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Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake

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Abstract Invertebrate predation on zooplankton was investigated in mesocosms in the shallow tropical Lake Monte Alegre, São Paulo State, Brazil, in the summer of 1999. Two treatments were applied: one with natural densities of prey and the predators *Chaoborus brasiliensis* and the water mite *Krendowskia* sp. (Pr+), and another without predators (Pr-). Three enclosures (volume: 6.6 m^3 of water per enclosure) per treatment were installed in the sediment of the deepest area of the lake (5.0 m). At the beginning, *Chaoborus* larvae were present in Pr- enclosures, because of technical difficulties in preventing their entrance, but they virtually disappeared in the course of the experiment. Water mites were almost absent in Pr- enclosures. *Chaoborus* predation negatively influenced the *Daphnia gessneri* population, but not the populations of the copepods *Tropocyclops prasinus* and *Thermocyclops decipiens* and the rotifers *Keratella* spp. Death rates of *Daphnia* were generally significantly higher in the Pr+ treatment; *Daphnia* densities increased after the disappearance of *Chaoborus* in Pr-. Copepod losses to predation in the experiment may be compensated by higher fecundity, shorter egg development time, and lower pressure on egg-bearing females, resulting in a lower susceptibility to *Chaoborus* predation. The predation impact of water mite on microcrustaceans and rotifers in the experiment was negligible.

Keywords *Chaoborus* predation · Copepods · *Daphnia* · Enclosure · Population dynamics

Introduction

In aquatic ecosystems, predation has been considered the major force in controlling densities and structure of zooplankton communities (Zaret 1980), compared with senescence, food shortage, parasitism, and limiting abiotic factors as the main cause of mortality (Gliwicz and Pijanowska 1989). The seasonal succession of species can be indirectly affected by predation (Gliwicz and Pijanowska 1989), in addition to direct effects on abundance, size structure, morphology, and organism behavior. In the absence of vertebrate predators, invertebrates can exert a strong impact on zooplankton populations (Zaret 1980; Lair 1990) and may be a key factor in the evolution of the life history of cladocerans (Lynch 1980).

Chaoborus larvae are among the most common invertebrate predators in fresh waters; their role in food webs is better known in temperate lakes than in

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tropical ones (e.g., Hare and Carter 1987; Saunders and Lewis 1988; Pagano et al. 2003). Vertebrates or invertebrates can regulate crustacean populations for a longer period in warm lakes than in temperate ones (Saunders et al. 1999), and therefore, predation by invertebrates can be more intense in the tropics than in the temperate zone.

Predation by water mites on zooplankton is not as well documented, because they are usually littoral dwellers. However, their impact on crustaceans can be considerable, especially when the mite densities exceed 100 ind. m^{-3} in the limnetic zone (Gliwicz and Biesiadka 1975; Matveev et al. 1989; Butler and Burns 1993).

Detritivory, piscivory, omnivory, insectivory, and herbivory are the main fish feeding guilds in Brazilian waters, where planktivores play only a minor role in food webs (Araújo-Lima et al. 1995; Arcifa et al. 1995). In Lake Monte Alegre, the pump filter-feeder adult *Tilapia rendalli* is the only planktivorous fish, feeding mostly on phytoplankton (Arcifa and Meschiatti 1993, 1996). Adults were not abundant in the lake and were inefficient in controlling zooplankton, whose densities increased significantly in the mesocosm with fish because of the phytoplankton enhancement (Silva 2004). Moreover, most fish larvae and juveniles do not prey on zooplankton (Meschiatti and Arcifa 2002), and both adult and young fishes are mainly littoral dwellers (Arcifa and Meschiatti 1993), resulting in a low predation pressure on zooplankton in the limnetic zone of the lake. Therefore, invertebrate predators can exert a larger influence on lake zooplankton than can fish. Instars III and IV of *Chaoborus brasiliensis*, and the limnetic water mite *Krendowskia* sp. are the main invertebrate predators in Lake Monte Alegre (Arcifa 2000; Cassano et al. 2002). Cyclopoid copepods do not seem to be important predators of microcrustaceans, because *Tropocyclops prasinus* could be maintained on a diet of algae in our laboratory, and *Thermocyclops decipiens* raised on protozoans and algae by Rietzler (1995). She found that in the field detritus, algae, and rotifers were the main items of its diet, and that *T. decipiens* preyed more heavily on rotifers if offered microcrustaceans and rotifers.

The aim of the present study was to evaluate the influence of invertebrate predation on the densities and dynamics of prey populations in a mesocosm experiment, to test the hypothesis (Arcifa et al. 1992) that in Lake Monte Alegre some zooplankton population can be regulated by the invertebrate predator *Chaoborus*. We applied two treatments in the mesocosms: one with *Chaoborus* and water mites, and one without predators. Since *Chaoborus brasiliensis* is a small species and early larval instars passed through the net holes of the predator-free treatment during the set up procedure, we tested: *a.* prey responses to natural densities of *Chaoborus* larvae and water mite (Pr+ treatment) and low densities of *Chaoborus* and no water mites (Pr- treatment) at the beginning of the experiment (Period 1), and *b.* prey responses to natural densities of larvae and mites (Pr+) and to lack of predators (Pr-), after the virtual disappearance of *Chaoborus* from the predator-free treatment (Period 2) .

