

Article

Competition of Cladocerans for Natural Seston from a Tropical Shallow Lake

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Abstract: The planktonic cladocerans *Ceriodaphnia richardi*, *Daphnia gessneri*, and *Daphnia birgei* inhabit the limnetic and littoral zones of Lake Monte Alegre, where the former species tends to be abundant. Laboratory experiments were carried out to investigate the competition for seston of the limnetic and littoral zones in cladocerans using life table data. In experiment 1, the species *C. richardi* and *D. gessneri* were fed seston from the limnetic zone (1–1.29 mg C L⁻¹); in experiment 2, the species *C. richardi* and *D. birgei* were fed seston from the littoral zone. Despite the relatively high concentration of sestonic algae (0.96–1 mg C L⁻¹), with predominance of nanoplankton, *C. richardi* outcompeted *D. gessneri* in the experiment with the limnetic seston. The species *C. richardi* and *D. birgei* benefited from the presence of each other in the experiment with littoral seston, where nanoplankton predominated, with increases in some parameters of the life table. *D. birgei*, however, showed better reproductive performance than *C. richardi*. A comparison between the results of the experiments suggests that the seston of the limnetic zone, in terms of quantity and quality, is better for *C. richardi* than the littoral seston.

Keywords: limnetic and littoral seston; phytoplankton; *Daphnia*; *Ceriodaphnia*; *Diaphanosoma*



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1. Introduction

Competition is considered a very important interaction in the structuring of communities [1,2], although predation has gained prominence, especially since the 1980s [3]. In interspecific competition, the superior species is more efficient in filtration, leading the inferior species to starvation [4]. Both the quantity and quality of food are important in exploitative competition [5,6].

Studies on competition using life tables are less common [7] than those based on abundance and population growth [6,8–10], due to the greater difficulty in obtaining data. “Parameters such as survivorship, average lifespan, life expectancy, fecundity, reproductive rate and generation time provide valuable insights into the suitability of the ambient conditions for zooplankton” [9]. The evaluation of reproductive parameters is more sensitive to competition for food resources than survival [4,9].

From the hypotheses proposed to explain competition and the superiority of species [11], the “small body size hypothesis” (e.g., [2]) suggests that smaller species are more efficient because they reach sexual maturity earlier and juveniles have a lower threshold food concentration than juveniles of larger species, giving an advantage when food is limited. In general, the “small body size hypothesis”, is supported by 17% of studies [11]. The concept of threshold food concentration (TFC), based on work by [12], can be used to explain exploitative competition and is defined as the concentration at a population growth rate equal to zero in the absence of predators, that is, the minimum food needed for population reproduction. The species with the lowest TFC is superior and can eliminate a

competitor [13–16]. At food concentrations below the TFC, the species that better resists starvation outcompetes another [17]. This hypothesis was supported by 36% of studies [11].

While most of the hypotheses proposed to explain competitive interactions are based on resource constraints, the hypothesis of the maximum intrinsic growth rate, r_{\max} [18], predicts the opposite. According to the hypothesis, the species capable of reaching the highest density when food is not limited can suppress species that do not increase at the same rate [17]. Small body size organisms are more likely to achieve a higher r_{\max} because of their short generation time [19]. Species that achieve high r_{\max} values are usually r -strategists that rapidly increase their densities when resources are not limited [17].

Facilitation, a positive interaction [20], caused changes in the concepts traditionally established in ecology [21]. According to models presented by the latter authors, there would be changes related to niche and competition, among others. In mutualism, both species benefit, and in facilitation, one of them benefits from the interaction. One species can feed on semi-digested fecal particles from another, thus benefiting from its presence [22], and facilitation effects may arise in exploitative competition [23].

Studies on exploitative competition between cladocerans have been carried out in the laboratory with controlled conditions, such as concentrations of unialgal food, temperature, and light. However, the influence of algae from natural communities on competitive interactions between cladocerans is less known [2,5,6,24].

An ample project developed in Lake Monte Alegre aimed to understand the role of interactions in the composition, abundance, and distribution of cladoceran populations. The issues that guided these studies focused on the relevance of interactions: 1. Is predation more important than competition? 2. Does predation by *Chaoborus* larvae prevail over fish and other invertebrates? 3. Does competition play a secondary role in structuring the cladoceran community? 4. Could food become limiting in the environment leading to competition between species? 5. Which hypotheses on competition would better explain the superiority of a species over others?

