

# Diel vertical migration of cladocerans in a tropical lake.

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## Abstract

The vertical migration of cladocerans was studied in shallow Lake Monte Alegre, in southeastern Brazil, in several years (1985/1986, 1999, 2001/2002). *Daphnia gessneri* and *Diaphanosoma birgei* showed a nocturnal pattern in all the periods, less pronounced in the second species, which was mainly distributed in the upper layers. *Bosmina tubicen* almost disappeared from the lake in 1999, changing from a nocturnal pattern in 1985-86 to a tendency to concentrate near surface in 2001-2002. The vertical distribution of *Bosmina* and *Diaphanosoma* and aggregates of *D. gessneri* resulted in lower spatial overlaps with potential invertebrate predators. Cladocerans' behavior might be strategies to cope with predation by larvae of the dipteran *Chaoborus brasiliensis* and the pelagic water mite *Krendowskia* sp.

**Key words:** cladocerans, vertical migration, predation by *Chaoborus* and water mite.

## Introduction

Diel vertical migration has been extensively studied, resulting in a large number of publications (reviews by Cushing, 1951; Bainbridge, 1961; Hutchinson, 1967; Longhurst, 1976; Kerfoot, 1985; Bayly, 1986; Haney, 1988; Ringelberg, 1993). Although doubts still remain on its ultimate causes, light is considered the main proximate cause, triggering and controlling the process (Buchanan and Haney, 1980; Ringelberg, 1980, 1991).

From the 70's onward, decrease of predation risk by visual and non-visual predators has assumed a higher importance as an ultimate cause (Zaret and Suffern, 1976; Wright *et al.*, 1980; Stich and Lampert, 1981; Ohman *et al.*, 1983; Lampert and Taylor, 1985; Gliwicz, 1986; Ohman, 1990). More recently, attention has been focused on diel horizontal migration and aggregate formation by zooplankton as adaptive mechanisms for decreasing predation risk (reviewed by Folt and Burns, 1999; Burks *et al.*, 2002).

Planktonic microcrustaceans, in Lake Monte Alegre, can be preyed on by invertebrates such as larvae of *Chaoborus brasiliensis* as mentioned by Arcifa (2000) and Castilho-Noll (2002) and the water mite *Krendowskia* sp. by Cassano *et al.* (2002), and by vertebrates such as adult *Tilapia rendalli* by Arcifa and Meschiatti (1996). Planktonic microcrustaceans are not a major dietary item for other adult fish or young fish in general (Arcifa and Meschiatti, 1993; Meschiatti and Arcifa, 2002).

Diel vertical migration of microcrustaceans has been studied in Lake Monte Alegre since 1985-1986, when larvae of the dipteran *Chaoborus* were the main invertebrate predator and water mites were virtually absent. More recently, in 1999, 2001-2002, new studies have been undertaken, which differ from the first period by the presence of a new predator, the water mite *Krendowskia* sp.

The aim of this paper is to compare the patterns of cladoceran vertical migration in the lake, in different periods, before and after the appearance of mites, predators of cladocerans

and *Chaoborus* larvae.

#### Study area

Lake Monte Alegre (21° 11'S, 47° 43'W) is a small (area = 7 ha), shallow (Z max. = 5 m, Mean z = 2.9 m), warm discontinuous polymictic reservoir (Arcifa *et al.*, 1990), located inside the campus of the University of São Paulo, in Ribeirão Preto, State of São Paulo, southeastern Brazil. It is considered naturally eutrophic (Arcifa, 1999), although cyanobacteria blooms are sporadic and not intense. The region is characterized by a tropical climate, with a marked dry-cool season (May-September) and a wet-warm season (October-April). Dominant and frequent cladocerans are *Daphnia gessneri* Herbst and *Daphnia ambigua* Scourfield. *Ceriodaphnia richardi* Sars, *C. cornuta* Sars, *Diaphanosoma birgei* Korinek, and *Moina micrura* Kurz occur only sporadically in the lake.

## Material and Methods

Samples were taken with a small electric pump, delivering 30 L.min<sup>-1</sup>, and the water was filtered through a 60 µm net, for catching zooplankton. In 1985-86 and 1999, samples were taken at each meter to near the bottom (5 m), and in 2001 and 2002 at surface, 1.5 m, 2.5 m and 4 m. Zooplankton samples were narcotized and preserved in 4% formaldehyde, according to Haney and Hall (1973).

