# Driving forces of the diel distribution of phytoplankton functional groups in a shallow tropical lake (Lake Monte Alegre, Southeast Brazil)

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(With 7 figures)

## Abstract

Phytoplankton vertical and diel dynamics in a small shallow lake (Lake Monte Alegre, Ribeirão Preto, state of São Paulo) were investigated in two climatological periods: July 2001 (cool-dry season) and March 2002 (warm-rainy season). Monte Alegre is a eutrophic reservoir, with a warm polymictic discontinuous circulation pattern. The lake was thermally stratified in both periods, although dissolved oxygen varied less in the cool-dry period. Phytoplankton biomass was higher in the warm-rainy season and the vertical distribution was stratified in both seasons. Flagellate groups ($L_m$, Y, $W_1$ and $W_2$) and functional groups typical of shallow eutrophic environments (J, $X_1$ and $S_n$) were important throughout the study period. The lake's thermal pattern strongly influenced the vertical distribution of the phytoplankton community in both periods. Biomass, functional groups and size classes of phytoplankton also were determined by the presence of more efficient herbivores in the lake, especially during the cool-dry period when phytoplankton biomass decreased.

*Keywords:* diel and vertical distribution, shallow tropical lake, thermal stratification, phytoplankton functional groups, grazing.

## Fatores direcionadores da distribuição nictemeral de grupos funcionais fitoplanctônicos de um lago brasileiro raso e tropical

## Resumo

As dinâmicas vertical e nictemeral do fitoplâncton de um lago pequeno e raso (Lago Monte Alegre, Ribeirão Preto, SP) foram investigadas em dois períodos climatológicos: julho/2001 (estação fria-seca) e março/2002 (estação quente-chuvosa). O lago esteve estratificado termicamente nos dois períodos de estudo, porém menores variações do oxigênio dissolvido foram observadas no período frio-seco. Maiores biomassas fitoplanctônicas foram registradas na estação quente-chuvosa e a distribuição vertical esteve estratificada nos dois períodos climatológicos. Grupos de flagelados ($L_m$, Y, $W_1$ e $W_2$), juntamente com grupos funcionais típicos de ambientes rasos e eutróficos (J, $X_1$ e $S_n$), foram importantes em todo o estudo. O padrão térmico do lago teve influência na distribuição vertical da comunidade fitoplanctônica nos períodos estudados. Biomassa, grupos funcionais e classes de tamanho do fitoplâncton também foram influenciados pela presença de herbívoros mais eficientes, principalmente durante o período frio-seco, quando ocorreram menores biomassas do fitoplâncton.

*Palavras-chave:* variação nictemeral e vertical, lago raso tropical, estratificação térmica, grupos funcionais fitoplanctônicos, herbivoria.

## 1. Introduction

In shallow tropical lakes, daily radiation input is mainly responsible for diel cycles of heat content and near-surface temperature. In these cycles, diurnal warming generates meaningful temperature-depth gradients that strongly affect biological processes (Talling, 2001).

Phytoplankton diel and vertical dynamics are driven by two main groups of factors: factors that produce small modifications in population growth rates, and factors that are responsible for population redistribution in the lake (George and Heavey, 1978; Reynolds, 2006). These dynamics are usually reported as dependent on: i) mixing patterns of the water body; ii) the presence of self-regulating populations by flagella or aerotopes; and iii) the occurrence of fast-growing species, which can fluctuate widely in numbers over a single diel cycle (Melo and Huszar, 2000; Melo et al., 2004).

Grazing may also control the vertical and diel distribution of phytoplankton. Zooplankton can be extremely efficient herbivores, consuming phytoplankton populations at great rates, and can move through the water column during the day in a phenomenon known as diel vertical migration (Reichwaldt and Stibor, 2005). Larvae of Chaoboridae (Arcifa, 1997) and some species of fish such as *Tilapia* spp. (Arcifa and Meschiatti, 1996; Starling et al., 2002) are also important plankton consumers.

Current studies on phytoplankton fluctuation divide this community into different functional groups and/or life strategies. The functional-group approach separates species of similar morphology and ecology according to their physiological responses (Reynolds, 1997; 2006; Reynolds et al., 2002). Phytoplankton is divided into 31 groups, based on its characteristics in habitat, tolerances and sensitivities. Many authors have obtained more adequate results with this approach than by using approaches related to higher taxonomic groups, which include organisms of different size, shape and physiology. The functional-groups scheme was successfully tested in temperate regions (Huszar and Caraco, 1998; Fabbro and Duivenvoorden, 2000; Romo and Villena, 2005) as well as in tropical and subtropical regions (Huszar et al., 2000; Marinho and Huszar, 2002; Kruk et al., 2002; Silva, 2004; Lopes et al., 2005; Devercelli, 2006; Nabout et al., 2005; Pivato et al., 2006; Soares et al., 2007).