Studies on competition between cladocerans from Lake Monte Alegre have focused on laboratory experiments, with defined concentrations of a single species of edible alga and controlled conditions of temperature, light, and photoperiod [10,25]. However, the current study used natural seston, with all its variability in algal composition and size, to test the possibility of competition in the environment, including the limnetic and littoral zones. With this aim, laboratory experiments were conducted to test the food effect on exploitative competitive interactions, regarding the quantity and quality of natural seston of the limnetic and littoral zones, using combinations of pairs of three species of cladocerans, *Ceriodaphnia richardi*, *Daphnia gessneri*, and *Diaphanosoma birgei*, which coexist in both zones of the lake. The limnological conditions of the lake and the characteristics of the phytoplankton during the experimental periods were also evaluated to show the conditions to which the organisms were submitted.

2. Materials and Methods

2.1. The Lake

Lake Monte Alegre (21°10'04" S, 47°51'28" W), where the cladocerans were collected, is a tropical shallow lake (area: 7 ha; Zmax: 5 m; mean depth: 2.9 m; altitude: 500 m above sea level) located in a Permanent Preservation Area within the campus of the University of São Paulo in southeastern Brazil. It was formed by damming the Laureano Creek of the Pardo River basin in 1942. Despite being a reservoir, it functions as a natural lake because the gate is not managed and its retention time (ca. 45 days) is relatively high for its dimensions. The climate is tropical, with two marked seasons: a cool–dry season (May–September) and a warm–wet one (October–April).

2.2. Algae Culture

The cladocerans were cultivated before the experiments, with the chlorophycean *Desmodesmus spinosus* (~10 µm; formerly *Scenedesmus spinosus*), which was cultivated in

MBL medium [26] in a germination chamber (FANEM, model CDG, São Paulo, SP, Brazil) at a temperature of 23 °C and with a photoperiod of 12:12 h. This temperature is equivalent to the average value of the water column over the year.

2.3. Sampling, Cultivation, and Acclimation of Cladocerans

Females cladocerans were collected in the lake, with a 58 µm meshed plankton net. Each species was cultivated separately before the beginning of the experiments for approximately 30 days.

The experiments followed a standard procedure used in the laboratory described by [25]: “the cladocerans were initially kept in 140 mL glass bottles, and then transferred to 600 mL bottles, after the increase of the organisms, for avoiding the crowding effect. The bottles were filled with lake water filtered on glass fiber membrane (Millipore AP20), plus 1 mg C L⁻¹ of the chlorophycean *D. spinosus* as food. The organisms were transferred to new bottles or discarded to maintain the limit of 20 individuals per bottle. Oviparous females were separated and transferred individually to small 40 mL test tubes containing filtered lake water + food, to obtain the neonates. All neonates born within 24 h were mixed and randomly selected, for the different treatments, to avoid a possible influence of maternal effects”.

2.4. Experiment 1: Competition between *Ceriodaphnia richardi* and *Daphnia gessneri* for Limnetic Seston

The experiment was carried out from 10 February 2014 to 13 March 2014 (warm–wet season), lasting 31 days. The experimental design was based on [4,22]. The cladocerans used in the experiment were *C. richardi* (maximum size 0.70 mm) and *D. gessneri* (max. size 1.22 mm) collected from the lake, as described in Section 2.3. These two species coexist in the limnetic zone of the lake.

Natural seston was used as a food source, collected daily from the central region of the lake with a 1 L Ruttner bottle at several depths in the euphotic zone between the surface and 3.5 m, and mixed in a 5 L recipient. The deepest layers were avoided due to low oxygen concentrations during periods of stratification. The water was filtered through a small 140 µm mesh net to eliminate large planktonic organisms, chaoborid larvae, and mites. The seston concentrations varied from 1 to 1.29 mg C L⁻¹ during the experimental period.

Randomly selected neonates were transferred to 140 mL bottles containing the freshly collected seston. The treatments were (4 replicates each): a. control with 10 neonates of *C. richardi* (Cr–); b. control with 10 neonates of *D. gessneri* (Dg–); and c. shared cultures with 5 neonates of each species (Cr+ and Dg+).