Two 24 h-samplings were made in 1985/1986, in July 1985 and in February/March 1986, four in 1999, in February, March, April, and November, three in 2001/2002, in June and July 2001, and March 2002. At the same time, physical and chemical measurements were taken: temperature and dissolved oxygen with a thermometer coupled to a Ruttner bottle and Winkler's method, respectively, in 1985/86, and with a Yellow Spring Inc., model 95, in the other periods; light intensity with a photometer LI-COR Inc., model 250, in 1999 and 2001/2002. Except 1985/1986, in the other years, at noon and midnight, water samples were taken for chlorophyll-*a* analyses by Lorenzen's method (1967).

Cladocerans were counted in 1, 2.5 or 5-ml subsamples, taken with Stempel pipettes, attaining to at least 60 individuals; several subsamples were counted in order to maintain a coefficient of variation lower than 0.20, according to recommendations of McCauley (1984) and Prepas (1984). *Chaoborus* larvae, water mites and low density samples were fully counted.

The vertical distribution of cladocerans was represented by isopleth diagrams. Spatial overlap between cladocerans and *Chaoborus* instar IV and water mites was obtained by first transforming all density values in percentages, and then evaluating the percentage overlap in each depth. Graphic representation was made by summing the overlap percentages in the water column at each time of a 24 h-sampling.

## Results

### Light

Light intensities fell to 30-50% of surface values in the first meter (Fig. 1). Light extinction occurred usually at around 4 m. Clear days during the dry-cool season (April 1999, July 2001) led to high intensities at surface waters.

### Temperature and dissolved oxygen

The lake was stratified in summer, in all sampling periods. A clear thermocline, with a gradient of 1-1.5°C, occurred within *ca.* 2.0 m and 3.0-3.5 m, influencing dissolved oxygen (DO) distribution, which decreased to *ca.* 2.0 mg.L<sup>-1</sup> or was depleted close to the bottom.

Stratification was unstable in autumn (April 1999) and spring (November 1999) and DO



concentrations were relatively high near the bottom (4-6 mg.L<sup>-1</sup>).

In the study periods in winter, the water column was isothermal and oxygen evenly distributed in the water column, temperature ranging from *ca.* 18 to 20°C.

#### Chlorophyll-*a*

Figure 2 presents the chlorophyll distribution in the water column in four occasions, on day and night samplings, chosen as representative for 1999 and 2001-2002. Two patterns can be observed: in summer (February) and autumn (April) of 1999 and late summer (March) of 2002, there was a trend for higher concentrations in deeper layers at night, whereas during the day higher concentrations were found within 1-3 m; in the autumn (June) of 2001, chlorophyll was evenly distributed in the water column.

#### Vertical distribution of cladocerans

In 1986, *Bosmina tubicen* migrated in a nocturnal pattern, with the population distributing mostly within the upper 3.5 m (Fig. 3). In July 2001 and March 2002, however, a trend to concentrate near surface can be observed. The animals did not discriminate between day and night regarding surface preference, but aggregates were denser at night. Part of the population can spread toward deeper layers at night, as in June 2001 and March 2002.

In 1986 and 1999, *Diaphanosoma birgei* was mostly distributed within the first two meters with weak up- and downward movements (Fig. 4). Only in November 1999, higher densities were found below 2 m. The distribution was similar in summer (February, March) as well as in autumn and spring (April and November).

Nocturnal migration of *Daphnia gessneri* was the general pattern observed in five of six occasions (Fig. 5). In the summer of 1999 (February), most individuals were distributed within the first 3 m, on a diel cycle, whereas in the other seasons, individuals moved to deeper waters during the day. A peculiar behavior, observed in March 1999, was the formation of dense aggregates, reaching up to *ca.* 1400 ind.L<sup>-1</sup> by day, the animals spreading in the water column at night. Part of the population can descend to deeper waters in the middle of the night, as in April 1999 and June 2001.