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 on the University of São Paulo campus, in Ribeirão Preto, State of São Paulo, southeastern Brazil. The lake was formed in 1942 by the damming of Laureano Creek, which belongs to the River Pardo basin. The region has a tropical climate, with a marked cool-dry season (May–September) and a warm-wet season (October–April). Since the outlet is superficial and the dam is not manipulated, the impoundment functions as a small lake, with a retention time of about 45 days at the end of the wet season. Stratification periods, particularly during summer, can lead to oxygen depletion in the narrow hypolimnion (Arcifa et al. 1990).

The lake is eutrophic, and has sporadic small cyanobacteria blooms. Eight planktonic cladoceran species were recorded in four periods (1985/86, 1988/89, 1998/99, and 2001/02) (Arcifa et al. 1992, 1998; Fileto 2001; Bunioto 2003): *Bosmina tubicen, Ceriodaphnia cornuta*, *C. richardi*, *Daphnia ambigua*, *D. gessneri, Diaphanosoma birgei, Moina micrura*, and *M. minuta*; and two cyclopoid copepod species: *Thermocyclops decipiens* and *Tropocyclops prasinus meridionalis*. Fifteen rotifer species have been found in the lake, including three species of *Keratella*: *K. americana*, *K. cochlearis micracantha*, and *K. tecta tecta* (Arcifa et al. 1992).

Materials and methods

The investigation was carried out in the lake from 9 to 25 February 1999. The enclosure was 5.5 m high, with a diameter of 1.3 m, and a volume of 6.6 m^3 (Fig. 1); the enclosure was made of non-toxic plastic sheet and double rounded aluminum frames. It was constructed and set up as described by Arcifa and Guagnoni (2003). The enclosure was lowered into the lake until it reached the lake bottom; it got filled with water on its way down. A floatation device, made of groups of six clear plastic bottles (volume −2 l, PET type, Coca Cola or similar), were attached to five short bars screwed around the upper frames of the enclosure. Six such enclosures were installed in the deepest area of the lake (5.0 m), in a systematic arrangement to prevent pseudoreplication. Two treatments with three replicates each were carried out: (1) Pr+, with free access of *Chaoborus brasiliensis* larvae and the water mite *Krendowskia* sp. to the water column and sediment; and (2) Pr-, provided with a 1 mm net close to the lower frames of the enclosure (Fig. 1), to block the entrance of organisms from the sediment. A 3 mm tulle fabric covered the Pr- enclosures, to prevent *Chaoborus* oviposition.

Despite efforts to exclude *Chaoborus* larvae from the Pr- (predator-free treatment), instars I, II, and III were present at the beginning of the experiment, although in low densities. The pore size of the net used to exclude predators could not be made smaller, in order to avoid exclusion of the prey. Thus, it was possible to evaluate predation effects on prey by analyzing the experiment in two periods: Period 1 (P1: day 1–9) characterized by higher and lower densities of *Chaoborus* larvae, respectively, in the treatments Pr+ and Pr-; and Period 2 (P2: day 13–16) marked by the virtual disappearance of *Chaoborus* in treatment Pr-.

The enclosures and the environment were monitored twice a week at sunset for 16 days, when *Chaoborus* larvae III and IV and mites were most abundant in the water. A total of 45 l of water were pumped from each enclosure with a bilge pump (Model 34,600-0000, Jabsco ITT Ind., Costa Mesa, USA) that delivered 30 l min^{-1} from the surface to *ca*. 4 m in the center of the water column, to avoid wall effects. The water was filtered through a 60 µm mesh net, and the organisms were narcotized and fixed (Haney and Hall 1973). Temperature, dissolved oxygen, and electrical conductivity were monitored

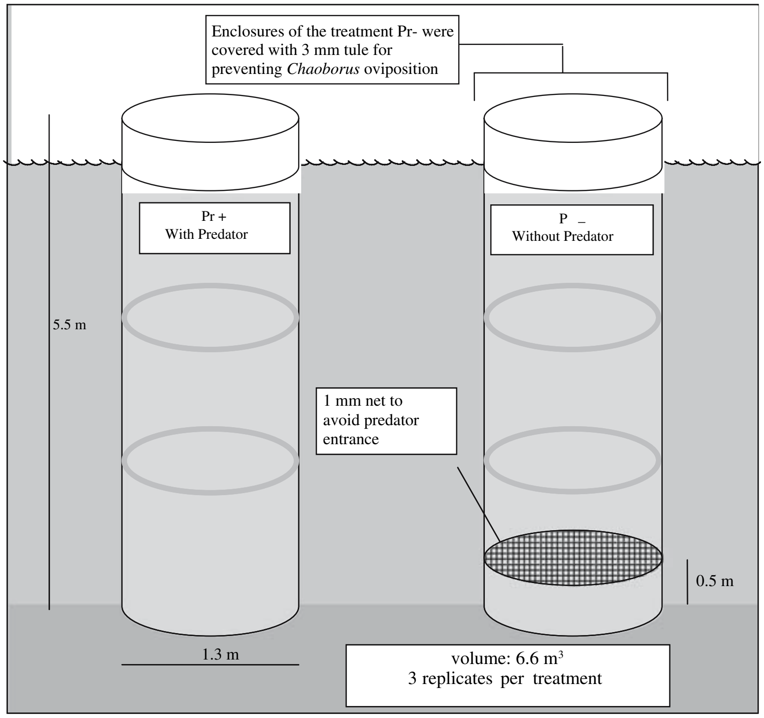


Fig. 1 Diagram of enclosures of both treatments

with Yellow Springs Inc. equipment, models 95 and 30.

