



Is competition an interaction as relevant as predation for tropical planktonic cladocerans?

Competição é uma interação tão relevante quanto a predação para cladóceros planctônicos tropicais?

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Abstract: Aim: To test the relevance of competition and predation for the two most abundant and frequent cladoceran populations, the medium-sized *Ceriodaphnia richardi* Sars, 1901 and the large-sized *Daphnia gessneri* Herbst, 1967, in a tropical shallow lake. **Methods:** Laboratory experiments and weekly samplings in the lake for a year were performed to evaluate: density fluctuations and reproduction; predation on juveniles and adults by larvae of *Chaoborus brasiliensis* Theobald, 1901; competitive interactions and possible implications of competition and predation on the fluctuations of populations in the lake. Juveniles and adults of both cladocerans were offered to larvae instar IV of chaoborid, for testing selective predation in laboratory experiment. Competitive interaction between the two cladocerans was tested in experiments, with high (0.70 mg C.L⁻¹) and low (0.25 mg C.L⁻¹) concentrations of the edible chlorophycean *Desmodesmus spinosus* Chodat. **Results:** *C. richardi* and *D. gessneri* were more abundant in the cool season, when their densities were inversely correlated, and when invertebrate predators, *C. brasiliensis* and the water mite *Krendowskia* sp., were less abundant. Despite higher concentrations of food and larger number of offsprings produced by the cladocerans in the warm season in the lake, their densities were lower, coincident with the increase of invertebrate predators, mainly chaoborid larvae. *C. brasiliensis* preyed on adult *C. richardi* and on young *D. gessneri*. In the competition experiments, the densities and the population growth rates of *C. richardi* were higher than those of *D. gessneri*. The competition results support the “small body size” and the “ r_{max} ” hypotheses. The exclusion of *D. gessneri* by *C. richardi* occurred only in experimental conditions, while they coexist in the lake, but without reaching their carrying capacity. **Conclusions:** Predation is the key factor influencing the populations of cladocerans, whereas competition seems to play a secondary role, probably restricted to some periods of lower food concentration in the cool season.

Keywords: experiments; *Chaoborus*; *Daphnia gessneri*; *Ceriodaphnia richardi*; field study.

Resumo: Objetivo: Testar a relevância da competição e da predação para as duas populações de cladóceros mais abundantes e frequentes, a de tamanho médio *Ceriodaphnia richardi* Sars, 1901, e a de tamanho grande *Daphnia gessneri* Herbst, 1967, em um lago tropical raso. **Métodos:** Foram feitos experimentos de laboratório e amostragens semanais durante um ano para avaliar: flutuações de densidade e reprodução; predação sobre jovens e adultos por larvas de *Chaoborus brasiliensis* Theobald, 1901; interações competitivas e possíveis implicações da competição e predação sobre as flutuações das populações no lago. Jovens e adultos de ambos os cladóceros foram oferecidos às larvas de estágio IV de caoborídeos, para testar predação seletiva em experimento de laboratório. A interação competitiva entre os dois cladóceros foi testada em experimentos com alta (0,70 mg C.L⁻¹) e baixa (0,25 mg C.L⁻¹)



concentrações da clorofíceia comestível *Desmodesmus spinosus* Chodat. **Resultados:** *C. richardi* e *D. gessneri* foram mais abundantes na estação fria, quando suas densidades foram inversamente correlacionadas e quando os predadores invertebrados, *C. brasiliensis* e o ácaro aquático *Krendowskia* sp., foram menos abundantes. Apesar de concentrações mais elevadas de alimento e maior número de descendentes produzidos pelos cladóceros na estação quente no lago, suas densidades foram menores, coincidindo com o aumento dos predadores invertebrados, principalmente caoborídeos. *C. brasiliensis* predou adultos de *C. richardi* e jovens de *D. gessneri*. Nos experimentos sobre competição, as densidades e as taxas de crescimento populacional de *C. richardi* foram maiores do que as de *D. gessneri*. Os resultados da competição apoiam as hipóteses de “pequeno tamanho” e “ r_{max} ”. A diferença entre os resultados de campo e laboratório é que a exclusão de *D. gessneri* por *C. richardi* ocorreu apenas em condições experimentais, enquanto estas espécies coexistem no lago, mas sem atingir sua capacidade de suporte. **Conclusões:** A predação é o fator chave que influencia as populações de cladóceros, enquanto a competição parece desempenhar um papel secundário, provavelmente restrito a alguns períodos de menor concentração de alimento na estação fria.

Palavras-chave: experimentos; *Chaoborus*; *Daphnia gessneri*; *Ceriodaphnia richardi*; estudo de campo.

1. Introduction

Competition has been regarded as the key agent in structuring plankton communities, losing primacy to predation, whose role has been most emphatically recognized from the decades of 1970 and 1980 (Zaret, 1980) onward. The controversy raised in these decades on the driving force in structuring communities led some authors to consider interspecific competition as a sporadic factor (e.g., Wiens, 1977). Other researchers, however, believed that competition was still an important factor in structuring communities (Schoener, 1982, 1983).

The factors or demographic parameters that would lead a species to be a superior competitor are basic for understanding and for predicting competitive interactions. Several hypotheses have been suggested in order to explain the competitive superiority of species, such as “size efficiency” (Brooks & Dodson, 1965), “small body size” (e.g. Neill, 1975) and “ r_{max} ” (Goulden et al., 1978). Large-bodied species are deemed more efficient in the exploitation of resources, although suffering higher losses by visual selective predation. The species superiority, however, is not necessarily based on its larger size, an aspect whose complexity has been revealed experimentally and in simulations, both showing the superiority of small species over large ones in low food concentrations (Romanovsky & Feniova, 1985). Bengtsson (1987) also reported relationship between feeding efficiency and small size under low food conditions. Milbrink et al. (2003) tested the hypotheses of r_{max} , size efficiency and small body size, with four species of *Daphnia*, including predation in their experiments. Their

findings support the r_{max} hypothesis, but do not uphold the size efficiency hypothesis.

Lower threshold food concentration (TFC) and greater resistance to starvation lead a species to outcompete other species. Gliwicz (1990) found an inverse relationship between body size of eight cladoceran species and TFC; on the other hand, lower TFCs were estimated for smaller cladocerans (review by DeMott, 1989). TFC can also have a non-linear relationship with body size in cladocerans, which can be positively related to size only up to 1.3 mm (Nandini & Sarma, 2003).

Some studies indicated competition as the most important factor controlling zooplankton (Neill, 1975; Lynch 1978; DeMott & Kerfoot, 1982), while in others predation is preponderant (Brooks & Dodson, 1965; Dodson, 1970; Allan, 1973). A review on the role of predation in reducing the effect of interspecific competition evidenced that it can lower, increase, or having no impact on competitive interaction (Chase et al., 2002). Competition and predation can be symmetrical interactions, the possibility of coexistence depending on the niche overlap regarding resource and predator (Chesson & Kuang, 2008).

According to Hutchinson (1961) the principle of competitive exclusion would not be supported in empirical conditions and many phytoplankton species that compete for the same resources could coexist in the natural environment. Underlying this context was the idea that in a variable environment the condition of non-equilibrium would enable the coexistence of species, in contrast to a stable environment in which the coexistence would be propitiated by the occupation of different niches (Schoener, 1974). However, variable resources in the environment, favouring differentially the

populations in time, and a lower niche overlap, reducing the possibility of competition, are concepts not mutually exclusive concerning the coexistence of species.

Competition experiments are limited as they confine individuals in vials under controlled conditions that do not mimic the natural environment, because of difficulties in testing competition in the ecosystem. Stable food resources and the absence of predation, under laboratory conditions, leading to the extinction of the subordinate species, have no parallel in the environment. Experiments are usually performed in small containers in the laboratory or in low-volume field enclosures (review by DeMott, 1989; Johnson & Havel, 2001; Dzialowski & O'Brien, 2004; Feniova et al., 2013; Chen et al., 2016). Johnson & Havel (2001) concluded, from studies with small field enclosures, that competition does not explain the seasonal succession of two *Daphnia* species in a North American reservoir. Bengtsson (1987) reported, reviewing twenty experiments on cladocerans, that hypotheses are not fully supported by laboratory or field experiments. This author considers that it is better to work with more than one competition hypothesis and that the competitive exclusion principle hardly applies to zooplankton in the environment. These studies show the difficulty of demonstrating the existence of competition, as well as the generalization of a single hypothesis.