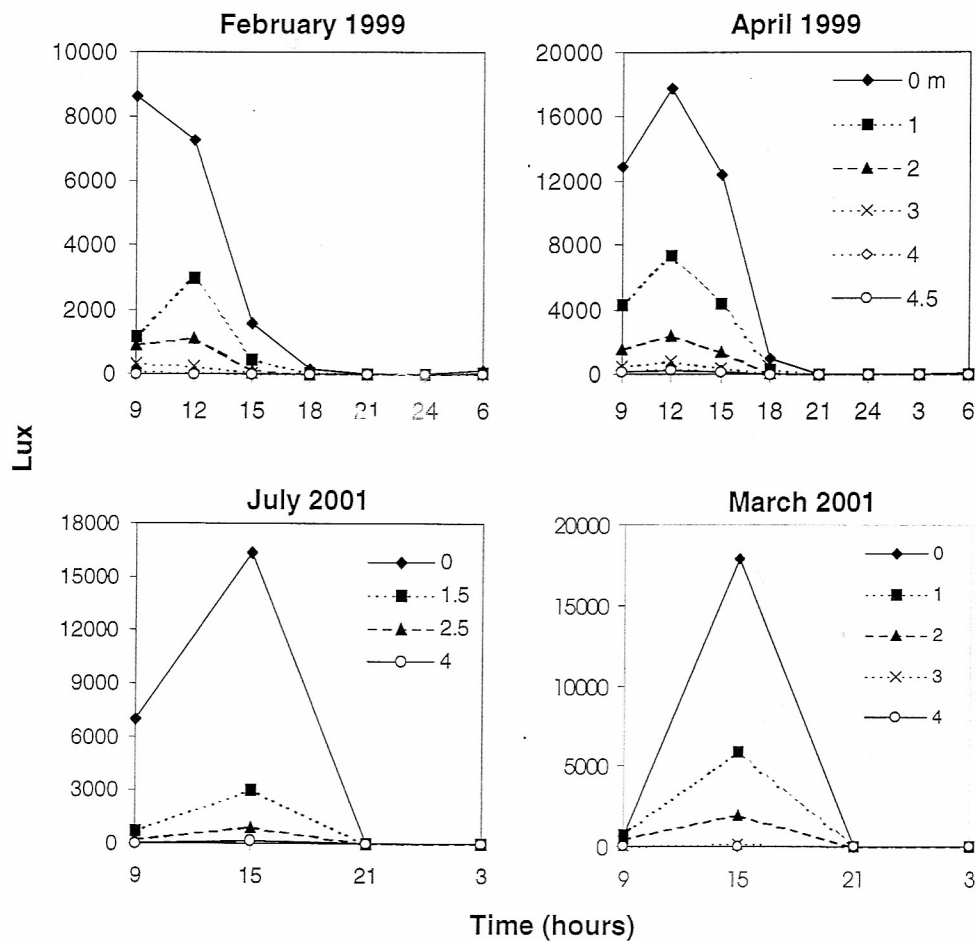
#### Spatial Overlap

In February-March 1986 and June 2001, when *Bosmina tubicen* descended to deeper layers, spatial overlap with potential predators was usually higher than when the population was mostly distributed in the first two meters of the water column, as in July 2001 and March 2002 (Fig. 6A, C).

The spatial overlap of *Daphnia gessneri* and potential predators in three different situations is shown in 1999 (Fig. 6B). When aggregates were formed followed by dispersion in the water column as in March, overlap was the lowest, on a diel cycle, compared to occasions when animals migrated nocturnally, as in February and April.

In the summer of 1986, when most *Chaoborus* instar IV moved to the sediment during the day, spatial overlap with *Bosmina* and *Daphnia* dropped, increasing at night when larvae ascended to the water column (Fig. 6A). In 1999, although being found in lower densities in the water at daytime, part of the *Chaoborus* larvae remained there, resulting in a relatively high overlap with potential prey (Fig. 6B, C).

As *Diaphanosoma birgei* was mostly distributed within the first two meters, a relatively low overlap with both invertebrate predators was found (Fig. 6B). When a higher number of individuals descended to deeper layers, as in November 1999 (Fig. 4), spatial overlap with *Chaoborus* instar



IV increased (Fig. 6B).

Figure 1: Light intensities in the water column, in 1999, 2001 and 2002.