Prey organisms were counted in 1 ml-subsamples taken with a piston pipette, and placed in a counting chamber and counted using a stereoscopic microscope. At least 60 individuals were enumerated in each subsample; the coefficient of variation did not exceed 0.20 as recommended (McCauley 1984). Low-density samples, as well as both predators in the samples were fully counted. Prey length was measured using a microscope or stereoscopic microscope and an ocular micrometer for calculating biomass.

Chaoborus diet was evaluated by counting prey extracted from the crop by gentle squeezing of the contents according to Arcifa (2000). Dietary item contribution in biomass was based on length-weight regressions established for lake crustaceans and *Chaoborus* larvae (Castilho-Noll and Arcifa, 2007) and biovolume for algae and rotifers. *Chaoborus* larvae were collected in the mesocosms and averaged over time for crop analysis.

The number of eggs/female, of egg-bearing females, and the egg development time for the main prey species–*Daphnia gessneri* and *Tropocyclops prasinus*–were quantified as measures of population dynamics. Egg development time for *Thermocyclops decipiens* was obtained from the literature (Rietzler 1995) and that of *D. gessneri* was determined by placing individually 10 neonates in 30 ml vessels containing lake seston <140 µm (mean concentration of 0.9 ± 0.3 mg C l^{-1}), maintained in an environmental chamber at 23–24°C (mean water-column temperatures in Lake Monte Alegre) and a 12:12 h photoperiod. The water was renewed daily, and observations were made every 3 h until eggs appeared and neonates hatched. The observed egg development time used in the calculations was 1.91 ± 0.12 days, which did not differ statistically from the time observed at 27°C, the mean temperature recorded in the experiment.

Non-ovigerous females of *Tropocyclops prasinus*, collected in the lake, were placed individually in ten 130 ml vessels, containing lake water filtered through a 20 µm mesh net, to which 1 mg C l^{-1} of the alga *Chlamydomonas reinhardtii* was added, and maintained at environmental chamber at 23–24°C and 12:12 h photoperiod. Observations were made frequently until eggs appeared and nauplii hatched; the mean time recorded for egg development was 1.72 ± 0.08 days. Females of *Thermocyclops decipiens* were raised at 23–24°C on a diet of protozoans and algae by Rietzler (1995), who found 1.33 ± 0.15 days for egg development time. Due to difficulties in differentiating nauplii and copepodites of the two-copepod species, the data for both were pooled. Hence, the egg development time used in the calculations (*D*) was the mean (1.52 days) for both copepods. Due to the egg development time of *T. decipiens* at 28°C was 0.94 ± 0.09 day (Rietzler 1995), the birth rates may be slightly underestimated in our experiment, because the mean temperature was around 27°C in the enclosures.

Birth (*b*), death (*d*), and growth (*r*) rates were calculated according to Edmondson (1968) and Paloheimo (1974).

One-way repeated-measures ANOVA (Systat®, version 9, 1999, SPSS, Chicago, IL, USA) was used for comparing means of the treatments. In order to supplement this analysis, a *post hoc* Tukey honest significant difference (HSD) test was performed to compare responses between treatments. The Spearman coefficient was used to test for correlations between predator densities and prey densities and population rates.

Results

Physical, chemical, and biological data

Temperature, electrical conductivity, and dissolved oxygen (DO) in the enclosures at the beginning, middle, and end of the experiment are presented in Table 1. Results from other sampling dates were excluded from the table, because the differences were negligible. Physical and chemical factors did not differ significantly between the treatments.

Thermal stratification was established in both treatments during the course of the experiment, with consequent stratification of dissolved oxygen and electrical conductivity. Dissolved oxygen values were ca. 1 mg l^{-1} near the bottom. Water parameters in the enclosures and in the environment were similar.

The organisms that were analyzed in the mesocosms for predator–prey relationship are: Cladocera, *Daphnia gessneri* (0.68–1.25 mm in length);

Table 1 Means and standard deviations of temperature, conductivity, and dissolved oxygen in the treatments Pr+ (with predator) and Pr- (without predator) at the beginning, middle, and end of the experiment

