

Experiments on invertebrate predation on cladocerans and its relationships with lake data

Tânia C. dos Santos Ferreira, Marlene S. Arcifa*

Departamento de Biologia, Universidade de São Paulo, Avenida Bandeirantes, 3900, 14040-901, Ribeirão Preto, São Paulo, Brasil

ABSTRACT

Until recently, knowledge of the impact of invertebrate predators on cladocerans in the Brazilian Lake Monte Alegre was limited to a few species. In order to assess the effects of predation on other cladoceran species, experiments were carried out with different pair-wise combinations of prey species. The experiments tested predation by fourth instar larvae of the dipteran *Chaoborus brasiliensis* Theobald on neonates and adults of the cladocerans *Daphnia gessneri* Herbst, *Diaphanosoma birgei* Kořinek, and *Ceriodaphnia richardi* Sars, and predation by the water mite *Krendowskia* sp. on neonates and adults of *C. richardi* and *D. gessneri*. In replicated treatments, the prey was offered alone or in combination with neonates and adults of two species and kept in bottles on a plankton wheel under controlled temperature, photoperiod, and light conditions. *Chaoborus* larvae preyed on neonates of *D. birgei* and *D. gessneri* and on adults of the former species. They preyed preferentially on neonates and adults of *D. birgei* over neonates and adults of *C. richardi*. The mite *Krendowskia* sp. preyed on only one species: neonates and adults of *D. gessneri*. Data on the distribution and strategies of prey in the lake are discussed in light of the experimental results, in an attempt to establish a link between laboratory data and field conditions.

INTRODUCTION

Predation is considered a driving factor in the evolution of the life history of cladocerans (Lynch, 1980), especially in the tropics, where this interaction tends to be more influential due to the longer period of predation in the annual cycle (Saunders *et al.*, 1999). Predation is the leading cause of mortality in planktonic populations, compared to senescence, hunger, parasitism, and abiotic factors such as extreme temperature or anoxia (Gliwicz and Pijanowska, 1989). As well as being identified as the most important factor in the regulation of zooplankton populations (Zaret, 1980), predation can interfere with competitive interactions (Chase *et al.*, 2002).

Predation can directly affect the abundance of prey populations when high ingestion rates decrease their densities and size, or when predation is selective towards particular size classes. The behavior of prey populations can also be affected when predation induces diel vertical migration (Percicarrari *et al.*, 2004; Minto *et al.*, 2010). Additionally, predation can indirectly affect prey populations in relation to seasonal succession, especially in the pelagic zone, where organisms are more susceptible to predation (Gliwicz and Pijanowska, 1989).

The predation risk for a given prey depends on its vulnerability and spatial and temporal overlap with the predator (Pastorok, 1981; Bezerra-Neto and Pinto-Coelho, 2002; Arcifa *et al.*, 2016). In their review, Gliwicz and Pijanowska (1989) indicated a series of morphological, physiological, and behavioral characteristics that influence prey vulnerability, such as size, shape, pigmentation, palatability, locomotion, and ability to escape. According to the authors, vulnerability combined with predator selectivity can lead to a drastic reduction in the density of the most affected prey. However, these authors add that the extinction of a population caused by predation should only occur if the impact of predation is persistent or the losses are not offset by the increased survival of juveniles and by reproduction. According to Gliwicz and Pijanowska (1989), the flexibility of the life history of prey allows a population to overcome intense predation since many parameters that are determinants of predation vulnerability (e.g., size at maturity) can be adjusted to decrease predation susceptibility, in addition to adjustments related to behavior and morphology. Some species show changes in life history in response to chemical signals released by predators (Gu *et al.*, 2017). Such changes are mainly related to size and age at maturity, size at first reproduction, and the number of eggs produced (Gu *et al.*, 2017). If the predator is a

Corresponding author: marcif@usp.br

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vertebrate (e.g., a fish), the main changes involve early reproduction, age and size reduction at sexual maturity, and increased reproductive effort and fertility (Hanazato, 1995; Dawidowicz *et al.*, 2010). In contrast, prey responses to invertebrate predators, such as the larvae of *Chaoborus*, are primarily related to a delay of first reproduction and a larger body size (Dzialowski *et al.*, 2003; Freitas *et al.*, 2007).

Predators can regulate crustacean populations for longer periods in tropical lakes than in temperate lakes (Saunders *et al.*, 1999). If predation is selective, the most vulnerable species are selected, in contrast to non-selective predation, when the most abundant species tend to suffer greater predation pressure (Gliwicz and Pijanowska, 1989). Visual planktivorous fish are the primary vertebrate predators responsible for the removal of large zooplankton taxa (Lynch, 1980). Equally important, predation by invertebrates can have a major impact on zooplankton populations, especially on smaller species, and can lead to extinction, especially in cases where predation by vertebrates is low or absent (Zaret, 1980).

Previous studies carried out in Lake Monte Alegre have identified the primary predators of microcrustaceans, which are (in order of importance): larvae of the dipteran *Chaoborus brasiliensis* (Arcifa, 2000; Castilho-Noll and Arcifa, 2007a, b), the water mite *Krendowskia* sp. (Cassano *et al.*, 2002), and adults of the exotic cichlid fish, *Tilapia rendalli* (Boulenger) (currently *Coptodon rendalli*) (Arcifa and Meschiatti, 1993, 1996). Although fishes are considered the most voracious predators of the zooplankton community (Gliwicz and Pijanowska, 1989), in Lake Monte Alegre, the pump filter-feeder *C. rendalli* exerts greater pressure on phytoplankton than on zooplankton and occurs in low abundance (Arcifa and Meschiatti, 1993); therefore, its impact on zooplankton taxa is considered negligible.

In the first studies of temporal variation carried out in Lake Monte Alegre (1985-86; 1988-89), the dipteran *Chaoborus brasiliensis* was identified as the principal regulator of the density of cladocerans, and its most significant effect on prey populations was found to occur during the warm season, when larvae were most abundant (Arcifa *et al.*, 1992; Arcifa *et al.*, 1998). Because they are omnivores (Arcifa, 2000) and opportunistic, *Chaoborus* larvae first select the most vulnerable species, with the number of captured prey dependent on both the frequency of the encounter with the predator, as well as the behavior, swimming speed, size, shape, and hardness of the prey body (Smyly, 1980).

The appearance of a new predator in the lake, the mite *Krendowskia* sp., in 1998-99, combined with the effect of predation by *C. brasiliensis*, was followed by the restructuring of the zooplankton community, which resulted in a greater abundance of copepods and a lower abundance of small cladocerans, such as *Bosmina tubicen* (Arcifa *et al.*, 2015). According to these authors, the impact of the new

predator, in addition to long-term predation by *Chaoborus*, resulted in the dominance of large and intermediate-sized cladocerans, such as *Daphnia gessneri* and *Ceriodaphnia richardi*, over small-sized ones such as *Bosmina tubicen*, *Bosminopsis deitersi*, *Moina micrura*, and *M. minuta*.

Considering the available knowledge regarding the main invertebrate predators inhabiting Lake Monte Alegre, laboratory experiments were carried out to test the influence of larvae of the dipteran *Chaoborus brasiliensis* and of the water mite *Krendowskia* sp. on the survival of the cladocerans *Ceriodaphnia richardi*, *Daphnia gessneri*, and *Diaphanosoma birgei*, which inhabit the limnetic zone, the littoral zone, or both zones of the lake, with the aim of better understanding their distribution in time and space.

Laboratory experiments were conducted to investigate the following: 1. predation of fourth instar larvae of *C. brasiliensis* on neonates and adults of *D. gessneri* and *D. birgei*; 2. predation of *C. brasiliensis* on neonates and adults of *C. richardi* and *D. birgei*; 3. predation of the mite *Krendowskia* sp. on neonates and adults of *C. richardi* and *D. gessneri*. Our hypothesis was that differential predation on different cladoceran developmental stages could explain the abundance and strategies of the species in the lake.