Laboratory experiments demonstrated the existence of interspecific competition, sometimes with extinction of zooplankton populations (e.g., Romanovsky & Feniova, 1985; Hurtado-Bocanegra et al., 2002). However, competition among zooplankton species is not always easily detectable in the natural environment where species coexist or succeed each other throughout the seasons of the year (review by DeMott, 1989), involving other factors, such as predation (review by Gliwicz & Pijanowska, 1989), and temperature (Feniova et al., 2011, 2013). Seasonal changes in the phytoplankton community in the environment are capable of altering the competitive ability of each species (Romanovsky & Feniova, 1985).

From the first study in Lake Monte Alegre, in 1985/86, a conceptual model of the main factors that might influence the zooplankton fluctuations was proposed (Arcifa et al., 1992). The model predicted that predation by invertebrate would be the main factor influencing zooplankton in the

warm season in the lake, whereas competition would be more important in the cool season. Indeed, the seston quantity and quality, tested in laboratory experiments, showed that cladocerans had a better performance in the spring and summer seston in contrast to winter seston (Ferrão-Filho et al., 2005).

The main limnetic predators in the lake are larvae of the dipteran *Chaoborus brasiliensis* Theobald, 1901 (maximum length ca. 7 mm), which are omnivores, with III and IV instars preying on zooplankton (Arcifa, 2000; Castilho-Noll & Arcifa, 2007a). Other less abundant predators that exert a lower pressure are the mite *Krendowskia* sp. (ca. 1.3 mm), which also preys on *Chaoborus* (Cassano et al., 2002), and the adults of the exotic cichlid fish *Tilapia rendalli* Boulenger, 1897. *Chaoborus* larvae prey on juveniles of larger species, such as *Daphnia gessneri* Herbst, 1967 (Arcifa, 2000; Castilho-Noll & Arcifa, 2007a), and caused the increase of mortality rates and decrease of population growth rates of *D. gessneri* in experiments in mesocosms (Castilho-Noll & Arcifa, 2007b). Mite can prey on adult *D. gessneri* (Cassano et al., 2002), but not on *C. richardi* Sars, 1901 (T. C. S. Ferreira, unpublished data). Zooplankton is a minor dietary item for the whole fish fauna, which is mostly confined to the littoral zone (Arcifa & Meschiatti, 1993) and fish associated to floating macrophytes feed mainly on non-planktonic microcrustaceans (Meschiatti & Arcifa, 2002). The only planktivorous fish is the pump filter-feeder adult *T. rendalli*, which feeds mostly on phytoplankton (Arcifa & Meschiatti, 1993, 1996). It is not very abundant (Arcifa & Meschiatti, 1993), influencing phytoplankton mainly through nutrient excretion in comparison to grazing (Silva et al., 2014) and exerting a low pressure on zooplankton even in a higher density in mesocosms (1 fish/2.5 m³) than in the lake (Silva, 2004).

The question still remains on the role of competition in this ecosystem, whether it may be seasonal, restricted to the cool season. Bearing this in mind we performed laboratory experiments on predation and competition with two cladocerans, whose density fluctuations were also followed in a field study. *Daphnia gessneri* and *Ceriodaphnia richardi* were selected for this study because they are the most abundant species of cladocerans recorded in the last two studies in the lake, the latter surpassing *D. gessneri* (Arcifa et al., 2015). The experiments performed in the laboratory were motivated by the negative correlation found

between the densities of both species during the cool season of 2011 and the increase of predators in the warm season of 2011-2012 (this study).

Competition between the cladocerans, the medium-sized *C. richardi* and the large-sized *D. gessneri*, under low and high food concentration and equilibrium conditions were then tested in laboratory in an attempt to find a possible interaction between them. Another experiment was conducted to verify whether *C. richardi* and *D. gessneri* can be selectively preyed on by larvae of *C. brasiliensis*.

Besides laboratory experiments, weekly data obtained in the lake during a year, allowed us to follow fluctuations of the two cladocerans and invertebrate predators, phytoplankton carbon fluctuations and the reproductive performance of cladocerans.

The issues addressed in this study are: I. fluctuations of the populations of prey and limnetic predators in an annual cycle in the lake; II. the intensity and selective predation by chaoborid larvae on the two cladocerans; III. the role of competition regarding seasons in the lake; IV. the superior and subordinate cladoceran species in laboratory experiments and in the field; V. laboratory support to the hypotheses of “small-body size” and “ r_{max} ” in competition.

2. Methods

2.1. Study area

Lake Monte Alegre (LMA) (21° 10' 04" S, 47° 51' 28" W) is located in Ribeirão Preto, southeastern Brazil, and was formed in 1942 by damming the Laureano Creek, belonging to the Pardo River basin. The region is characterized by a tropical climate, with two well-defined seasons: a cool-dry season (May to September) and a warm-wet season (October to April). The reservoir is eutrophic, small, shallow (area: 7 ha; Z_{max} : 5 m) and warm discontinuous polymictic (Arcifa et al., 1990). Despite being a reservoir, it functions similarly to a lake because the dam is not manipulated and the retention time is relatively high (~ 45 days) for its dimensions.

2.2. Temporal variations in the lake

Populations of both cladocerans, *C. richardi* and *D. gessneri*, the predators *C. brasiliensis* and *Krendowskia* sp., as well as physical and chemical factors and chlorophyll-*a* were monitored in the lake. Samplings were carried out every week during one year, from May 2011 to April 2012, between

15 and 16 hours, at a deepest station (5 m) in the center of the lake and the littoral zone (1 m). In this study only the limnetic samples were used for assessing the fluctuations of populations.

Three replicates were sampled (150 L each), in an area around the central station, with a pump (Jabsco ITT, model 34600-000), delivering 30 L.min⁻¹ and integrating the whole water column. The water was filtered through a 58 µm-mesh net to collect microcrustaceans, *Chaoborus* larvae and water mites. The samples were fixed with 4% formaldehyde after addition of sucrose, according to Haney & Hall (1973), to prevent loss of eggs by cladocerans. The organisms were identified and counted under a stereomicroscope, in subsamples of 1, 2.5 and 5 mL, depending on the abundance of each species, maintaining the coefficient of variation of 0.20, according to McCauley (1984). The instars III and IV of *C. brasiliensis* and the mite *Krendowskia* sp. were entirely counted. Twenty of the largest ovigerous females of the cladocerans were selected from each sample for counting eggs, for preventing a bias regarding female size and number of eggs. The average number of eggs per female was calculated to evaluate the fecundity of cladocerans during the year.

For evaluating the field conditions for cladocerans and predators, the limnological factors analysed were: temperature and dissolved oxygen, with Yellow Springs Inc. probes, model 95, electrical conductivity, at 25°C (YSI 30) and pH (YSI 60). Transparency was measured with a white Secchi disc 30 cm in diameter. The limit of the euphotic zone was calculated: $ZE = DS \times 2.7$, where ZE = depth of the euphotic zone and DS = Secchi disc depth (m). Chlorophyll-*a* was analysed according to Jeffrey & Humphrey (1975). The conversion of chlorophyll into carbon was based on the ratio chlorophyll/algae, assuming that the chlorophyll is 1.25% of the dry weight of algae, within the limits reported by Reynolds (1984), and that carbon represents 50% of the algal dry weight.

The Spearman coefficient (SigmaStat, Version 3.5, Systat Software Inc.) was used to test correlations between the densities of *C. richardi* and *D. gessneri*, in the cool season, between the clutch size of both species and the algal carbon concentration and between prey and predators throughout the year.

2.3. Algal culture

The algal strain of *Desmodesmus spinosus* Chodat (former *Scenedesmus spinosus*) was cultivated in MBL medium (Stemberger, 1981) in an environmental

chamber (FANEM, model 347 CDG), at a temperature of 23°C and a photoperiod of 12:12 h. This chlorophycean was used as food for the cladocerans, because it is suitable for promoting the best growth rates for most cladocerans of the lake (Ferrão-Filho et al., 2005).

2.4. Predation experiment

The cladocerans were obtained from samples collected in the lake and cultivated in the laboratory for several generations. In the laboratory, cladocerans were cultivated in 600 mL-bottle filled with lake water filtered in glass fiber filter, at 23°C and photoperiod of 12:12 h, on a plankton wheel (turning 1 min every 5 min). The cultivated chlorophycean *D. spinosus* was added to the filtered water, at a concentration of 1 mg C.L⁻¹. Before the experiment (about 24-36 hours), ovigerous females were separated and individually transferred to test tubes (40 mL), containing filtered lake water plus the chlorophycean, for obtaining the neonates used in the experiment.

