

## The dominance of desmids in tropical monomictic lakes (SE Brazil)

Luciana G. Barbosa<sup>1,\*</sup>, Francisco A. R. Barbosa<sup>2</sup>, Gabrielle J. M. Araujo<sup>1</sup> and Carlos E. de M. Bicudo<sup>3</sup>

<sup>1</sup> Limnology Laboratory, Plant Technology and Environmental Sciences Department, Center for Agrarian Sciences, Universidade Federal da Paraíba, Campus II, 58397-000 Areia, PB, Brazil.

<sup>2</sup> Limnology Laboratory, General Biology Department, Institute of Biological Sciences, Universidade Federal de Minas Gerais, PO Box 486, 30161-970 Belo Horizonte, MG, Brazil.

<sup>3</sup> Center for Ecology Research, Instituto de Botânica, PO Box 68041, 04045-972 São Paulo, SP, Brazil.

\* Corresponding author: lucianabarbosa@cca.ufpb.br

Received: 4/4/12

Accepted: 8/2/13

### ABSTRACT

#### The dominance of desmids in tropical monomictic lakes (SE Brazil)

Disturbance is a concept used to explain the structure of communities. This concept emphasizes the effects of disturbance on the “break” of biomass stability in stable environments and the opportunities for the development of other species. The major disturbances in natural warm monomictic lakes include the contrasting effects of seasonal changes and long-term in thermal stability, as well as short-term changes in the mixing layer. This study investigated the effects of disturbance and abiotic environmental factors on the biomass of desmids, based on samples collected monthly from January 2002 through December 2006 in the limnetic region of two natural lakes, Carioca (small and shallow) and Dom Helvécio (large and deep), located in Rio Doce State Park, Minas Gerais State, southeast Brazil. At Lake Dom Helvécio, the extensive banks of aquatic macrophytes, the lake’s dendritic shape and the period of clear water produced higher richness values and facilitated the occurrence of relatively large (maximum linear dimension >20 µm) desmid species, primarily species belonging to *Staurastrum* and *Staurodesmus*. In contrast, less richness and a dominant group of relatively small (maximum linear dimension <20 µm) desmid species, especially species belonging to the genus *Cosmarium*, were observed at Lake Carioca in conjunction with a sparse macrophyte cover. The lakes showed a seasonal thermal stratification characterized by high temperature (25-32 °C), thermal stability and higher desmid biomass. The stability of the epilimnetic desmid biomass was an indicator of the adaptive flexibility of the desmid species and the capacity of the biomass to recover after the mixing period.

**Key words:** Biomass stability, desmid, seasonal variability, thermal stability.

### RESUMEN

#### Dominio de desmidiáceas en lagos monomícticos tropicales (SE Brasil)

La perturbación es un concepto utilizado para explicar la estructura de las comunidades, con énfasis en sus efectos sobre la “ruptura” de la estabilidad de la biomasa en ambientes estables y sobre las oportunidades para el desarrollo de nuevas especies. Entre las perturbaciones más importantes encontradas en lagos naturales monomícticos destaca el efecto de las variaciones estacionales y de largo plazo en la estabilidad térmica, así como los cambios a corto plazo en la profundidad de la mezcla. En este trabajo se describe el efecto de la estratificación y mezcla del lago así como de otros factores abióticos sobre la biomasa de desmidiáceas en lagos tropicales. Los muestreos se realizaron mensualmente entre enero de 2002 y diciembre de 2006 en la región pelágica de dos lagos naturales monomícticos cálidos, Carioca (pequeño y poco profundo) y Dom Helvécio (grande y bastante profundo) ubicados en el Parque Estadual do Rio Doce (Estado Minas Gerais, SE Brasil). En el lago Dom Helvécio, las grandes acumulaciones de macrófitas acuáticas, la forma dendrítica del lago y el período de aguas transparentes influyeron de forma sinérgica en una mayor riqueza de especies y de tamaños grandes, mayores de 20 µm, siendo principalmente especies de *Staurastrum* y *Staurodesmus*. Sin embargo, en el Lago Carioca se observó una menor riqueza y el dominio de desmidiáceas de pequeño tamaño (<20 µm), especialmente *Cosmarium*. Este último lago presentó también una cobertura escasa de macrófitas. Los lagos mostraron un patrón estacional caracterizado, durante la estratificación térmica, por el aumento de la temperatura (25-32 °C), estabilidad térmica y mayor biomasa de desmidiáceas.

*La estabilidad de la biomasa epilimnética fue indicativo de una flexibilidad adaptiva y recuperación después del período de mezcla.*

**Palabras clave:** *Desmidiáceas, estabilidad de la biomasa, estabilidad térmica, variabilidad estacional.*

## INTRODUCTION

Brook (1981) stated that the primary challenging questions associated with desmid ecology worldwide include the spatial and temporal distribution of the group and the multiplicity of factors controlling this distribution. In the past decades, relatively few advances have been made on these problems (Gerrath, 1993). Descriptive and experimental studies of desmid ecology in tropical regions are extremely scarce, and the need for such studies is great.

Desmids are important components of freshwater phytoplankton but very seldom play a major role in terms of biomass. For this reason, it is difficult to conduct investigations of characteristics related to the seasonal fluctuations of desmid biomass. Few desmid species have been found to occur in eutrophic environments (Gerrath, 1993; Coesel, 2001). Highly sensitive to environmental changes, desmids are considered good indicators of the ecological quality of water and of the saprobity level of different environments. They are commonly used as a tool for aquatic environment conservation and management (Coesel *et al.*, 1978; Coesel, 2001; Ngearnpat & Peerapompisal, 2007).

### Factors associated with the dominance of planktonic desmids

Desmids are frequently associated with periphytic and epiphytic communities, but the following hypotheses can explain the success of planktonic desmids in lakes and reservoirs:

1. Chemical factors: the distribution of desmids in continental waters is always related to the chemistry of the system (Woelkerling & Gough, 1976). Among the most important factors controlling desmid distributions are water conductivity, pH and CO<sub>2</sub> (Moss, 1972, 1973;

Coesel, 1986, 1993; Coesel & Kooijman-van-Blokland, 1991; 1994).

2. Physical features associated with temperature and thermal stability: desmids are also extremely well adapted to turbulent environments (Brook, 1981) and have an optimal temperature between 25 and 30 °C (Coesel & Wandenaar, 1990). These organisms' population maxima in the Northern Hemisphere are usually associated with the summer and fall seasons (June-August or September-October) (Canter & Lund, 1966; Lund, 1971; Coesel & Kooijman-van-Blokland, 1991). In the tropics and subtropics, however, the occurrence of population maxima is associated with atelomixis, a singular characteristic of warm monomictic lakes in which thermal stability is noticeably high (Barbosa & Padišák, 2002; Tavera & Martínez-Almeida, 2005). Atelomixis occurs during the night and early morning, allowing the identification of total mixing during the entire dry period or partial mixing of the epilimnion during the rainy period (Barbosa & Padišák, 2002).

3. The association of desmids with underwater light conditions is underexplored: small desmids are adapted to low light intensities and eutrophic lakes, whereas large desmids dominate in oligotrophic lakes, where organic matter is scarce and light is more available (Coesel, 1982). The eutrophication process may decrease the abundance of desmids, and the structural diversity of desmids may also decrease as the richness of the aquatic vegetation decreases (Coesel, 1978).