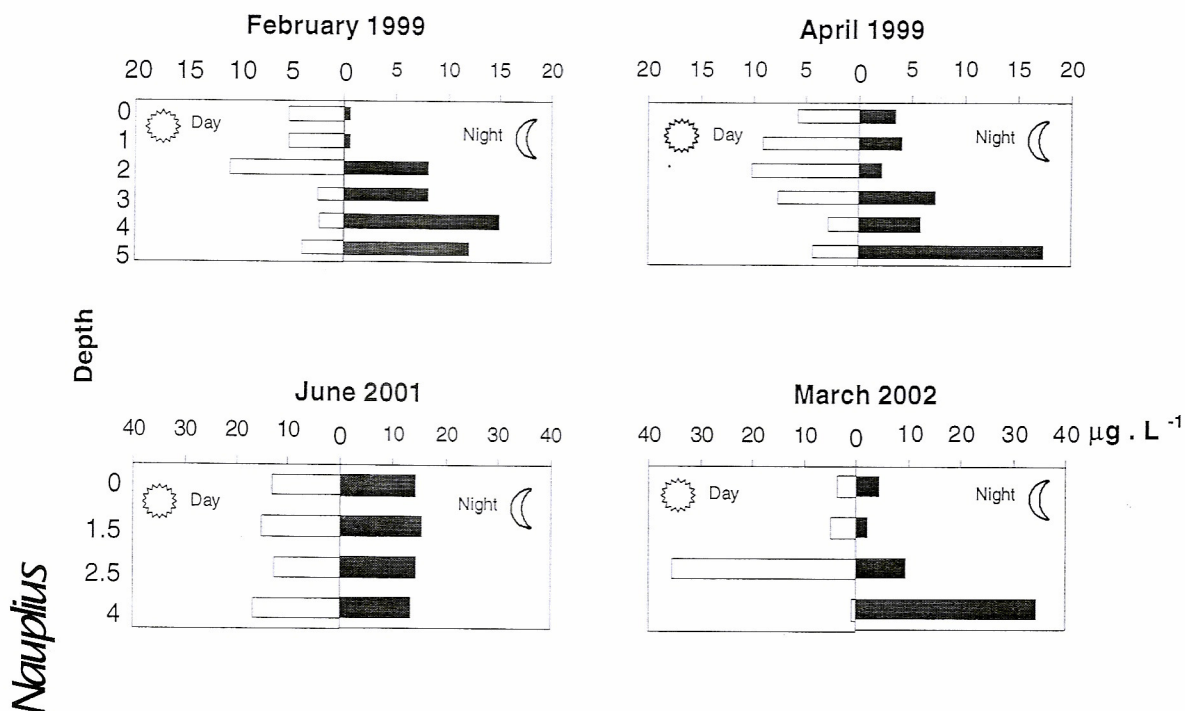


Figure 2: Chlorophyll-a concentrations, in the water column, at midday and midnight, in 1999, 2001, and 2002.



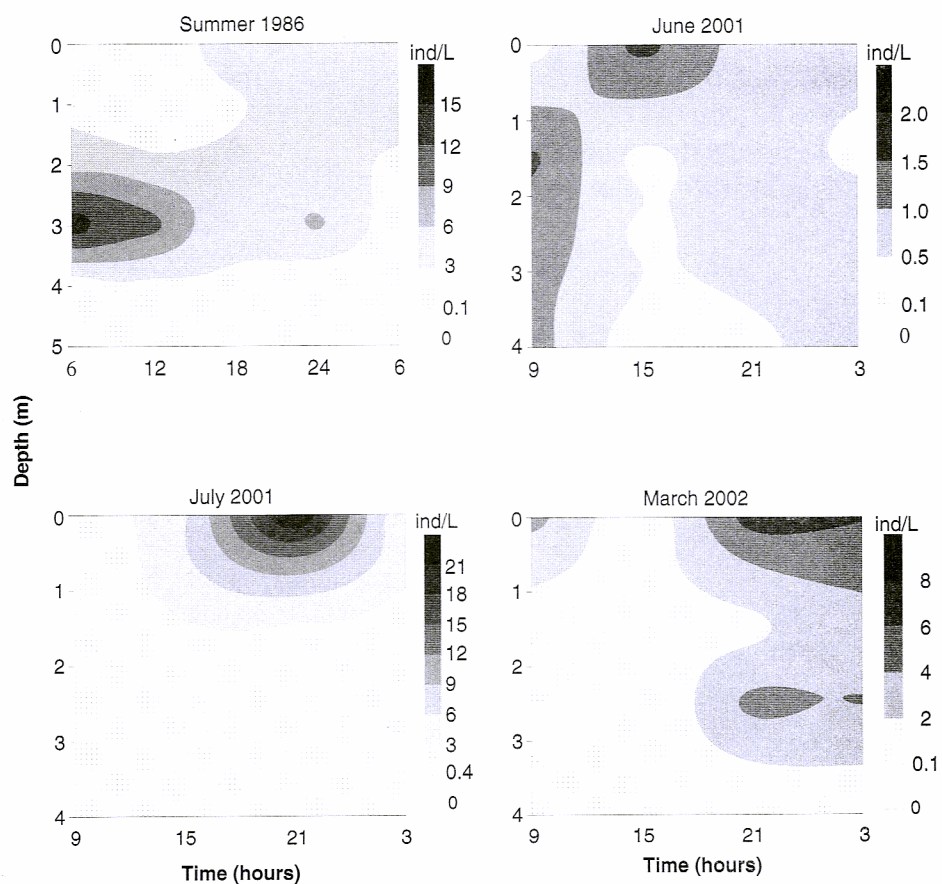


Figure 3: Vertical distribution of *Bosmina tubicen*, in day and night samplings, in 1986, 2001, and 2002.