The medium was changed daily and all survivors and neonates produced were counted. The survivors were transferred to new bottles containing a new medium, and the neonates were narcotized and fixed according to [27]. The experiment was performed in a laboratory with dim lighting, mimicking the lake conditions, at 23 °C and with a 12:12 h photoperiod on a plankton wheel (rotating 1 min every 5 min), ending after the death of all individuals.

The main parameters of the life table analyzed were survival (l_x), fertility (b_x), gross reproductive rate (Grr), net reproductive rate (R_0), generation time (G), and population growth rate (r) [28].

$$\text{Survivalprofile}(l_x) = \frac{S(x)}{S(0)} \quad (1)$$

$$\text{Fecundityprofile} = \frac{b(x)}{S(x)} \quad (2)$$

$$\text{Grossreproductiverate}(Grr) : \sum_0^{\infty} b_x \quad (3)$$

$$\text{Netreproductiverate}(R_0) : \sum_0^{\infty} lx.bx \quad (4)$$

$$\text{Generationtime}(G) : \sum_0^{\infty} lx.bx.x \quad (5)$$

$$\text{Approximatepopulationgrowthrate}(r) : \frac{\ln R_0}{G} \quad (6)$$

$$r - \text{corrected}(\text{EulerEquation}) : \sum_{x=w}^n e^{-rx}.lx.bx = 1 \quad (7)$$

where (1) lx is the probability that an individual will survive to a certain age class; (2) b_x is the per capita birth rate for females, that is, the average number of offspring produced by a female of a certain age per unit of time; (3) R_0 is the average number of offspring produced per female over a lifetime, adjusted to the survival profile; (4) G is the average number of offspring produced per female over a lifetime, disregarding mortality ($lx = 1$); (5) G is the average age of the parents of all descendants produced by a population; (6) r corrected is the intrinsic rate of population growth corrected by the Euler equation. Reproductive effort (R_0 /reproductive period) was calculated according to [4].

2.4.1. Physical and Chemical Factors, Algal Carbon, and Phytoplankton Composition and Size in the Lake during the Experimental Period

The limnological factors analyzed in the lake during the experimental period were temperature and dissolved oxygen (Yellow Springs Inc., model 95, Yellow Springs, OH, USA), electrical conductivity (YSI 30), and pH (YSI 60). The factors were measured in a meter from the surface to 3.5 m depth (euphotic zone). The water transparency was measured with a 30 cm diameter white Secchi disk. The euphotic zone was calculated by $ZE = DS \times 2.7$, where ZE = thickness of the euphotic zone and DS = Secchi disk value (m), according to [29]. The chlorophyll *a* was measured in water samples collected in the euphotic zone (see Section 2.4) to feed the cladocerans, according to [30]. The transformation of chlorophyll concentration into carbon (mg C L^{-1}) was based on the chlorophyll/algae ratio, assuming that chlorophyll represents 1.25% of the dry weight of algae, within the limits reported by [31], and carbon represents 50% of the dry weight of algae.

For phytoplankton analyses, samples were collected in a water column in integrated samples in the euphotic zone, as described in Section 2.4, and fixed with Lugol's solution. Phytoplankton populations were concentrated by sedimentation and counted in random fields [32] under an inverted microscope (Zeiss Oberkochen Axiovert 10, Carl Zeiss, Jena, Germany) with 400x magnification [33]. The phytoplankton taxonomic groups were defined according to the criteria established by [34] except for cyanobacteria [35–37] and diatoms [38], and the infrageneric categories are those usually registered in the specialized literature.

2.5. Experiment 2: Competition between *Ceriodaphnia richardi* and *Diaphanosoma birgei* for Littoral Seston

This experiment was carried out between 4 and 24 July 2014 (cool–dry season) for 21 days with the cladocerans *C. richardi* and *D. birgei* (max. size 0.87 mm). These species coexist in the littoral zone, where *D. birgei* is commonly found in lower densities than *C. richardi* [39].