The adaptive survival strategies of desmids are characterized by K tendencies (the tendency to act as S-strategists). Desmids are strong competitors in the epilimnion in the presence of

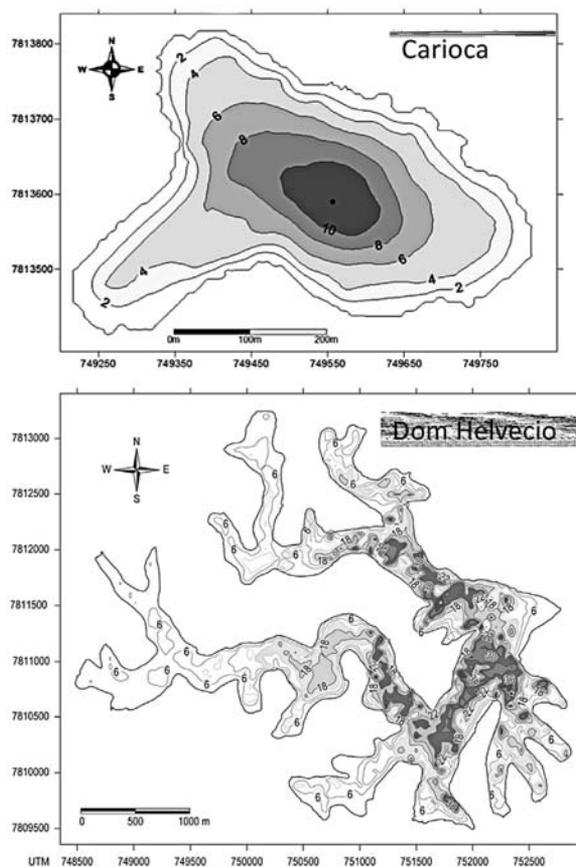
biomass stability during the thermal stratification period (Reynolds, 1984). Desmids were formerly included by Reynolds *et al.* (2002) in the **N** and **P** functional groups, both proposed for epilimnetic species living in low-latitude or temperate lakes during the summer. These groups show a strong reliance on physical mixing and, consequently, require a continuous or semi-continuous mixing layer. These groups are representative of shallow lakes whose mean depth is 2-3 m or slightly deeper. The groups are also representative of the epilimnion of stratified lakes, where mixing occurs. Padisák *et al.* (2009) suggested that group **N** should be restricted to temperate environments and that all low-latitude species should be transferred to group **Na** according to the Souza *et al.* (2008) criteria. This group would include all desmid species with small isodiametric cells such as those of *Cosmarium*, *Staurodesmus* and *Staurastrum*. It would also include filamentous individual organisms (e.g., *Teilingia* and *Spondylosium*) that are sensitive to mixing and typical of oligo-mesotrophic lakes subjected to atelomixis. Species of functional group **P** have very similar requirements to those of group **N**. However, they are able to live in more eutrophic waters and tolerate low light availability.

The present study aimed to describe the effects of different disturbance events and abiotic factors on desmid biomass in two warm monomictic lakes: Dom Helvécio (large and deep) and Carioca (small and shallow).

## METHODS

### Study area

Rio Doce State Park is located approximately in the middle of the Rio Doce Lake District, southeast Brazil (19°29'S, 42°28'W) (Meis & Tundisi, 1997). Among the lakes in Rio Doce State Park are Lake Carioca, which is mesotrophic, shallow and round-shaped, with a surface area of 0.14 km<sup>2</sup> and a maximum depth of 11.8 m, and Lake Dom Helvécio, which is oligotrophic and dendritic in shape, with a surface area of 5.27 km<sup>2</sup> and a maximum depth of 39.2 m



**Figure 1.** Bathymetry of Lakes Carioca and Dom Helvécio, southeast Brazil, with depth isolines (Bezerra-Neto & Pinto-Coelho 2008; Bezerra-Neto *et al.* 2010). *Batimetría de los lagos Carioca y Dom Helvécio, sureste de Brasil.*

(Bezerra-Neto & Pinto-Coelho, 2008). Both lakes are warm monomictic, are stratified between September and April and are basically isothermal from May through August (Henry & Barbosa, 1989) (Fig. 1).

### Sampling

Monthly samples were collected over a five-year period (January 2002-December 2006) in the limnetic region of the two lakes. The percentage of incident light was estimated from Secchi disk measurements (Cole, 1994). Vertical profiles of water temperature, pH and electrical conductivity were obtained with a multiparameter probe (Horiba<sup>®</sup> sensor 220 model U 22). The

stability of stratification was calculated according to Idso (1973). The mixing zone ( $Z_{\text{mix}}$ ) was identified from the temperature profiles, and the  $Z_{\text{eu}} : Z_{\text{mix}}$  ratio was used as a light availability index (Jensen *et al.*, 1994).

Nutrients and phytoplankton samples were collected monthly with a van Dorn bottle from the subsurface (100 % incident light), the Secchi disk depth (15 % incident light), three times the Secchi disk depth (1 % incident light) and the aphotic zone. Total phosphorus (TP), soluble reactive phosphorus (SRP  $\rightarrow$   $\text{PO}_4^{-3}$ ), total nitrogen (TN) and dissolved inorganic nitrogen (DIN  $\rightarrow$   $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ) were measured according to Golterman *et al.* (1978) and Mackereth *et al.* (1978), respectively. The DIN:SRP molar ratio was used to evaluate possible nitrogen or phosphorus limitation, where: DIN:SRP < 13 indicates limiting nitrogen, DIN:SRP > 50 indicates limiting phosphorus, and  $13 < \text{DIN:SRP} < 50$  indicates that neither of these nutrients is limiting (Morris & Lewis, 1988; Kosten *et al.*, 2009).

For specific and infra-specific identification of the taxa, classical taxonomic literature was consulted (Teiling, 1967; Croasdale, *et al.*, 1983; Prescott, 1975; Prescott *et al.*, 1972, 1975, 1977, 1981, 1982).

Desmids were quantitatively estimated according to Utermöhl (1958). The sedimentation time determinations followed Lund *et al.* (1958). The biomass and the surface:volume ratio (S:V) were obtained in terms of geometric shapes (Hillebrand *et al.*, 1999), assuming that the unit of fresh weight, expressed in terms of mass, was  $1 \text{ mm}^3 \text{ L}^{-1} = 1 \text{ mg L}^{-1}$  (Wetzel & Likens, 2000).

Desmid species were classified according to the following criteria:

1. Frequency of occurrence (%):

- |             |                              |
|-------------|------------------------------|
| rare        | ( $F \leq 10$ %),            |
| common      | ( $10$ % < $F \leq 50$ %) or |
| very common | ( $F > 50$ %).               |

2. Habit or life form: simple (*Cosmarium*), filamentous (intact filaments of *Spondylosium* and *Teilingia*), complex (*Staurastrum*), intermedi-

ate (*Staurodesmus*) or cylindrical (*Closterium* and *Pleurotaenium*).

3. MLD, Maximum Linear Dimension (adapted from Sieburth *et al.*, 1978): class 1 (<10  $\mu$  m, ultraplankton), class 2 (11-20  $\mu$  m, nanoplankton), class 3 (21-50  $\mu$  m, microplankton) or class 4 (>50  $\mu$  m, net plankton).
4. Functional groups (*sensu* Reynolds *et al.*, 2002; Padišák *et al.*, 2009).

A multivariate descriptive analysis of the five-year abiotic and biotic variables was performed with canonical correspondence analysis (CCA). A Monte Carlo test was used, and the variability of the data was explained in terms of the canonic coefficient (Ter-Braak, 1986). The Pearson correlation coefficient ( $r$ ) resulting from the relationship between the ordination values was used, as well as the individual variables for the ordination (McCune & Mefford, 1997).