Lake Monte Alegre is a small tropical reservoir that behaves as a lake. Limnological studies since the 1980s have characterized the abiotic variables and the different communities. The reservoir is eutrophic and warm polymictic discontinuous, with long periods of stratification (Arcifa et al., 1990; Huszar et al., 1998). The plankton composition, fluctuations and interactions with other communities are well known. Composition and fluctuation has been described for the following communities: bacterioplankton and protozooplankton (Gomes, 1991), phytoplankton (Silva, 1995; 1999; 2004), zooplankton (Arcifa et al., 1992; Arcifa et al., 1998; Arcifa, 1999), zoobenthos (Cleto-Filho, 2006), larval Chaoboridae (Arcifa, 1997; Arcifa, 2000) and fish (Arcifa and Meschiatti, 1996; Meschiatti and Arcifa, 2002). Biomass and densities of small zooplankton species during spring (Arcifa et al., 1998) are related to phytoplankton biomass, which is dominated by a large species (>60 µm, *Aulacoseira granulata* (Ehrenb.) Simons.), limiting zooplankton growth. During the cool-dry period, lower phytoplankton biomass was observed, when high densities of larger and more efficient filterers such as *Daphnia gessneri* Herbst and *D. ambigua* Scourf. were found (Arcifa et al., 1998; Silva, 2004). Analyses of the main herbivores have shown a feeding preference for bacteria and small algae (1 to 17 µm); and laboratory experiments on zooplankton groups have also demonstrated better zooplankton growth when fed nanoplanktonic algae (Fileto et al., 2004). Vertical distribution of zooplankton has been studied as well (Perticarrari et al., 2003; 2004; Perticarrari, 2005). Studies on seasonal phytoplankton dynamics have indicated a strong influence of abiotic and biotic disturbances (Arcifa et al., 1998; Silva, 2004).

The present study aimed to analyze diel and vertical dynamics of phytoplankton in Lake Monte Alegre in two seasons: cool-dry and warm-rainy. Considering the reservoir mixing patterns and available knowledge of its communities, we expected: i) a more even vertical distribution of phytoplankton in the cool-dry period, when circulation is expected; ii) differences in phytoplankton distribution in the various depths during the warm-rainy period, due to likely stratification of the water column; iii) lower phytoplanktonic biomasses at night, due to higher pressure by herbivores; and iv) predominance of phytoplankton functional groups typical of shallow eutrophic environments.

## 2. Material and Methods

### *2.1. Study area*

Lake Monte Alegre (21° 11' S and 47° 43' W) is a small (area = 7 ha), shallow reservoir with maximum depth ($z_{max}$) of 5 m and mean depth ($z_{mean}$) of 2.9 m, located on the campus of the University of São Paulo in Ribeirão Preto, state of São Paulo, southeastern Brazil (Figure 1). The climate is in between tropical and highland tropical, with two well-defined seasons: cool-dry (May to September) and warm-rainy (October to April). It is a eutrophic, warm polymictic discontinuous reservoir. It frequently stratifies for long periods (at least a month), especially during summer, leading to oxygen depletion near the bottom. Several factors contribute to the stability of the reservoir: the dam is not manipulated, the outlet is at the surface, there is little input from streams, the annual water level fluctuation is low (~0.40 m), and the winds are gentle with no predominant direction (Arcifa, 1999).

### *2.2. Sampling*

Climatological data (air temperature, rainfall and average winds) were obtained at the Agronomy Institute,

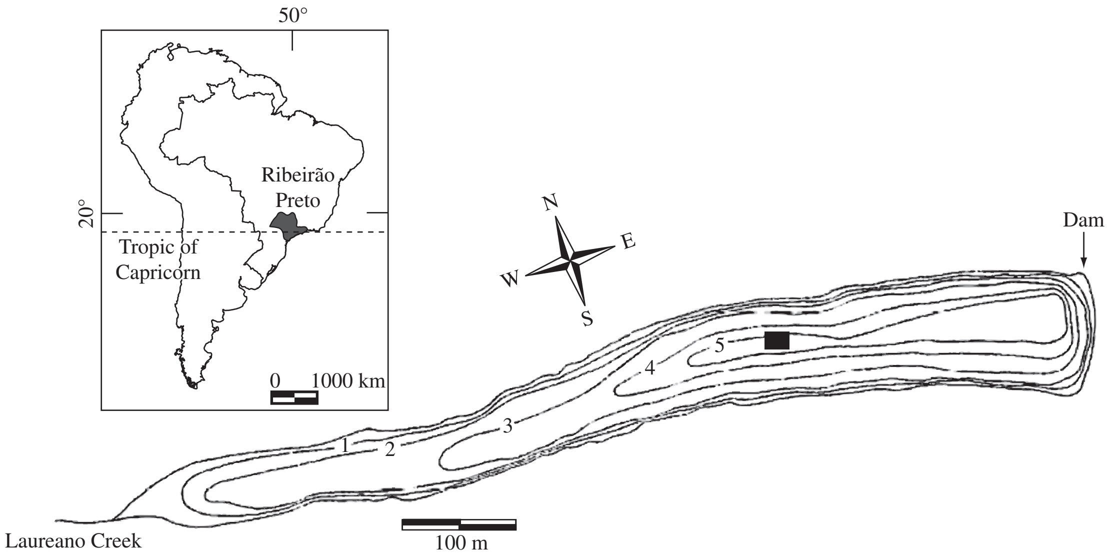


**Figure 1.** Morphometry and geographical location of Lake Monte Alegre, showing the location of the sampling station (■).

Ribeirão Preto Experimental Station, located ca. 5 km from the reservoir.