The experiment was conducted in June 2015, during 24 h, using the same chlorophycean and the same concentration aforementioned and the cladocerans placed in 140 mL-bottles, each one containing two larvae of instar IV of *Chaoborus*. The larvae were collected 24-36 h before the experiment, and acclimated in the laboratory with food. The test was made in a short time and with high density of predator to preclude prey death unrelated to predation. The treatments were (4 replicates each): a. 10 neonates (0.30 ± 0.01 mm) of *C. richardi*; b. 10 neonates (0.60 ± 0.01 mm) of *D. gessneri*; c. 10 neonates of *C. richardi* + 10 neonates of *D. gessneri*; d. 10 neonates of *C. richardi* + 10 adult females (1.20 ± 0.02 mm) of *D. gessneri*; e. 10 adult females (0.70 ± 0.01 mm) of *C. richardi* + 10 adult females of *D. gessneri*. The treatments were kept under the same conditions of light and temperature of the cladoceran culture, on the plankton wheel, with dim light to mimic lake conditions. After 24 hours, survivors were counted at the end of the experiment, in order to detect predation, as well as the body conditions of remaining individuals to evaluate unsuccessful attacks by the predator.

The data of each treatment were statistically compared by *t*-test (Statistica, Version 8.0, StatSoft Inc.), for alternative hypothesis ($p < 0.05$). The ingestion rate was calculated according to the formula: $IR = IP_{control} - IP_{experimental} / T * N$, where $IP_{control}$ = initial number of prey, $IP_{experimental}$ = final number of intact prey,

T = experiment duration, N = number of predator. One-way repeated ANOVA and the *post hoc* Tukey test were used for statistical analysis of ingestion rate.

2.5. Competition experiments

C. richardi (max. length 0.70 mm) and *D. gessneri* (max. length 1.2 mm) were collected in the lake with a 58 µm-mesh net. The organisms were kept in beakers containing lake water filtered through a glass fiber filter, at a constant temperature of 23°C and 12:12 h photoperiod, in the environmental chamber, for acclimation during 24-48 h. The cladocerans were acclimated in the same concentrations of *D. spinosus* of each experiment. The temperature of 23°C was chosen because it is favourable to both cladocerans and our purpose was to test one factor (food resource), without the influence of a second one (temperature). At a low temperature (-19°C), *D. gessneri* had a worse performance, indicated by several life-table parameters (Bunioto & Arcifa, 2007).

Two experiments were carried out, one in January and the other in February 2012, to evaluate possible interaction between the daphniids. Two different food concentrations were used: high (0.70 mg C.L⁻¹), in the first experiment and low (0.25 mg C.L⁻¹), in the second experiment. The lower concentration, 0.25 mg C.L⁻¹ is above the threshold and the incipient limiting level for these cladocerans, both levels able to negatively influence reproduction of the species, based on Bunioto & Arcifa (2007). Therefore, both threshold and the incipient limiting level were taken into consideration here, otherwise the populations alone could be affected by food and competition could not be tested in mixed cladoceran populations; the second reason is that the concentrations used in the experiments were close respectively to the maximum (0.62 mg C.L⁻¹) and minimum (0.20 mg C.L⁻¹) algal carbon concentrations found in the cool season in the lake in the present study.

After acclimation, 10 individuals of mixed age groups of each species were randomly taken for each treatment, most of them juveniles and non-ovigerous adults. The treatments of each experiment (three replicates each) were: a. control with the species *C. richardi* in individual vials (10 ind.); b. control with the species *D. gessneri* in individual vials (10 ind.); c. both species placed in the same vial (10 ind. each).

The organisms were maintained in transparent 600 mL-bottles, containing lake water filtered through glass fiber filter plus the alga *D. spinosus*,

in order to evaluate the population growth of each species. The vials were kept on the plankton wheel to avoid algae sedimentation. The experiments were maintained at a room temperature of 23°C, which represents the annual average temperature in the lake and the laboratory was kept in dim light, to mimic the lake conditions for cladocerans. The medium was renewed every other day, for maintaining the food concentration, when the number of survivors and neonates were counted. The organisms were carefully collected with a pipette, for avoiding killing the individuals, and transferred to new bottles with fresh food.

The population rate of increase (r) was calculated during the whole experiment, using the equation (Krebs, 1985): $r = (\ln N_t - \ln N_0)/t$ where: N_0 and N_t are the initial and final densities, respectively, and t is time (days). The " r_{max} " values for both species were considered those recorded in the high food concentration, during the exponential growth. One-way repeated ANOVA (Statistica, Version 8.0, StatSoft Inc.), and the *post hoc* Tukey test were used for statistical analysis of competition experiments.

3. Results

3.1. Physical and chemical factors in the lake

Lower temperatures were recorded from May to September 2011, during the cool season, when the minimum was close to 18°C near the bottom (Table 1), but lasted a short time. This period showed frequent circulation but the dissolved oxygen was unevenly distributed. Thermal stratification was observed during the warm season, when temperatures ranged from 23 to 31°C in the water column. From December 2011 to April 2012 stratification was more stable. Low dissolved oxygen

concentrations were found near the bottom of the lake, especially in the warm season.

Higher pH values were recorded in top layers in the warm season (Table 1). Values of pH varied throughout the year in the water column, having weak connection with periods of thermal stratification and circulation in the lake. The euphotic zone was deeper in the cool season, almost extending to the bottom, and decreasing in the warm season, particularly from January to April 2012.

The concentrations of algal carbon varied, during the year, from 0.2 to 2.1 mg C.L⁻¹, with the lowest concentrations recorded in the cool season, generally below 0.70 mg C.L⁻¹ (Figure 1). The values increased, during the warm season, when concentrations above 1 mg C.L⁻¹ were common.

The clutch sizes of *C. richardi* and *D. gessneri* were lower in the cool season (Figure 1) compared

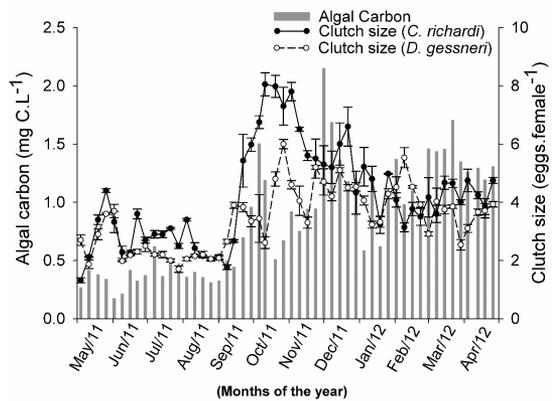


Figure 1. Weekly variation of algal carbon and clutch size of *C. richardi* and *D. gessneri* in Lake Monte Alegre, in the period May 2011 to April 2012. Bars are standard error of the means (\pm) based on three replicates.

Table 1. Maximum and minimum values of temperature, dissolved oxygen and pH at surface and bottom of the lake, and the limit of the euphotic zone, in the cool and warm seasons.

Physical and chemical factors	Cool season		Warm season	
	Max.	Min.	Max.	Min.
Temperature (°C)				
Surface (1 m)	25.9	18.9	30.3	25.6
Bottom (5 m)	23.1	18.2	26.3	23.3
Dissolved oxygen (mg.L⁻¹)				
Surface (1 m)	9.1	5.9	10.5	5.9
Bottom (5 m)	7.3	1.4	3.9	0.9
pH				
Surface (1 m)	8.5	6.1	8.5	6.6
Bottom (5m)	7.4	4.2	7.3	5.4
Limit of the euphotic zone (m)	5.0	3.5	4.4	2.5

Food, reproduction and densities of cladocerans and of the invertebrate predators in the lake.

to the warm season (ANOVA, $F = 36.15$, $p < 0.001$, and, $F = 48.90$, $p < 0.001$, respectively). The clutch size of both species increased mainly in spring (September–November 2011), when *C. richardi* produced up to 8 eggs.female⁻¹, and *D. gessneri* up to 6 eggs.female⁻¹. The clutch size was positively correlated to algal carbon concentrations, for *C. richardi* ($r = 0.52$, $p < 0.001$) and *D. gessneri* ($r = 0.53$, $p < 0.001$).

Despite the larger clutch sizes produced during the warm season, *C. richardi* and *D. gessneri* were more abundant during the cool season (Figure 2). *C. richardi* was the most abundant species, reaching 98 ind.L⁻¹, while *D. gessneri* did not exceed 15 ind.L⁻¹. There was a negative correlation between the densities of *C. richardi* and *D. gessneri* ($r = -0.54$, $p = 0.01$), in the cool season. Both populations declined in late cool season-early warm season, maintaining low densities in the latter period, attaining a maximum of 4–6 ind.L⁻¹. Two peaks were reached by *D. gessneri*, one before the increase of *C. richardi* population in early May, and another after a sharp decrease of *C. richardi* in September.

The III and IV instars of *C. brasiliensis* were the dominant limnetic invertebrate predators in this study, compared to the water mite *Krendowskia* sp. (Figure 3). Chaoborid larvae were present in the lake throughout the year, but in higher densities in the warm season, when they reached a maximum value of 2 ind.L⁻¹. In the cool season, the densities were below 1 ind.L⁻¹, except the peaks in May and September 2011.