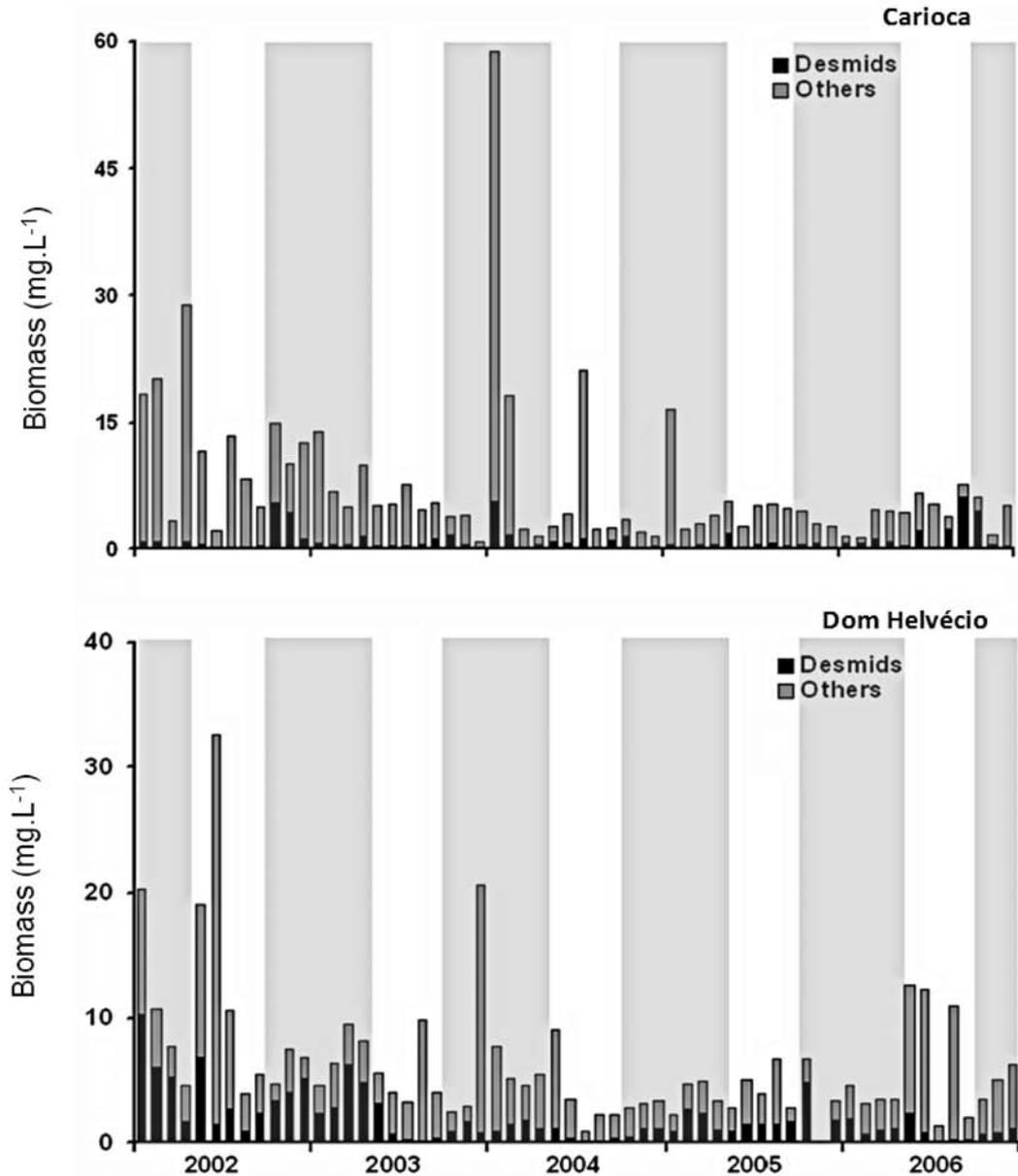
For a descriptive multivariate analysis of the variables at a monthly scale, the thermal stability,  $Z_{\text{mix}}$ , Secchi disc depth and light attenuation coefficient were selected from a principal component analysis (PCA) (Barbosa *et al.*, 2012). The biomass was integrated arithmetically ( $\text{mm}^3 \cdot \text{m}^{-2}$ ) including monthly values at each depth. The arithmetic integration of the water column was performed in terms of the sum of the area of each stratum (depth), composed of two axes: the depth of the water column and the other variable to be integrated (biomass). The programs used were FITOPAC (Shepherd, 1996), for the transformation of data, and PC-ORD for Windows, version 5.0 (McCune & Mefford, 1997).

The average depth of desmid occurrence ( $Pm_i$ ), i.e., the depth at which the mean biomass ( $\text{mg L}^{-1}$ )  $i$  is located in the water column, was calculated with the Dini *et al.* (1993) formula, used to describe the daytime vertical migration (DVM) of zooplankton. In this study, this formula was used to assess the difference in the maximum biomass between the stratification and mixing periods. Different months were compared with a two-tailed t test. These analyses were performed with Statistica software, version 5.1 (Statsoft).

## RESULTS

During stratification, significant differences in desmid biomass were observed between depths in Lake Dom Helvécio (one-way Anova,  $p = 0.001$ ,  $n = 60$ ). The maximum value of des-

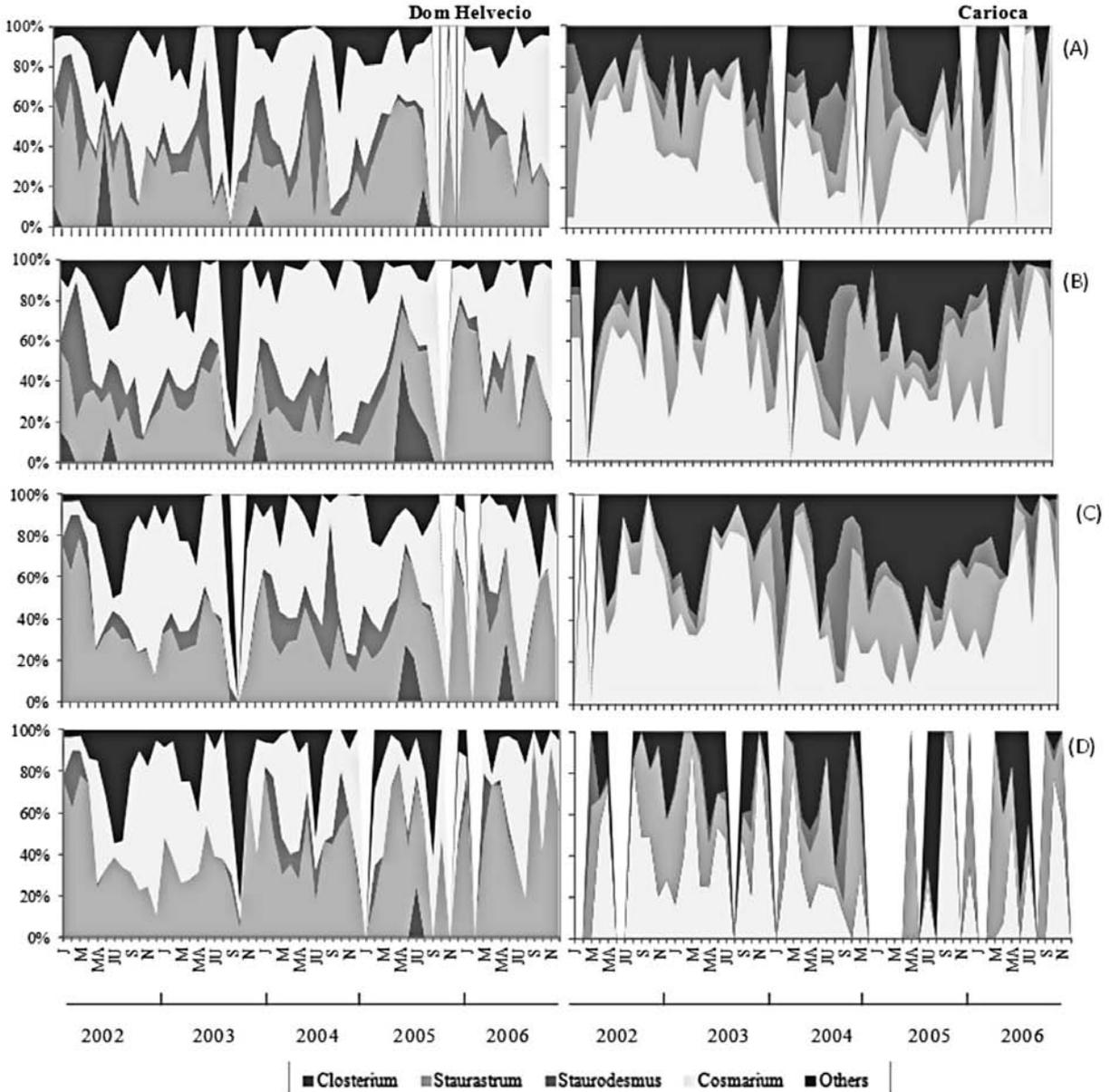
mid biomass ( $4.97 \text{ mg L}^{-1}$ ) was measured during stratification in January 2002, at 10 % light incidence. During the mixing period, maximum values ( $3.99 \text{ mg L}^{-1}$ ) were measured in May 2002 at 1 % light incidence (Figs. 2a-b). In both lakes, the three most representative



**Figure 2.** Biomass of desmids and other algal classes ( $\text{mg L}^{-1}$ ) at Lakes Carioca and Dom Helvécio during 2002-2006. Clear spaces: non-sampling period. Grey stripes correspond to stratification periods. *Biomasa ( $\text{mg L}^{-1}$ ) de las desmidiáceas y otras clases de algas en los lagos Carioca y Dom Helvécio durante el período 2002-2006. Espacios en blanco: periodo sin muestreo. Columnas grises corresponden a los períodos de estratificación.*

genera (maximum 90 % of total desmid biomass) were *Cosmarium*, *Staurastrum* and *Staurodesmus* (Fig. 3). *C. asphaerosporum* var. *strigosum* was the dominant species (>50 %) along the entire temporal scale.

