

DIEL VERTICAL MIGRATION OF COPEPODS IN A BRAZILIAN LAKE: A MECHANISM FOR DECREASING RISK OF *Chaoborus* PREDATION?

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(With 8 figures)

ABSTRACT

A comparison between two studies on diel vertical migration of two cyclopoid copepod species, in Lake Monte Alegre, undertaken in 1985/86 and 1999, revealed a change in their migratory behavior. In summer, during a period of marked stratification with low dissolved oxygen near the bottom, the organisms avoided the deepest layers, and migration was nocturnal or undetectable, in both periods. On other occasions, with partial or total circulation in the lake, a weak twilight migration of copepodites and adults in 1985 was replaced by the reverse in 1999. Differences were found among stages, with the weakest or undetectable migration being observed for nauplii. The migratory pattern change for copepodites and adults might be related with a recent predation pressure increase by *Chaoborus* larvae on copepods, after the virtual disappearance of their main cladoceran prey.

Key words: reverse migration, cyclopoid copepods, *Chaoborus* predation.

RESUMO

A migração vertical de copépodos em um lago brasileiro: um mecanismo para diminuir o risco de predação por *Chaoborus*?

A comparação entre dois estudos sobre migração vertical diária de duas espécies de copépodos ciclo-póides no Lago Monte Alegre, realizados entre 1985/86 e 1999, revelou mudança em seu comportamento migratório. No verão, durante período de marcada estratificação, com pouco oxigênio dissolvido próximo ao fundo, as camadas mais profundas foram evitadas pelos organismos e a migração foi noturna ou não ocorreu. Em outras ocasiões, com circulação parcial ou total do lago, uma fraca migração crepuscular de copepoditos e adultos, em 1985, foi substituída por reversa em 1999. Foram encontradas diferenças entre os estágios, sendo que os náuplios não migraram ou migraram fracamente. A mudança do padrão migratório de copepoditos e adultos poderia estar relacionada a recente aumento da predação de copépodos por larvas de *Chaoborus*, depois do desaparecimento virtual do cladóceros, sua presa principal.

Palavras-chave: migração reversa, copépodo ciclo-póide, predação por *Chaoborus*.

INTRODUCTION

Despite extensive research on diel vertical migration (reviews by Cushing, 1951; Bainbridge,

1961; Hutchinson, 1967; Longhurst, 1976; Kerfoot, 1985; Bayly, 1986; Haney, 1988; Ringelberg, 1993), questions still remain about its ultimate causes. If light is considered the most important factor for

triggering and controlling the process (Buchanan & Haney, 1980; Ringelberg, 1980, 1991), there is no agreement concerning the adaptive value.

Decrease of predation risk by visual and non-visual predators as a result of prey vertical migration, gained greater importance as an ultimate cause from the seventies on (Zaret & Suffern, 1976; Wright *et al.*, 1980; Stich & Lampert, 1981; Ohman *et al.*, 1983; Lampert & Taylor, 1985; Gliwicz, 1986; Ohman, 1990). Nocturnal migration has been reported as the common zooplankton behavior while reverse migration is regarded as an unusual pattern (Bayly, 1986). Reverse migration by smaller zooplanktonic organisms might lower predation by larger planktonic invertebrates which, on the other hand, migrate nocturnally to escape from visual vertebrate predators (Lampert, 1993).

In Lake Monte Alegre, known predators of planktonic microcrustaceans are *Chaoborus* larvae (Arcifa, 2000; Castilho-Noll, 2002), a water mite (Cassano *et al.*, 2002), and adult *Tilapia rendalli* (Arcifa & Meschiatti, 1996). Water mites prey on cladocerans but not on copepods, and tilapias are mainly phytoplanktivores, catching mostly cladocerans in the water current produced by their pumping filter-feeding. *Chaoborus* larvae II-IV are the main copepod predators.

Two studies done 13 years apart on diel vertical migration of microcrustaceans in Lake Monte Alegre allowed a comparison of patterns under different predation pressure degrees by *Chaoborus* larvae. The virtual disappearance of their favorite cladoceran prey (Arcifa, 2000) resulted in an increase of larvae predation on copepods (Castilho-Noll, 2002).