Natural seston was used as a food source, collected daily from the littoral zone of the lake. The sampling, selection, and cultivation of cladocerans; the experimental design; the laboratory conditions; and the life table parameters analyzed were the same as described in experiment 1. The seston concentration given to cladocerans varied from 0.96 to 1 mg C L^{-1} .

The treatments were (4 replicates each) a. control with 10 neonates of *C. richardi* (Cr−); b. control with 10 neonates of *D. birgei* (Db−); and c. shared cultures with 5 neonates of each species (Cr+ and Db+).

Physical and Chemical Factors, Algal Carbon, and Phytoplankton Composition and Size in the Lake during the Experimental Period

The limnological factors analyzed in the lake were the same as described in experiment 1 (Section 2.4.1). Measurements were taken at the surface and at 1 m in the littoral zone of the lake. For phytoplankton analysis, samples were collected at 0.5 m, close to the bank of the emergent macrophyte, composed mainly of *Ludwigia* sp. The evaluation of phytoplankton composition and size in the lake was the same as described in experiment 1 (Section 2.4.1). Turbidity values were measured in integrated samples from the surface and 1 m deep by a turbidimeter (Turbidimeter HACH, model 2100p, Loveland, CO, USA).

2.6. Data Analysis

One-way ANOVA was used in the treatment of the data of the analyzed parameters of the life table with the post hoc Fisher test. The software STATISTICA 8.0—StatSoft was used for data processing, with significance level $p < 0.05$.

3. Results

3.1. Experiment 1: Competition between *C. richardi* and *D. gessneri* for Limnetic Seston

In the control treatment of *C. richardi* (Cr−) and together with *D. gessneri* (Cr+), there was a constant mortality throughout life, with a more pronounced mortality in Cr− between 5 and 6 days, expressed as a decrease of ca. 25% in survivorship (Figure 1a,b, respectively). *D. gessneri*, in turn, had a higher mortality at the beginning of the experiment, affecting younger individuals, in both the control (Dg−) and in the shared treatment (Dg+), with increased adult mortality from the 11th day in Dg+, with death of all individuals on the 17th day (Figure 1c,d, respectively). In the shared treatment with *C. richardi*, the survival of *D. gessneri* was shortened to 16 days, while alone it was 25 days. The survival time for *C. richardi* was shortened by only one day in the shared treatment (29 days), but with increased survival of the young adults (Figure 1a,b).

The age at first reproduction was anticipated by one day in the shared treatment for both *C. richardi* (Figure 2b) and *D. gessneri* (Figure 2d) in relation to their respective controls (Figure 2a,c, respectively). The first clutch of *C. richardi* occurred on the 5th and 4th day in Cr− and Cr+, respectively, while for *D. gessneri* it was recorded on the 7th and 6th day, in Dg− and Dg+, respectively. The reproductive period lasted 29 days for *C. richardi* in Cr− and Cr+, while for *D. gessneri* it lasted 23 days in Dg− and 14 days in Dg+. Daily peaks of neonate production, throughout the reproductive period, were higher for the small *C. richardi* (~10 offspring female^{−1} day^{−1}) than for the large *D. gessneri* (~4 offspring female^{−1} day^{−1}).

There was no balance between survival and fecundity in terms of the allocation of energy in *D. gessneri*, as both were affected in the shared treatment with *C. richardi*.

The values of the life table parameters of *C. richardi* and *D. gessneri* in the control and shared treatments are detailed in Table 1. *C. richardi* showed no difference between the parameters in the control and in association with *D. gessneri*. On the contrary, although not significant, several parameters increased in the shared treatment with *D. gessneri*. On the other hand, the presence of *C. richardi* caused a significant reduction in the average life span and in the gross reproductive rate of *D. gessneri*. There was no relationship between life span and reproductive effort.