Temperature and dissolved oxygen were measured with a portable digital meter from Yellow Springs YSI, model 95. Light intensity was obtained with a LI-COR Inc., model 250 photometer. Phytoplankton samples were taken with a Ruttner bottle in two periods, in each of the two main climatological seasons: July 26th and 27th, 2001 (cool-dry season) and March 20th and 21st, 2002 (warm-rainy season), at a central point of the reservoir, at the surface, 1.5 m, 2.5 m and 4 m, at 9:00 AM, 3:00 PM, 9:00 PM and 3:00 AM. They were fixed with a modified Lugol solution, according to Vollenweider (1974). Zooplankton was sampled using an electric pump, delivering 30 L/min. A 60 µm net was used for water filtration. Sampling depths and time were the same for phytoplankton. Samples were narcotized and preserved in 4% formaldehyde (Haney and Hall, 1973).

*2.3. Sample analysis*

Phytoplankton was quantified by the Utermöhl (1958) sedimentation method. Individuals (colonies, filaments, cells) were counted in random fields according to Uhelinger (1964). Whenever possible, 100 individuals of the most frequent species were counted, with an error rate less than 20%, at a 95% significance level (Lund et al., 1958). Cladocerans and copepods were counted in 1, 2.5 or 5 mL subsamples, taken with Stempel pipettes; a minimum of 60 individuals were counted. Several subsamples were counted in order to maintain a coefficient of variation lower than 0.20 (McCauley, 1984; Prepas, 1984). Zooplankton data were taken from Perticarrari (2005) and Perticarrari et al. (2003; 2004).

*2.4. Data analysis*

Specific phytoplankton biovolume was estimated according to Edler (1979) and Hillebrand et al. (1999), and population volume was calculated by multiplying the population density of each species by the mean volume of individuals. Biomass (fresh weight) was obtained from the mean biovolume, assuming specific density of the phytoplankton cells as approximately 1 $g.cm^{-3}$. Population size structure (GALD – "Greatest Axial Linear Dimension") was defined in three size classes: I: 2-20 µm; II: 20-50 µm; III: > 50 µm. Species richness was expressed as the number of taxa present in each sample. Functional groups were defined for species that contributed at least 5% of the mean phytoplankton biomass in each period (Reynolds et al., 2002, Reynolds, 2006).

## 3. Results

*3.1. Climate data*

The air temperature did not differ significantly between the cool-dry (ranging from 30.4 to 17.8 °C) and warm-rainy (ranging from 29.7 and 20.6 °C) periods. There was moderate rain the day before the sampling in the warm-rainy period. In both sampling periods, the winds were gentle or absent.

*3.2. Limnological data*

Lake Monte Alegre was stratified in both sampling periods (Figure 2). However, during the cool-dry season the thermocline was poorly structured. Temperatures ranged from 20.0 to 23.2 °C. With cooling at night, by 03:00 AM the mixing layer had deepened to 2.5 m (Figure 2). In the warm-rainy season, stratification was strong, with a marked thermocline between 1.5 and 2.5 m during the entire period, with no modification during night cooling. The water-column temperature ranged from 29.4 to 25.4 °C. In both periods, dissolved oxygen contents at the surface were high, and sharply reduced towards the bottom, mainly during the warm-rainy season (Figure 2). In the cool-dry season, the dissolved oxygen profile was clinograde without a clear oxycline, with concentrations ranging from 1 mg.L$^{-1}$ (bottom) to 11 mg.L$^{-1}$ (surface). During the warm-rainy season, dissolved oxygen ranged from 1 mg.L$^{-1}$ (bottom) to 14 mg.L$^{-1}$ (surface), with a lasting oxycline between 2 and 3 m depth.

Light intensity decreased to about 50% of the surface level in the first meter and extinction occurred at about 4 m in both study periods; thus, the entire water column was illuminated.

### *3.3. Phytoplankton community*

During the study, the phytoplankton assemblages included 110 taxa belonging to 8 taxonomic classes (11 Cyanobacteria, 5 Dinophyceae, 6 Cryptophyceae, 4 Chrysophyceae, 7 Bacillariophyceae, 11 Euglenophyceae, 49 Chlorophyceae and 17 Zygnematophyceae). Fewer species were found during the cool-dry season (76 taxa) than the warm-rainy period (104 taxa). Lower species richness (27 to 45 taxa per sample) was also found in the cool-dry period compared to the warm-rainy one (38 to 86 taxa per sample).

During the cool season, higher phytoplankton biomass was observed at daytime, between 2.0 and 4.0 m, and at night down to 1.0 m and from 2.0 m on, oscillating from 2.2 mg.L$^{-1}$ (surface) to 5.4 mg.L$^{-1}$ (bottom; Figure 3). At 9:00 PM, phytoplankton biomass was greater at the surface and at the bottom. In the warm season, higher biomass was always found between 1.0 m and 3.0 m, and varied from 4 mg.L$^{-1}$ to 22 mg.L$^{-1}$ (Figure 3).

Phytoplankton biomass was dominated by size classes I (< 20 µm) and II (20-50 µm; Figure 4) during the cool season at all sampling times and depths. In the warm season, the distribution fluctuated, with dominance of class II during the night and class I throughout the day (Figure 4).