	1st day		6th day		16 th day	
Temperature (°C)	Pr+	Pr-	Pr+	Pr-	Pr+	Pr-
Surface	28.2 ± 0.0	28.3 ± 0.1	29.5 ± 0.2	29.8 ± 0.2	27.3 ± 0.5	28.3 ± 0.2
Bottom (4.5 m)	26.0 ± 0.1	26.1 ± 0.1	25.7 ± 0.1	25.6 ± 0.1	25.6 ± 0.1	25.7 ± 0.1
Conductivity (μs cm^{-1})						
Surface	68.2 ± 0.7	68.7 ± 0.5	70.4 ± 0.7	71.3 ± 0.5	65.2 ± 1.5	66.3 ± 0.1
Bottom (4.5 m)	81.9 ± 2.6	89.0 ± 3.4	69.3 ± 2.8	73.2 ± 7.8	79.9 ± 3.7	77.4 ± 4.4
DO (mg l^{-1})						
Surface	8.6 ± 0.2	8.7 ± 0.1	8.2 ± 0.6	8.0 ± 0.4	8.2 ± 0.1	8.3 ± 0.7
Bottom (4.5 m)	0.9 ± 0.1	0.6 ± 0.1	1.9 ± 0.1	1.8 ± 1.1	1.0 ± 0.1	1.1 ± 0.1

Copepoda, adult *Tropocyclops prasinus* (0.47–0.61 mm) and adult *Thermocyclops decipiens* (0.71–0.77 mm); Rotifera, *Keratella* spp. (0.08–0.11 mm); Diptera, *Chaoborus brasiliensis* Instar I (1.47–1.87 mm), Instar II (2.05–3.23 mm), Instar III (4.07–4.70 mm), and Instar IV (5.68–6.92 mm); and Hydracarina, *Krendowskia* sp. (0.99–1.33 mm).

Feeding habits of *Chaoborus* larvae in the enclosures

Microcrustaceans contributed the most to the diet of Instars III and IV, as shown in the crop contents (Fig. 2). The dinophycean *Peridinium* and the rotifer *Keratella* were numerically the dominant prey of instar II (Fig. 2a), while copepodites prevailed in biomass (Fig. 2b). Instars III and IV had higher dietary diversity, as adult copepods, *Daphnia gessneri* (small size 0.68–0.80 mm), and *Chaoborus* larvae were included in their diets. The main prey items in terms of biomass were *Tropocyclops prasinus* and *Thermocyclops decipiens* (Fig. 2b). About 81 percent of the copepods ingested by late instars were males and non-egg-bearing females. The diet of Instar I could not be evaluated, because all the individuals had empty crops.

Temporal variation of predators in the enclosures

The two periods (P1 and P2) were marked by variations in predation pressure in both treatments, with (Pr+) and without predators (Pr-) (Figs. 3a, 4).

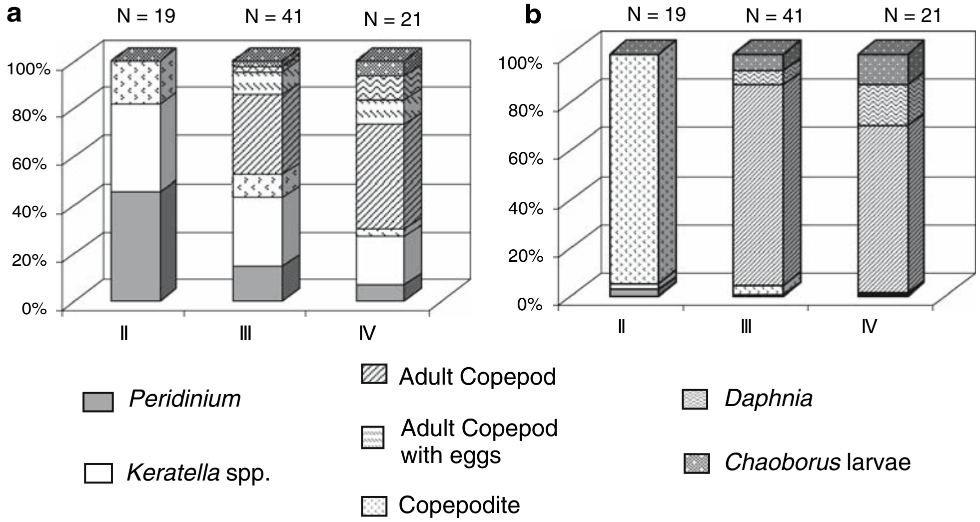
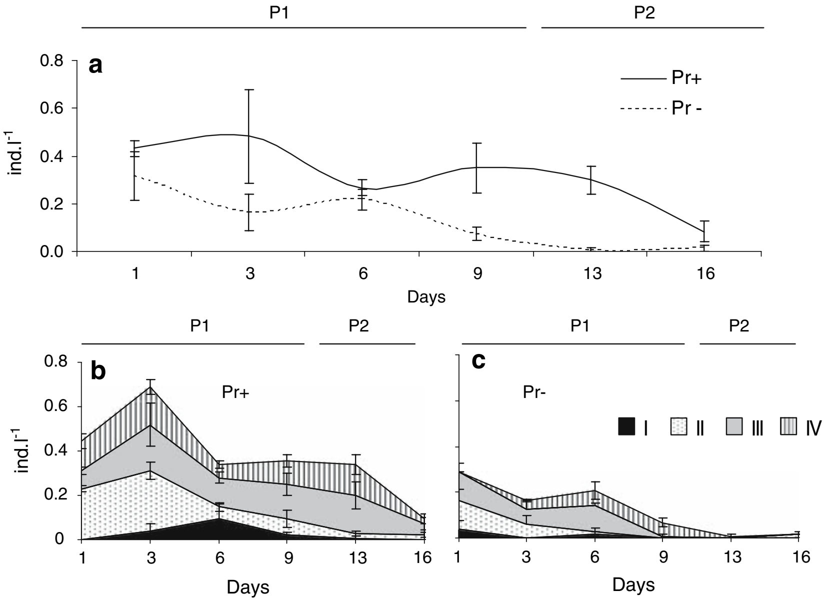