METHODS

The Lake

Lake Monte Alegre (21° 10' 04" S, 47° 51' 28" W) is located within the campus of the University of São Paulo, Ribeirão Preto, São Paulo State, Brazil, in an environmentally protected area surrounded by a fence. Use of the lake is restricted to research and teaching. It is a shallow tropical reservoir (area = 7 ha, max. depth = 5 m, average depth = 2.9 m), resulting from damming of the Laureano Creek of the Pardo River basin, in 1942. Owing to several characteristics, such as a lack of a sluice gate management and a relatively high residence time (~45 days) for its dimensions and surface outlet, it behaves like a natural lake. The cladoceran species used in the experiments, *C. richardi*, *D. gessneri*, and *D. birgei*, coexist in the lake in the limnetic and littoral zones, except for *D. birgei*, which currently inhabits only the littoral zone. The predators, the larvae of the dipteran *C. brasiliensis*, and the planktonic mite *Krendowskia* sp., are most abundant in the limnetic zone and in the warm-wet season (i.e., from October to April).

Experiment 1: Predation of *Chaoborus brasiliensis* on *Daphnia gessneri* and *Diaphanosoma birgei*

Sampling, cultivation, and acclimation of cladocerans

Cladocerans were collected from Lake Monte Alegre using a 58 µm plankton net. In the laboratory, each species was cultivated separately for approximately 2-3 months

before the experiments, starting with the cultures from single females. During cultivation, the cladocerans were kept in 140 mL glass bottles and transferred to 600 mL bottles after the first generation because of the exponential increase in the number of individuals. The bottles were filled with lake water filtered through a glass fiber membrane (Millipore AP20) and a cultivated chlorophycean, *Desmodesmus spinosus* (Chodat) E. Hegewald, at a concentration of 1 mg C L⁻¹, to feed the cladocerans. After several generations, ovigerous females were separated and transferred individually to small 40 mL test tubes containing filtered lake water and food, to obtain the neonates. Cultures were maintained at a constant temperature of 23°C and a photoperiod of 12:12 h on a plankton wheel (rotation of 1 min every 5 min) under dim light.

Desmodesmus spinosus (formerly *Scenedesmus spinosus*) was grown in MBL medium (Stemberger, 1981) in a germination chamber (FANEM, model CDG), at a temperature of 23°C and a 12:12 h photoperiod.

The size of the prey (*C. richardi*, *D. gessneri*, and *D. birgei*) and predators (*C. brasiliensis* and *Krendowskia* sp.) are shown in Tab. 1. At least 20 individuals of each prey species, obtained from the pre-existing laboratory cultures, were measured. To obtain data on the size of adult prey, individuals at least 10 days old were removed from the cultures, narcotized with sucrose, fixed with formaldehyde, and measured. Different ovigerous females were separated until the neonates were obtained, which were mixed (to reduce genetic effects), narcotized, fixed, and measured to obtain data on the size of neonates. Carapace spines of the species were excluded from the measurements.

In this experiment, starting on June 2, 2016, neonates and adults of the cladocerans *D. gessneri* and *D. birgei* were offered as prey, and the predators were fourth instar larvae of *C. brasiliensis*. Cladoceran ovigerous females, previously cultivated in the laboratory, were isolated 24-36 h before the experiment for the hatching of neonates. Previously cultivated adult prey were selected for this

experiment. Chaoborid larvae were collected using a 58 µm plankton net, 48 h before the beginning of the experiments, acclimated, and fed cultured cladocerans in the laboratory to avoid the hunger effect (Butler and Burns, 1993). During the experiment, the cladocerans were fed the same chlorophycean of the cultures (1 mg C L⁻¹) to avoid death due to food limitation. To perform a test simulating high predation, the cladocerans were placed in 140 mL glass bottles, each containing two fourth instar larvae of *Chaoborus*. The bottles were kept on a plankton wheel under the same conditions as the cultures throughout the experiment. The treatments were as follows (4 replicates each): a) 10 neonates of *D. gessneri*; b) 10 neonates of *D. birgei*; c) 5 neonates of *D. gessneri* + 5 neonates of *D. birgei*; d) 5 neonates of *D. gessneri* + 5 adult females of *D. birgei*; e) 5 neonates of *D. birgei* + 5 adult females of *D. gessneri*; f) 5 adult females of *D. gessneri* + 5 adult females of *D. birgei*. After 24 h, the experiment was completed, all survivors were counted, and the replicates were also examined for prey death unrelated to predation. The ingestion rate was calculated according to the following formula (Gilbert and Burns, 1999):

$$IR = IP_{control} - IP_{experimental} / T * N,$$

where IP_{control} = initial number of intact prey, IP_{experimental} = final number of intact prey, T = duration of the experiment, N = number of predators.

Experiment 2: Predation of *Chaoborus brasiliensis* on *Ceriodaphnia richardi* and *Diaphanosoma birgei*

The experiment started on June 24, 2016, with neonates and adults of *C. richardi* and *D. birgei* used as prey items. The experimental design and conditions for the preparation and execution of the experiment were the same as those described in Experiment 1. The treatments were (4 replicates each): a) 10 neonates of *D. birgei*; b) 10 neonates of *C. richardi*; c) 5 neonates of *C. richardi* + 5 neonates of *D. birgei*; d) 5 neonates of *C. richardi* + 5 adult females of *D. birgei*; e) 5 neonates of *D. birgei* + 5 adult females of *C. richardi*; f) 5 adult females of *C. richardi* + 5 adult females of *D. birgei*. Two fourth instar larvae of *Chaoborus* were added to each treatment.

After 24 h, the experiment was completed, all survivors were counted, and the ingestion rate was calculated. The same care was taken to evaluate the prey deaths unrelated to predation.

Experiment 3: Predation of the water mite *Krendowskia* sp. on *Ceriodaphnia richardi* and *Daphnia gessneri*

The experiment started on August 09, 2016, the prey were neonates and adults of *C. richardi* and *D. gessneri*, and the predator was the water mite *Krendowskia* sp. The procedures regarding prey sampling and the preparation

Tab. 1. Average size (± SD) of prey (neonates and adults) and predators used in the experiments.

Prey	Size (mm)
<i>Ceriodaphnia richardi</i>	Neonate: 0.30±0.03
	Adult: 0.70±0.0
<i>Diaphanosoma birgei</i>	Neonate: 0.30±0.02
	Adult: 0.87±0.03
<i>Daphnia gessneri</i>	Neonate: 0.55±0.02
	Adult: 1.22±0.01
Predator	
<i>Chaoborus brasiliensis</i>	(IV instar): 6.14±0.74 *
<i>Krendowskia</i> sp.	Adult: 1.14±0.03 °

*Arcifa (2000); °Cassano et al. (2002).

of the experiments followed the methods described in Experiment 1.

The mites were collected in the lake with a 58 µm plankton net 48 h before the beginning of the experiments, acclimated, and fed in the laboratory with cultured cladocerans to avoid the hunger effect (Butler and Burns, 1993). During the experiment, *D. spinosus* was used to feed the cladocerans at a non-limiting concentration of 1 mg C L⁻¹.

The organisms were kept in 100 mL test tubes, each containing one predator, to avoid interference between predators, as recommended by Matveev *et al.* (1989). The treatments were (4 replicates each): a) 10 neonates of *C. richardi*; b) 10 neonates of *D. gessneri*; c) 5 neonates of *C. richardi* + 5 neonates of *D. gessneri*; d) 5 neonates of *C. richardi* + 5 adult females of *D. gessneri*; e) 5 neonates of *D. gessneri* + 5 adult females of *C. richardi*; f) 5 adult females of *C. richardi* + 5 adult females of *D. gessneri*.

The tubes were kept in a germination chamber (FANEM, model CDG) at 23°C with a 12:12 h photoperiod under dim light, to mimic the lake conditions. After 24 h, the experiment was completed, all survivors were counted, and the ingestion rate was calculated. A search was performed in the replicates to evaluate death due to other causes since the mite causes a perforation in the cladoceran carapace that is easy to identify.