Species that contributed at least 5% to the mean phytoplankton biomass in the cool period were represented by five functional groups typical of shallow and/or eutrophic environments: $L_m$, $W_1$, $W_2$, Y, J (Table 1; Figure 5). Greater biomass of $L_m$ group (*Peridinium umbonatum Stein*, *P. volzii Lemm*) was widely distributed throughout the water column, with larger biomass concentrations in the morning in the deeper layers, and a more homogeneous distribution at the beginning of the afternoon. Euglenophyceae of $W_1$ (*Lepocinclis fusiformis* (H. J. Cart.) Lemm. *emend.* Conr., *L. ovum* (Ehrenb.) Lemm.) appeared mainly during the day, decreasing throughout the water column beginning at 9:00 PM. Group $W_2$ (*Trachelomonas armata* (Ehrenb.) Stein f. *inevoluta* Defl., *Trachelomonas raciborskii* Wolosz.) showed a higher contribution at night, when the biomass increased from 1.5 m towards the bottom layers. Cryptophyta, belonging to group Y (*Cryptomonas erosa* Ehrenb., *C. marssonii* Skuja, *C. platyuris* Skuja, *C. brasiliensis* Castro, D.Bic. and E.Bic.) were concentrated in deeper layers in daytime; at night there was a large decrease, especially in the layers near the metalimnion. Group J (*Coelastrum sphaericum* Näg) also contributed more during the morning, mainly between 1.0 and 3.0 m, with biomass reduction beginning at 9:00 PM (Figure 5).

During the warm period, in addition to the functional groups present in the cool period, $S_N$ and $X_1$ also contributed more than 5% of the total phytoplankton biomass (Table 2; Figure 6). Groups $L_m$, $W_1$ and Y showed the same type of behaviour as in the cool period. Group $W_2$

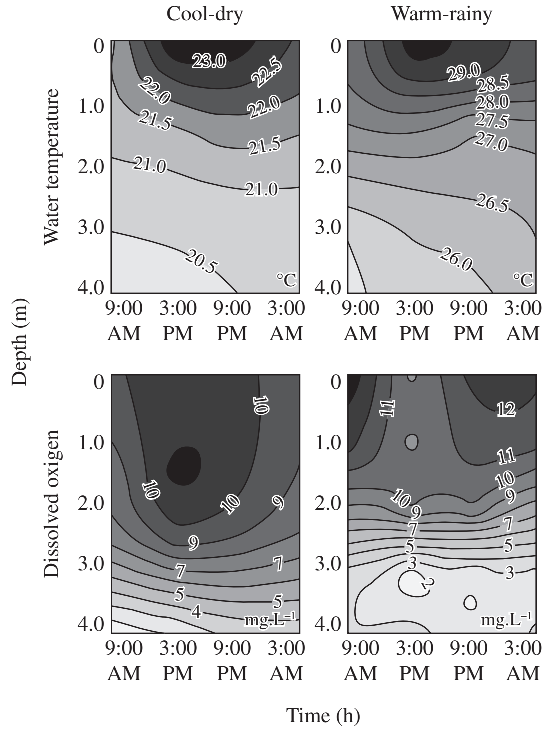


**Figure 2.** Depth-time diagrams of water temperature (°C) and dissolved oxygen (mg.L$^{-1}$) during the cool-dry and warm-rainy seasons.