Mites were also more abundant in the warm season with higher densities from October to December 2011, when maximum values of 0.25 ind.L⁻¹ were attained (Figure 3). In the cool season, mites were sampled only in May and June, but at very low densities.

An inverse correlation, between cladocerans and chaoborid larvae, was significant only for *C. richardi* ($r = -0.33$, $p = 0.01$), considering densities of the whole year.

3.2. Predation experiment

In the treatments a and b (neonates of *Daphnia* and *Ceriodaphnia* placed in separate vials), predators significantly reduced only the density of *D. gessneri* ($p < 0.001$; Figure 4a), but not that of *C. richardi* (Figure 4b). Similarly, in the treatment c (neonates of *Daphnia* and *Ceriodaphnia*), only the density of *D. gessneri* was significantly reduced by the predator ($p = 0.04$; Figure 4c). In the treatment d

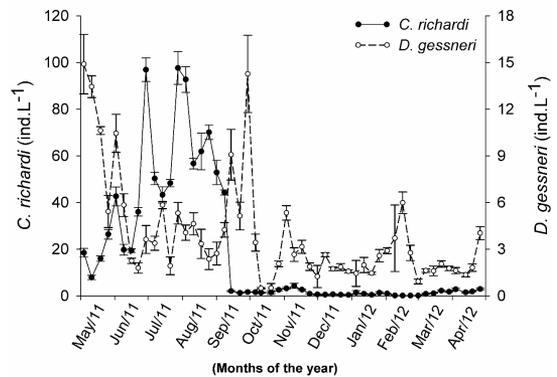


Figure 2. Weekly variation of the densities of the cladocerans *C. richardi* and *D. gessneri* in Lake Monte Alegre, from May 2011 to April 2012. Bars are standard error of the means (\pm) based on three replicates. Note the different scales for the species.

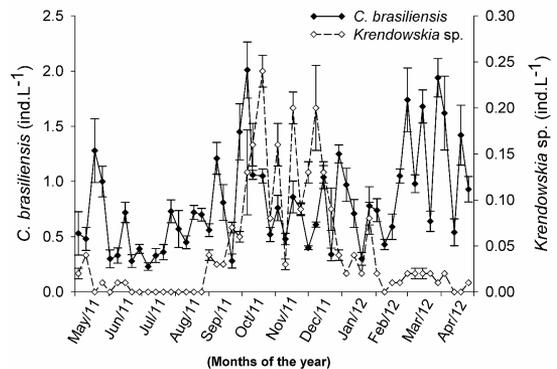


Figure 3. Weekly variation of the densities of III and IV instars of *C. brasiliensis* and the aquatic mite *Krendowskia* sp., in Lake Monte Alegre, in the period May 2011 to April 2012. Bars are standard error of the means (\pm) based on three replicates. Note the different scales for the species.

(neonates of *Ceriodaphnia* and adults of *Daphnia*), adults of *D. gessneri* were not eaten, although some individuals had signs of the predator attack, while density of *C. richardi* was not affected (Figure 4d). In the treatment e (adults of both species), only the density of *C. richardi* was significantly reduced ($p = 0.002$; Figure 4e).

Average daily ingestion rates showed that the larvae consumed preferentially neonates of *Daphnia* than of *Ceriodaphnia* (ANOVA, *post hoc* Fisher test, $p < 0.001$) (Figure 5). However, adult *Ceriodaphnia* was the favorite prey, when paired with adult *Daphnia* (*post hoc* Fisher test, $p = 0.003$). Average daily ingestion rates varied from 0 to 0.2 neonate.*Chaoborus*⁻¹.day⁻¹ and 0.8 adult.*Chaoborus*⁻¹.day⁻¹ for

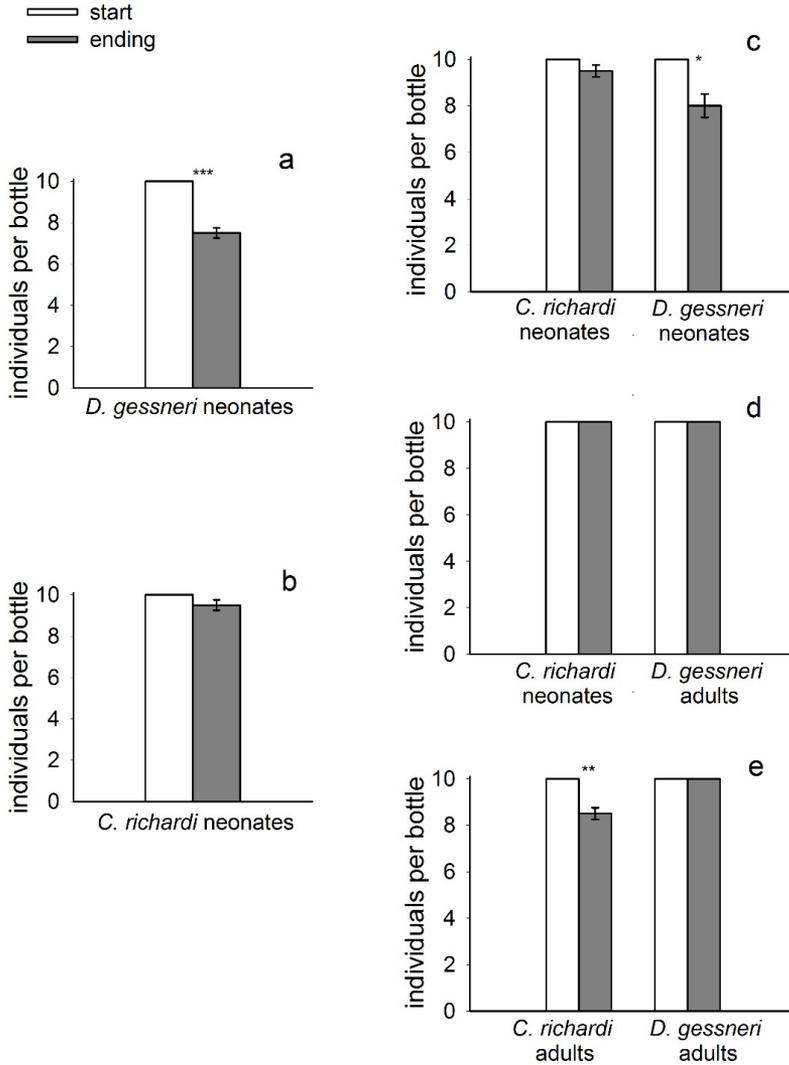


Figure 4. Number of prey of *C. richardi* (Cr) and *D. gessneri* (Dg) at the beginning (white) and its average number at the end (grey) of the experiment, after individuals were exposed to predation by *Chaoborus brasiliensis*; neonates of Dg (a), neonates of Cr (b), neonates of Cr + neonates of Dg (c), neonates of Cr + adults of Dg (d) and adults of Cr + adults of Dg (e). Significant differences are * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

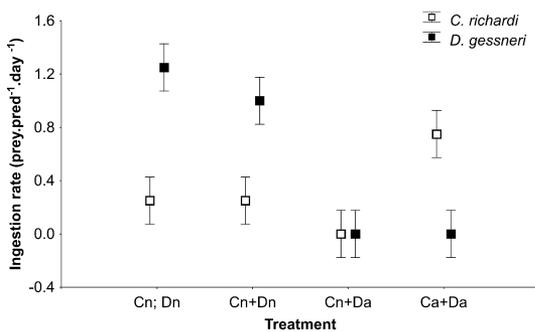


Figure 5. Ingestion rates of prey, *C. richardi* and *D. gessneri*, by the instar IV of *C. brasiliensis*. Cn and Dn are neonates and Ca and Da adults of the prey species, respectively. Bars are standard error of the means (\pm) based on four replicates.

C. richardi and 1 to 1.2 neonates.*Chaoborus*⁻¹.day⁻¹ and zero adult for *D. gessneri*.

3.3. Competition experiments

The medium-sized *C. richardi* and the large-sized *D. gessneri* showed different responses to the food availability and competitive interaction.