The purpose of this paper is to compare the diel vertical migration behavior in Lake Monte Alegre, in 1985/86 and 1999, of copepods subject to lower and higher predation pressure by *Chaoborus* larvae. The effect, in both periods, of low oxygen concentrations as a counteracting stimulus influencing vertical migration pattern is also discussed.

STUDY AREA

Lake Monte Alegre (21°11'S, 47°43'W) is a small, shallow, eutrophic reservoir (area 7 ha, $Z_{\max} = 5$ m). Located in Ribeirão Preto, São Paulo State, at a 500 m altitude, it resulted from damming the Laureano Creek, of the Pardo River Basin in 1942. As the outlet is superficial, the dam is not manipulated by man, and the retention time (ca. 45 days) is

relatively high for the lake dimensions it functions as a lake. It may stratify for relatively long periods in the warm season, resulting in low concentrations of, or depleted oxygen near the bottom. Surface temperatures range from 19 to 30°C, conductivity from 47 to 96 $\mu\text{S} \cdot \text{cm}^{-1}$, and pH from 5.5 to 8.0. The lake is located in a tropical climate region with a marked dry-cool season (May-September) and wet-warm season (October-April). General abiotic and biotic features of the lake can be found in Arcifa (1999).

MATERIAL AND METHODS

Samples were taken, from each meter of the water column, with a small electric pump delivering 30 L \cdot min⁻¹; the water was filtered in a 60 μm net. Zooplankton was narcotized and preserved in formaldehyde 4%, according to Haney & Hall (1973).

Two 24 h-samplings were made in 1985/1986, in July 1985 and in February/March 1986, and four in 1999, in February, March, April, and November. 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 YSI 95 in 1999; light intensity with a photometer LI 250 in 1999. At noon and midnight in 1999, water samples were taken at each meter, filtered through Sartorius glass fiber filters, and the chlorophyll-a was analyzed by Lorenzen's method (1967).

Juvenile and adult copepods were counted in 1, 2.5, or 5 ml subsamples, taken with Stempel pipettes, attaining at least a minimum of 60 individuals in each one; 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 and low density samples were fully counted.

For November 1999, the vertical distribution of copepods was represented by quartile curve diagrams (Pennak, 1943) and also by a isopleth diagram.

Spatial overlap between adult copepods and *Chaoborus* instar IV was obtained by first transforming all density values into percentages, and then evaluating the percentage overlap for each depth. Graphic representation was made by summing the overlap percentages in the water column, on each time a within 24 h-sampling.

RESULTS

Physical and chemical factors

Surface temperatures ranged from 27° to 30°C in the warm season, and 19° to 25°C in the cool season in both periods (1985/86 and 1999).

Also, in both periods lake stratification was established in summer, with a thermocline located between 2 and 3 to 3.5 m, having a gradient of ca. 1.5°C. In February 1986 and 1999 as a consequence of thermal stratification, dissolved oxygen (DO) was unevenly distributed in the water column (Figs. 1A, 2A). Below 4 m, DO dropped to near-zero in 1999, or was depleted in 1986. During the cool season in the winter of 1985 (July) and the autumn of 1999 (April), DO concentrations were relatively high in the water column, indicating a period of partial or total circulation (Figs. 1B, 2B). In March 1999, oxygen distribution was similar to that in February, but with higher values near the bottom; in November, it was like that in April.

Light was quickly attenuated in the water column in all sampling periods in 1999, as shown by light intensity profiles of February and April (Fig. 2C, D).

Chlorophyll-a distribution

In February and April 1999 (Fig. 3A, B), as well as in March and November, by day, chlorophyll concentrations were higher in the upper layers, and increased in deeper ones at night.

Vertical distribution of copepods in 1985/1986 and 1999

In both February/March 1986 and February 1999 (Figs. 4A, 5A), most juveniles and adults avoided the deepest layers, where oxygen concentrations were very low or depleted in summer.

In the summer of 1986, some of the adults of *Tropocyclops prasinus* ascended to upper layers after sunset, in a weak nocturnal migration (Fig. 4A). In the winter of 1985, nauplii, copepodites, and adults of *T. prasinus* showed a weak twilight vertical pattern (Fig. 4B).