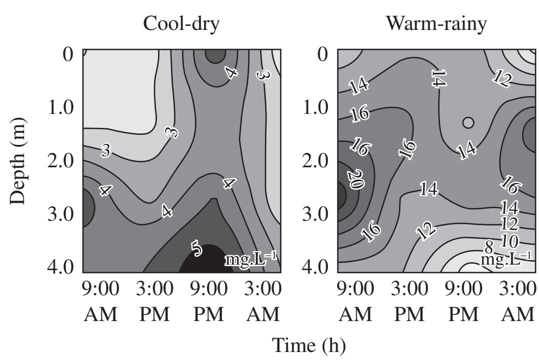


**Figure 3.** Depth-time diagrams of phytoplankton biomass (mg.L$^{-1}$) during the cool-dry and warm-rainy seasons.

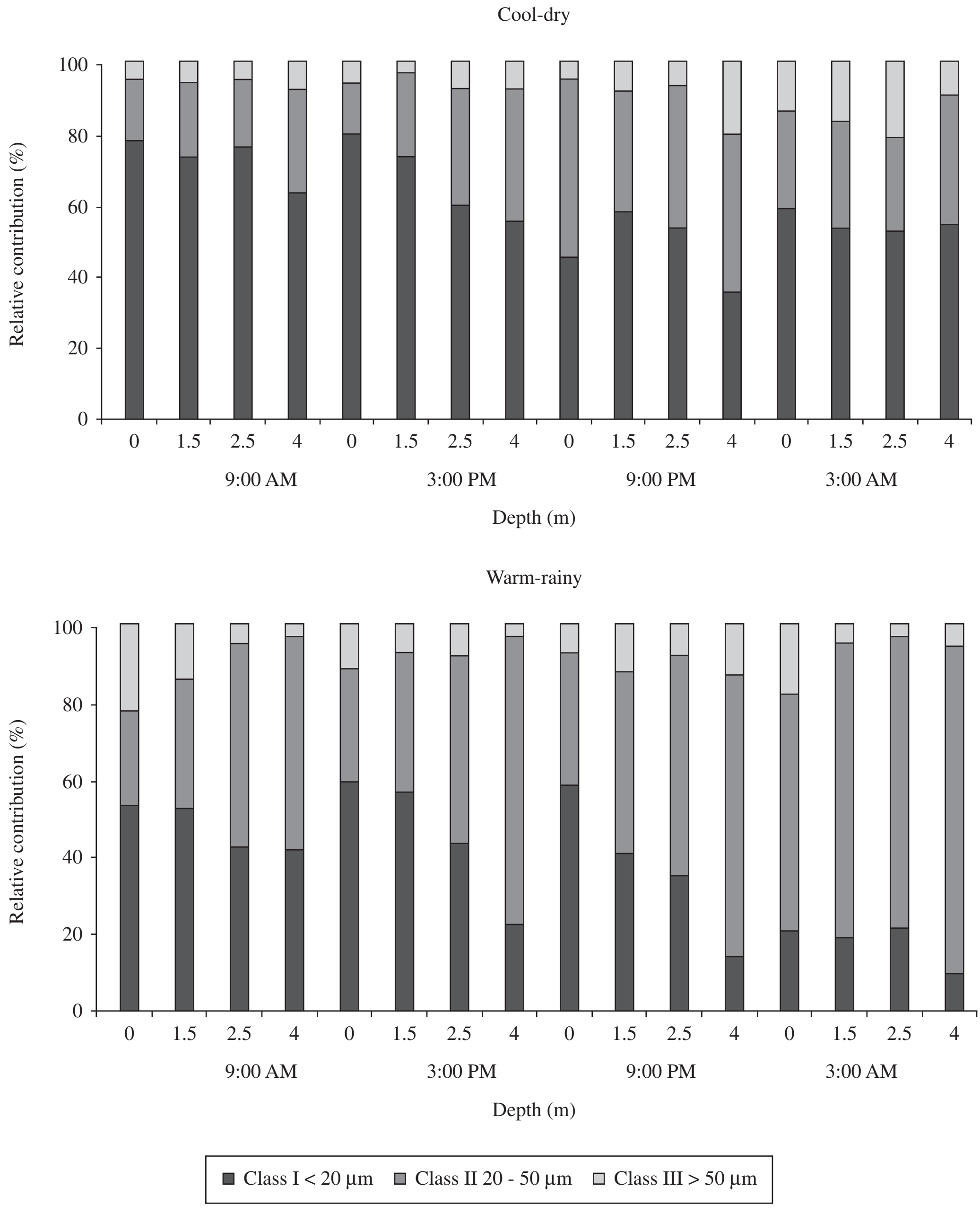


**Figure 4.** Relative contribution to phytoplankton biomass (%) of size classes in the cool-dry and warm-rainy seasons.

was concentrated in the morning, especially in deeper layers, with an upward movement to the surface layers throughout the day, moving to the bottom from 9:00 PM to 3:00 AM. Functional groups J and $X_1$ (*Actinotaenium perminutum* (G. S. West) Teil) were important mainly during the day in the surface layers, decreasing during the night. Functional group $S_N$ (*Cylindrospermopsis raciborskii* (Wol.) Seen. and Sub. Raju) was highly concentrated during daytime, and then became more homogeneously distributed in the water column (Figure 6).

*3.4. Zooplankton*

Higher zooplankton densities occurred during the cool season, with the most important herbivores reaching 75 ind.$L^{-1}$, mainly after 3:00 PM in the entire lake. During the night, herbivores became more concentrated in the upper layers. *Daphnia ambigua* and *Ceriodaphnia richardi* Sars were concentrated most densely (Figure 7). During the warm season, herbivores reached 12 ind.$L^{-1}$, with important contributions of *Bosmina tubicen* Brehm and *Daphnia ambigua*. Higher

**Table 1.** Characteristics of the main functional groups in Lake Monte Alegre in the cool-dry season (modified from Reynolds et al., 2002).

| Codon | Habitat | Monte Alegre representatives | Tolerance | Sensitivities |
|---|---|---|---|---|
| Y | small enriched lakes | *Cryptomonas erosa, C. marssonii, C. platyuris*, *C. brasiliensis* | low light | phagotrophs |
| $L_m$ | summer epilimnia in eutrophic lakes | *Peridinium umbonatum, P. volzii*, Dinoflagellate 1, Dinoflagellate 2 | very low C | mixing, poor stratification light |
| J | shallow, enriched lakes ponds and rivers | *Coelastrum sphaericum* | - | settling into low light |
| $W_1$ | small organic ponds | *Lepocinclis fusiformis, L. ovum, Euglena* sp. | high BOD | grazing |
| $W_2$ | shallow mesotrophic lakes | *Trachelomonas armata* f. *inevoluta*, *Trachelomonas raciborskii* | unknown | unknown |