The performance of *C. richardi* was better than that of *D. gessneri* in both food concentrations, with similar density (Figure 6a) and population growth rate in the control (Cr-) and mixed (Cr+) with *D. gessneri* (Figure 6b). There was no significant difference in the densities and population growth rates between treatments (Cr- and Cr+) in any food concentration (Table 2), indicating that the species

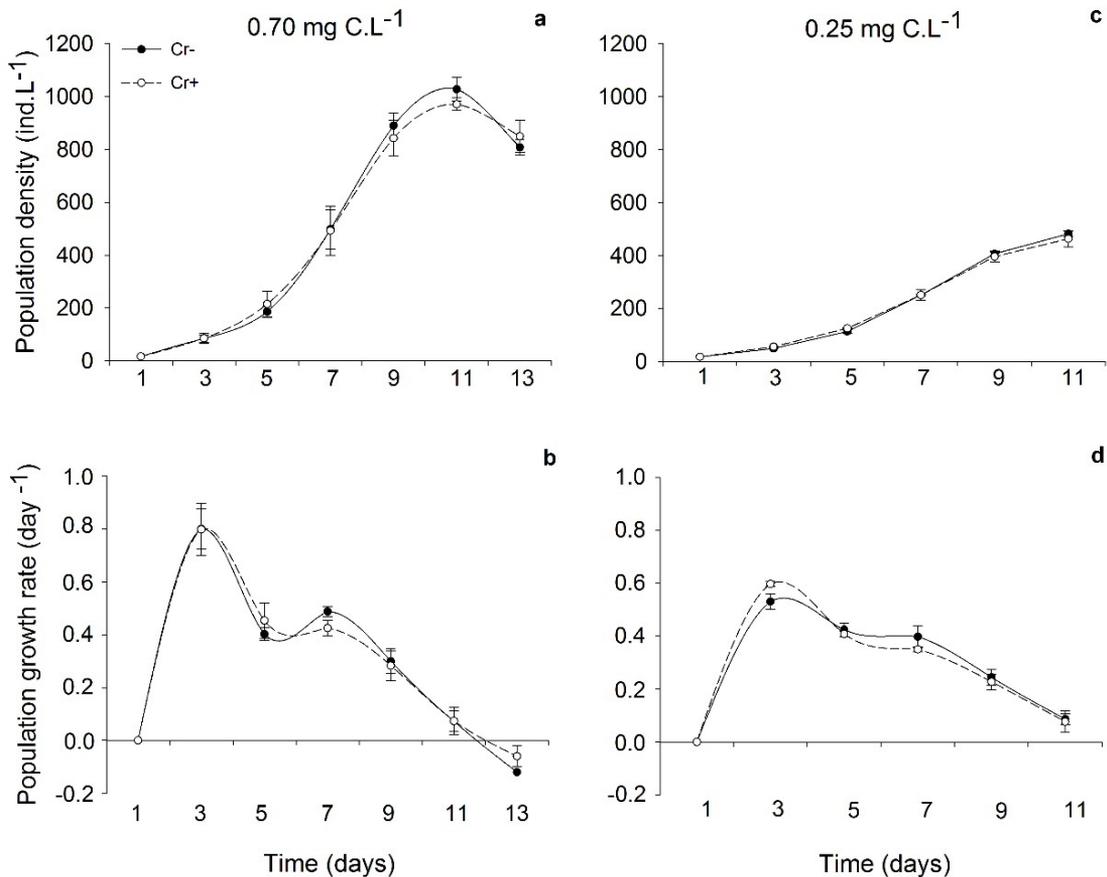
Ceriodaphnia richardi

Figure 6. Population growth curves (a, b) and population growth rate (r) per day (c, d) of *C. richardi* alone (Cr-) and cultured together (Cr+) in high (0.70 mg C.L⁻¹) and low (0.25 mg C.L⁻¹) food concentrations, respectively. The vertical bars represent the standard error of the mean (\pm) based on three replicates.

was not influenced by the presence of *D. gessneri*. The densities of *C. richardi*, in the controls (Cr-), increased in the high food concentration (Figure 6a), significantly higher than in the low food concentration (Figure 6c; *post hoc* Tukey test, $p = 0.00$). Population growth rates were not significantly different between food concentrations (Figures 6b and d).

D. gessneri performance was worse, with lower densities in the low food concentration (Figures 7a and b). The species reached its highest density in the control (Dg-) of the high food concentration (43 ind.L⁻¹) that was significantly different than that recorded in the low food concentration (33 ind.L⁻¹) (*post hoc* Tukey test, $p = 0.03$). There were significant differences between treatments (Dg- and Dg+), and over time, concerning densities and population growth rates in both food concentrations (Table 2). The density and population growth rates in the treatment Dg- were

significantly higher than in Dg+, in both high (*post hoc* Tukey test, $p = 0.04$ and 0.02 , respectively), and low food concentrations (*post hoc* Tukey test, $p < 0.001$ and $p < 0.01$, respectively).

The r_{max} in the control treatment, with high food concentration (0.70 mg C.L⁻¹), was significantly higher for *C. richardi* (0.8.day⁻¹) compared to *D. gessneri* (0.3.day⁻¹) (*post hoc* Tukey test, $p = 0.01$).

4. Discussion

Despite larger populations expected by the larger number of offsprings produced by the species in the warm season, their lower densities compared to the cool season indicate the stronger influence of factors other than food resources, particularly predation. The sudden decrease of *C. richardi* and low densities during the warm season can be related to the increase of chaoborid larvae, also indicated by the inverse correlation between them. Low densities (mean - 5 ind.L⁻¹) of *C. richardi* were

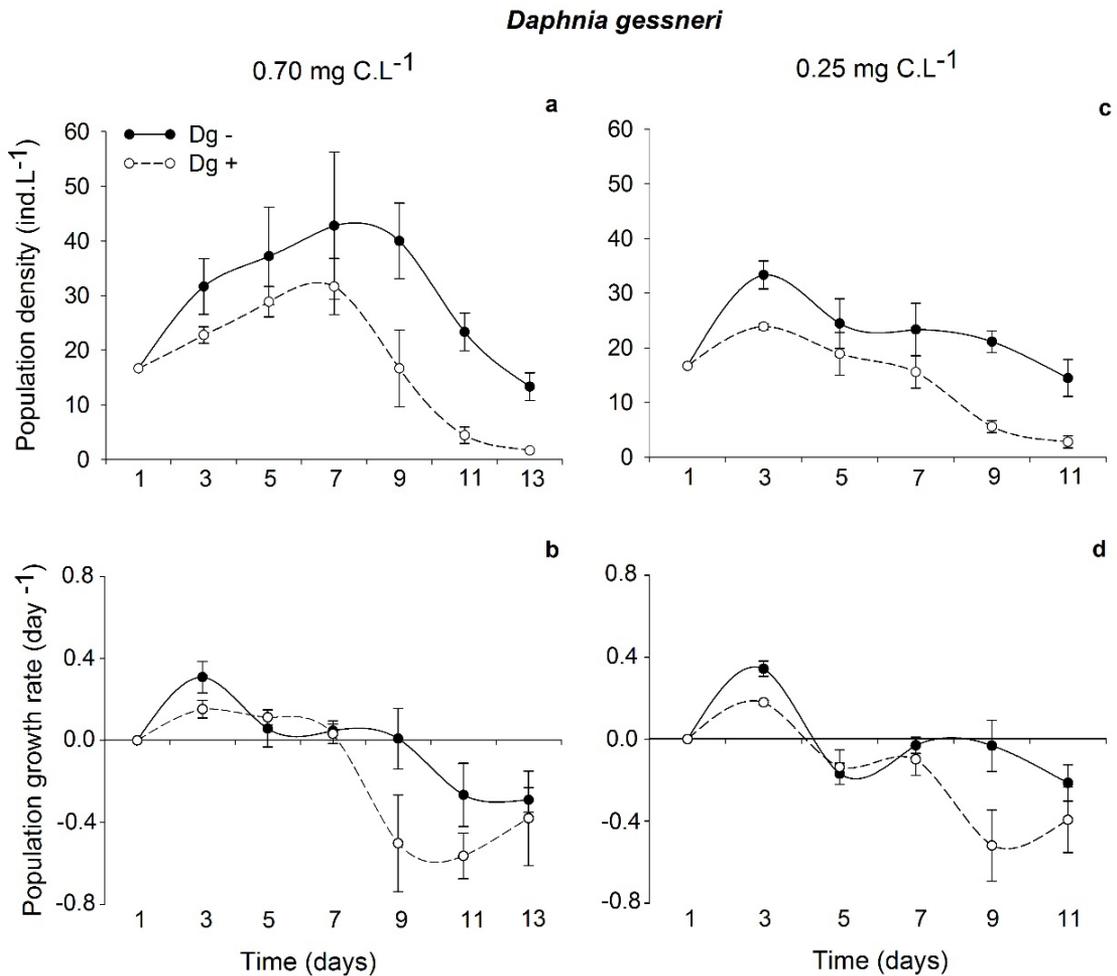


Figure 7. Population growth curves (a, b) and population growth rate (r) per day (c, d) of *D. gessneri* alone (Dg-) and cultured together (Dg+) in high (0.70 mg C.L⁻¹) and low (0.25 mg C.L⁻¹) food concentrations, respectively. The vertical bars represent the standard error of the mean (\pm) based on three replicates.

kept in mesocosms with *Chaoborus*, in contrast to 42 ind.L⁻¹, in the treatment without *Chaoborus* (Peticarrari, 2005). Average densities of *D. gessneri* lower than 8 ind.L⁻¹ were recorded in enclosures with *Chaoborus*, in comparison with 40 ind.L⁻¹ in the predator-free treatment (Castilho-Noll & Arcifa, 2007b). The densities of both species, in the warm season in the lake in this study (4-6 ind.L⁻¹), are similar to those of the aforementioned treatments with chaoborid larvae.