In 1999, migration was undetectable for nauplii except in February when a nocturnal pattern was observed (Fig. 5). After a slight trend towards nocturnal or undetectable migration in February (Fig. 5A), copepodites and adults of both species reverse migrated in March and April (Fig. 5B, C). For November, the pattern for *T. prasinus* copepodites and adults is not clearly shown by quartile curves (Fig. 5D), although they seemed to remain in the same layer day and night, with only part of them ascending at sunset. The isopleth diagram was more effective in showing that most copepodites remained in deeper layers on a diel cycle, while most adults were distributed in upper layers at daytime, occupying the deepest one after sunset (Fig. 6). Therefore, in general, copepodites and adults showed a strong tendency for reverse migrating.

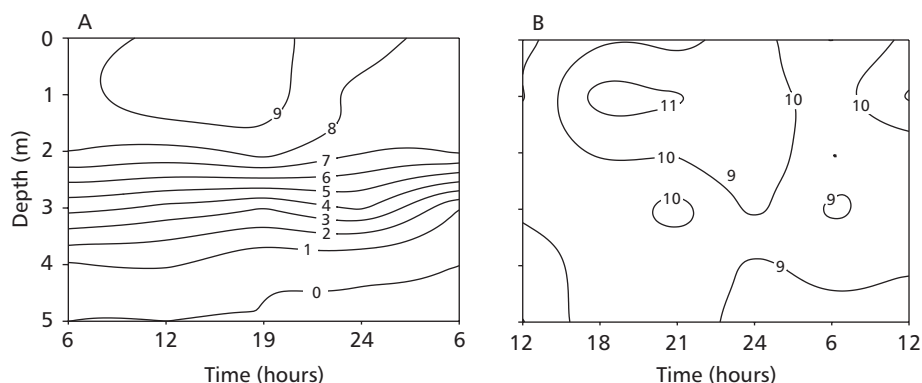


Fig. 1 — Dissolved oxygen isopleths, at intervals of 1 mg.L⁻¹, in 24 h periods, in the summer of 1986 (A) and the winter of 1985 (B).

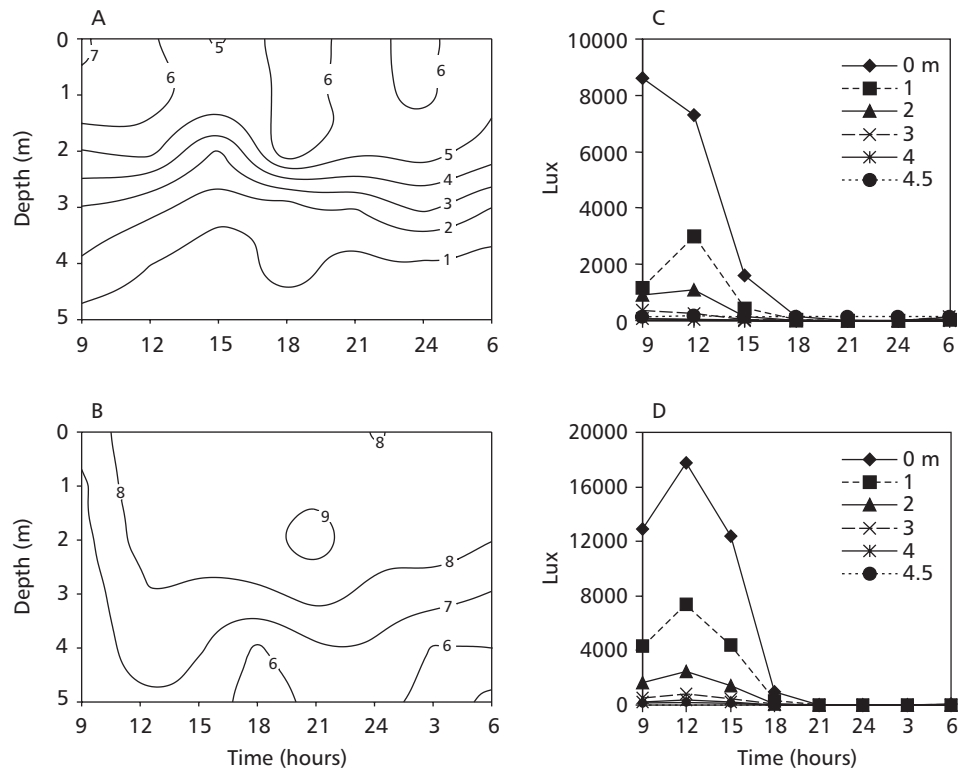


Fig. 2 — Dissolved oxygen isopleths, at intervals of 1 mg.L⁻¹, in 24 h periods, in February (A) and April (B), and light intensity in the water column in February (C) and April (D) of 1999.