Data analysis

The Student’s *t*-test was used to compare the mean number of survivors with the initial numbers for each treatment of the experiments. A one-way ANOVA was used with the post-hoc Fisher test to compare the ingestion rates of each predator. The ingestion rates for all treatments in each experiment were included in the analyses. All analyses were performed using STATISTICA 8.0. StatSoft software. The level of significance was set at P<0.05.

RESULTS

Experiment 1: Predation of *C. brasiliensis* on *D. gessneri* and *D. birgei*

The predator significantly reduced the number of *D. gessneri* and *D. birgei* (*t*-test, P<0.001; for both) in treatments with neonates placed alone (Figs. 1a and b, respectively) and together (*t*-test, P<0.001 for both, Fig. 1c). The numbers of adults of *D. birgei* and neonates of *D. gessneri* were also significantly reduced by the predator (*t*-test, P<0.001 and P=0.003, respectively) when placed together (Fig. 1d). When the prey offered were adults of *D. gessneri* and neonates of *D. birgei*, only the second species

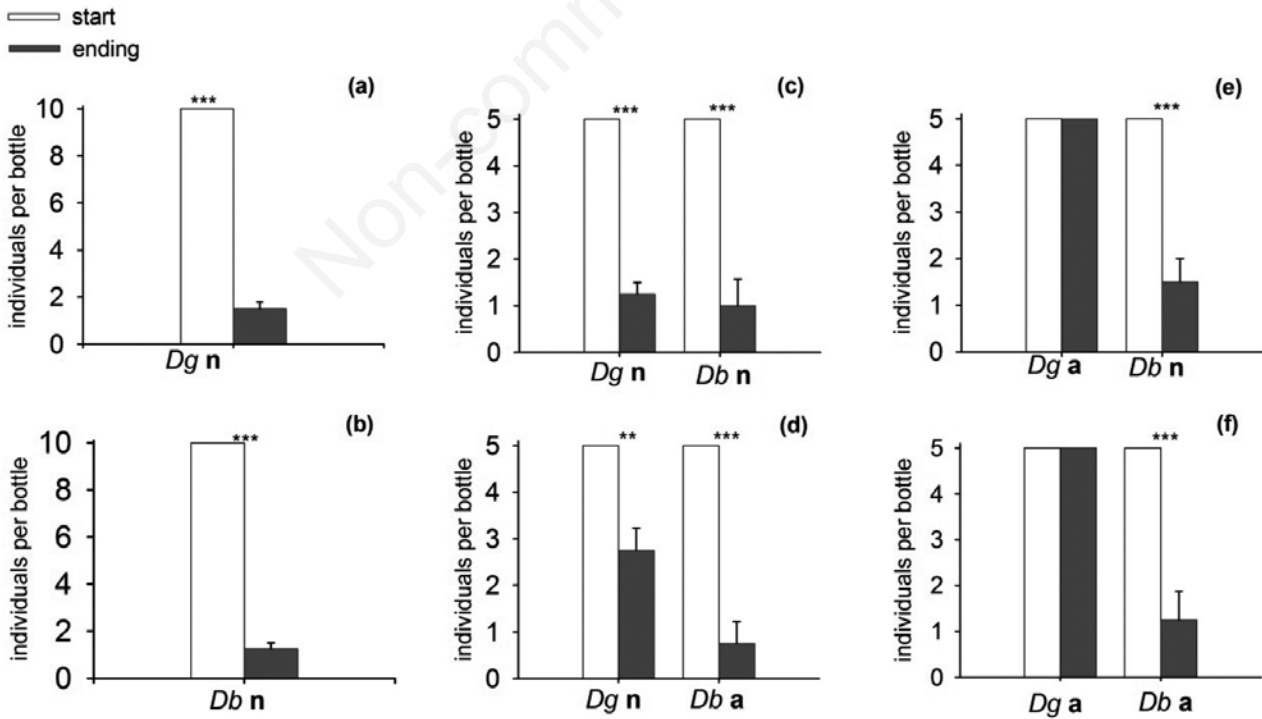


Fig. 1. Number of *D. gessneri* and *D. birgei* individuals, at the beginning (white) and end (black) of the experiment, exposed to the predator *C. brasiliensis*; “Dgn” and “Dbn” represent neonates of both species, respectively; “Dga” and “Db a”, represent adults, respectively. Bars are standard error of the mean (±); *P<0.05; **P<0.01; ***P<0.001.

was significantly preyed upon (*t*-test, $P < 0.001$) (Fig. 1e). Predation on adults of both species placed together only occurred on *D. birgei* (Fig. 1f), which was significantly reduced by *Chaoborus* (*t*-test, $P < 0.001$).

The prey ingestion rate was density dependent since neonates in treatments alone (10 individuals) were consumed more than when 5 neonates of each species were offered together. Daily means of ingestion rate of *D. gessneri* and *D. birgei* by *C. brasiliensis* differed between treatments (one-way ANOVA, $F = 8.21$, $P < 0.001$) (Fig. 2). Ingestion rate of neonates of *D. gessneri* by *C. brasiliensis* ranged from 1.1 to 4.3 prey predator⁻¹ day⁻¹, while the ingestion rate of *D. birgei* neonates ranged from 1.8 to 4.4 prey predator⁻¹ day⁻¹. There was no difference between predator ingestion rates of *D. gessneri* and *D. birgei* neonates placed in separate bottles (*Dgn*, *Dbn*) or together (*Dgn* + *Dbn*). However, when the prey were neonates of *D. gessneri* and adults of *D. birgei* placed together (*Dgn* + *Dbn*), the predator ingested the second species (post hoc Fisher test, $P = 0.02$). *C. brasiliensis* preyed on *D. birgei* at any developmental stage.

Experiment 2: Predation of *C. brasiliensis* on *C. richardi* and *D. birgei*

C. richardi and *D. birgei* were preyed on by *C. brasiliensis* in all treatments (Fig. 3). In individual treatments, the number of neonates of *C. richardi* (Fig. 3a) and *D. birgei* (Fig. 3b) was significantly reduced by the predator (*t*-test, $P < 0.001$ for both). A similar result was observed when the neonates were placed together (Fig. 3c),

with a significant reduction in the number of both species (*t*-test, $P < 0.001$ for both). The predator also significantly reduced the number of adults of *D. birgei* and neonates of *C. richardi* (*t*-test, $P < 0.001$ and $P = 0.02$, respectively), placed together (Fig. 3d). A similar situation occurred when the prey were adults of *C. richardi* and neonates of *D. birgei* (*t*-test, $P = 0.01$, and $P < 0.001$, respectively) (Fig. 3e). There was also predation on adults, with a significant reduction in *C. richardi* (*t*-test, $P = 0.02$) and *D. birgei* (*t*-test, $P < 0.001$) when together (Fig. 3f).

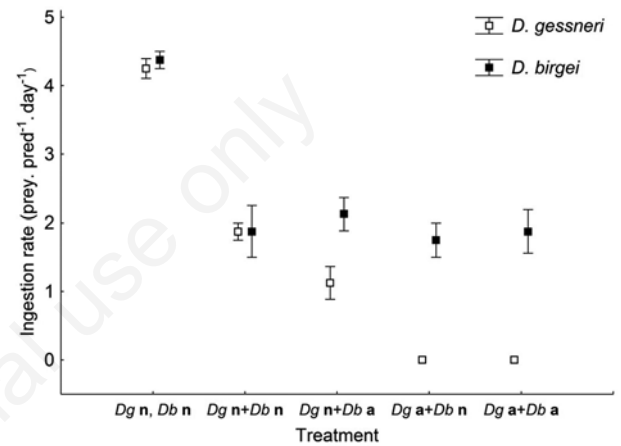


Fig. 2. Ingestion rates of neonates and adults of *D. gessneri* and *D. birgei* by *C. brasiliensis*; “Dgn” and “Dbn” represent the neonates of both species, respectively; “Dga” and “Dba”, represent the adults of the species, respectively. Bars indicate the standard error of the mean (\pm).