During stratification at Lake Carioca, coexistence of *C. asphaerosporum* var. *strigosum* (40 %), *S. panduriforme* (13 %), *T. granulata* (10 %), *C. bioculatum* (7 %) and *S. iotanium* var. *iotanium* (5 %) was detected at depths up to 1 %



**Figure 3.** Relative abundance (%) of the major desmid genera at four depths in Lakes Carioca and Dom Helvécio during 2002-2006. Sub-surface (A), 10 % light incidence (B), 1 % light incidence (C) and aphotic zone (D). Clear spaces: non-sampling period. *Abundancia relativa (%) de los principales géneros de desmidiáceas a lo largo de las cuatro profundidades de muestreo en los lagos Carioca y Dom Helvécio durante el período 2002-2006. Sub-superficie (A), 10 % de incidencia de luz (B), 1 % de incidencia de luz (C) y zona afótica (D). Espacios en blanco: período sin muestreo.*

light incidence (3-6 m), corresponding to 80 % of the desmids' total biomass (Table 1).

The maximum biomass of *C. asphaerosporum* var. *strigosum* (3.37 mg L<sup>-1</sup>) was identified in September 2006 at the 1 % light incidence

depth. The molar dissolved ratio was relatively high (DIN:SRP = 102), and the maximum value recorded for NO<sub>3</sub><sup>-</sup> was 46 µg L<sup>-1</sup>. In January 2004, *C. bioculatum* (1.15 mg L<sup>-1</sup>), *T. granulata* (2.16 mg L<sup>-1</sup>) and *S. panduriforme* (0.86 mg L<sup>-1</sup>)

**Table 1.** Classification of desmids of Lakes Carioca and Dom Helvécio (MLD: Size structure, FG: Functional Group, \*: occurrence only at Lake Dom Helvécio, \*\*: species with biomass (mg L<sup>-1</sup>) below 1 %). *Clasificación de las desmidiáceas de los lagos Carioca y Dom Helvécio: (MLD: Máxima Dimensión Linear, FG: Grupo Funcional, \*: ocurrencia restringida al lago Dom Helvécio, \*\*: especies con biomasa (mg L<sup>-1</sup>) menor a 1 %).*

Species	Abreviation	Form	Carioca		Dom Helvécio	
			MLD	FG	MLD	FG
<i>Closterium aciculare</i> West	Clac	Cylindrical	4	**	4	P
<i>C. moliniferum</i> Ehr. ex Ralfs	Clmol	Cylindrical	*	**	4	**
<i>Cosmarium asphaerosporum</i> Nordst. var. <i>strigosum</i> Nordst.	Cosasp	Simple	1	Na	1	**
<i>C. bioculatum</i> Bréb.	Cosbio	Simple	1	**	1	**
<i>C. contractum</i> Kirchn. var. <i>contractum</i>	Coscont	Simple	2	**	2	Na
<i>C. moniliforme</i> (Turp.) Ralfs	Cosmon	Simple	1	**	1	**
<i>Cosmarium regnelii</i> Wille	Cosregn	Simple	1	**	1	**
<i>Pleurotaenium trabecula</i> (Ehr.) ex Näg.	Pleurotr	Cylindrical	*	**	4	**
<i>Spondylosium panduriforme</i> (Heim.) Teil.	Spontan	Simple	1	Na	1	**
<i>Staurastrum erostellum</i> West & West	Staeros	Complex	-	-	2	**
<i>S. forficulatum</i> Lund.	Stafor	Complex	3	**	3	**
<i>S. gemelliparum</i> Nordst.	Stagemel	Complex	2	**	2	**
<i>S. gracile</i> Ralfs	Stagrac	Complex	-	-	3	**
<i>S. hirsutum</i> (Ehr.) Ralfs	Stahirs	Complex	*	**	2	**
<i>S. iotantum</i> Wolle var. <i>iotantum</i>	StaiotG	Complex	2	**	2	**
<i>S. iotantum</i> Wolle Morphotype 1	StaiotG	Complex	2	**	2	**
<i>S. laeve</i> Ralfs	Stalae	Complex	2	**	2	**
<i>S. laeve</i> Morphotype 1	StalaeP	Complex	2	**	2	**
<i>S. leptocladum</i> Nordst. var. <i>cornutum</i> West & West	Stalepto	Complex	*	**	4	**
<i>S. muticum</i> (Bréb.) ex Ralfs var. <i>muticum</i>	Stamut	Complex	4	**	4	**
<i>S. rotula</i> Nordst.	Starot	Complex	2	Na	2	Na
<i>S. smithii</i> (G.M. Smith) Teil.	Stasmi	Complex	*	**	1	Na
<i>Staurastrum</i> sp.	Stasp	Complex	3	**	3	**
<i>S. subcruciantum</i> Cook & Wills	Stsubc	Complex	2	**	-	**
<i>S. subunguiferum</i> Fritsch & Rich	Stasubun	Complex	2	**	2	**
<i>S. taylorii</i> Grönbl.	Statayl	Complex	1	**	1	Na
<i>S. tetracerum</i> (Kütz.) Ralfs ex Ralfs var. <i>tetracerum</i> f. <i>tetracerum</i>	Sttetet	Complex	1	**	1	**
<i>S. tetracerum</i> var. <i>tetracerum</i> (Kütz.) Ralfs ex Ralfs var. <i>tortum</i> (Teil.) Borge	Statetor	Complex	1	**	1	**
<i>S. trifidum</i> Nordst. var. <i>glabrum</i> Lag.	Statrif	Complex	2	**	**	**
<i>S. wolleanum</i> Butl.	Stawol	Intermediate	-	**	4	**
<i>S. convergens</i> (Ehr. ex Ralfs) Teil.	Stocon	Intermediate	3	**	3	**
<i>S. crassus</i> (West) Flor.	Stocra	Intermediate	2	Na	2	Na
<i>S. cuspidatus</i> (Bréb.) Teil.	Stocusp	Complex	-	-	2	**
<i>S. dejectus</i> (Bréb.) Teil.	Stodej	Intermediate	3	**	3	**
<i>S. incus</i> (Bréb.) Teil. var. <i>ralfsii</i> (W. West) Teil.	StoinR	Intermediate	1	**	1	**
<i>S. jaculiferus</i> (West & West) Teil.	Stojacu	Intermediate	*	**	3	**
<i>Teilingia granulata</i> (Roy & Biss.) Bourr.	Teilgra	Simple	1	Na	1	Na
<i>Teilingia granulata</i> (Roy & Biss.) Bourr. Morfotipo 1	TeilgraG	Simple	1	Na	1	**
<i>Xanthidium concinnum</i> Arch.	Xconc	Complex	**	**	1	**
<i>Xanthidium</i> sp.	Xsp	Complex	**	**	2	**

maximum values were identified at the 1 % light incidence depth. The  $Z_{eu} : Z_{mix} = 1.3$  ratio indicated a clear epilimnion (Fig. 4).