Fig. 2 Proportion of food items in the crops of *Chaoborus brasiliensis* larvae II, III and IV in both treatments, during the experiment. (**a**) Percentage in number, (**b**) Percentage in biomass. *N* = number of specimens analyzed

Fig. 3 (**a**) Mean densities and standard errors of *Chaoborus brasiliensis* larvae in both treatments; (**b**) Contribution of *C. brasiliensis* instars in the treatment with predator (Pr +); c) Contribution of *C. brasiliensis* instars in the treatment without predator (Pr -). P1 = period 1; P2 = period 2



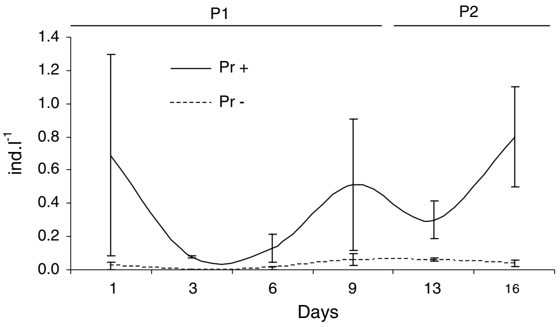


Fig. 4 Mean densities and standard errors of *Krendowskia* sp. (Hydracarina) in both treatments. P1 = period 1; P2 = period 2

The Anova showed that there were significant differences in *Chaoborus* densities between treatments (*post hoc* Tukey test, $P = 0.005$) and over time ($P = 0.01$) (Table 2). Densities of the water mite *Krendowskia* did not differ statistically in the treatments (Table 2).

During P1 (days 1–9), all *Chaoborus* instars were present in Pr+ (Fig. 3b), and the mean densities of larvae III + IV ranged from 0.19 to 0.38 ind. l^{-1}. In P2 (days 13–16) there was a general trend toward decreasing numbers of instars I and II, and the densities of larvae III + IV varied from 0.04 to 0.39 ind. l^{-1}. Adult emergence and larval mortality were responsible for density variations during the experiment, and may explain the decline of *Chaoborus* by the end of the experimental period. Since the larvae were trapped inside the enclosures, density declines in the water, followed by an increase on the next sampling date, could result from a larger number of individuals remaining in the sediment. Oviposition was ineffective despite the absence of a tulle screen over the Pr+ enclosures, as shown by the disappearance of instar I.

The most conspicuous shifts occurred in the Pr- treatment, in which initial densities of instars III + IV (0.06 to 0.17 ind. l^{-1}), in P1, decreased in the following period, the larvae virtually disappearing from the enclosures (Fig. 3a, c). Larvae disappearance can be attributed to the lack of female oviposition, precluded by the tulle screen over the Pr- enclosures, their isolation from the sediment by the 1 mm net located near the lower frame of the cylinder, mortality, and completion of the life cycle by the remaining larvae. Instar IV did not pass through the holes of the 1 mm net during the set up procedure, and appeared in the enclosures a few days later after the early instars developed (Fig. 3c).

Water mite were almost absent in Pr-, confirming the efficiency of the 1 mm net in preventing the entrance of the animals into the enclosures (Fig. 4). An increase in their densities in Pr+ during P2 probably resulted from better reproductive performance, because the enclosure walls provided an extra substrate for egg deposition. Although the same factor could have favored mites in Pr-, their daytime

Table 2 One-way repeated-measures ANOVA for the treatment effects, with predator (Pr+) or without predator (Pr-), and the effect of time (*T*) on density of *Chaoborus*, *Krendowskia*, and *Keratella*, and on density and population rates of *D. gessneri* and Copepoda

Source	df	MS	*F*	*P*
(i) *Chaoborus* density				
Pr + x Pr-	1	0.317	32.181	0.005
T	5	0.083	3.987	0.01
Pr + x Pr- x T	5	0.022	1.076	0.403
(ii) *D. gessneri* density				
Pr + x Pr-	1	888.934	65.526	0.001
T	5	429.277	16.169	<0.001
Pr + x Pr- x T	5	368.110	13.865	<0.001
(iii) *D. gessneri* birth rate				
Pr + x Pr-	1	0.025	3.702	0.127
T	5	0.056	4.063	0.010
Pr + x Pr- x T	5	0.023	1.670	0.188
(iv) *D. gessneri* death rate				
Pr + x Pr-	1	0.515	27.179	0.006
T	5	0.275	6.771	<0.001
Pr + x Pr- x T	5	0.336	8.275	<0.001
(v) *D. gessneri* growth rate				
Pr + x Pr-	1	0.312	25.245	0.007
T	5	0.364	10.028	<0.001
Pr + x Pr- x T	5	0.233	6.411	0.001
(vi) Copepoda density				
Pr + x Pr-	1	0.003	0.000	0.993
T	5	78.722	4.000	0.011
Pr + x Pr- x T	5	9.028	0.459	0.802
(vii) Copepoda birth rate				
Pr + x Pr-	1	0.002	1.192	0.336
T	5	0.004	3.490	0.020
Pr + x Pr- x T	5	0.001	1.383	0.272
(viii) Copepoda death rate				
Pr + x Pr-	1	0.002	0.302	0.612
T	5	0.062	7.211	0.001
Pr + x Pr- x T	5	0.005	0.640	0.672
(ix) Copepoda growth rate				
Pr + x Pr-	1	0.006	1.629	0.271
T	5	0.048	6.570	0.001
Pr + x Pr- x T	5	0.005	0.621	0.686
(x) *Keratella* density				
Pr + x Pr-	1	119205.6	3.090	0.154
T	5	110693.7	11.993	<0.001
Pr + x Pr- x T	5	27214.26	2.948	0.037
(xi) *Krendowskia* sp. density				
Pr + x Pr-	1	1.365	6.208	0.067
T	5	0.142	0.967	0.461
Pr + x Pr- x T	5	0.122	0.831	0.542