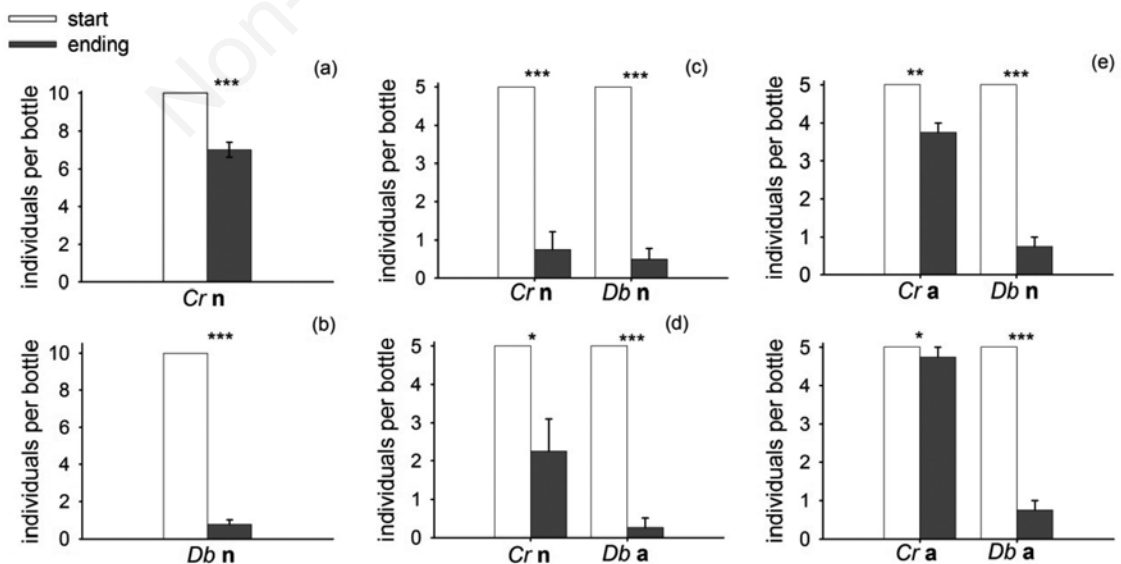


Fig. 3. Number of *C. richardi* and *D. birgei* individuals at the beginning (white) and end (black) of the experiment, exposed to the predator *C. brasiliensis*; “Crn” and “Dbn” represent neonates of both species, respectively; “Cra” and “Dba”, represent adults, respectively. Bars are the standard error of the mean (\pm); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

As observed in experiment 1, the ingestion rate was density dependent, but only for neonates of one species, *D. birgei*. Daily average ingestion rates of *C. richardi* and *D. birgei* by *C. brasiliensis* differed among treatments (one-way ANOVA, $F = 15.29$, $P < 0.001$) (Fig. 4). The daily ingestion rate of neonates of *C. richardi* by chaoborid larvae varied from 1 to 2 prey predator⁻¹ day⁻¹ and from 2 to 5 prey predator⁻¹ day⁻¹ of *D. birgei*, while for adults, it varied from 0.4 to 0.6 prey predator⁻¹ day⁻¹ and from 2.1 to 2.4 prey predator⁻¹ day⁻¹ for the first and second species, respectively. In individual treatments (*Crn*, *Dbn*), the predator consumed significantly more neonates of *D. birgei* than of *C. richardi* (post hoc Fisher test, $P < 0.001$). At the same time, there was no difference for neonates placed together (*Crn + Dbn*). There was also no difference between the ingestion rates of neonates of *C. richardi* and adults of *D. birgei* when placed together (*Crn + Dba*). The predator preferentially consumed neonates and adults of *D. birgei* over adults of *C. richardi*; the ingestion rates were significantly higher for the first species in *Cra + Dbn* and *Cra + Dba* (post-hoc Fisher test, $P < 0.001$ for both treatments).

Experiment 3: Predation of the water mite *Krendowskia* sp. on *C. richardi* and *D. gessneri*

Predation by *Krendowskia* sp. was limited to a single prey, *D. gessneri*, while neither the neonates (Fig. 5 a,c,e)

nor the adults (Fig. 5 d,f) of *C. richardi* were consumed by the predator. The predator consumed but did not significantly reduce the number of neonates of *D. gessneri* in the individual treatments (Fig. 5b). In contrast, there was a significant reduction in the number of neonates of *D.*

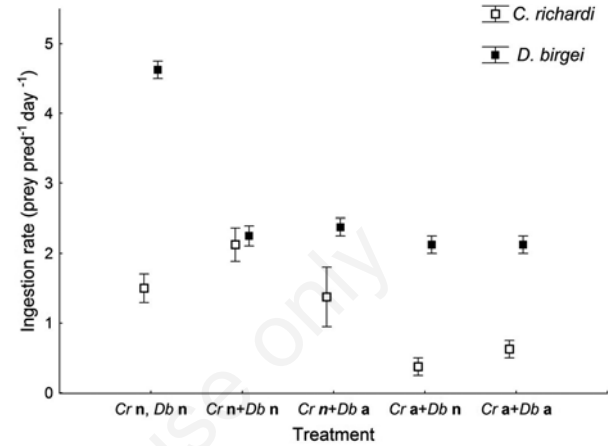


Fig. 4. Ingestion rates of neonates and adults of *C. richardi* and *D. birgei* by *C. brasiliensis*; “Crn” and “Dbn” represent the neonates of both species, respectively; “Cra” and “Dba”, represent the adults of the species, respectively. Bars indicate the standard error of the mean (\pm).

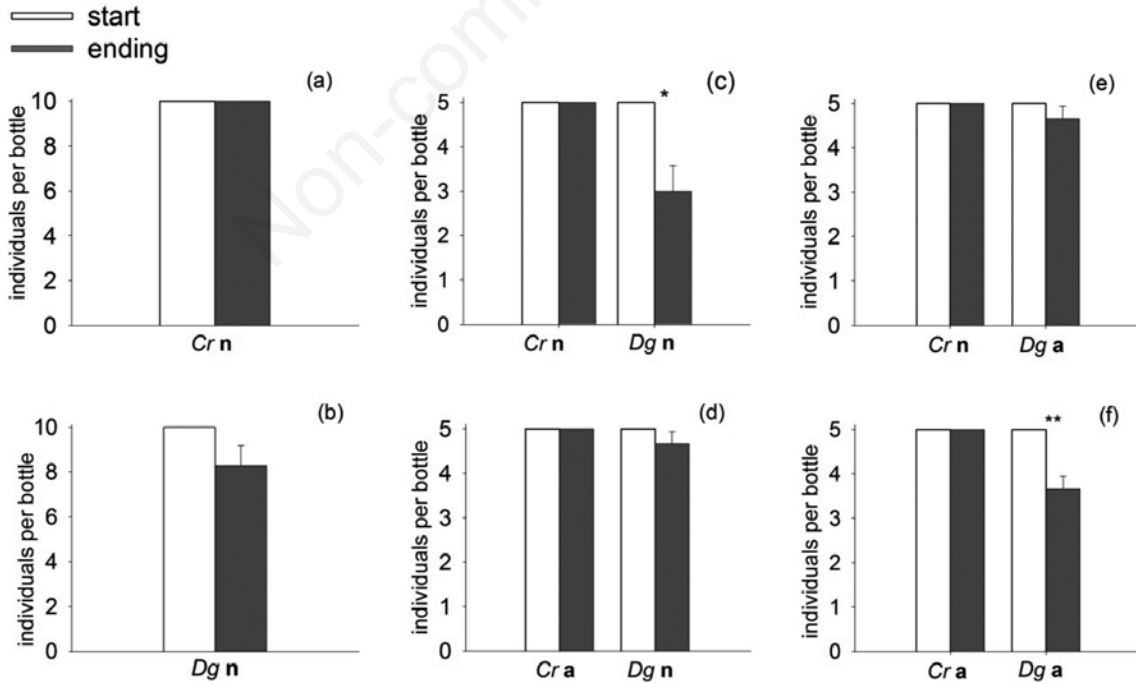


Fig. 5. Number of *C. richardi* and *D. gessneri* individuals at the beginning (white) and end (black) of the experiment, exposed to the predator *Krendowskia* sp.; “Crn” and “Dgn” represent neonates of both species, respectively; “Cra” and “Dga”, represent adults, respectively. Bars are the standard error of the mean (\pm); * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

gessneri (*t*-test, $P=0.02$) when placed together with neonates, but not with adults of *C. richardi* (Fig. 5c and d, respectively). Adults of *D. gessneri* were not significantly reduced in the presence of neonates of *C. richardi* (Fig. 5e). However, the reduction was significant (*t*-test, $P=0.01$) in the presence of adults of the second species (Fig. 5f).