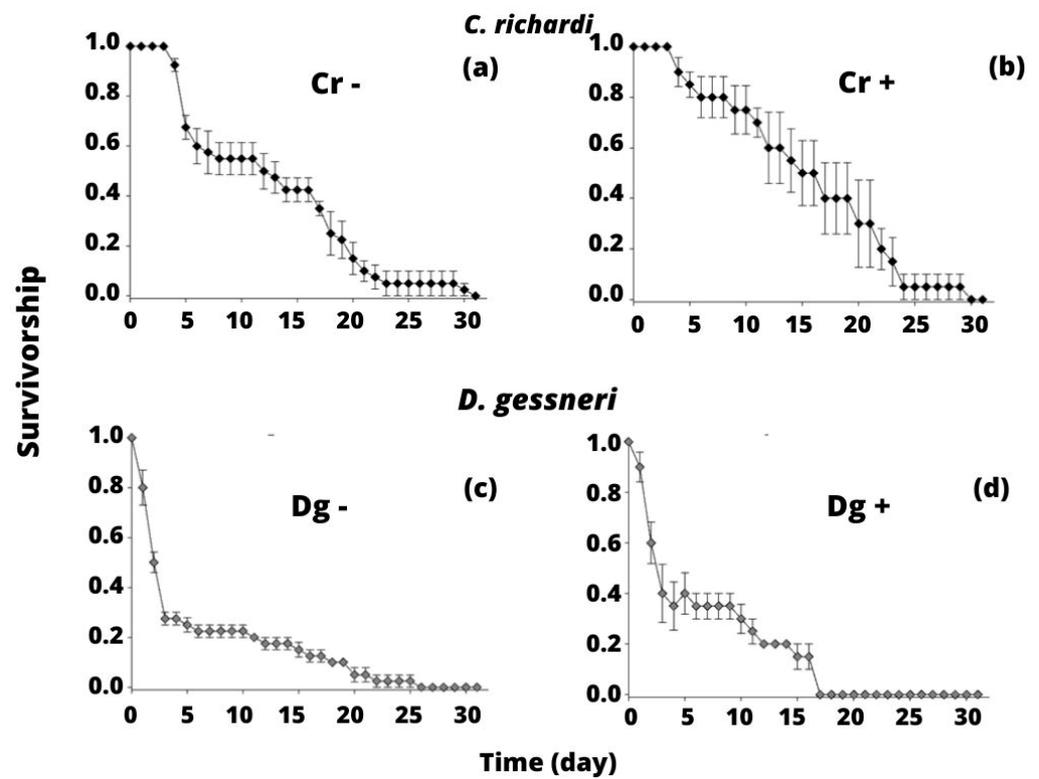


Figure 1. Survival curves at specific age (lx) of the species *C. richardi* (a,b) and *D. gessneri* (c,d) grown in natural seston from the limnetic zone alone (Cr−, Dg−) and in association with each other (Cr+, Dg+). Bars indicate the standard error of the mean based on the four replicates.