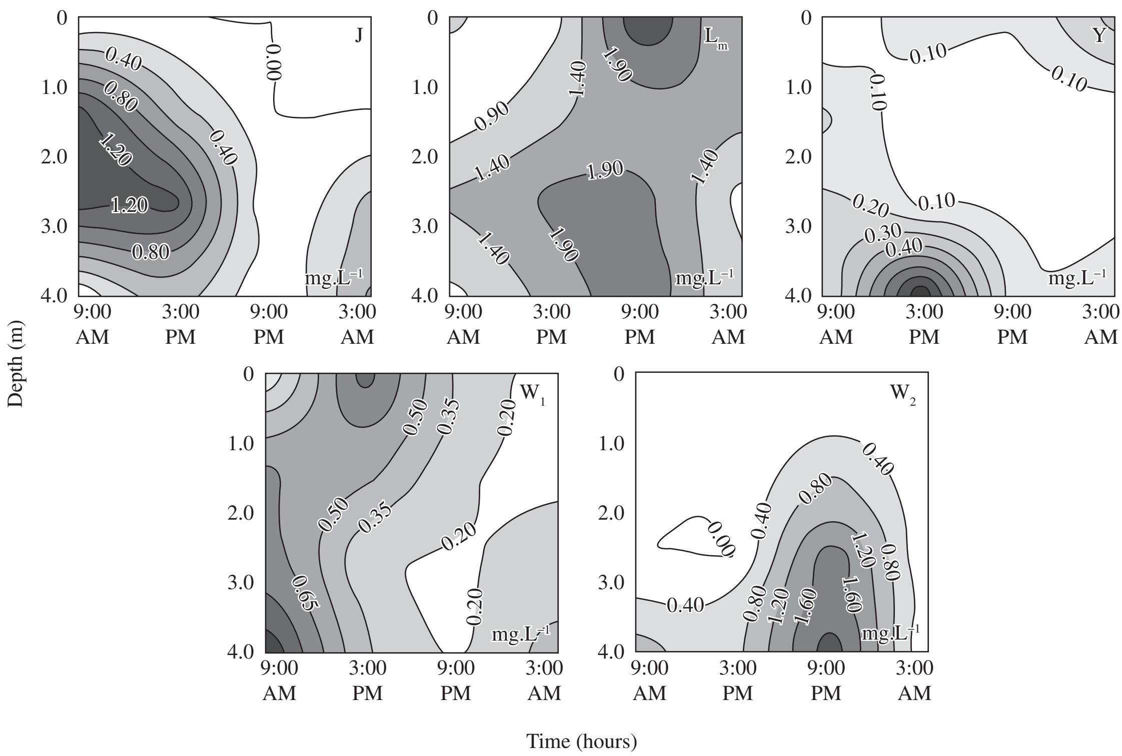


**Figure 5.** Depth-time diagrams of the biomasses (mg.$L^{-1}$) of the J, $L_m$, Y, $W_1$ and $W_2$ functional groups during the cool-dry season.

concentrations occurred during the second half of the illuminated period, also with a trend towards the upper layers at night (Figure 7).

## 4. Discussion

Physical and chemical properties of water directly influence aquatic organisms, and may affect their vertical distribution. Phytoplankton biomass in Lake Monte Alegre was related to the thermal structure in both seasons, especially during the warm-rainy period, when higher phytoplankton biomass coincided with the level of the metalimnion. Melo et al. (2004) suggested that in periods of thermal stratification, most phytoplankton groups concentrate at the metalimnion. During the cool-dry period, the phytoplankton did not concentrate at a particular layer, because of the lack of a defined thermocline and deepening of the mixing layer throughout the day.

Several groups of flagellates were important to the phytoplankton biomass in both study periods ($L_m$, $W_1$, $W_2$, Y). Flagellates have selective advantages over non-motile species, especially in stratified periods, and seem to have overwhelmed the water column stratification. The flagellate of group $W_2$ (*Trachelomonas armata* f. *inevoluta*, *Trachelomonas raciborskii*), adapted to

**Table 2.** Characteristics of the main functional groups in Lake Monte Alegre in the warm-rainy season (modified from Reynolds et al., 2002).

| Codon | Habitat | Monte Alegre representatives | Tolerance | Sensitivities |
|---|---|---|---|---|
| $S_n$ | Warm mixed layers | *Cylindrospermopsis raciborskii* | light-, nitrogen-deficient | - |
| $X_1$ | Shallow mixed layers in enriched conditions | *Actinotaenium perminutum* | stratification | nutient deficiency filter feeding |
| Y | Small enriched lakes | *Cryptomonas curvata, C. erosa, C. platyuris*, *C. brasiliensis* | low light | phagotrophs |
| J | Shallow, enriched lakes ponds and rivers | *Coelastrum sphaericum* | - | settling into low light |
| $L_m$ | Summer epilimnia in eutrophic lakes | *Peridinium umbonatum, P. volzii*, Dinoflagellate 1, Dinoflagellate 2 | very low Carbon | mixing, poor stratification, light |
| $W_1$ | Small organic ponds | *Lepocinclis fusiformis*, *L. ovum* | high BOD | grazing |
| $W_2$ | Shallow mesotrophic lakes | *Trachelomonas armata* f. *inevoluta*, *Trachelomonas raciborskii* | unknown | unknown |