Both *D. gessneri* (Arcifa, 2000; Castilho-Noll & Arcifa, 2007a, this study) and *C. richardi* (Peticarrari, 2005; this study) are preyed on by chaoborid larvae, and the first species is also preyed on by mite (Cassano et al., 2002; T. C. S. Ferreira, unpublished data). Predation by chaoborid larvae on adult *Ceriodaphnia* in our study seems to cause a greater population effect because predation also

falls on its reproductive stage, reflecting on the recruitment. Predation on ovigerous females has a greatest impact on a population, since it affects both natality and mortality, with a direct effect on density (Gliwicz & Pijanowska, 1989).

Although lower number of eggs was produced by cladocerans in the cool season than in the warm season in the lake, in agreement with lower food resources, the densities were higher. The reproductive performance may have been affected by more than one factor, in the cool season. Laboratory experiments showed that at the lowest winter temperature in the lake (19°C), the fecundity and population growth of *D. gessneri* decreased and first reproduction was delayed in comparison to a higher temperature (27°C), which is the mean water column temperature in summer (Bunioto & Arcifa, 2007). *C. richardi* seems to be less sensitive

Table 2. One-way repeated-measures ANOVA for the treatment effects, with species *C. richardi* and *D. gessneri*, alone (Cr- and Dg-) or mixed (Cr+ and Dg+), and the effect of time (T) on density and population growth rates.

Source	df	MS	F
Maximum population density			
<i>C. richardi</i>			
<i>0.70 mg C.L⁻¹</i>			
Cr- x Cr+	1	576	0.239 ns
T	5	370840.9	153.901***
Cr- x Cr+ x T	5	573	0.238 ns
<i>0.25 mg C.L⁻¹</i>			
Cr- x Cr+	1	6.5	0.063 ns
T	4	53946.4	518.217***
Cr- x Cr+ x T	4	37.8	0.363 ns
<i>D. gessneri</i>			
<i>0.70 mg C.L⁻¹</i>			
Dg- x Dg+	1	448.028	9.7811**
T	5	179.894	3.9273**
Dg- x Dg+ x T	5	37.094	0.8098 ns
<i>0.25 mg C.L⁻¹</i>			
Dg- x Dg+	1	158.70	18.45***
T	4	71.70	8.33***
Dg- x Dg+ x T	4	17.36	2.01 ns
Population growth rate			
<i>C. richardi</i>			
<i>0.70 mg C.L⁻¹</i>			
Cr- x Cr+	1	0.000225	0.0285 ns
T	5	0.503712	63.7834***
Cr- x Cr+ x T	5	0.001872	0.2370 ns
<i>0.25 mg C.L⁻¹</i>			
Cr- x Cr+	1	0.000083	0.053 ns
T	4	0.271583	171.166***
Cr- x Cr+ x T	4	0.002717	1.712 ns
<i>D. gessneri</i>			
<i>0.70 mg C.L⁻¹</i>			
Dg- x Dg+	1	0.216225	6.429421*
T	5	0.336072	9.993045***
Dg- x Dg+ x T	5	0.071792	2.134715 ns
<i>0.25 mg C.L⁻¹</i>			
Dg- x Dg+	1	0.138	7.22*
T	4	0.241	12.58***
Dg- x Dg+ x T	4	0.065	3.38*

ns: non-significant ($p > 0.05$); * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

to low temperature, since densities were high even when the mean water column temperatures ranged from 18.5 to 20.6°C, during winter in our study. Food quantity and quality can be also responsible for worse reproductive performance of cladocerans, in the cool season in the lake (Ferrão-Filho et al., 2003, 2005). These previous studies may indicate that food and temperature can be included among the relevant factors in the cool season in our study. The influence of these factors may fall on different

developmental stages of organisms, indicated by the inverse relationship between temperature and the embryonic development time of cladocerans (Hall, 1964; Munro & White, 1975; Hardy & Duncan, 1994); the effect of food concentration can be stronger on the post-embryonic development (Hardy & Duncan, 1994), indicated by juvenile growth rates (Bunioto & Arcifa, 2007).

Since quantity and quality of food resources in the environment are variable and other factors may also affect competitive interactions, the extrapolation of results in the laboratory to the natural environment is always viewed with caution (review by DeMott, 1989; Milbrink et al., 2003).

In the environment, predation by invertebrates, in addition to other factors, may mediate competitive interactions and the two species coexist in varying densities, related to seasons. Depending on the interaction between competition and predation, coexistence is promoted or predictions are supported by the stronger interaction (Chesson & Kuang, 2008).

The numerical dominance of *C. richardi* regarding *D. gessneri* in the cool season was detected in the lake since its appearance in 2001-02, the first species reaching its highest densities in this study. The negative correlation between densities of *C. richardi* and *D. gessneri* in the cool season, and peaks of *D. gessneri* when densities of *C. richardi* were lower (*ca.* 20 ind.L⁻¹), may indicate the dominance of the smaller species also in the lake. The maximum densities of *C. richardi* (482 ind.L⁻¹) and *D. gessneri* (33 ind.L⁻¹) in the low food concentration in the experiments, well above those of the cool season in the lake (max. 98 ind.L⁻¹ and 15 ind.L⁻¹, respectively), indicated that the populations did not reach their carrying capacities in the field. Since part of the algal carbon in the lake can be unsuitable to cladocerans (Fileto et al., 2004), the amount of edible algae can be lower in the environment compared to the low concentration used in the experiment. Moreover, the influence of multiple factors in the lake, including competition, should be taken into account.

Competitive superiority would not be based on a single hypothesis, but rather on some features that would add undeniable advantages to the species (Bengtsson, 1987). The “size-efficiency” hypothesis is not supported by our experiments, similarly to findings by Milbrink et al. (2003), whereas the “small body size hypothesis” is reinforced. Besides smaller size, the population growth rates of *C. richardi* being greater than that of *D. gessneri*

in the high food concentration (0.70 mg C.L^{-1}), agree also with the “ r_{max} hypothesis”. But it is worth examining the underlying factors that led the smaller species to have advantages over the larger one, using subsidies of previous studies, since these factors were not dealt with here.

The threshold food concentration (TFC), when mortality equals natality, for both species has not been determined and is below the lowest concentration used in experiments ($0.025 \text{ mg C.L}^{-1}$; Bunioto & Arcifa, 2007). Juvenile growth rate of *D. gessneri* was more impaired at food concentrations within and below the incipient limiting level ($0.1\text{-}0.2 \text{ mg C.L}^{-1}$) than that of *C. richardi*. The juvenile growth rate was always higher for *C. richardi*, reaching 1.57 times that of *D. gessneri* in the highest food concentration (0.2 mg C.L^{-1}), which is near the lower concentration used in our experiments. The advantage of the smaller species (*C. richardi*) already outlined at the level of juveniles in the experiments by Bunioto & Arcifa (2007), suggests that it has lower TFC. Besides, higher juvenile growth rates lead to better fitness and a larger abundance of the species population (Feniova et al., 2013).

Variable results have been observed for competitive superiority of smaller species, in particular of the genus *Ceriodaphnia*, which depends on the species involved. Smith & Cooper (1982) define the *Ceriodaphnia* - *Daphnia* interaction as very complex, with a non-linear relationship concerning the advantage of one over the other. Neill (1975) observed, in one of the experiments, that the smaller species, *Ceriodaphnia quadrangula*, was able to exclude most juveniles of *Daphnia magna*, because these were very sensitive to resource depletion. A similar situation was observed by Lynch (1978) who also found changes in competitive relationships between *Daphnia pulex* and *Ceriodaphnia reticulata*. *Daphnia magna* and *D. pulex* had a higher population growth rate than *Ceriodaphnia reticulata* only when food was abundant (Tessier & Goulden, 1987). Romanovsky & Feniova (1985) observed that *Ceriodaphnia reticulata* was superior to *Daphnia pulex* in lower food concentrations; juveniles of larger cladocerans do not reach maturity under severe food limitation. However, when other factor, such as temperature, is involved the competitive advantage of large and small species can change in relation to food concentration (Feniova et al., 2013).