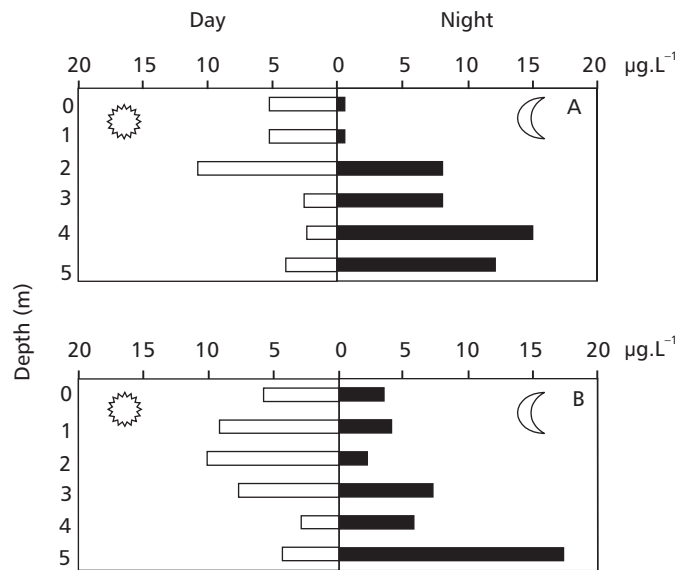


Fig. 3 — Vertical distribution of chlorophyll-*a*, in µg.L⁻¹, in February (A) and April (B) of 1999.

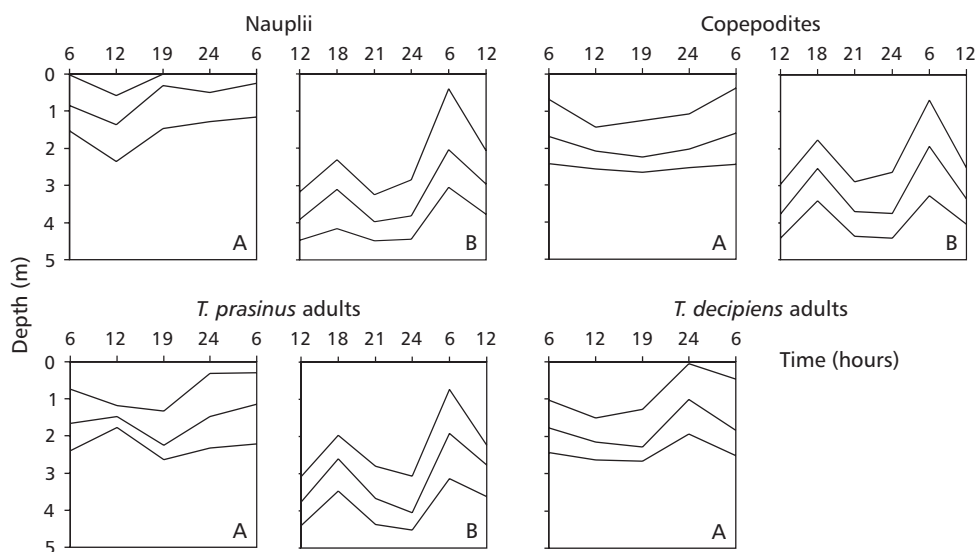


Fig. 4 — Vertical distribution of copepod stages represented by quartile curves, in February-March of 1986 (A) and July of 1985 (B).

In the summer of 1986, the clearly established nocturnal migration of *Chaoborus* instar IV led to a very low spatial overlap with *T. prasinus*, during the day (Fig. 7A). When adult copepods migrated in a weak nocturnal way, as in February 1999, the spatial overlap with *Chaoborus* instar IV was, generally, higher than when they (in the other months) on a diel cycle (Fig. 7B, C). This holds specially for *Tropocyclops prasinus* (Fig. 7B).