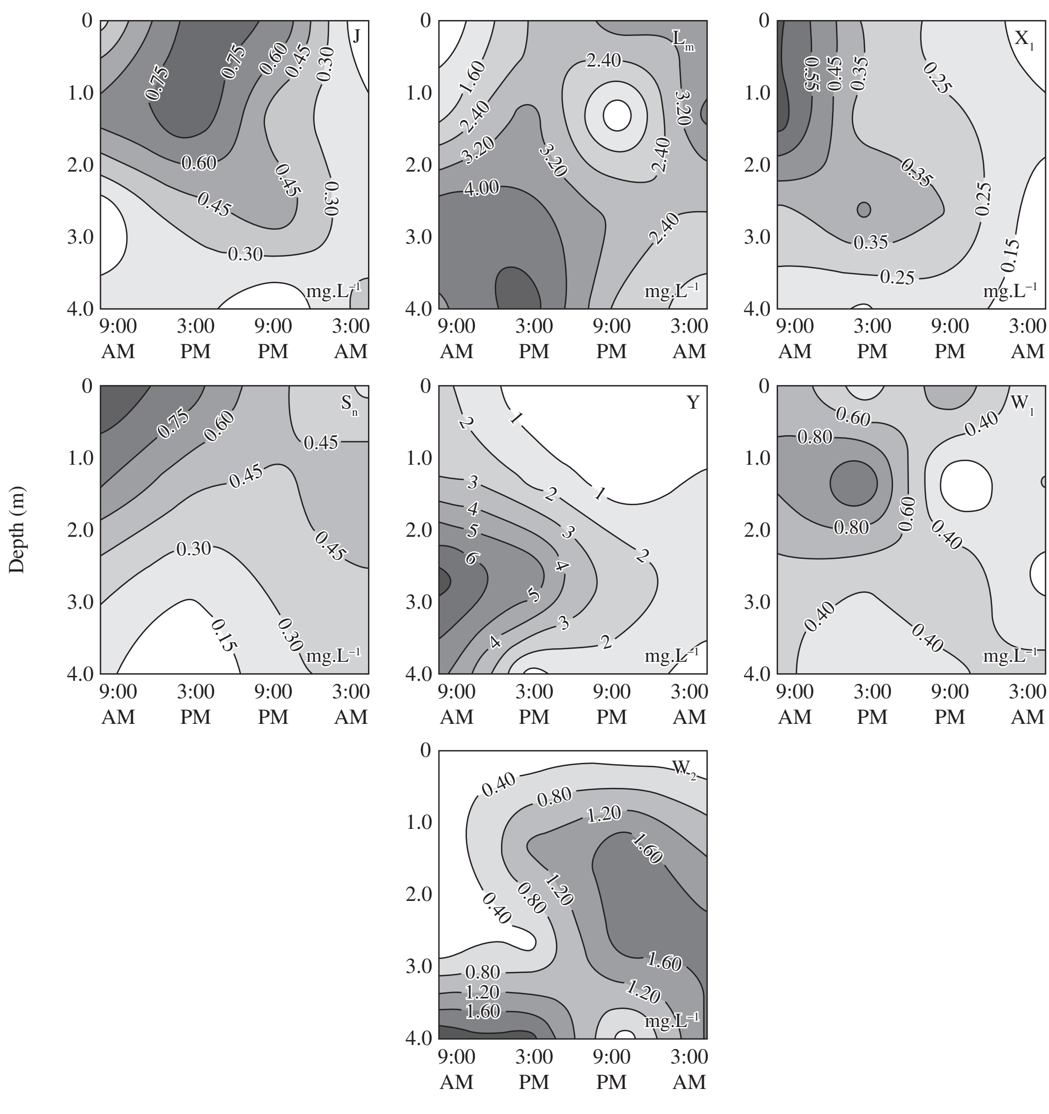


**Figure 6.** Depth-time diagrams of the biomasses (mg.L$^{-1}$) of the J, $L_m$, $X_1$, $S_n$, Y, $W_1$ and $W_2$ functional groups during the warm-rainy season.