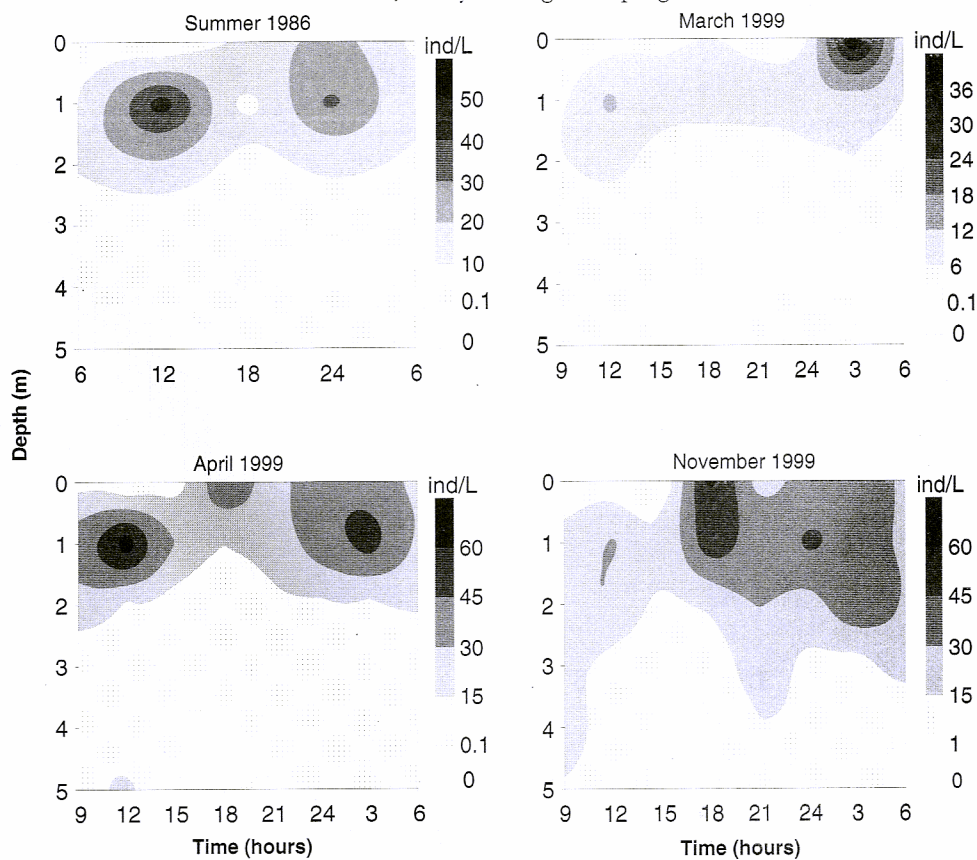


Figure 4: Vertical distribution of *Diaphanosoma birgei*, in 24-hour periods, in 1986 and 1999.