During the mixing period, however, *C. asphaerosporum* var. *strigosum* ( $0.9\text{--}3.4 \text{ mg L}^{-1}$ ) maximum values were measured at the  $Z_{eu}$  from June to September 2006. During this period, the  $\text{N-NO}_3^-$  concentration at  $Z_{eu}$  varied between  $2.6$  and  $20.1 \text{ mg L}^{-1}$ , and  $\text{N-NH}_4^+$  varied from  $115.8$  to  $77.2 \text{ } \mu\text{g L}^{-1}$ . Their molar ratio (DIN:SRP) was always  $> 50$  if  $Z_{mix}$  reached the lake bottom.

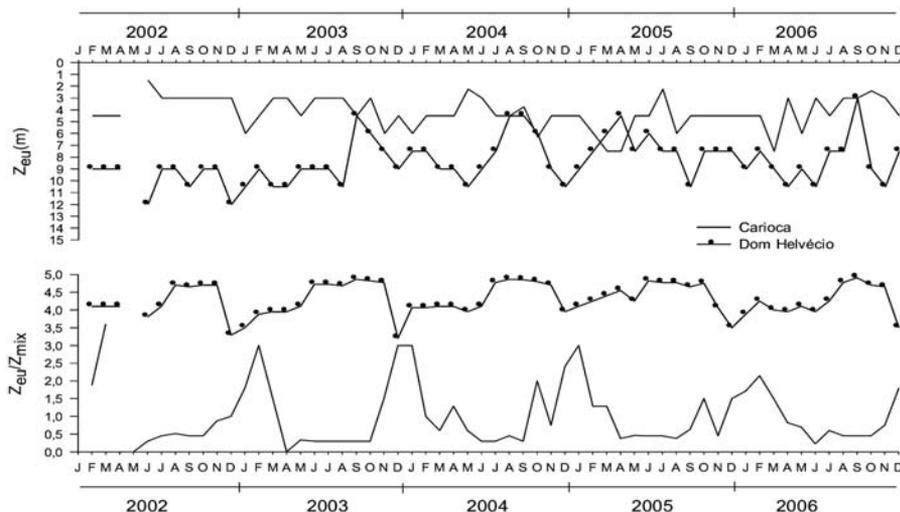
The analysis of the intermediate and complex desmid forms (*Staurastrum* and *Staurodesmus*) with  $\text{MLD} < 20 \text{ } \mu\text{m}$  showed that the maximum values were recorded between the surface and the 1 % light incidence depth during the stratification period, corresponding to the epilimnetic and metalimnetic layers. *S. crassus* (maximum  $0.67 \text{ mg L}^{-1}$ ), *Staurastrum* sp. (maximum  $0.45 \text{ mg L}^{-1}$ ), *S. incus* var. *ralfsii* (maximum  $0.43 \text{ mg L}^{-1}$ ), *S. iotatum* var. *iotatum* (maximum  $0.35 \text{ mg L}^{-1}$ ) and *S. laeve* (maximum  $0.29 \text{ mg L}^{-1}$ ) were the most common species during the stratification period.

Rarely occurring species (complex forms) with  $\text{MLD} > 20 \text{ } \mu\text{m}$  were best documented below the 10 % light incidence depth. Among these species were *S. rotula* ( $1.34 \text{ mg L}^{-1}$ , May 2005),

*S. dejectus* ( $0.89 \text{ mg L}^{-1}$ , February 2004), *S. trifidum* ( $0.48 \text{ mg L}^{-1}$ , September 2006), *S. cuspidatus* ( $0.36 \text{ mg L}^{-1}$ , August 2006) and *S. gemelliparum* ( $0.25 \text{ mg L}^{-1}$ , December 2002). However, in contrast to the observations at Lake Dom Helvécio, morphologically complex forms ( $\text{MLD} > 20 \text{ } \mu\text{m}$ ) showed maximum biomass values very similar to those of the rarely occurring forms.

At Lake Dom Helvécio, the co-occurrence of *C. contractum* (22 %), *S. taylorii* (17 %), *C. asphaerosporum* var. *strigosum* (15 %), *S. crassus* (13 %), *T. granulata* (6 %) and *S. laeve* (5 %) was recorded during stratification at the 1 % light incidence depth (approximately 9 m).

A maximum of *C. asphaerosporum* var. *strigosum* ( $1.09 \text{ mg L}^{-1}$ ) was detected in May 2002 at the 1 % light incidence depth, with  $Z_{mix}$  located at a depth of 10 m and  $Z_{eu}$  at a depth of 9 m ( $Z_{eu} : Z_{mix} = 0.9$ ). In November and December 2003, maximum values for *C. contractum* ( $1.39\text{--}2.47 \text{ mg L}^{-1}$ ) were found between the surface and the 1 % light incidence depth. During these months, the  $Z_{eu} : Z_{mix}$  ratio was 0.95, and the concentrations of both  $\text{P-PO}_4^{3-}$  ( $2.2\text{--}3.5 \text{ } \mu\text{g L}^{-1}$ ) and  $\text{N-NO}_3^-$  ( $3.6\text{--}12 \text{ } \mu\text{g L}^{-1}$ ) were comparatively low. Maxima for *S. panduriforme* ( $0.33 \text{ mg L}^{-1}$ ) and *T. granulata* ( $0.54 \text{ mg L}^{-1}$ )



**Figure 4.** Monthly variation in the euphotic zone and the euphotic zone:mixing zone ratio in Lakes Carioca and Dom Helvécio during the study period (2002-2006). Variación mensual de la zona eufótica y de la relación zona eufótica:zona de mezcla en los lagos Carioca y Dom Helvécio durante el período de estudio (2002-2006).

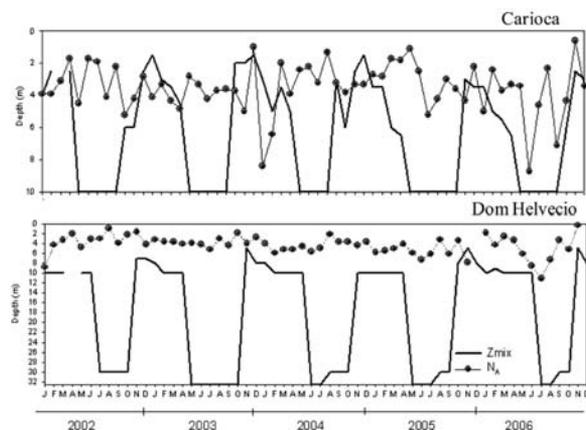
$L^{-1}$ ) were observed between the surface and the 1 % light incidence depth (March-May 2003).

The analysis of the intermediate and complex forms (*Staurastrum* and *Staurodesmus*) with an MLD up to 20  $\mu\text{m}$  showed that the maximum values occurred during the stratification period at  $Z_{\text{mix}}$  ( $Z_{\text{mix}} = 12$  m). Among the commonly occurring species, *S. crassus* (maximum 2.5  $\text{mg L}^{-1}$ , February-March 2002), *S. taylorii* (maximum 2.25  $\text{mg L}^{-1}$ , January-February 2002), *S. laeve* (maximum 0.35  $\text{mg L}^{-1}$ , May 2002) and *S. tetracerum* var. *tetracerum* f. *tetracerum* (maximum 0.64  $\text{mg L}^{-1}$  at  $Z_{\text{aph}}$ , October 2005) were noteworthy. The commonly occurring species with MLD > 20  $\mu\text{m}$  also had their greatest occurrence between the surface and the 1 % light incidence depth, occasionally during the mixing period (June-September) and frequently during stratification (October-February). Among the commonly occurring species, *S. wolleanum* (0.37  $\text{mg L}^{-1}$ , January 2006), *S. rotula* (0.35  $\text{mg L}^{-1}$ , December 2002), *S. muticum* (0.1  $\text{mg L}^{-1}$ , January 2005) and *S. gemelliparum* (0.03  $\text{mg L}^{-1}$ , January 2002) were noteworthy. Rarely occurring species were also identified, including *S. leptocladum* (0.13  $\text{mg L}^{-1}$ , October 2002) and *S. dejectus* (0.02  $\text{mg L}^{-1}$ , April and July 2003).