DISCUSSION

In Lake Monte Alegre in the summers of 1985/86 and 1999, copepods occupied mostly the upper layers, occurring in lower numbers in the deepest ones. This was the result of a counteracting stimulus (Ringelberg, 1980) represented by low dissolved oxygen concentrations beneath 3.5 m. Avoidance of poorly oxygenated layers by migratory crustaceans is common and has been reported for other Brazilian water bodies (Okano, 1980; Fisher *et al.*, 1983; Matsumura-Tundisi *et al.*, 1984).

Comparing copepod diel migration in both 1985/86 and 1999, there was a clear trend towards reverse migration in the latter, except during a stronger thermal and oxygen stratification period (February). This raises the question of what has changed in the lake from the first to the second period

and whether the new copepod migration pattern is related to any adaptive value.

In both periods but in different proportions, *Chaoborus* larvae always included copepods in their diets. Copepods contributed ca. 4% to the diet of instars III and IV in 1985/86, and 13% and 18%, respectively, in 1999 (Fig. 8). The cladoceran *Bosmina tubicen*, which was the favorite prey in the eighties (Arcifa, 2000), virtually disappeared from the lake in 1999 (Fileto, 2001). In 1985/86, lower densities of the cladoceran prey *B. tubicen* and *Daphnia gessneri*, at some times in the lake, ended in a higher consumption of alternative items (Arcifa, *op. cit.*). When this happened, the usual contribution of copepods to the diets of larvae III and IV (2.5 to 5%) increased to, 14% or 15%, respectively. Therefore, copepods occasionally faced a higher predation pressure in 1985/86, which was the rule in 1999.

Chaoborus larvae II-IV migrated nocturnally in 1985/86, the last instar disappearing from the water column at noon (Arcifa, 1997). Migratory behavior of the larvae was not so clearly defined in 1999 as it had been in the previous period (Peticarrari, 2000). Three kinds of behavior were observed in 1999: larvae were either distributed in the water column, or migrated nocturnally, or even showed a slight trend to reverse migration. Instars III and IV, however, were

found during the day in the sediment in higher densities which decreased at night (S. E. N. Cleto Filho, in preparation). So, at least a part of the oldest larvae descends to the sediment during the day, ascending to the water column at night. *Chaoborus* larvae can be preyed on by fish (Arcifa & Meschiatti, 1993) and the water mite *Krendowskia* sp. (Cassano *et al.*, 2002). In 1999, mites were present in the lake and usually migrated nocturnally (Peticarrari, 2000), but were virtually absent in 1985/86. Larvae migratory behavior in 1999 could be related to the presence of a new predator.

It is possible that the reverse diel migration adopted by both copepod species in Lake Monte Alegre in 1999 was a response to an increase in predation pressure by *Chaoborus* larvae after the virtual disappearance of their previous favorite prey, *Bosmina tubicen*. Although both prey and predator still in the water column, when prey encountered reverse migrated there was a lower spatial overlap at some hours compared to that existing when it migrated nocturnally (February). The lower spatial overlap with *Chaoborus*, on a diel cycle, is possibly advantageous for prey.