Predation and competition in Lake Monte Alegre may vary throughout the year, with different

strength in the seasons. It is possible, however, to suppose that predation, although weaker during the cool season, collaborates for maintaining *C. richardi*'s population well below its carrying capacity, leading to coexistence with the subordinate *D. gessneri*. Predation was the driving force, in the warm season, and we suppose that prey were not extinct due also to escape strategies developed by cladocerans in this lake. The two species showed different strategies of spatial occupation (Arcifa et al., 2013; Arcifa et al., 2016), resulting in a partial overlap between them. *C. richardi* seems to be more skilled to escape from invertebrate predation, such as a more effective use of the littoral zone and the uppermost layer of the water column, leading to a lower spatial overlap (42%) with *Chaoborus* larvae than *D. gessneri* (75%) (Arcifa et al., 2016). Nevertheless, mortality of *C. richardi*'s population was weakly offset by the larger number of offsprings, shorter egg development, and escape ability, when predation was stronger in the warm season. It is plausible to suppose that predation, falling on the reproductive phase, has greater impact over this population than on *D. gessneri*.

The conspicuous influence of predation by invertebrates in our study was also detected in the long-term study in Lake Monte Alegre (Arcifa et al., 2015). While the influence of predation is more evident on the potentially competing populations, exploitative competition possibly has a more sporadic role, when food resources are lower in the cool season.

Coexistence of the two potentially competing cladocerans in the lake may be propitiated by resource partitioning, absent in laboratory experiments. Taken into account two niche dimensions, food and habitat, it seems that a partial habitat segregation due to the horizontal and vertical distribution of *C. richardi* and *D. gessneri* in the lake (Arcifa et al., 2016) may lower resource overlap. Based on the assumption of partial overlap, due to the possibility of resource exploitation in different lake zones, and that the predator was shared, type b of Figures 3 and 4 of Chesson & Kuang (2008) can offer a better explanation to the interactions between these two cladocerans in the lake. In this case, niche overlap would be a function of relative predation intensity. When predation attains the highest strength in the lake in the warm season, the species *C. richardi* is subject to a stronger impact than *D. gessneri*, leading to very low densities, compared to those of the cool season. These observations support our conclusion that predation

on adult females of *C. richardi* has a stronger impact on the population than predation on neonates of *D. gessneri*.

Our results suggest that food, temperature, and competition could be the main factors influencing the cladocerans in the cool season and predation by invertebrates in the warm season in the lake. Although predation is lower in the cool season, it can mediate competition by preventing the populations to reach high densities.

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References

- ALLAN, J.D. Competition and the relative abundances of two cladocerans. *Ecology*, 1973, 54(3), 484-498. <http://dx.doi.org/10.2307/1935334>.
- ARCIFA, M.S. and MESCHIATTI, A.J. Distribution and feeding ecology of fishes in a Brazilian reservoir: Lake Monte Alegre. *Interciencia*, 1993, 18(6), 302-313.
- ARCIFA, M.S. and MESCHIATTI, A.J. *Tilapia rendalli* in the Lake Monte Alegre, a case of planktivory. *Acta Limnologica Brasiliensia*, 1996, 8(1), 221-229.
- ARCIFA, M.S. Feeding habits of Chaoboridae larvae in a tropical Brazilian reservoir. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2000, 60(4), 591-597. <http://dx.doi.org/10.1590/S0034-71082000000400008>. PMID:11241957.
- ARCIFA, M.S., BUNIOTO, T.C., PERTICARRARI, A. and MINTO, W.J. Diel horizontal distribution of microcrustaceans and predators throughout a year in a shallow neotropical lake. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2013, 73(1), 103-114. <http://dx.doi.org/10.1590/S1519-69842013000100012>. PMID:23644793.
- ARCIFA, M.S., FERREIRA, T.C.S., FILETO, C., CASTILHO-NOLL, M.S.M., BUNIOTO, T.C. and MINTO, W.J. A long-term study on crustacean plankton of a shallow tropical lake: the role of invertebrate predation. *Journal of Limnology*, 2015, 74(3), 606-617.
- ARCIFA, M.S., GOMES, E.A.T. and MESCHIATTI, A.J. Composition and fluctuations of the zooplankton of a tropical Brazilian reservoir. *Archiv für Hydrobiologie*, 1992, 123(4), 479-495.
- ARCIFA, M.S., MESCHIATTI, A.J. and GOMES, E.A.T. Thermal regime and stability of a tropical shallow reservoir: Lake Monte Alegre, Brazil. *Revue d'Hydrobiologie Tropicale*, 1990, 23, 271-281.
- ARCIFA, M.S., PERTICARRARI, A., BUNIOTO, T.C., DOMINGOS, A.R. and MINTO, W.J. Microcrustaceans and predators: diel migration in a tropical lake and comparison with shallow warm lakes. *Limnetica*, 2016, 35(2), 281-296.
- BENGTSSON, J. Competitive dominance among Cladocera: Are single-factor explanations enough? *Hydrobiologia*, 1987, 145(1), 245-257. <http://dx.doi.org/10.1007/BF02530285>.
- BROOKS, J.L. and DODSON, S.I. Predation, body size and composition of plankton. *Science*, 1965, 150(3692), 28-35. <http://dx.doi.org/10.1126/science.150.3692.28>. PMID:17829740.
- BUNIOTO, T.C. and ARCIFA, M.S. Effects of food limitation and temperature on cladocerans from a tropical Brazilian lake. *Aquatic Ecology*, 2007, 41(4), 569-578. <http://dx.doi.org/10.1007/s10452-007-9114-2>.
- CASSANO, C.R., CASTILHO-NOLL, M.S.M. and ARCIFA, M.S. Water mite predation on zooplankton of a tropical lake. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2002, 62(4A), 565-571. <http://dx.doi.org/10.1590/S1519-69842002000400002>. PMID:12659004.
- CASTILHO-NOLL, M.S.M. and ARCIFA, M.S. *Chaoborus* diet in a tropical lake and predation of microcrustaceans in laboratory experiments. *Acta Limnologica Brasiliensia*, 2007a, 19(2), 163-174.
- CASTILHO-NOLL, M.S.M. and ARCIFA, M.S. Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake. *Aquatic Ecology*, 2007b, 41(4), 587-598. <http://dx.doi.org/10.1007/s10452-007-9112-4>.
- CHASE, J.M., ABRAMS, P.A., GROVER, J.P., DIEHL, S., CHESSON, P., HOLT, R.D., RICHARDS, S.A., NISBET, R.M. and CASE, T.J. The interaction between predation and competition: a review and synthesis. *Ecology Letters*, 2002, 5(2), 302-315. <http://dx.doi.org/10.1046/j.1461-0248.2002.00315.x>.
- CHEN, R., TANG, H., ZHAO, F., WU, Y., HUANG, Y. and YANG, Z. Food availability and initial relative abundance determine the outcome of interspecific competition between two different-sized cladocerans. *International Review of Hydrobiology*, 2016, 101(3-4), 105-112. <http://dx.doi.org/10.1002/iroh.201501832>.
- CHESSON, P. and KUANG, J.J. The interaction between predation and competition. *Nature*, 2008, 456(7219), 235-238. <http://dx.doi.org/10.1038/nature07248>. PMID:19005554.
- DEMOTT, W.R. and KERFOOT, W.C. Competition among cladocerans: nature of the interactions