migration into the sediment was precluded by the 1 mm net, which probably affected population growth.

Population dynamics of prey

The *Daphnia gessneri* population was sensitive to predation-pressure variation, reacting to the disappearance of *Chaoborus* in Pr- with a sharp increase in densities in P2 (Fig. 5a). Significant density differences were found between treatments (Anova, Table 2, *post hoc* Tukey test, $P = < 0.001$). A conspicuous increase of males in Pr- in P2 (Fig. 5b) took place concurrently with a high abundance of parthenogenetic females, indicating the effect of crowding on sexual reproduction.

Daphnia birth rates did not significant differ between treatments (Table 2, Fig. 6a). Death and growth rates differed statistically between treatments (Anova, *post hoc* Tukey test, $P = 0.007$ and $P = 0.007$, respectively), generally with higher death rates and lower growth rates in Pr+ (Fig. 6b, c). There was a significant negative correlation between the densities of *Daphnia* and *Chaoborus* in the Pr- treatment ($r = -0.70$; $p = 0.05$). In both treatments the correlations between *Daphnia* population rates and predator densities were not significant.

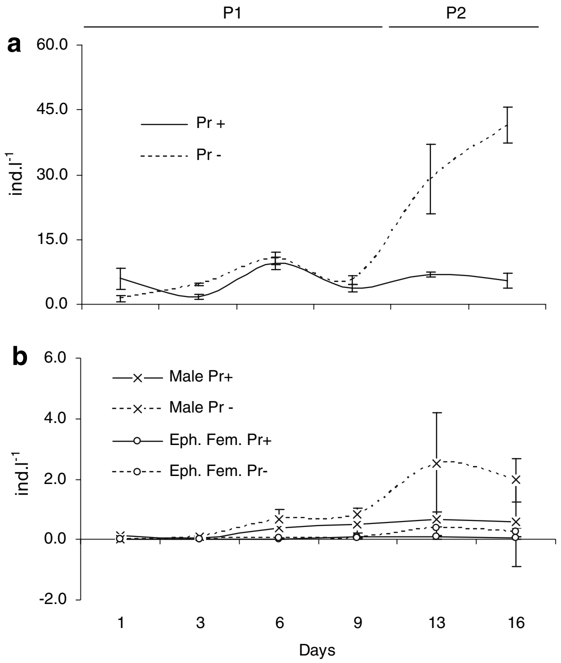


Fig. 5 (**a**) Mean densities and standard errors of parthenogenetic *Daphnia gessneri* in both treatments. (**b**) Mean densities and standard errors of males and ephippial females of *D. gessneri* in both treatments. P1 = period 1; P2 = period 2

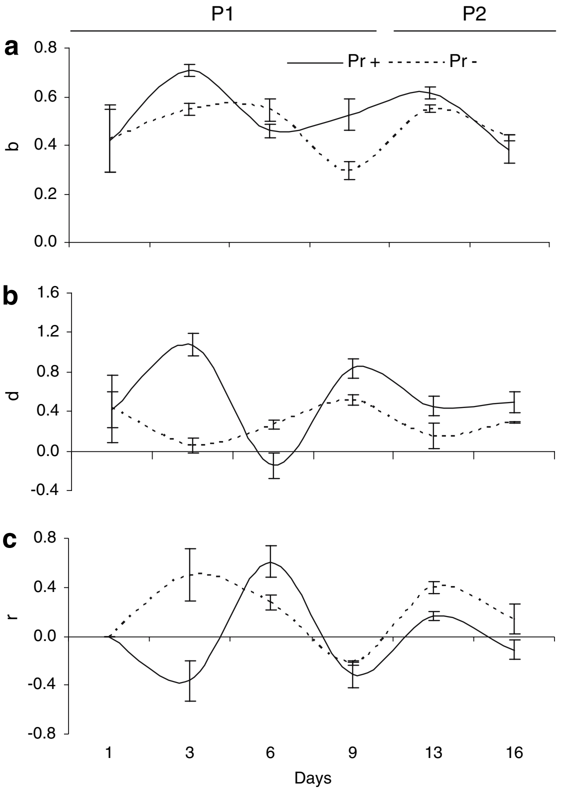


Fig. 6 Means and standard errors of (**a**) population birth rates, (**b**) population death rates, and (**c**) population growth rates of *Daphnia gessneri* in both treatments. P1 = period 1; P2 = period 2

The densities of adult copepods did not differ between the two treatments during the experimental period (Table 2, Fig. 7a). In both treatments growth rates were positive, except at the beginning of period P2 (Fig. 7d), when densities remained stable (Fig. 7a). The birth, death, or growth rates did not significantly differ between treatments (Table 2), and the correlation between densities of copepods and *Chaoborus* was not significant. Copepods have higher clutch size and fecundity (eggs/total females) and a shorter egg development time than *Daphnia* (Table 3).