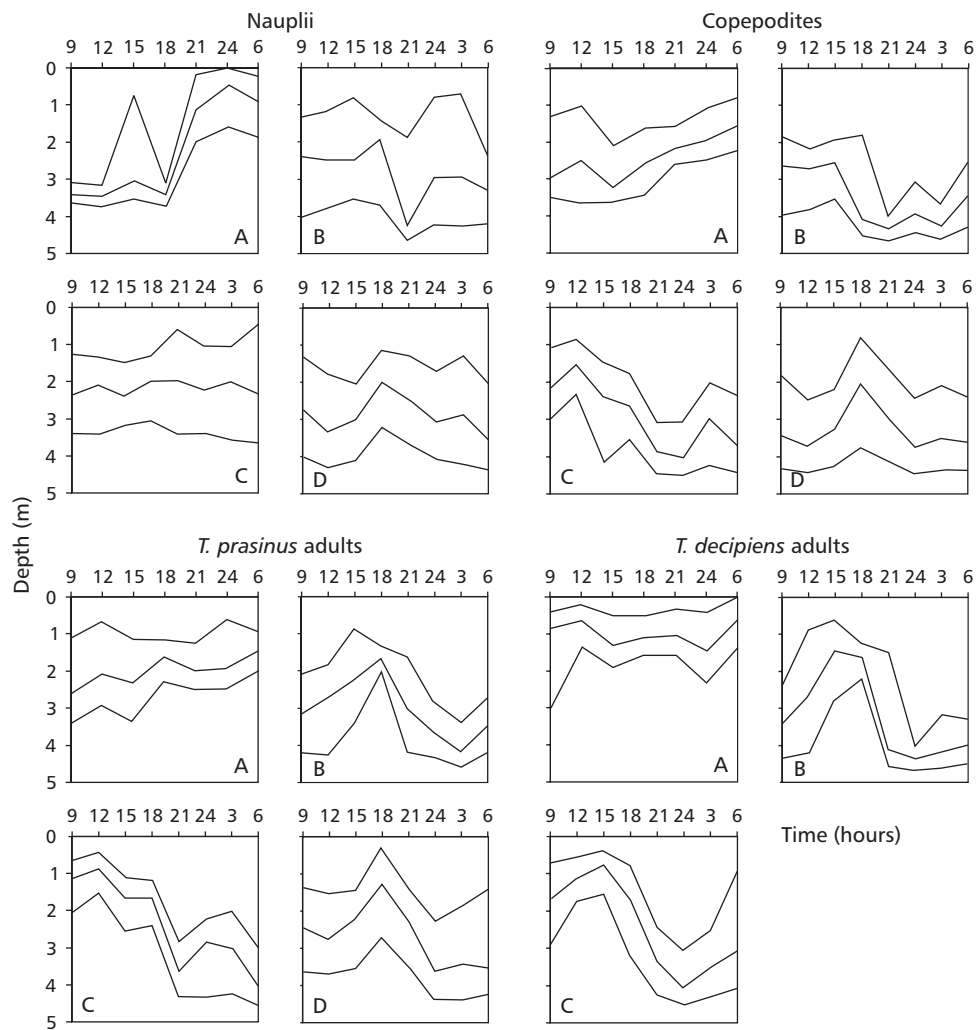


Fig. 5 — Vertical distribution of copepod stages represented by quartile curves, in February (A), March (B), April (C), and November (D) of 1999.

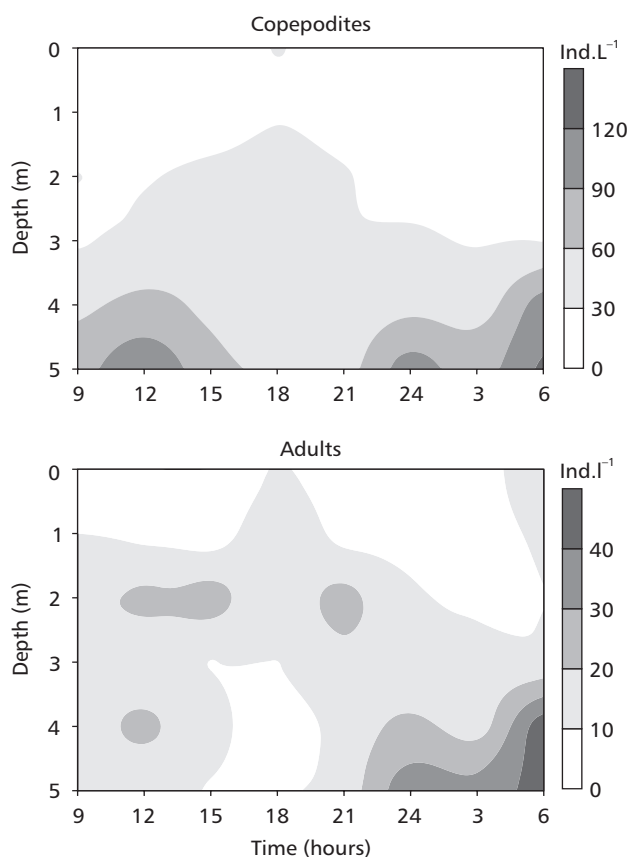


Fig. 6 — Vertical distribution of *Tropocyclops prasinus* represented by isopleths, in November of 1999.