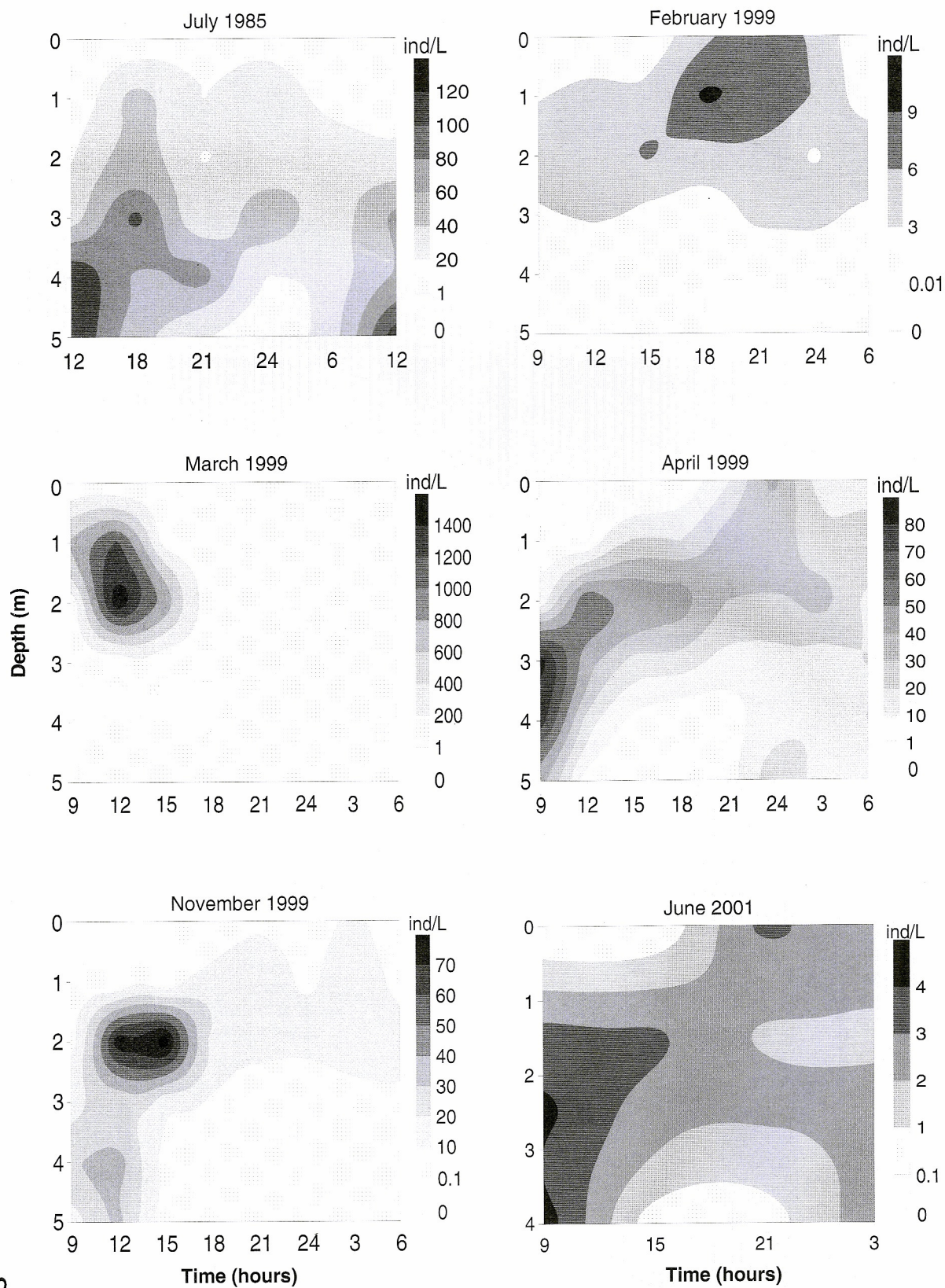


Figure 5: Vertical distribution of *Daphnia gessneri*, in 24-hour periods, in 1985, 1999, and 2001.

