa & Padisák (2002) the small stratifications/ destratifications at Dom Helvécio's surface layers during a 24 hour period (atelomixis) generate turbulence, re-suspending these organisms and increasing their permanence within the euphotic zone. Moreover, in this condition of partial mixing algae density reaches its maximum value since there is neither limitation by light nor losses due to sinking making nutrients the main restriction to phytoplankton production (Diehl, 2002). On the other hand, in the decreased stability (low temperatures), the netplankton fraction was favored. Filamentous Cyanobacteria are competitively superior when light availability becomes limiting. Thus, they maintained larger biovolume in spite of not being abundant. Increase in the mean cellular biovolume during dry seasons compensated the fact that they did not reach high population densities. The observed constancy of algae total biovolume in Dom Helvécio Lake can not be inferred to be a result of a stable phytoplankton community. In fact, it occurs in Dom Helvécio Lake as a consequence of significant changes in size structure of phytoplankton.

Considering the high temporal fluctuation of zooplankton community along years it was difficult to identify a clear top-down control over the phytoplankton. Although the highest algae density was recorded when zooplankton density was lowest (rainy period 2002) the increased copepods or rotifers population densities did not coincide with lower algae contributions (dry period 2002 and rainy season 2004). However, in these two seasons larger Cyanophyceae relative abundance might suggest interaction with non-edible phytoplankton species. Therefore, the compositional phytoplankton change might also have responded to zooplankton pressure.

The other size fractions and taxonomic classes depended on variations within years to change significantly but no association with the environment was evident, a community feature also described by Huszar & Caraco (1998). Nevertheless, 2002 was marked by greater phytoplankton biovolume and density, when the occurrence of El Niño-ENSO climatic event (Kerr, 2002) might have driven the system entirely favoring phytoplankton community, thus evidencing the major influence of weather on phytoplankton development in individual years as suggested by Temponeras et al. (2000).

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