In a mesocosm experiment run from 9/II to 8/III/1999 on *Chaoborus* predation on zooplankton, copepods were less affected by predators than were cladocerans (Castilho-Noll, 2002). Mortality rates of *Daphnia gessneri*, which migrated nocturnally in the lake (Peticarrari, 2000), were significantly higher than those of copepods in enclosures with predators. As the experimental period and the first two 24 h-samplings (February, March) mostly coincided, it is plausible to suppose that microcrustaceans behaved in the same way in the lake and in the enclosures with *Chaoborus*. Thus, while oxygen concentrations were lower near the bottom at the start of the experiment, copepodites and adults possibly migrated within the upper layers or remained there day and night (as in Fig. 5A). However, from the middle to the end of the experimental period, when oxygen was above 1 mg.L^{-1} , they possibly reverse migrated.

Reverse diel migration can be advantageous for zooplankton by reducing predation risk by

invertebrate predators, which migrate nocturnally to escape from visual vertebrate predators.

A marine copepod, *Pseudocalanus* sp., exhibited an unusual reverse diel migration, whereas their invertebrate predators migrated nocturnally (Ohman *et al.*, 1983). A small reduction of mortality rate of adult female copepods, due to decrease of spatial overlap with predators, was advantageous for migratory individuals. Later (Ohman, 1990), *Pseudocalanus newmani* was reported exhibiting three migratory behaviors: nocturnal where diurnal predation by planktivorous fish was most important; reverse, under higher predation pressure by invertebrates migrating in a nocturnal way; and non-migrating, when predation was low in surface waters. Ohman also found that copepodites I to III, which suffered a lower predation pressure by invertebrates, did not exhibit a detectable migration. In 1999, in Lake Monte Alegre, nauplii, which is a minor *Chaoborus* prey

(Fig. 8), also showed an undetectable pattern on three sampling occasions, and nocturnal migration on one (February).

Enclosure experiments with addition of *Chaoborus* larvae resulted in reverse migration of the copepod *Diaptomus kenai*, a quick response (< 4 h) of previously non-migrating individuals (Neill, 1990). Copepods used to reverse migrate when *Chaoborus* was present in the lake, stopped migrating after predator elimination by trout, introduced 28 months before the enclosure experiments. In addition, Fedorenko (1975a, b) found that *D. kenai* reverse migrated and states that a lower spatial overlap between *Chaoborus* and copepod may result in lower predation.

Daphnids shifted from nocturnal to reverse migration after the removal of surface-orienting insects from manipulated ponds (Herwig & Schindler, 1996). The authors considered the new behavior as a way

to reduce overlap with *Chaoborus* IV, which became the main predator and continued to migrate nocturnally.

Food distribution is another aspect to be taken into account in Lake Monte Alegre. Considering that chlorophyll-a concentrations increased towards the bottom at night in 1999, it would have been advantageous for herbivores to descend for feeding nocturnally. Cyclopoid nauplii are obligate herbivores (Pourriot & Lescher-Moutoué, 1983) while older stages are usually omnivores. Nauplii should reverse migrate to feed on algae where they are most abundant, whether in the upper layers during the day or the deeper ones at night. But, instead, copepodites and adults are the ones that reverse migrate.

Therefore, it is plausible to suppose that the reverse migration pattern of copepods, shown recently in Lake Monte Alegre, is more advantageous for decreasing *Chaoborus* predation pressure.