The common planktonic species included *C. aciculare* and *C. moniliferum*. The maximum values of *C. aciculare* were observed in July 2002 (1.01  $\text{mg L}^{-1}$ ) and June-September 2005 (0.08-0.30  $\text{mg L}^{-1}$ ), always at the lake subsurface. This species was also present during the stratification period (0.2-0.4  $\text{mg L}^{-1}$ ).

### Effects of thermal stability and underwater light climate on desmid biomass

The average depth of biomass ( $\text{mg L}^{-1}$ ) for functional group **Na** (Fig. 5) indicated that typical desmid epilimnetic communities occurred at both Carioca (MLD < 20  $\mu\text{m}$ ) and Dom Helvécio (MLD > 20  $\mu\text{m}$ ) Lakes. A comparison between the data for the stratification period and the data for the mixing period for both lakes noted no significant differences ( $p > 0.05$ ). The only differences occurred in the quantitative decrease in species biomass ( $\leq 80$  %) during the mixing period.



**Figure 5.** Annual variation in the mean depth of the biomass ( $\text{mg L}^{-1}$ ) of functional group **Na** at Lakes Carioca (A) and Dom Helvécio (B) during 2002-2006. Continuous lines: mixing layer. *Variación anual de la profundidad promedio del grupo funcional Na en los lagos Carioca (A) y Dom Helvécio (B) durante el período 2002-2006. Línea continua: zona de mezcla.*

A Canonical Correspondence Analysis performed with 39 species and 6 abiotic factors resulted in eigenvalues of  $\lambda = 0.13$  and  $\lambda = 0.036$  for axes 1 and 2, respectively. The species-environment correlations for axes 1 (0.89) and 2 (0.685) were high, indicating a strong correlation between the distribution of the desmid species and the environmental variables used for ordination (Table 2). A Monte Carlo permutation test showed that axes 1 and 2 were both statistically significant, as simultaneously identified by CCA ( $p < 0.01$ ), indicating an absence of random events and the presence of relationships between environmental variables and desmid species (Fig. 6). The sampling units for Lake Dom Helvécio formed a group to the right of axis 1, and the units for Lake Carioca formed a group to the left of this axis. The canonical coefficients for axis 1 and axis 2 showed that thermal stability and the Secchi disk depth were the most important environmental variables for the ordination.

The canonical coefficients indicated that thermal stability ( $r = -0.63$ ), the mixing layer ( $r = -0.59$ ) and the light attenuation coefficient ( $r = 0.35$ ) were the most important factors associated with the axis 1 ordination. Axis 2 presented higher canonical coefficients for the Secchi disk depth ( $r = -0.77$ ), thermal stability ( $r = 0.54$ ), electrical conductivity ( $r = -0.46$ ),



species group showed a close relationship with thermal stability ( $r = -0.68$ ). The other group combined the species *P. trabecula* ( $r = -0.93$ ), *S. hirsutum* ( $r = -0.85$ ), *S. rotula* ( $r = -0.71$ ), all associated with  $Z_{\text{mix}}$  ( $r = -0.61$ ) and water transparency ( $r = -0.57$ ).

On the positive side of axis 1, species characteristic of Lake Carioca were grouped together based on the high light attenuation coefficient ( $r = 0.42$ ) and  $\text{N-NH}_4^+$  ( $r = 0.33$ ) concentration. The highest correlations were found for *S. iotatum* var. *iotatum* ( $r = 0.77$ ), *S. laeve* ( $r = 1.17$ ) and *S. incus* var. *ralfsii* ( $r = 0.98$ ). In the central portion of the ordination, a group was observed corresponding to the common species association between the two lakes and the months.

## DISCUSSION

The long stratification period (202 days) associated with high temperatures ( $>25^\circ\text{C}$ ) and high thermal stability, acidic water ( $\text{pH} < 7$ ), low light availability, high availability of nutrients and structural changes at a lower  $Z_{\text{mix}}$  (Lake Carioca: 1.5-6.5 m) or larger scale (Lake Dom Helvécio: 5-12 m) significantly affected the biomass of desmids, as indicated by the CCA results. Previous studies have shown that in certain tropical lakes, the largest desmid populations occur during the period of thermal stratification (summer). Furthermore, the growth of these algae has been detected in the epilimnion of tropical lakes (Barbosa & Padisák, 2002; Tavera & Martínez-Almeida, 2005; Souza *et al.*, 2008).

The adaptation of desmids to turbulent environments (Brook, 1981) requires an optimum temperature between 25 and 30 °C (Coesel & Wandenaar, 1990) and the ability to tolerate nutritional deficits (Reynolds *et al.*, 2002), conditions observed in the epilimnion of lakes in general. Yinxin & Minjuan (2005) reported that *Cosmarium*, *Staurastrum*, *Staurodesmus* and *Closterium* (> 70 % of the density and biomass) were dominant at six stations during three seasons (spring, summer and autumn) but not during the winter. Desmid populations associated with increased surface temperature have also been

previously identified in tropical lakes (Clarke, 2008), particularly if the increase in temperature is associated with thermal stratification.

A greater biomass of desmids was found in the epilimnion of the lakes, and the physical stability of the lakes had a substantial influence on the long-term maintenance of this biomass. However, the biomass values decreased drastically ( $\geq 70\%$ ) during the mixing period. Consequently, the desmid community would show a low adaptive flexibility and persistence in unstable pelagic lakes (i.e., during the mixing period), thus reinforcing the hypothesis that desmids exhibit high ecological resilience in the face of significant fluctuations between the stratification and mixing periods. Despite their preference or affinity for the thermal stratification period, *C. asphaerosporum* var. *strigosum*, *S. taylorii* and *C. aciculare* also occurred during the mixing period.

Most of the desmids collected ( $\text{MLD} < 20$ ) belonged to functional group **Na**. Species of functional group **P**, which show requirements very similar to those of group **N**, were also found in both lakes and were represented by *C. aciculare*, which attained maximum values at Lake Dom Helvécio during the mixing period. *Closterium* species were very well adapted to the higher levels of organic matter and the lower levels of light intensity in the monomictic lakes (Brook & Williamson, 1988). These species also gained a strong adaptive benefit from their physiological affinity to the mixing conditions (Pollinger, 1986) in the monomictic lakes.

The  $Z_{\text{eu}} : Z_{\text{mix}}$  ratio identified a well-lighted epilimnion in Lakes Carioca ( $0.9 < Z_{\text{eu}}/Z_{\text{mix}} < 3.6$ ) and Dom Helvécio ( $0.9 < Z_{\text{eu}}/Z_{\text{mix}} < 1.8$ ). This result suggested that desmid communities are most likely not light limited. Lower transparency (0.5-2.5 m) and greater light attenuation (0.85-3.4 m) were observed in Lake Carioca due to its high content of pigmented organic matter (Bezerra-Neto *et al.*, 2006). Eutrophic swamps and wetlands tend to be dominated by small desmids with short generation times (e. g., *Cosmarium granatum* Brébisson, *Cosmarium subgranatum* Nordstedt and *Cosmarium subtumidum* Nordstedt), whereas oligotrophic lakes are dominated by large desmids (e. g., *Micraste-*

rias, *Tetmemorus* and *Pleurotaenium*) (Coesel, 1982), situations similar to those observed in Lakes Carioca and Dom Helvécio, respectively. Studies of the effect of light on phytoplankton morphology in wetlands have shown that small organisms occur in light-limited environments, whereas larger forms occur if light is relatively abundant (O'Farrel *et al.*, 2007).