The density dependence of the ingestion rates was not observed for this predator. There was a difference in the ingestion rates obtained for the different treatments (one-way ANOVA, $F = 2.94$, $P=0.046$) (Fig. 6). Daily averages of ingestion rates for *D. gessneri* ranged from 1 to 3 prey predator⁻¹ day⁻¹ for neonates, 1 to 2 prey predator⁻¹ day⁻¹ for adults, and was null for *C. richardi*.

DISCUSSION

Experiment 1: Predation of *C. brasiliensis* on *D. gessneri* and *D. birgei*

The predation pressure exerted exclusively on young *D. gessneri* supports the hypothesis that larvae of chaoborids do not prey on adults of the species (Arcifa, 2000; Castilho-Noll and Arcifa, 2007a).

Gape-limited predation of invertebrates, as happens with *Chaoborus*, favors large zooplankton (Zaret, 1980). The increase in body size and mouth diameter in these predators allows late instars to capture and ingest larger prey (Arcifa, 2000; Castilho-Noll and Arcifa, 2007a). However, the incidence of *Chaoborus* predation pressure on juveniles of large species is common, as reported in several studies, especially in *Daphnia* species (Lewis,

1977; Pastorok, 1981; Arcifa, 2000; Castilho-Noll and Arcifa, 2007a). *Chaoborus* larvae tend to remove small prey items as the attack efficiency decreases with increasing prey size (Mumm, 1997). In Lake Monte Alegre, an analysis of the crop contents of the four larval instars of chaoborids collected from 1985-86 revealed that more than 50% of the dietary items of I and II instars were composed of the dinophycean *Peridinium*, while the same proportion of cladocerans, especially *Bosmina tubicen*, made up the diet of III and IV instars (Arcifa, 2000). In the period 1998-99 (Castilho-Noll and Arcifa, 2007a), *B. tubicen* was replaced by *Peridinium*, copepods, and rotifers when *Bosmina* decreased in the lake (Fileto, 2001). This drastic reduction in the densities of *B. tubicen* in the lake led to small *D. gessneri* occupying the position of the most consumed cladoceran by the III and IV instars of chaoborid larvae (Castilho-Noll and Arcifa, 2007a).

Chaoborus predation on *Diaphanosoma* has been reported in several studies (Fedorenko, 1975; Lewis, 1977; Winner and Greber, 1980; Neill, 1981; Mumm, 1997), and before being confirmed in our experiment, was unknown in Lake Monte Alegre, despite the low densities of *D. birgei* suggesting the existence of predation influence (Ferreira, 2013; Souza, 2015). Predation on young and adult *D. birgei* can affect its population more than that of *D. gessneri* because predation also affects its reproductive phase. According to DeMott (1989), the reproduction of a species can be most affected if adults are also preyed on, further decreasing their densities. In experiments, Neill (1981) found that *Diaphanosoma brachyurum* was severely suppressed by *Chaoborus*. However, the mortality was compensated by the rapid growth of the species in summer, preventing the species from being eliminated by the predator.

D. birgei can be even more affected by predation, considering the higher ingestion rates of *C. brasiliensis* in its young and adult stages in this study, in comparison to the ingestion rates of young *D. gessneri*. Mumm (1997) also found through experiments that in the German Lake Plußsee, the abundance of *Diaphanosoma brachyurum* was reduced in four of the five experiments, while the abundance of the large cladoceran, *Daphnia 'longispina'* (a complex of species), was not significantly reduced in any of them. In a similar study, Winner and Greber (1980) observed that *Chaoborus punctipennis* larvae consumed 100% of *Diaphanosoma leuchtenbergianum*, 67% of *Daphnia parvula*, and 57% of *Diaptomus pallidus* in the control treatments, whereas 90% of *D. leuchtenbergianum*, 10% of *D. parvula*, and <1 % of *D. pallidus* were ingested in the shared treatments. The authors found that *Diaphanosoma* is vulnerable to *Chaoborus* predation and observed that, in Lake Acton, it is primarily confined to the upper 3 m, whereas *Chaoborus* is abundant in layers deeper than 3 m.

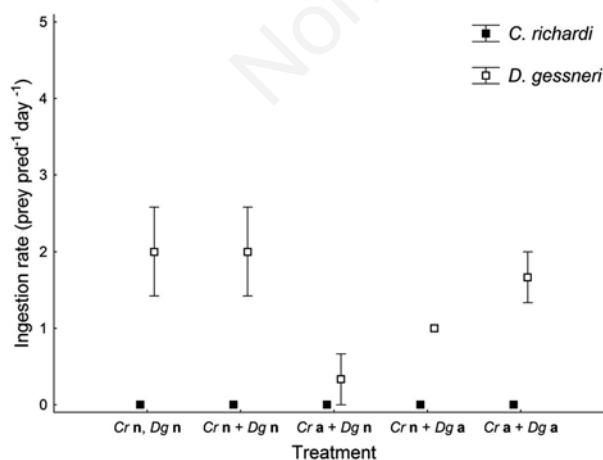


Fig. 6. Ingestion rates of neonates and adults of *C. richardi* and *D. gessneri* by the water mite *Krendowskia* sp.; “Crn” and “Dgn” represent the neonates of both species, respectively; “Cra” and “Dga”, represent the adults of the species, respectively. Bars indicate the standard error of the mean (\pm).

Experiment 2: Predation of *C. brasiliensis* on *C. richardi* and *D. birgei*

The higher predation of *C. brasiliensis* on juveniles and adults of *D. birgei* in relation to juveniles and adults of *C. richardi*, as indicated by the ingestion rates, agrees with several experimental studies that reported different species of *Diaphanosoma* as the preferred prey of this predator (Fedorenko, 1975; Lewis, 1977; Winner and Greber, 1980). Considering the similarity of the average size of neonates and adults of *C. richardi* (0.30 and 0.70 mm, respectively) and *D. birgei* (0.30 and 0.60-0.90 mm, respectively), the preference of chaoborid larvae for the second species may be related to the facility to locate, attack, and ingest it, and not its body size. According to Swift and Fedorenko (1975), the prey choice by the predator may depend on prey availability and the chances of contact between them, which are affected by the swimming behavior and escape responses of the prey. They add that once the contact is made, the prey size, shape, and behavior are responsible for successful ingestion by the predator. For Smyly (1980), these characteristics justify the choice of one prey over the other. In experiments, the author observed that, when the prey shape and size were similar, *Chaoborus* predation was more intense on the most active swimmer. In the present study, *D. birgei* was the most active species in relation to *C. richardi* due to its fast-swimming behavior, hampering its capture with a pipette during the experiment.

Due to their opportunism, *Chaoborus* larvae consume more individuals of some species than others, choosing the easiest prey to capture (Swift and Fedorenko, 1975). Winner and Greber (1980) related *Diaphanosoma leuchtenbergianum* vulnerability to its cylindrical body, swimming movements, and responses to tactile stimuli, which are more similar to those of a copepod than those of a daphnid. Copepods are also among the preferred prey of *Chaoborus* (Lewis, 1977; Riessen, 1982; Butler and Burns, 1993; Castilho-Noll and Arcifa, 2007a). However, although *Chaoborus* selectivity is high for *Diaphanosoma* and copepods, the preference is greater for cladocerans (Lewis, 1977). Other experimental studies also point to greater selectivity of *Chaoborus* for *Diaphanosoma* than for copepods (Fedorenko, 1975; Lewis, 1977).