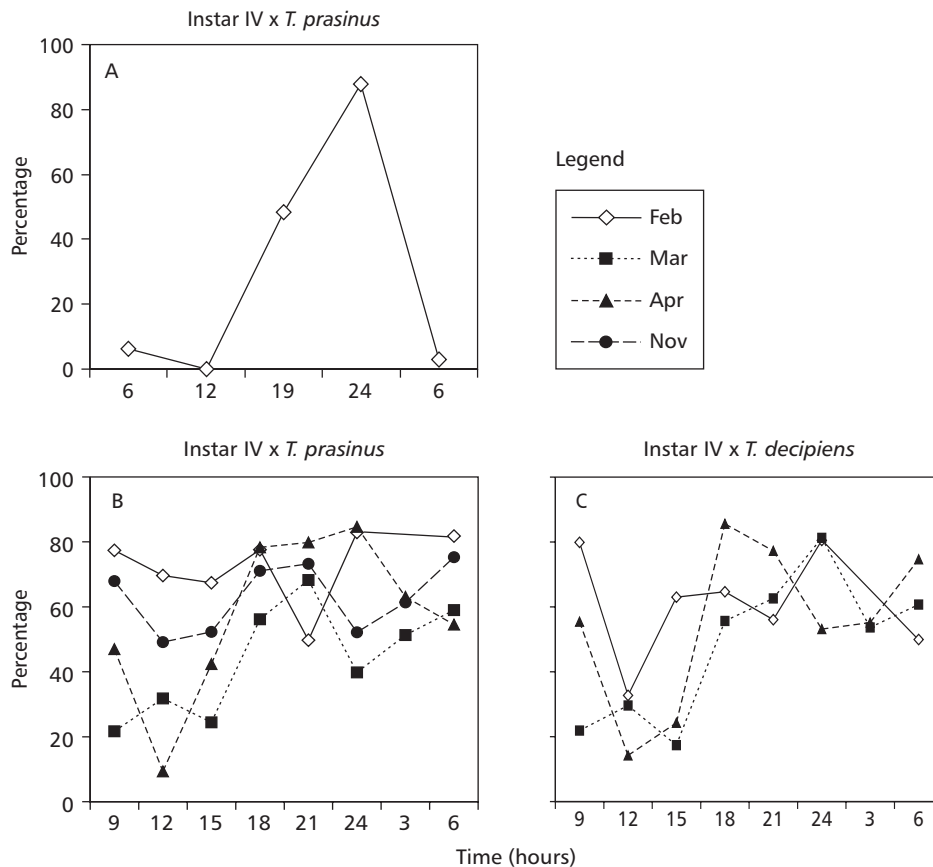


Fig. 7 — Spatial overlap between *Chaoborus* instar IV and adult copepods, in the summer of 1986 (A), and in 1999 (B, C).

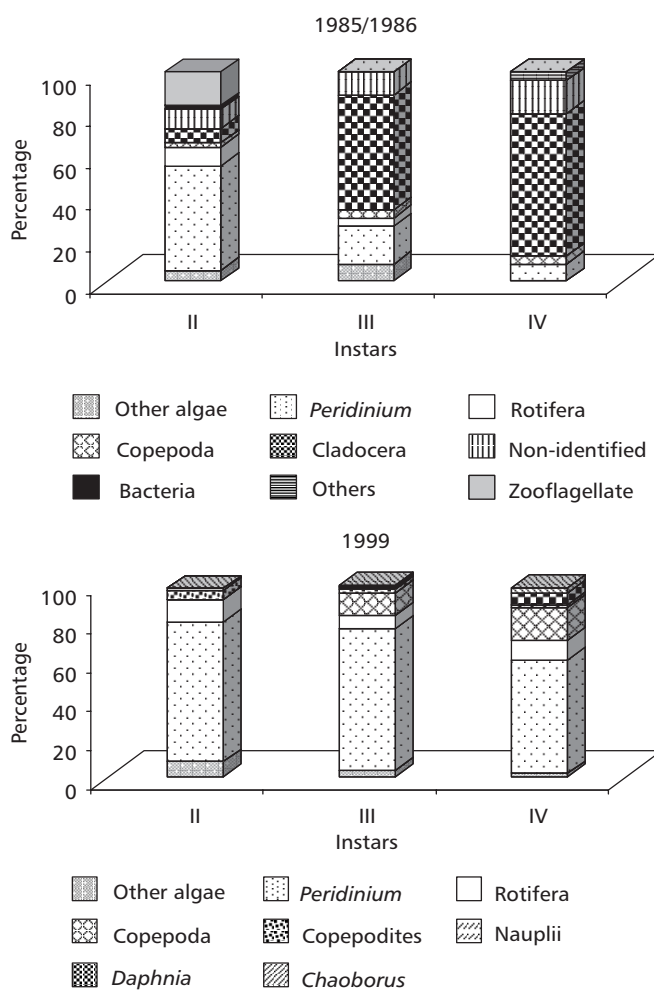


Fig. 8 — Relative volume of items in the diet of *Chaoborus* larvae II to IV, in 1985/86 and 1999. Sources: Arcifa (2000) and Castilho-Noll (2002).

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