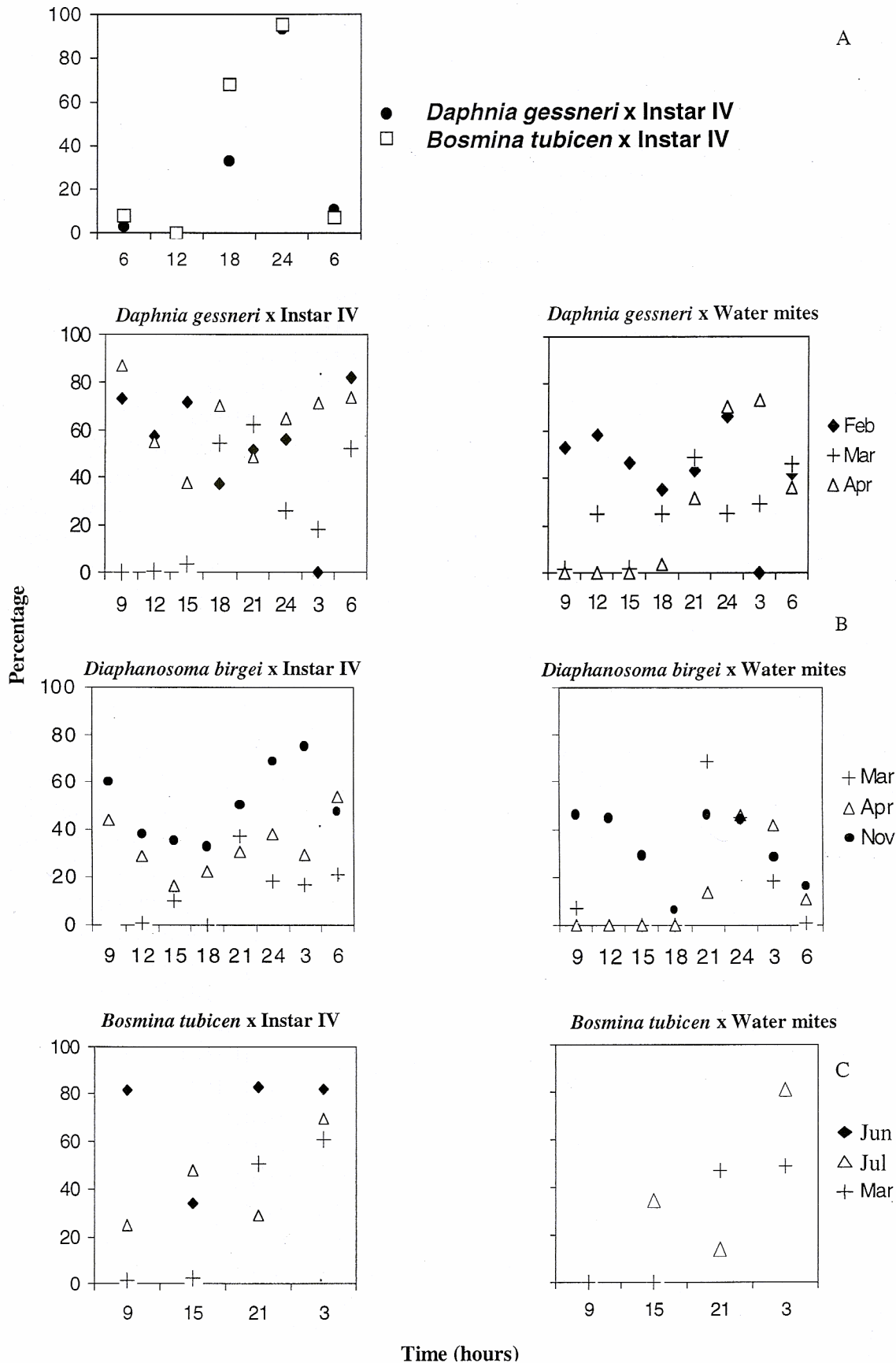


Figure 6: Spatial overlap between cladocerans and instar IV of *Chaoborus* and water mites; A. 1986, B. 1999, and C. 2001/2002.



## Discussion

Low oxygen concentrations or anoxia near the bottom of the lake, in the warm season, limited the vertical displacement of most cladocerans to the upper 3-3.5 m. Low oxygen also represented a barrier for the vertical movement of *Daphnia gessneri* in an Amazonian lake (Fisher *et al.*, 1983), and *Diaphanosoma birgei* and copepods in Itaipu Reservoir (Tomm *et al.*, 1992). Reverse migration by copepods, in Lake Monte Alegre, did not occur in the warm season, when oxygen dropped to concentrations lower than 1 mg.L<sup>-1</sup> near the bottom (Percicarrari *et al.*, in press).

The same pattern has been observed for *Diaphanosoma birgei* in 1986 and 1999, which migrated in a weak nocturnal pattern mainly restricted to the upper layers of Lake Monte Alegre. *D. birgei* was not identified as prey of *Chaoborus* larvae or of the water mite *Krendowskia* in Lake Monte Alegre (Arcifa, 2000; Cassano *et al.*, 2002; Castilho-Noll, 2002). *Diaphanosoma* can be a prey for water mites, ranked fourth in preference by *Piona constricta* (Riessen, 1982). The vertical distribution pattern of *D. birgei* in the lake might be one of the reasons for low predation, as overlap with invertebrate predators was usually below 50%. Despite a low predation pressure, *D. birgei* appears only sporadically, usually peaking when *Daphnia gessneri* is less abundant (Arcifa *et al.*, 1992, 1998).

*Bosmina tubicen* was frequent and abundant in the lake, in 1985-1986, reaching up to 90 ind.L<sup>-1</sup> (Arcifa *et al.*, 1992). It was the favorite cladoceran prey of larvae III and IV of *Chaoborus* at that time (Arcifa, 2000), when water mites were absent from the lake. In 1999, it disappeared from *Chaoborus*' diet (Castilho-Noll, 2002), declined to low densities (0.01 ind.L<sup>-1</sup>) in the lake (Fileto, 2001), what has been ascribed to predation by both *Chaoborus* and water mites (Cassano *et al.*, 2002). In 2001-2002, *B. tubicen* densities increased relatively to 1999 (Bunioto, 2003); not attaining, however, the high values recorded in the eighties.

In the summer of 1986, *Chaoborus* III and especially the instar IV showed a clear nocturnal migration, rarely being found in the water column, by day during 1985-86 (Arcifa, 1997). In 1999, the instars III and IV were found in the water column during the day and the migration pattern was not so clearly defined as in the previous period (Percicarrari, 2000). Although most of the larvae, especially the instar IV, are located in the sediment during the day (Cleto Filho, unpub.), the permanence of part of the larvae in the water has occurred after the increase of the water mite population. As *Chaoborus* can be preyed on by the water mite (Cassano *et al.*, 2002), the change of its migratory behavior might be related to the predator vertical distribution. Mites migrate nocturnally (Percicarrari, 2000), most individuals searching the sediment by day (Cleto Filho, unpub.).