At Lake Carioca, the maximum biomass was associated with the nanoplanktonic fraction (MLD < 20 µm). In Lake Dom Helvécio, the nano- and microplanktonic (> 20 µm) species coexisted. Brook (1981) reported that desmid species tend to behave as K-strategists, with high volumes and low intrinsic growth rates, low rates of population increase (Coesel & Kooijman-van-Blokland, 1991) and high light demands (Reynolds, 1984). However, the dominant desmids in Lakes Carioca and Dom Helvécio have a lower MLD ( $\leq 20$  µm), a small volume ( $< 10^3$ ) and greater dispersion. These characteristics would allow rapid colonization and nutrient absorption. In addition to these factors, a low sinking rate would also be potentially favored by the morphological features cited above. These features would facilitate the establishment of forms with the ability to achieve dominance under stressful conditions (i.e., low light and nutrient availability) (Reynolds, 2006).

Planktonic desmids are commonly associated with oligo-mesotrophic waters (Nygaard, 1949; Coesel, 1975, 2001). However, the relationship between the trophic level of a lake and the species richness, diversity and biomass of planktonic desmids is highly debatable. In addition to their association with oligotrophic lakes, the great majority of desmid species (except for the cosmopolitan species) are considered oligosaprobic (Coesel, 1983), i.e., not tolerant to organic pollution. Although planktonic desmids are commonly associated with oligo-mesotrophic waters, their trophic relationships and level are still very uncertain (Coesel, 1975, 2001).

The presence of *P. trabecula* and *C. aciculare* at Lake Dom Helvécio indicates a low to medium level of pollution (Coesel, 1983; Negearnpat & Peerapornpisal, 2007). However, the floristic composition of the desmids in Lake Carioca

included both species typical of eutrophic lakes and species associated with oligotrophic lakes. This result indicated that, although the lake is located in an area in which the environment is protected, the changes occurring in the lake are typical of shallow ponds. Eutrophication processes are associated with decreases in the richness of desmids (Coesel, 1978). This association results from the increase in organic pollution, which decreases the structural diversity of the environment in conjunction with the decreased richness of the aquatic vegetation (Coesel *et al.*, 1978). A decrease in diversity in Lake Donghu (China) was identified between 1960 and 1990 and related to increases in phosphorus and nitrogen and a decrease in water transparency (Yinxin & Minjuan, 2005). A relatively low richness of desmids may be favored by several factors intrinsic to Lake Carioca, including shading by the terrestrial vegetation, a lower richness of macrophytes and low water transparency, (Felisberto & Rodrigues, 2005).

In summary, the physical stability of the lakes is the principal driver favoring the dominance of desmids in tropical warm monomictic lakes, although stress due to the limitation of inorganic nutrients (Lake Dom Helvécio) and the limited amount of light (Lake Carioca) also determines the composition and abundance of functional groups and adaptive strategies.

## ACKNOWLEDGMENTS

LGB thanks CNPq, Conselho Nacional de Desenvolvimento Científico e Tecnológico, for doctoral scholarship and financial support of the Brazilian Long Term Ecological Research Program (Grant n° 520031/1998-1999). CEMB also thanks CNPq for a Research Fellowship (Grant n° 303876/2004-2).

## REFERENCES

- BARBOSA, F. A. R. & J. PADISÁK. 2002. The forgotten lake stratification pattern: atelomixis, and its ecological importance. *Verhandlungen der*

- Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 28: 1385–1395.
- BARBOSA, L. G., F. A. R. BARBOSA & C. E. de M. BICUDO. 2012. Inter-annual chemical stratification in Brazilian natural lakes: meromixis and hypolimnetic memory. *Acta Limnologica Brasiliensia*, 24(2) 127–139.
- BEZERRA-NETO, J. F., L. S. BRIGUENTI & R. M. PINTO-COELHO. 2010. A new morphometric study of Carioca Lake, Parque Estadual do Rio Doce (PERD), Minas Gerais State, Brazil. *Acta Scientiarum. Biological Sciences*, 32: 49–54.
- BEZERRA-NETO, J. F. & R. M. PINTO-COELHO. 2008. Morphometric study of Lake Dom Helvécio, Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil: a re-evaluation. *Acta Limnologica Brasiliensia*, 20: 161–167.
- BEZERRA-NETO, J. F., P. M. BARBOSA & F. A. R. BARBOSA. 2006. Temporal variation of attenuation of the visible radiation in four lakes of Parque Estadual do Rio Doce (PERD), Minas Gerais, Brasil. *Acta Limnologica Brasiliensia*, 18: 39–46.
- BROOK, A. J. 1981. *The Biology of Desmids*. Oxford: Blackwell Scientific Publications. 275 pp. (Botanical Monographs, 16).
- BROOK, A. J. & D. B. WILLIAMSON. 1988. The survival of desmids on the drying mud of a small lake. In: *Algae and the aquatic environment*. F. E. Round (ed.): 185–196. Biopress. Bristol.
- CANTER, H. M. & J. W. G. LUND. 1966. The periodicity of planktonic desmids in Windermere, England. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 16: 163–172.
- CLARKE, E., O. M. OLARINMOYE, F. G. OWODEINDE, A. O. ADEBOYEJO, A. JIMOH, S. L. AKINTOLA, & O. J. ADERINOLA, 2008. The dynamics of *Desmidacean* populations in Ologe lagoon, Lagos, Nigeria. *Journal of Cell and Animal Biology*, 2: 021–030.
- COESEL, P. F. M. 1975. The relevance of desmids in the biological typology and evaluation of fresh waters. *Aquatic Ecology*, 9: 93–101.
- COESEL, P. F. M. 1978. Environmental changes in the Oisterwijk pool area, as evident from the composition of the desmid flora. *Aquatic Ecology*, 12: 52–53.
- COESEL, P. F. M. 1982. Structural characteristics and adaptations of desmid communities. *Journal of Ecology*, 70: 163–177.
- COESEL, P. F. M. 1983. The significance of desmids as indicators of the trophic status of freshwaters. *Schweizerische Zeitschrift für Hydrologie*, 45: 388–393.
- COESEL, P. F. M. 1986. Structure and dynamics of desmid communities in hydrosere vegetation in a mesotrophic quivering bog. *Beihefte zum Nova Hedwigia*, 56: 119–143.
- COESEL, P. F. M. 1993. Poor physiological adaptation to alkaline culture conditions in *Closterium acutum* var. *variabile*, a planktonic desmid from eutrophic waters. *European Journal of Phycology*, 28: 53–57.
- COESEL, P. F. M. 2001. A method for quantifying conservation value in lentic freshwater habitats using desmids as indicator organisms. *Biodiversity and Conservation*, 10: 177–187.
- COESEL, P. F. M. & H. KOOIJMAN-VAN-BLOK-LAND. 1991. Seasonality of planktonic desmid species in Lake Maarsseveen (The Netherlands) related to experimentally determined growth rates in a temperature-light gradient. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 24: 763–767.
- COESEL, P. F. M. & H. KOOIJMAN-VAN-BLOK-LAND. 1994. Distribution and seasonality of desmids in the Maarsseveen Lakes area. *Netherlands Journal of Aquatic Ecology*, 28: 19–24.
- COESEL, P. F. M., R. KWAKKESTEIN & A. VERSCHOOR. 1978. Oligotrophication and eutrophication tendencies in some Dutch moorland pools, as reflected in their desmid flora. *Hydrobiologia*, 61: 21–31.
- COESEL, P. F. M. & K. WANDENAAR. 1990. Growth responses of planktonic desmids in a light-temperature gradient. *Freshwater Biology*, 23: 551–560.
- COLE, G. A. 1994. *Textbook of Limnology*. Waveland Press. Illinois. 412 pp.
- CROASDALE, H. T., C. E. M. BICUDO & G. W. PRESCOTT. 1983. A Synopsis of North American Desmids. University Nebraska Press. Lincoln. 2(5): 470 pp.
- DINI, M. L., P. A. SORANNO, M. SCHEUERELL & S. R. CARPENTER. 1993. Effects of predators and food supply on diel vertical migration of *Daphnia*. In: *The trophic cascades in lakes*. S. R. Carpenter & J. F. Kitchell (eds.): 153–171. Cambridge University Press. Cambridge.
- FELISBERTO, S. A. & L. RODRIGUES. 2005. Influência do gradiente longitudinal (riobarragem) na similaridade das comunidades de desmídias