The populations of *Keratella* spp. decreased during the experiment to very low values at the end (Fig. 8). Values were higher in Pr+ but not significantly different from Pr- (Table 2).

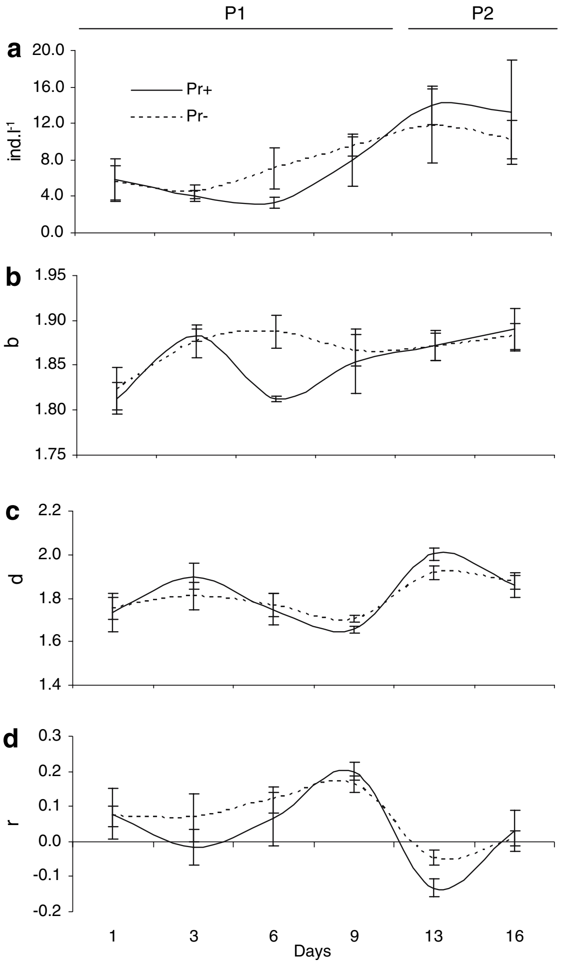


Fig. 7 Means and standard errors of (**a**) densities, (**b**) population birth rates, (**c**) population death rates, and (**d**) population growth rates of Copepoda in both treatments. P1 = period 1; P2 = period 2

Table 3 Comparison of some reproductive characteristics between *Daphnia gessneri* and Copepoda (*Tropocyclops prasinus* + *Thermocyclops decipiens*) during the experiment

	D. gessneri	Copepoda
Clutch size	3.4 ± 0.5	16 ± 0.7
Fecundity (eggs/total female)	1.6 ± 0.5	4.7 ± 1.3
Proportion of ovigerous female (%)	18 ± 0.08	30 ± 0.1
Egg development time (days)	1.91 ± 0.1	1.52 ± 0.1

There was no significant correlation between the densities of *Daphnia gessneri* and mites in Pr+. The increase of density in both cases in P2, indicated a lower predation impact by mites on prey.

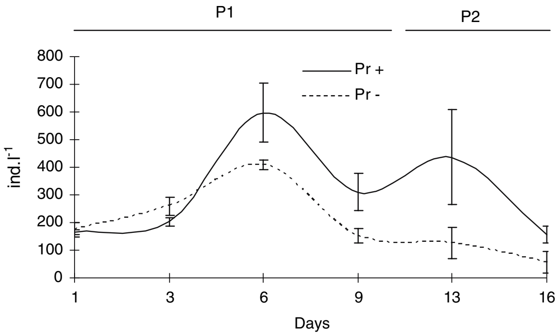


Fig. 8 Mean densities and standard errors of *Keratella* spp. in both treatments. P1 = period 1; P2 = period 2

Discussion

In experiments on invertebrate predation in enclosures it is difficult to exclude predators without excluding prey. Examples can be found in the literature, e.g., the experiment by Mumm (1997), who was also unable to prevent the entrance of *Chaoborus* larvae in the predator-free treatment, but considered predation negligible because only younger instars were present, which had low impact on cladocerans. However, a minimum of 5–6 days (Moore 1986) and a maximum of 12–13 days (Cressa and Lewis 1986) is the time range for instar I of two *Chaoborus* species to reach instar III. Thus, even though only early instars were initially present in the predator-free enclosures in Mumm's experiments (Mumm 1997), the larvae eventually reached a stage at which they could predate on crustaceans. In our study, in the predator-free enclosures instars I, II, and III were present at the beginning of the experiment, because *Chaoborus brasiliensis* is a relatively small species and larvae passed through the net holes in a vertical position, during the enclosure set up in the lake. However, once the enclosure was installed, the net was efficient in blocking the entrance of new larvae, because they swim horizontally. Thus, the effect of the lack of *Chaoborus* predation could be evaluated at the end of period 1 and during period 2, when larvae occurred in very low densities or were virtually absent in the Pr- treatment. The mite *Krendowskia* sp. can prey on *Daphnia gessneri* (Cassano et al. 2002), but in the experiment there is no indication of its impact on the daphnid population and for this reason *Chaoborus* predation was mainly focused.