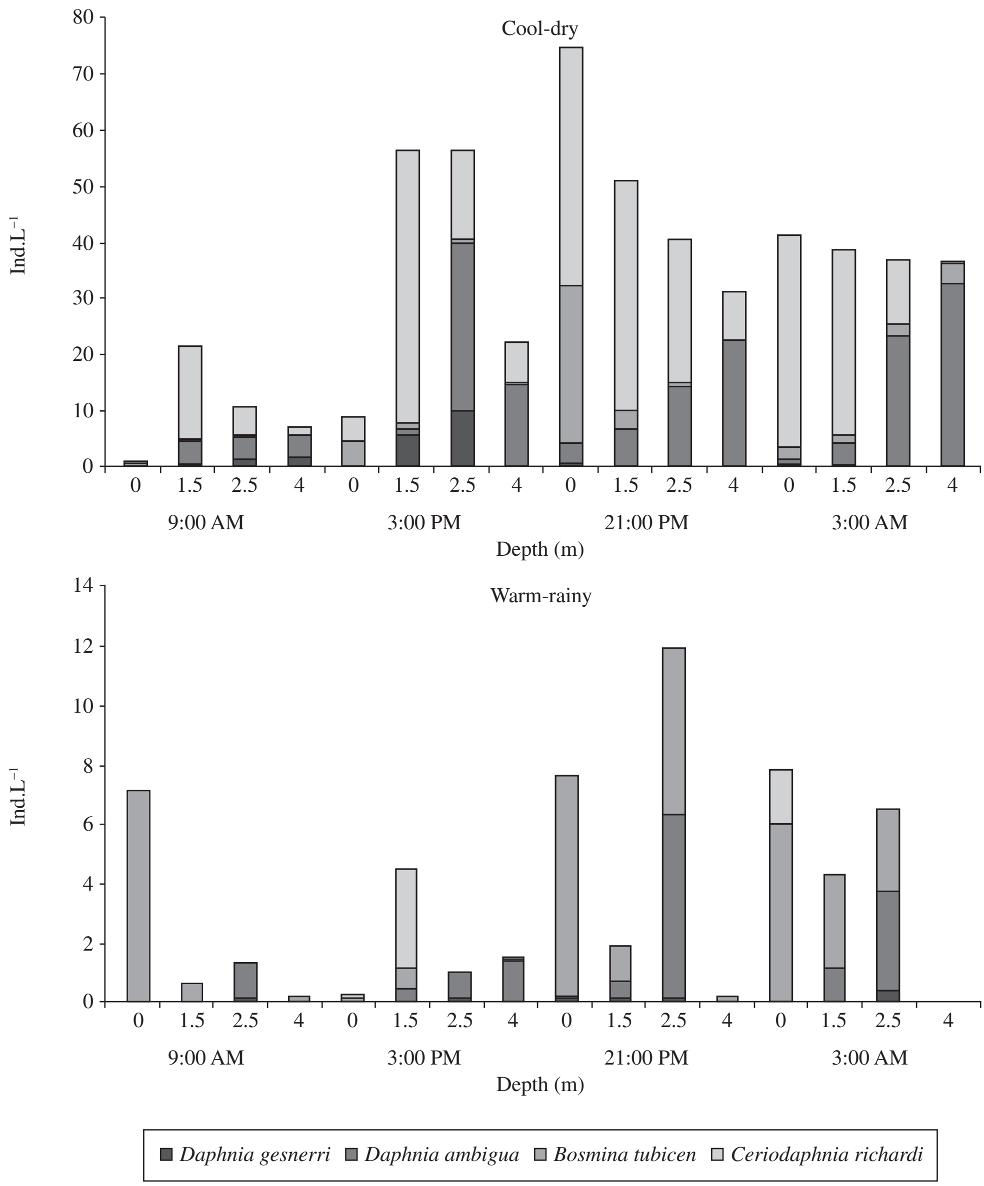


**Figure 7.** Relative contributions to density (ind.$L^{-1}$) of the main herbivores (cladocerans) in Lake Monte Alegre during the cool-dry and warm-rainy seasons.

mixotrophic conditions, seem to have been favored by the hipoxic hypolimnion.

Functional group $L_m$, able to live in epilimnia of eutrophic lakes (Reynolds et al., 2002), had great importance in both study periods. Members of this functional group can rapidly migrate vertically throughout the water column, reaching great depths, and thus can exploit light and nutrients and avoid grazing and sedimentation (Liebermann et al., 1994; Graham and Wilcox, 2000).

Chaoborid larvae can consume algae, mainly phytoflagellates (Elser et al., 1987; Hare and Carter, 1987; Shei et al., 1988; Moore, 1988; Moore et al., 1994). Studies on chaoborid larvae in Lake Monte Alegre have shown that the dinoflagellate *Peridinium* is an important component of the diet of these larvae, mainly for instars I and II (Arcifa, 2000). In a vertical migration study (Arcifa, 1997), the early instars were present in the entire water column, and instars II, III and IV performed nocturnal vertical migration. It is possible to hypothesize that chaoborid larvae influenced the diel vertical distribution of the $L_m$ group, which seemed to concentrate at night until early morning in the deeper layers and then move to better-lighted layers during the day.

Functional groups, $X_1$ and Y are efficiently consumed by herbivores, which may control phytoplankton biomass and induce changes in its composition (Reynolds et al., 2002). Reductions in biomass of these groups were observed at night. Cryptophytes are extremely edible for zooplankton and contain high concentrations of PUFA (Polyunsaturated fatty acids; Ahlgren et al., 1992), and are an important food item of these herbivores (Gullati and DeMott, 1997; Ferrão-Filho et al., 2003a). An experimental study has suggested that high cryptophycean biomass in the summer may have contributed to increased growth of cladocerans in Lake Monte Alegre (Ferrão-Filho et al., 2003b).

Group $X_1$ is composed of small green algae, and is more appropriate for zooplankton consumption. The influence of two seston fractions: < 20 µm (nanoplankton) and ≥ 20 µm (microplankton) on growth and reproduction of cladoceran species of different sizes was evaluated; nanoplankton was more suitable for most cladocerans, and microplankton for the largest species (Fileto et al., 2004). Higher densities of these efficient filter-feeders in the cool-dry period may explain the small contribution of $X_1$ in this period.

Group $S_N$ seemed to be favored by particular hydrological conditions in the lake during the warm-rainy period, such as high temperature and thermal stability of the water column (Branco and Senna, 1994; Tucci and Sant'Anna, 2003; Silva, 2004). Its distribution did not seem to be influenced by grazing, probably because of the ample availability of algae of appropriate sizes for herbivores.

Zooplankton, especially large cladocerans, maintain important control over phytoplankton in most lakes (Scheffer, 1998). During this study, the reductions of phytoplankton densities were observed to be related to zooplankton distribution, especially during the cool-dry season, when zooplankton densities were higher. Silva (2004), in an experimental study, observed that the most efficient filter-feeders in Lake Monte Alegre, such as *Daphnia* species, were capable of controlling phytoplankton biomass. Therefore, besides the reduction observed in some functional groups, the reduction of size Class I (<20 µm) was noted in both periods of this study, especially at nighttime, as it is an especially suitable food for the herbivores.

In conclusion, our results show that the thermal pattern of the water column was the main driving factor acting upon the vertical distribution of the phytoplankton community in both study periods. The thermal stratification that occurred in both study periods seemed to have favored a heterogeneous distribution of the phytoplankton biomass. Furthermore, the presence of more efficient herbivores in the lake, especially during the cool-dry period, determined the lower phytoplankton biomass as well as total biomass distribution patterns, phytoplankton functional groups and size classes.

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