- perifíticas. *Revista Brasileira de Botânica*, 28: 241–254.
- GERRATH, J. F. 1993. The biology of desmids: a decade of progress. In: *Progress in Phycological Research*. F. E. Round, D. J. Chapman (eds.): 79–193. Biopress Ltd. Bristol.
- GOLTERMAN, H. L., R. S. CLYMO & M. A. M. OHMSTAD. 1978. *Methods for physical and chemical analysis of freshwaters*. Blackwell Scientific Publications. Oxford. 214 pp.
- HARRIS, G. P. 1986. *Phytoplankton ecology: structure, function and fluctuation*. Chapman and Hall. London. 384 pp.
- HENRY, R. & F. A. R. BARBOSA. 1989. Thermal structure, heat content and stability of two lakes in the National Rio Doce Valley Lakes (Minas Gerais, Brazil). *Hydrobiologia*, 181: 189–199.
- HILLEBRAND, H., C. D. DÜRSELEN, D. KIRSCHTEL, D. POLLINGER & T. ZOHARY. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, 35: 403–424.
- HUSZAR, V. L. M., L. H. S. SILVA, P. DOMINGOS, M. MARINHO & S. MELO. 1998. Phytoplankton species composition is more sensitive than OECD criteria to the trophic status of three Brazilian tropical lakes. *Hydrobiologia*, 369–370: 59–71.
- IDSO, S. 1973. On the concept of lake stability. *Limnology and Oceanography*, 18: 681–683.
- JENSEN, P., E. JEPPESEN, K. OLRİK & P. KRISTENSEN. 1994. Impact of nutrients and physical factors on the shift from Cyanobacterial to Chlorophyte dominance in shallow Danish lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 1692–1699.
- KOROLEFF, F. 1976. Determination of ammonia. In: *Methods of seawater analysis*. K. Grasshoff (ed.): 126–133. Verlag Chemie. Weinheim.
- KOSTEN, S., V. L. M. HUSZAR, N. MAZZEO, M. SCHEFFER, L. S. L. STERNBERG, & E. JEPPESEN. 2009. Lake and watershed characteristics rather than climate influence nutrient limitation in shallow lakes. *Ecological Applications*, 19: 1791–1804.
- LUND, J. W. G. 1971. The seasonal periodicity of three planktonic desmids in Windermere. *Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 19: 3–25.
- LUND, J. W. G., C. KIPLING & E. D. LECREN. 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., J. HERON & J. F. TALLING. 1978. *Water Analysis. Scientific Publication (n° 36)*. Freshwater Biological Association. Ambleside. 120 pp.
- MCCUNE, B. & M. J. MEFFORD. 1997. *PC-ORD. Multivariate analysis of ecological data, Version 3.0*. MjM Software Design. Oregon.
- MEIS, M. R. M. & J. G. TUNDISI. 1997. Geomorphological and limnological process as a basis for lake typology. The middle Rio Doce lake system. In: *Limnological Studies in the Rio Doce Valley Lakes*. J. G. Tundisi & Y. Saijo (eds.): 25–50. Brazilian Academy of Sciences, São Carlos, 25–50.
- MORRIS, D. P. & W. M. LEWIS. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. *Freshwater Biology*, 20: 315–327.
- MOSS, B. 1972. The influence of environmental factors on the distribution of freshwater algae: an experimental study, 1: introduction and the influence of calcium concentration. *Journal of Ecology*, 60: 917–932.
- MOSS, B. 1973. The influence of environmental factors on the distribution of freshwater algae: an experimental study, 2: the role of pH and the carbon dioxide-bicarbonate system. *Journal of Ecology*, 61: 157–177.
- NASELLI-FLORES, L., J. PADISÁK, M. T. DOKULIL & I. CHORUS. 2003. Equilibrium/steady-state concept in phytoplankton ecology. *Hydrobiologia*, 502: 395–403.
- NGEARNPAT, N. & Y. PEERAPOMPISAL. 2007. Application of desmid diversity in assessing the water quality of 12 freshwater resources in Thailand. *Journal of Applied Phycology*, 19: 667–674.
- NYGAARD, G. 1949. Hydrobiological studies on some Danish ponds and lakes, 2: the quotient hypothesis and some new or little known phytoplankton organisms. *Kongelige Danske Videnskaberne Selskab*, 7: 1–293.
- O'FARRELL, I., P. TEZANOS-PINTO & I. IZAGUIRRE. 2007. Phytoplankton morphological response to the underwater light conditions in a vegetated wetland. *Hydrobiologia*, 578: 65–77.
- PADISÁK, J., L. O. CROSSETTI & L. NASELLI-FLORES. 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia*, 621: 1–19.

- POLLINGER, U. 1986. Phytoplankton periodicity in a subtropical lake (Lake Kinneret, Israel). *Hydrobiologia*, 138: 127–138.
- PRESCOTT, G. W. 1975. *Algae of the western great lakes area*. Wm. C. Brown Company Publishers. 6<sup>th</sup> edition. 977 pp.
- PRESCOTT, G. W., H. T. CROASDALE & W. C. VINYARD. 1972. *A Synopsis of North American Desmids*. University Nebraska Press. Lincoln. 1(2): 84 pp.
- PRESCOTT, G. W., H. T. CROASDALE & W. C. VINYARD. 1975. *A Synopsis of North American Desmids*. University Nebraska Press. Lincoln. 2(1): 267 pp.
- PRESCOTT, G. W., H. T. CROASDALE & W. C. VINYARD. 1977. *A Synopsis of North American Desmids*. University Nebraska Press. Lincoln. 2(2): 413 pp.
- PRESCOTT, G. W., H. T. CROASDALE, W. C. VINYARD & C. E. M. BICUDO. 1981. *A Synopsis of North American Desmids*. University Nebraska Press. Lincoln. 2(3): 720 pp.
- PRESCOTT, G. W., W. C. VINYARD & C. E. M. BICUDO. 1982. *A Synopsis of North American Desmids*. University Nebraska Press. Lincoln. 2(3): 700 pp.
- REYNOLDS, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press. Cambridge. 365 pp.
- REYNOLDS, C. S. 2006. *Ecology of phytoplankton*. Cambridge University Press. Cambridge. 535 pp.
- REYNOLDS, C. S., V. HUZSAR, C. KRUK, L. NASELLI-FLORES & S. MELO. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, 24(5): 417–428.
- SHEPHERD, G. J. 1996. *FITOPAC 1: manual de usuá-rio*. Universidade Estadual de Campinas, Campinas. 95 pp.
- SIEBURTH, J. McN., V. SMETACEK & J. LENZ. Pelagic ecosystem structure: heterotrophic compartments of plankton and their relationship to plankton size fractions. *Limnology and Oceanography*, 23: 1256–1263.
- SOUZA, M. B. G., C. BARROS, F. A. R. BARBOSA, E. HAJNAL & J. PADISÁK. 2008. Role of atelomixis in replacement of phytoplankton assemblages in Dom Helvécio Lake, Southeast Brazil. *Hydrobiologia*, 607(1): 211–224.
- TAVERA, R. & V. MARTÍNEZ-ALMEIDA. 2005. A hydrobiological study to interpret the presence of desmids in Lake Zirahuén, Mexico. *Limnologica*, 35: 61–69.
- TEILING, E. 1967. *The desmid genus Staurodesmus. A taxonomic study*. Arkiv für Botanik, 6(11): 467–629.
- TER-BRAAK, C. J. F. 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67: 1167–1179.
- UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitative Phytoplankton-methodik. *Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 9: 1–38.
- WETZEL, R. G. & G. E. LIKENS. 2000. *Limnological analyses*. Springer-Verlag New York Inc. New York. 391 pp.
- WOELKERLING, W. J. & S. B. GOUGH. 1976. Wisconsin desmids, 3: desmid community composition and distribution in relation to lake type and water chemistry. *Hydrobiologia*, 51: 3–32.
- YINXIN, W. & Y. MINJUAN. 2005. New desmids material from Donghu Lake, Wuhan, China. *Chinese Journal of Oceanology and Limnology*, 23(2): 210–217.