Comparing the vertical distribution pattern of *Bosmina* in 1986 and 2001-2002 in the lake, a trend to concentrate near surface, day and night, was observed, with the formation of larger aggregates especially at night, in the latter period. This behavior led to a relatively lower spatial overlap with predators, on a diel cycle, than the nocturnal migration, in 1986, or the movement to deeper layers, in March 2002. In 2001-2002, studies on microcrustacean horizontal migration, showed that *Bosmina* moved onshore at night, where both *Chaoborus* and mites were less abundant (Bunioto, 2003; Percicarrari, unpub.). The tendency of concentrating near surface or migrating to shallower areas, in 2001-2002, seem to be part of a strategy of *Bosmina* population to cope with the predation pressure by both invertebrate predators. Other microcrustaceans, such as copepodites and adult copepods, have also apparently developed a strategy for facing an increase in *Chaoborus* predation. In 1999, after the virtual disappearance of *Chaoborus* favorite prey, *Bosmina tubicen*, copepods became the main microcrustacean prey (Percicarrari *et al.*, in press). In 1999, copepods performed reverse migration, whereas in 1985-1986, when copepods were a minor dietary item (Arcifa, 2000), twilight migration was the common pattern.

Diel reverse migration can be advantageous for reducing predation risk by invertebrates, which, on the other hand, migrate nocturnally. There are examples of copepods and cladocerans

migrating reversally when invertebrate predators migrated in a nocturnal pattern (Fedorenko, 1975; Ohman, 1990; Ohman *et al.*, 1983; Neill, 1990; Herwig and Schindler, 1996).

However, *Daphnia gessneri* continued to migrate in a nocturnal pattern in 1999 and 2001, as in 1985-1986, in Lake Monte Alegre, regardless of the presence of water mites, a new predator. Instar IV selects young *Daphnia* (Arcifa, 2000; Castilho-Noll, 2002) and a trend for juveniles to be more superficially located in the water column than adults was found in 1999, on a diel cycle, resulting in a little lower spatial overlap with *Chaoborus* as mentioned by Sousa (2003). The difference between young and adult behavior could be adaptive for decreasing *Chaoborus* predation, as well as the formation of aggregates could reduce invertebrate predation risk in general. But mites prey on adult *Daphnia* according to Cassano *et al.* (2002), and they overlap in the lake in relatively high values (Sousa, 2003). Castilho-Noll (2002), in experiments with mesocosms in the lake, found that there was an increase in the natality rate of *D. gessneri* in mesocosms with invertebrate predators, mainly *Chaoborus brasiliensis*, compared with those without predators. It seems that *Daphnia* population has adopted mechanisms, other than vertical migration, for minimizing the negative effects of invertebrate predation.

Copepods are more successful than cladocerans in facing predation pressure in the lake, due to their ability to change from nocturnal to reverse migration (Percarrari *et al.*, in press), the fact they are not the main microcrustacean prey of fish (Arcifa and Meschiatti, 1996), and are not preyed on by water mites (Cassano *et al.*, 2002).

In Lake Monte Alegre, microcrustaceans were a dietary item of *Tilapia rendalli*, usually a leaf chopper (Fryer and Iles, 1972). This species occurs in relatively low number in the lake, where only adult tilapias are pump-filter feeders, catching mostly phytoplankton, but also some zooplankton, especially those organisms with lower escape ability (Arcifa and Meschiatti, 1993; 1996). *Daphnia gessneri* and *Bosmina tubicen* were selected by tilapia, which avoid adult copepods (Arcifa and Meschiatti, 1996). Adults of tilapia were caught mainly offshore, distributing from 1 to 4 m of the water column (Arcifa and Meschiatti, 1993), although also occurring inshore during the reproductive period, in summer (Arcifa, unpub.). Predation would be restricted to daytime due to the diurnal habits of the fish (Munro, 1967; Uieda, 1984). In aquaria, *T. rendalli* uses a visually-oriented search for a pumping site, either just below the surface or near the bottom (Starling, 1993).

Aggregates of cladocerans, mostly during the day in the lake, or their concentration near surface do not seem to be advantageous relatively to predation by tilapia, seeming to be more adaptive regarding invertebrate predation. Prey aggregation horizontally or as a result of vertical migration decreases individual predation risk (Folt and Burns, 1999), and surface location of prey increases the distance between the organisms and invertebrate predators. Therefore, aggregates of *Daphnia gessneri*, preferential distribution of *Bosmina tubicen* and *Diaphanosoma birgei* in upper layers seem to be advantageous for avoiding invertebrate predation.

Herbivores could benefit from vertical migration, ascending at night to upper layers, where algae are most abundant. However, maximum food biomass in Lake Monte Alegre, evaluated as chlorophyll concentrations, and peaks of microcrustaceans in the water column were not always coincident. Therefore, it is doubtful any relationship between microcrustacean diel vertical migration and feeding optimization.

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