The morphology of *Ceriodaphnia* facilitated manipulation by *Chaoborus* in experiments by Lynch (1979) and Smyly (1980). In Smyly's (1980) experiments, *Ceriodaphnia quadrangula* was the most preyed on item by *Chaoborus* when paired with similar-sized prey, that is, *Diaptomus gracilis* (currently *Eudiaptomus gracilis*) and young *Daphnia obtusa*. According to the author, the continuous swimming mode facilitated the capture of *Ceriodaphnia* and was easily manipulated due to its size. The characteristics shared by *Ceriodaphnia* and

Diaphanosoma (size and swimming behavior) seem to justify *Chaoborus* selection for both species. However, *Ceriodaphnia cornuta*, from Lake Monte Alegre, was avoided by chaoborid larvae, even at high densities (Arcifa, 2000), probably owing to the presence of spines on the carapace. In Mumm's (1997) experiments, *Ceriodaphnia quadrangula* and *Diaphanosoma brachyurum* were the most affected species, and *Daphnia 'longispina'* the species least affected by *Chaoborus* predation. Lynch (1979) observed significant changes in the composition of the zooplankton community with an increase in *Chaoborus americanus*. The author observed that *Bosmina longirostris* was the first species to decline, followed by *Ceriodaphnia reticulata*, nauplii, adults of *Diaptomus clavipes* (currently *Agladiaptomus clavipes*), *Daphnia pulex*, and *D. galeata mendotae*.

Experiment 3: Predation of *Krendowskia* sp. on *C. richardi* and *D. gessneri*

The finding that the mite *Krendowskia* sp. consumed neither neonates nor adults of *C. richardi* agrees with that of Balseiro (1992), who found no evidence of predation of the water mite *Limnesia patagonica* on juveniles and adults of *Ceriodaphnia dubia*. Similarly, nymphs of *Krendowskia* sp. did not prey on another congeneric cladoceran species, *C. cornuta*, in the experiments of Cassano *et al.* (2002) with species from Lake Monte Alegre. Contrary to the results presented here, some experimental studies mention different species of *Ceriodaphnia* among the prey of aquatic mites (Gliwicz and Biesiadka, 1975; Riessen, 1982; Butler and Burns, 1991, 1993), in agreement with the hypothesis that morphological and behavioral differences between different prey species make some more vulnerable than others to predation (Riessen, 1982; Gliwicz and Pijanowska, 1989).

The selection pattern of aquatic mites mainly depends on the ability of the prey to detect the predator and flee before being attacked, more than on the size and thickness of the prey carapace (Riessen, 1982). Observations made during the current experiment showed that *C. richardi* avoided the deeper layers of the tubes, where the mites were concentrated and remained close to the surface. This behavior can be a strategy to avoid encounters with the predator. Spatial segregation between prey and predator decreases the predation rate, especially in enclosures (Matveev *et al.*, 1989). The smaller size of neonates of *C. richardi* relative to those of *D. gessneri*, is another factor that could favor the species due to the lower frequency of encounters with the predator.

The number of prey captured by a mite depends on several factors, mainly related to experimental conditions (Matveev *et al.*, 1989), such as temperature (Davids *et al.*, 1981), interference between predators (Matveev *et al.*,

1989), initial prey density (Fedorenko, 1975; Butler and Burns, 1993), and different prey identities (Riessen, 1982). These factors justify the wide difference in the predation rates of aquatic mites obtained in several experimental studies: 9-25 prey predator⁻¹ day⁻¹ (Butler and Burns, 1993); 3-4 prey predator⁻¹ day⁻¹ (Gliwicz and Biesiadka, 1975); 10-15 prey predator⁻¹ day⁻¹ (Riessen, 1982); 24-168 prey predator⁻¹ day⁻¹ (Matveev *et al.*, 1989); 7 prey predator⁻¹ day⁻¹ (Cassano *et al.*, 2002); and 1-3 prey predator⁻¹ day⁻¹ in the present study. The low predation rate of *Krendowskia* sp. on *D. gessneri* in our experiment may be related to the fact that the mites were fed before the experiment, during the acclimation period, unlike other studies that induced the hunger effect before the experiments (Riessen, 1982; Matveev *et al.*, 1989; Cassano *et al.*, 2002). Butler and Burns (1993) used two different methods of acclimating the mites in their experiments (with and without food) and found that the predation rates of the mites, which were deprived of food 24 h before the experiment, were significantly higher than those that were pre-conditioned along with the initial prey densities.

Predation of aquatic mites on *Daphnia gessneri* has also been found in other experimental studies on *Daphnia* species (Riessen, 1982; Butler and Burns, 1991; Cassano *et al.*, 2002), despite the formation of helmets and caudal spines in *Daphnia* spp. (Riessen, 1982). In the experiments of Cassano *et al.* (2002), out of the five organisms offered to the mite *Krendowskia* sp., including two cladocerans, *Daphnia gessneri*, and *Ceriodaphnia cornuta*, two copepods, *Thermocyclops decipiens* and *Tropocyclops prasinus*, and III and IV instar larvae of *C. brasiliensis*, only the cladoceran *D. gessneri* was preyed on. The effect of predation by the mite *Piona* sp. on different populations of cladocerans from an Argentine lake may have been responsible for more than 50% of the mortality of *Daphnia laevis* (Matveev *et al.*, 1989).

Linking experiments and lake data

Knowledge of predation on different developmental stages of the studied cladocerans allowed us to better understand on the abundance and spatial distribution of cladoceran populations in the lake.

The experiments showed that cladoceran populations are not equally susceptible to predation by *Chaoborus* and water mites, as the predators can feed on all stages or a single developmental stage of the different prey species. Thus, the population of *D. gessneri* would be less susceptible than those of *C. richardi* and *D. birgei* to predation by *Chaoborus* larvae, since only juveniles are preyed on, while the populations of the other two cladocerans also lose adults to predators. On the other hand, *D. gessneri* is more sensitive to predation by mites (Cassano *et al.*, 2002; this study).

Strategies to decrease predation impact have been detected in the cladoceran populations in the lake. The low abundance of *D. birgei* in the limnetic zone of the lake (Ferreira, 2013) could be attributed to predation by *Chaoborus*, which is more abundant in this zone (Arcifa *et al.*, 2016), as well as to its preference for the littoral zone of the lake (Souza *et al.*, 2017), which decreases spatial overlap with the predator (Arcifa *et al.*, 2016). The lack of sensitivity of this species to kairomones released by *Chaoborus* larvae (Ferreira and Arcifa, in preparation) increases its vulnerability to predation. On the other hand, high reproductive rates and the rapid development of *D. birgei* (Ferreira and Arcifa, in preparation) could offset mortality due to predation. These characteristics would explain why this species is still present in the lake. *D. birgei* occurred in the limnetic zone, as observed in the studies carried out in 1985-86 (Arcifa *et al.*, 1992) and 1988-89 (Arcifa *et al.*, 1998), that is, before the appearance of the mite *Krendowskia* sp. in 1998-99 (Arcifa *et al.*, 2015). Although there are no data on predation of this species by mites, *Chaoborus* predation increased in the limnetic zone after the appearance of the second predator because there was a change in the diel vertical migratory behavior of fourth instar of *Chaoborus* larvae. During the day, the mites migrated to the bottom of the lake (Arcifa *et al.*, 2016), and as they prey on *Chaoborus* larvae, as seen in direct observations on the stereomicroscope (Cassano *et al.*, 2002), the larvae started to occupy the water column during the day in greater abundance, increasing predation pressure.