- between *Bosmina* and *Daphnia*. *Ecology*, 1982, 63(6), 1949-1966. <http://dx.doi.org/10.2307/1940132>.
- DEMOTT, W.R. The role of competition in zooplankton succession. In: U. SOMMER, ed. *Plankton ecology: succession in plankton communities*. Berlin: Springer-Verlag, 1989, pp. 195-252. http://dx.doi.org/10.1007/978-3-642-74890-5_6.
- DODSON, S.I. Complementary feeding niches sustained by size selective predation. *Limnology and Oceanography*, 1970, 5(1), 131-137. <http://dx.doi.org/10.4319/lo.1970.15.1.0131>.
- DZIALOWSKI, A.R. and O'BRIEN, W.J. Is competition important for arctic zooplankton community structure? *Freshwater Biology*, 2004, 49(9), 1103-1111. <http://dx.doi.org/10.1111/j.1365-2427.2004.01250.x>.
- FENIOVA, I.Y., PALASH, A.L., RAZLUTSKIJ, V.I. and DZIALOWSKI, A.R. Effects of temperature and resource abundance on small- and large-bodied cladocerans: Community stability and species replacement. *Open Journal of Ecology*, 2013, 3(02), 164-171. <http://dx.doi.org/10.4236/oje.2013.32020>.
- FENIOVA, I.Y., RAZLUTSKY, V.I. and PALASH, A.L. Temperature effects of interspecies competition between cladoceran species in experimental conditions. *Inland Water Biology*, 2011, 4(1), 65-71. <http://dx.doi.org/10.1134/S1995082910041017>.
- FERRÃO-FILHO, A.S., ARCIFA, M.S. and FILETO, C. Influence of seston quantity and quality on growth of tropical cladocerans. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2005., 65(1), 77-89. <http://dx.doi.org/10.1590/S1519-69842005000100011>. PMID:16025906.
- FERRÃO-FILHO, A.S., ARCIFA, M.S. and FILETO, C. Resource limitation and food quality for cladocerans in a tropical Brazilian lake. *Hydrobiologia*, 2003, 491(1-3), 201-210. <http://dx.doi.org/10.1023/A:1024496611829>.
- FILETO, C., ARCIFA, M.S., FERRÃO-FILHO, A.S. and SILVA, L.H.S. Influence of phytoplankton fractions on growth and reproduction of tropical cladocerans. *Aquatic Ecology*, 2004, 38(4), 503-514. <http://dx.doi.org/10.1007/s10452-004-4087-x>.
- GLIWICZ, Z.M. and PIJANOWSKA, J. The role of predation in zooplankton succession. In: U. SOMMER, ed. *Plankton ecology: succession in plankton communities*. Berlin: Springer-Verlag, 1989, pp. 253-296. http://dx.doi.org/10.1007/978-3-642-74890-5_7.
- GLIWICZ, Z.M. Food thresholds and body size in cladocerans. *Nature*, 1990, 343(6259), 638-640. <http://dx.doi.org/10.1038/343638a0>.
- GOULDEN, C.E., HORNIG, L.L.P. and WILSON, C. Why do large zooplankton species dominate? *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 1978, 20, 2457-2460.
- HALL, D.J. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. *Ecology*, 1964, 45(1), 94-112. <http://dx.doi.org/10.2307/1937111>.
- HANEY, J.F. and HALL, D.J. Sugar-coated *Daphnia*: A preservation technique for Cladocera. *Limnology and Oceanography*, 1973, 18(2), 331-333. <http://dx.doi.org/10.4319/lo.1973.18.2.0331>.
- HARDY, E.R. and DUNCAN, A. Food concentration and temperature effects on life cycle characteristics of tropical cladocera (*Daphnia gessneri* Herbst, *Diaphanosoma sarsi* Richard, *Moina reticulata* (Daday): 1. Development time. *Acta Amazonica*, 1994, 24(1/2), 119-134. <http://dx.doi.org/10.1590/1809-43921994242134>.
- HURTADO-BOCANEGRA, M.D., NANDINI, S. and SARMA, S.S.S. Combined effects of food level and inoculation density on competition between *Brachionus patulus* (Rotifera) and the cladocerans *Ceriodaphnia dubia* and *Moina macrocopa*. *Hydrobiologia*, 2002, 468(1/3), 13-22. <http://dx.doi.org/10.1023/A:1015261625982>.
- HUTCHINSON, G.E. The paradox of the plankton. *American Naturalist*, 1961, 5(3), 137-146. <http://dx.doi.org/10.1086/282171>.
- JEFFREY, S.W. and HUMPHREY, G.F. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c1* and *c2* in higher plants, algae, and natural phytoplankton. *Biochimie und Physiologie der Pflanzen*, 1975, 167(2), 191-194. [http://dx.doi.org/10.1016/S0015-3796\(17\)30778-3](http://dx.doi.org/10.1016/S0015-3796(17)30778-3).
- JOHNSON, J.L. and HAVEL, J.E. Competition between native and exotic *Daphnia*: *in situ* experiments. *Journal of Plankton Research*, 2001, 23(4), 373-387. <http://dx.doi.org/10.1093/plankt/23.4.373>.
- KREBS, C.J. *Ecology: the experimental analysis of distribution and abundance*. 3. ed. New York: Harper and Row, 1985.
- LYNCH, M. Complex interactions between natural co-exploiters *Daphnia* and *Ceriodaphnia*. *Ecology*, 1978, 59(3), 552-564. <http://dx.doi.org/10.2307/1936585>.
- MCCAULEY, E. The estimation of the abundance and biomass of zooplankton in samples. In: J.A. DOWNING and F.H. RIGLER, eds. *A Manual on methods for the assessment of secondary productivity in fresh waters*. London: Blackwell Scientific, 1984, pp. 228-265.
- MESCHIATTI, A.J. and ARCIFA, M.S. Early life stages of fish and the relationships with zooplankton in a tropical Brazilian reservoir: Lake Monte Alegre. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2002, 62(1), 41-50. <http://dx.doi.org/10.1590/S1519-69842002000100006>. PMID:12185922.

- MILBRINK, G., KRUSE, M.L. and BENGTTSSON, J. Competitive ability and life history strategies in four species of *Daphnia*: *D. obtusa*, *D. magna*, *D. pulex* and *D. longispina*. *Archiv für Hydrobiologie*, 2003, 157(4), 433-453. <http://dx.doi.org/10.1127/0003-9136/2003/0157-0433>.
- MUNRO, I.G. and WHITE, R.W.G. Comparison of the influence of temperature on the egg development and growth of *Daphnia longispina* O.F. Muller (Crustacea: Cladocera) from two habitats in Southern England. *Oecologia*, 1975, 20(2), 157-165. <http://dx.doi.org/10.1007/BF00369028>. PMID:28308822.
- NANDINI, S. and SARMA, S.S.S. Population growth of some genera of cladocerans (Cladocera) in relation to algal food (*Chlorella vulgaris*) levels. *Hydrobiologia*, 2003, 491(1-3), 211-219. <http://dx.doi.org/10.1023/A:1024410314313>.
- NEILL, W.E. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology*, 1975, 56(4), 809-826. <http://dx.doi.org/10.2307/1936293>.
- PERTICARRARI, A. *Distribuição espacial e interação entre presas e predadores invertebrados no lago Monte Alegre* [Tese de Doutorado]. Ribeirão Preto: Universidade de São Paulo, 2005.
- REYNOLDS, C.S. *The ecology of freshwater phytoplankton*. Cambridge: Cambridge University Press, 1984.
- ROMANOVSKY, Y.E. and FENIOVA, I.Y. Competition among Cladocera: effect of different levels of food supply. *Oikos*, 1985, 44(2), 243-252. <http://dx.doi.org/10.2307/3544696>.
- SCHOENER, T.W. Field experiments on interspecific competition. *American Naturalist*, 1983, 122(2), 240-285. <http://dx.doi.org/10.1086/284133>.
- SCHOENER, T.W. Resource partitioning in ecological communities. *Science*, 1974, 185(4145), 27-39. <http://dx.doi.org/10.1126/science.185.4145.27>. PMID:17779277.
- SCHOENER, T.W. The controversy over interspecific competition. *American Scientist*, 1982, 70, 586-595.
- SILVA, L.H.S. *Fitoplâncton de um pequeno reservatório eutrófico (Lago Monte Alegre, Ribeirão Preto, SP): dinâmica temporal e respostas do fitoplâncton à ação do zooplâncton e peixes* [Tese de Doutorado]. Rio de Janeiro: Universidade Federal do Rio de Janeiro, 2004.
- SILVA, L.H.S., ARCIFA, M.S., SALAZAR-TORRES, G. and HUSZAR, V.L.M. *Tilapia rendalli* increases phytoplankton biomass of a shallow tropical lake. *Acta Limnologica Brasiliensia*, 2014, 26(4), 429-441. <http://dx.doi.org/10.1590/S2179-975X2014000400010>.
- SMITH, D.W. and COOPER, S.D. Competition among Cladocera. *Ecology*, 1982, 63(4), 1004-1015. <http://dx.doi.org/10.2307/1937240>.
- STEMBERGER, R.S. A general approach to the culture of planktonic rotifers. *Canadian Journal of Fisheries and Aquatic Sciences*, 1981, 38(6), 721-724. <http://dx.doi.org/10.1139/f81-095>.
- TESSIER, A.J. and GOULDEN, C.E. Cladoceran juvenile growth. *Limnology and Oceanography*, 1987, 32(3), 680-686. <http://dx.doi.org/10.4319/lo.1987.32.3.0680>.
- WIENS, J.A. On competition and variable environments: populations may experience "ecological crunches" in variable climates, nullifying the assumptions of competition theory and limiting the usefulness of short-term studies of population patterns. *American Scientist*, 1977, 65, 590-597.
- ZARET, T.M. *Predation and freshwater communities*. New Haven: Yale University Press, 1980.

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