The population of *Daphnia gessneri* responded more clearly to shifts in predator densities than the populations of copepods and rotifers (*Keratella* spp.) in the experiment, with higher death rates and lower densities and lower growth rates in the treatment with predators. The daphnids did not exhibit any strategy to prevent their predation by *Chaoborus* in our experiment.

Densities and population rates of copepods do not seem to be strongly influenced by invertebrate predation in the experiment. Higher clutch size, fecundity, and shorter egg development time of *Tropocyclops prasinus* and *Thermocyclops decipiens*, enhancing birth rates, are plausible explanations that compensate for the lower predation impact on copepods compared with *Daphnia gessneri*. Also a lower predation on egg-bearing copepod females (19% of the total individuals consumed) and nauplii could explain the lower predation on copepods. Differential predation by *Chaoborus* larvae on males and females of copepods has been earlier reported. Higher predation pressure on males has been observed, because their quicker movement is more easily detected by *Chaoborus* mechanoreceptors (Blais and Maly, in Svensson 1997). On the other hand, both Svensson (1997) and Maier et al. (2000) have observed higher predation on egg-bearing females and mating couples, while males were better able to escape.

Sutor et al. (2001) reported that predation effects in enclosures depended on the density and migratory behavior of *Chaoborus*. They found no difference in predation impact between treatments with maximum larvae IV densities of 0.1 and 0.5 ind. l^{-1} and concluded that these densities were not high enough to affect prey, which also took refuge from predation through the predator diel vertical migration. Our data in the experiment do not corroborate these conclusions, because *Chaoborus brasiliensis* is a migratory species in the lake (Arcifa 1997; Perticarrari et al. 2003), and significantly lower densities and higher death rates of *Daphnia* were found when densities of *Chaoborus* instar III + IV were around 0.4 ind. l^{-1} compared with 0.1 ind. l^{-1}.

The stronger predation impact on cladocerans than on copepods in the experiment supports the work of Arcifa et al. (1992) on Lake Monte Alegre, where a higher *Chaoborus* predation in the warm season did not affect copepod populations, but caused decreases of *Daphnia gessneri* and *Bosmina tubicen* populations. Perticarrari et al. (2004) suggested that reverse vertical migration could be a response of copepods to higher *Chaoborus* predation. The migratory pattern of copepods in Lake Monte Alegre differed in 1985/86 from that of 1999 when they contributed more to *Chaoborus* diet. Reverse migration was performed by copepods in 1999, whereas in 1985/86, when the cladoceran *Bosmina* was the main *Chaoborus* prey, a twilight pattern (ascent in the water column at sunset and dawn) was observed. Reverse migration can be a response of the copepod to higher predation pressure by larvae (e.g., Ohman et al. 1983; Neill 1990). Lack of predation by water mites (Cassano et al. 2002) confers an advantage to copepods in relation with cladocerans. The only strategy of *Daphnia* in the lake against predation is that juveniles, which are selectively preyed upon by *Chaoborus*, were distributed higher in the water column than adults, leading to lower spatial overlap with the predator (Sousa 2003).

Conflicting data on the predation impact by *Chaoborus* on zooplankton in different lakes can be caused by differences in predator abundance and migratory behavior of both prey and predator and their feeding habits, and sizes. Wissel and Benndorf (1998) reported a strong predation effect on zooplankton by a large species of *Chaoborus*, *C. obscuripes*, which replaced a smaller one, *C. flavicans*. The mouth gapes for instar IV of these species ranged from 689 to 734 µm in *C. obscuripes* and 450 to 650 µm in *C. flavicans*. The smallest North American *Chaoborus*, *C. punctipennis* (Instar IV gape diameter 425–500 µm and 7.8 mm in body length; Moore and Gilbert 1987; Moore 1988), was unable to control a prey population, which was attributed to its small size (Rodusky and Havens 1996). *Chaoborus brasiliensis* from Lake Monte Alegre is even smaller (instar IV length 6.0 mm and 290 µm in mouth diameter; Arcifa 1997), but is able to control a part of the prey population because in this tropical lake its prey are relatively small, a characteristic of the tropical zooplankton compared with the temperate one (Arcifa 1984).

In conclusion, experimental results corroborated the formulated hypothesis based on field data, that some zooplankton populations, such as *Daphnia gessneri*, can be regulated by invertebrate predation, particularly *Chaoborus*, in Lake Monte Alegre (Arcifa et al. 1992). Negative predation effects on copepods and rotifers were not observed in the experiment, just as in the field (Arcifa et al. 1992; Arcifa 2000). Although water mite preyed on *Daphnia gessneri* in laboratory experiments, its impact on *Daphnia* population seems to be negligible in the mesocosms, as increase in predator densities did not affect prey densities.

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