Unlike *Diaphanosoma birgei*, *Ceriodaphnia richardi* is abundant in both limnetic and littoral zones of the lake (Souza *et al.*, 2017). When assessing the food quality in the littoral zone of the lake, Souza *et al.* (2017) found that it is suitable for the development of both cladocerans and, therefore, food supply probably has no influence on the distribution of these organisms in the lake. Among the main factors that influence the abundance of cladocerans, that is, available food, competition, and predation pressure (Lazareva, 2012), the first factor seems to have a lesser impact on the species. Although the mechanisms involved in the distribution of these species in the lake are not fully understood, it is evident that the occupation of the littoral zone by both species reduces their encounters with limnetic predators. However, the incidence of *Chaoborus* predation also on adults of *Ceriodaphnia* and *Diaphanosoma* might affect the abundance of species in the lake, especially in the warm season, when predators are more abundant (Arcifa *et al.*, 2015). On the other hand, the high reproductive potential of both species (Souza *et al.*, 2017) would offset the mortality imposed by predators in the lake.

However, the occupation of the littoral zone of the lake can expose cladocerans to other predators that inhabit

this area, including notonectids and gerrids. Notonectids occur in higher densities in the littoral zone ($\sim 140 \text{ ind m}^{-2}$) than in the limnetic zone, and their juveniles preyed on *Ceriodaphnia richardi* and *Daphnia gessneri* in laboratory experiments (Domingos and Arcifa, 2017a). Gerrids are also more abundant in the littoral zone, although at lower densities ($\sim 7 \text{ ind m}^{-2}$) than notonectids (Domingos and Arcifa, 2017b). The cladocerans *C. richardi* and *D. gessneri* were preyed on by gerrids in experiments, with gerrid juveniles preying on both species and adults preying only on *Daphnia* (Domingos and Arcifa, 2017b). DNA extracted from the digestive tube of notonectids and gerrids from the lake revealed the ingestion of cladocerans, such as *Daphnia* and *Diaphanosoma*.

Diel horizontal migration of cladocerans is not an escape strategy from invertebrate predators in this lake, or in most tropical shallow lakes (Arcifa *et al.*, 2016). However, nocturnal or reverse diel vertical migration could be a strategy to decrease predation (Percicarrari *et al.*, 2004; Minto *et al.*, 2010; Arcifa *et al.*, 2016).

Water mite predation is considered relevant when their density exceeds 100 ind m^{-3} (Riessen, 1982). The mite densities recorded in Lake Monte Alegre ranged from 250 ind m^{-3} to 2000 ind m^{-3} between 1998 and 2012 (Percicarrari, 2000; Fileto, 2001; Ferreira *et al.*, 2018). Such densities could affect the mortality of cladoceran species (Matveev *et al.*, 1989; Balseiro, 1992). This predator has a potential impact on cladocerans in the lake, but its impact is probably lower than that caused by the dipteran *C. brasiliensis* (Arcifa *et al.*, 2015).

Changes in the composition and density of cladoceran species in Lake Monte Alegre are more evident in the warm season (spring and summer) than in the cool season, along with an increase in *Chaoborus* density (Arcifa *et al.*, 2015). A sharp reduction in *Ceriodaphnia* density was observed in this season (Ferreira *et al.*, 2018), while *Diaphanosoma* remained less abundant throughout the year in the limnetic zone (Ferreira, 2013). The laboratory experiments in the present study provide evidence that *Chaoborus* predation is of significant importance for lake grazers and that both cladoceran species, *D. birgei* and *C. richardi*, can be strongly affected by it, the first being the most affected species. However, predation by *Chaoborus* larvae is less intense in the natural community than in the laboratory, as lower prey densities and spatial segregation between predator and prey in the environment reduce the encounter rate between them.

The results obtained in the present study confirm the occurrence of predation by the mite *Krendowskia* sp. on *Daphnia*, but not on *Ceriodaphnia*. The impact of mite predation on juveniles and adults of *D. gessneri*, in addition to the predation impact exerted by chaoborids on juveniles of the species (Arcifa, 2000; Castilho-Noll and

Arcifa, 2007a, present study), is in agreement with the hypothesis of Arcifa *et al.* (2015) that predation may be one of the most important factors that influence the structure of the zooplankton community in Lake Monte Alegre. Competition could be another important factor, but experiments using seston from the lake as food did not result in clear competition among cladocerans (Ferreira and Arcifa, in preparation), although it occurs when a laboratory alga was offered in limited concentrations. Experiments on competition between *Daphnia gessneri* and *Ceriodaphnia richardi* under food limitation showed that *C. richardi* was a superior competitor to *D. gessneri* (Ferreira *et al.*, 2018). However, in the lake, the fluctuations of the populations of the two species indicated the prevalence of predation, because although there was a higher carbon concentration and a higher egg production per female in the warm season, their abundance was lower, particularly for *C. richardi* (Ferreira *et al.*, 2018). Lower predation pressure by *Chaoborus* larvae and mites allowed higher abundances of the two species of cladocerans in the cool season, despite lower food concentrations (Ferreira *et al.*, 2018).

According to Arcifa *et al.* (2015), the success or recovery of some cladoceran populations after the appearance of predatory water mites in Lake Monte Alegre may be related to their ability to occupy the littoral zone of the lake, where *Chaoborus* and water mites are much less abundant, as observed for other cladocerans, such as *Bosmina tubicen*, *C. richardi*, and *D. birgei*. Arcifa *et al.* (2015) suggested, however, that the littoral zone is not a permanent habitat for these species, but it can allow the species to maintain a minimum population density, ensuring the reoccupation of the limnetic zone when conditions are more favorable.

CONCLUSIONS

Juveniles of *D. gessneri* are preyed on by *C. brasiliensis* while adults of *D. gessneri* are preyed on by *Krendowskia* sp.; *C. richardi* is preyed on by *C. brasiliensis* (both juvenile and adult) but not by *Krendowskia* sp., whereas *D. birgei* is preyed on by *C. brasiliensis* (juvenile and adult), but predation by *Krendowskia* sp. in the lake is unknown. The predation pressure exerted by *C. brasiliensis* and *Krendowskia* sp. varies with prey species, prey body size, swimming behavior, predator food preference, and prey availability. Such information supports the hypothesis that differential predation over different developmental stages of species, resulting in a greater impact on populations whose juveniles and adults are preyed on, could explain species abundance and strategies in the field.

The ability of the predator to prey on more than one species of different size classes can allow prey populations to re-establish themselves in the lake after

periods of intense predation (warm season), in addition to controlling competition by decreasing the abundance of prey populations. Prey strategies can reduce predation impact, for example, through the occupation of the littoral zone, where the predators are less abundant, or by changing their diel migratory behavior.

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REFERENCES

- Arcifa MS, 2000. Feeding habits of Chaoboridae larvae in a tropical Brazilian reservoir. *Braz. J. Biol.* 60:591-597.
- Arcifa MS, Ferreira TCS, Fileto C, Castilho-Noll MSM, Bunioto TC, Minto WJ, 2015. A long-term study on crustacean plankton of a shallow tropical lake: the role of invertebrate predation. *J. Limnol.* 74:606-617.
- Arcifa MS, Gomes EAT, Meschiatti AJ, 1992. Composition and fluctuations of the zooplankton of a tropical Brazilian reservoir. *Arch. Hydrobiol.* 123:479-495.
- Arcifa MS, Meschiatti AJ, 1993. Distribution and feeding ecology of fishes in a Brazilian reservoir: Lake Monte Alegre. *Interciencia* 18:302-313.
- Arcifa MS, Meschiatti AJ, 1996. *Tilapia rendalli* in the Lake Monte Alegre, a case of planktivory. *Acta Limnol. Brasil.* 8:221-229.
- Arcifa MS, Peticarrari A, Bunioto TC, Domingos AR, Minto WJ, 2016. Microcrustaceans and predators: diel migration in a tropical lake and comparison with shallow warm lakes. *Limnetica* 35:281-296.
- Arcifa MS, Silva LHS, Silva MHL, 1998. The planktonic community in a tropical Brazilian reservoir: composition, fluctuations and interactions. *Rev. Brasil. Biol.* 58:241-254.
- Balseiro EG, 1992. The role of pelagic water mites in the control of cladoceran populations in a temperate lake of Southern Andes. *J. Plankton Res.* 14:1267-1277.
- Bezerra-Neto JF, Pinto-Coelho RM, 2002. Population dynamics and secondary production of *Chaoborus brasiliensis* (Diptera - Chaoboridae) in a small tropical reservoir: Lagoa do Nado, Belo Horizonte (MG). *Acta Limnol. Brasil.* 3:145-161.
- Butler MI, Burns CW, 1991. Predation by a water mite (*Piona exigua*) on enclosed populations of zooplankton. *Hydrobiologia* 220:30-48.
- Butler MI, Burns CW, 1993. Water mite predation on planktonic Cladocera: parallel curve analysis of functional responses. *Oikos* 66:5-16.
- Cassano CR, Castilho-Noll MSM, Arcifa MS, 2002. Water mite predation on zooplankton of a tropical lake. *Braz. J. Biol.* 62:565-571.
- Castilho-Noll MSM, Arcifa MS, 2007a. *Chaoborus* diet in a tropical lake and predation of microcrustaceans in laboratory experiments. *Acta Limnol. Brasil.* 19:163-174.
- Castilho-Noll MSM, Arcifa MS, 2007b. Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake. *Aquat. Ecol.* 41:587-598.
- Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ, 2002. The interaction between predation and competition: a review and synthesis. *Ecol. Lett.* 5:302-315.
- Davids C, Beintema EF, Mulder R, Weekenstroo JE, 1981. Feeding rate and egg production in water mites in relationship with temperature. *Verh. Internat. Verein. Limnol.* 21:1603-1606.
- DeMott WR, 1989. The role of competition in zooplankton succession, 195-252. In: U. Sommer (ed.), *Plankton Ecology: Succession in plankton communities*. Springer-Verlag.
- Domingos AR, Arcifa MS, 2017a. Distribution and fluctuations of backswimmers (Notonectidae) in a shallow tropical lake and predation on microcrustaceans. *Braz. J. Biol.* 77:108-117.
- Domingos AR, Arcifa MS, 2017b. Spatial and temporal distribution of gerrid (Heteroptera) and predation on microcrustaceans from a tropical shallow lake. *Braz. J. Biol.* 77:289-298.
- Dzialowski AR, Lennon JT, O'Brien WJ, Smith VH, 2003. Predator-induced phenotypic plasticity in the exotic cladoceran *Daphnia lumholtzi*. *Freshw. Biol.* 48: 1593-1602.
- Fedorenko AY, 1975. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. *Limnol. Oceanogr.* 20:250-258.
- Ferreira TCS, 2013. [Competição, predação e variação temporal de microcrustáceos planctônicos no Lago Monte Alegre]. [Master Thesis in Portuguese]. University of São Paulo, Brazil.
- Ferreira TCS, Arcifa MS, Domingos AR, 2018. Is competition an interaction as relevant as predation for tropical planktonic cladocerans? *Acta Limnol. Brasil.* 30 e1.
- Freitas, GTP, Crispim MC, Hernández MIM, 2007. Changes in life-history parameters of cladoceran *Ceriodaphnia cornuta* (Sars, 1886) in the presence of *Chaoborus* larvae. *Acta Limnol. Brasil.* 30:295-303.
- Fileto C, 2001. [O zooplâncton do Lago Monte Alegre: variação temporal e a influência das frações do fitoplâncton sobre o crescimento e reprodução de cladóceros]. [Master Thesis in Portuguese]. University of São Paulo, Brazil.
- Gilbert JJ, Burns C, 1999. Some observations on the diet of the backswimmer, *Anisops wakefieldi* (Hemiptera: Notonectidae). *Hydrobiologia* 412:111-118.
- Gliwicz ZM, Biesiadka E, 1975. Pelagic mites (Hydracarina) and their effect on the plankton community in a neo-tropical man-made lake. *Arch. Hydrobiol.* 76:65-88.
- Gliwicz ZM, Pijanowska J, 1989. The role of predation in zooplankton succession, 253-296. In: U. Sommer (ed.), *Plankton Ecology: Succession in plankton communities*. Springer-Verlag.

- Gu L, Lyu K, Dai Z, Fan M, Zhu X, Wang J, Wang X, Yang Z, 2017. Predator-specific responses of *Moina macrocopa* to kairomones from different fishes. *Int. Rev. Hydrobiol.* 102:83-89.
- Hanazato T, 1995. Combined effect of the insecticide carbaryl and the *Chaoborus* kairomone on helmet development in *Daphnia ambigua*. *Hydrobiologia* 310:95–10.
- Lazareva VI, 2012. The distribution of species of the genus *Diaphanosoma* (Crustacea, Cladocera) in reservoirs of Volga and Sheksna Rivers: impact of environmental factors. *Inland Water Biol.* 5:257–265.
- Lewis WM Jr, 1977. Feeding selectivity of a tropical *Chaoborus* population. *Freshwater Biol.* 7:311-325.
- Lynch M. 1979. Predation, competition, and zooplankton community structure: An experimental study. *Limnol. Oceanogr.* 24:253-272.
- Lynch M, 1980. The evolution of cladoceran life histories. *Q. Rev. Biol.* 55:23–42.
- Matveev VT, Martinez CC, Frutos SM, 1989. Predatory-prey relationships in subtropical zooplankton: water mite against cladocerans in an Argentine lake. *Oecologia* 79:489-495.
- Minto WJ, Arcifa MS, Peticarrari A, 2010. Experiments on the influence of *Chaoborus brasiliensis* on the diel vertical migration of microcrustaceans from Lake Monte Alegre. *Braz. J. Biol.* 70:25-35.
- Mumm H, 1997. Effects of competitors and *Chaoborus* predation on the cladocerans of a eutrophic lake: an enclosure study. *Hydrobiologia* 360:253-264.
- Neill WE, 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. *Oecologia* 48:164-177.
- Pastorok RA, 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62:1311-1324.
- Peticarrari A, 2000. [Migração vertical de microcrustáceos, Chaoboridae e Hydracarina no Lago Monte Alegre]. [Master Thesis in Portuguese]. University of São Paulo, Brazil.
- Peticarrari A, Arcifa MS, Rodrigues RA, 2004. Diel vertical migration of copepods in a Brazilian lake: a mechanism for decreasing risk of *Chaoborus* predation? *Braz. J. Biol.* 64:289-298.
- Saunders PA, Porter KG, Taylor BE, 1999. Population dynamics of *Daphnia* spp. and implications for trophic interactions in a small, monomictic lake. *J. Plankton Res.* 21:1823-1845.
- Smyly WJP, 1980. Food and feeding of aquatic larvae of the midge *Chaoborus flavicans* (Meigen) (Diptera: Chaoboridae) in the laboratory. *Hydrobiologia* 70:179-188.
- Riessen H, 1982. Predatory behavior and prey selectivity of the pelagic water mite *Piona constricta*. *Can. J. Fish. Aquat. Sci.* 39:1569-1579.
- Souza BB, 2015. [Variação espacial e temporal de microcrustáceos planctônicos do lago Monte Alegre e experimentos abordando a influência da qualidade do alimento sobre o desempenho dos cladóceros]. [Master Thesis in Portuguese]. University of São Paulo, Brazil.
- Souza BB, Arcifa MS, Ferreira TCS, Silva LHS, Fileto C, Domingos AR, 2017. Are the littoral zone conditions suitable for tropical planktonic microcrustaceans? *Ann. Limnol.-Int. J. Lim.* 53:281-291.
- Stemberger, RS, 1981. A general approach to the culture of planktonic rotifers. *Can. J. Fish. Aquat. Sci.*, 38:721-724.
- Swift MC, Fedorenko AY, 1975. Some aspects of prey capture by *Chaoborus* larvae. *Limnol. Oceanogr.* 20:418-426.
- Winner RW, Greber JS, 1980. Prey selection by *Chaoborus punctipennis* under laboratory conditions. *Hydrobiologia* 68:231-233.
- Zaret TM, 1980. *Predation and freshwater communities*. Yale University Press, New Haven: 187 pp.