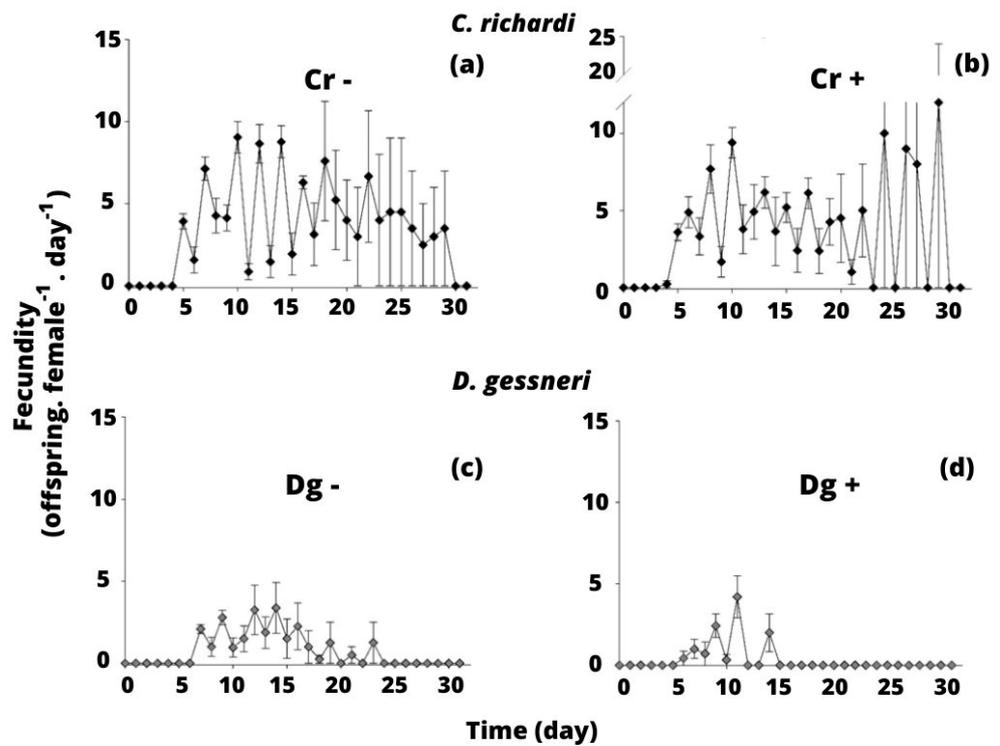


Figure 2. Fertility curves at specific age (bx) of the species *C. richardi* (a,b) and *D. gessneri* (c,d) grown in natural seston from the limnetic zone alone (Cr−, Dg−) and in association with each other (Cr+, Dg+). Bars indicate the standard error of the mean based on the four replicates.

Table 1. Life table parameters: average lifespan (day), Grr—gross reproductive rate (offspring female⁻¹ lifetime⁻¹), R₀—net reproductive rate (offspring female⁻¹ lifetime⁻¹), G—generation time (day), r—population growth rate, and reproductive effort (R₀/reproductive period) of *C. richardi* and *D. gessneri* alone (Cr−, Dg−) and in association with each other (Cr+, Dg+). Ns = non-significant; n = 4 replicates.

Species	Average Lifespan	Gross Reproductive Rate	Net Reproductive Rate	Generation Time	Population Growth Rate	Reproductive Effort
Cr−	23 ± 2.7	113.2 ± 38.0	43.5 ± 18.3	12.8 ± 1.0	0.4 ± 0.0	2.4 ± 0.4
Cr+	23 ± 2.1	119.1 ± 42.4	60.9 ± 21.1	12.6 ± 1.6	0.5 ± 0.0	3.2 ± 0.9
	ns	ns	ns	ns	ns	ns
Dg−	21 ± 1.4	24.8 ± 4.5	4.3 ± 1.1	11.9 ± 0.6	0.1 ± 0.0	0.3 ± 0.0
Dg+	15 ± 0.3	11.1 ± 3.4	3.2 ± 1.2	10.1 ± 0.8	0.1 ± 0.0	0.4 ± 0.1
<i>p</i>	0.004	0.05	ns	ns	ns	ns
Cr−	23 ± 2.7	113.2 ± 38.0	43.5 ± 18.3	12.8 ± 1.0	0.4 ± 0.0	2.4 ± 0.4
Dg−	21 ± 1.4	24.8 ± 4.5	4.3 ± 1.1	11.9 ± 0.6	0.1 ± 0.0	0.3 ± 0.0
<i>p</i>	ns	0.03	0.04	ns	0.000	0.01

In the control treatments, the gross reproductive rate of *C. richardi* exceeded that of *D. gessneri* (100 and 25 offspring female⁻¹ lifetime⁻¹, respectively), with a significant difference, as well as the net reproductive rate, which reached 40 and 4 offspring female⁻¹ lifetime⁻¹ in Cr− and Dg−, respectively (Table 1). The population growth rate and reproductive effort were also significantly higher for *C. richardi* in comparison with *D. gessneri*.

Physical and Chemical Factors, Algal Carbon, and Phytoplankton Composition and Size in the Lake during the Experimental Period

Physical and chemical factors and algal carbon concentration in the water column recorded in the lake on three occasions during the experimental period are shown in Table 2. In the warm–wet season, slightly higher temperatures were recorded at the surface, where the temperature difference between the surface and at 3.5 m (euphotic zone) was approximately 1 °C. Dissolved oxygen concentrations and the pH were lower at 3.5 m compared to the surface layer, especially on 11 of February, but not anoxic. Electrical conductivity values did not show great variations between layers or along the experimental period, and neither did the algal carbon concentrations, which varied from 1 to 1.29 mg C L⁻¹.

Table 2. Limnological factors at the surface and at 3.5 m and algal carbon in the limnetic zone, recorded in the lake during the experimental period in February–March (warm–rainy season).

Factors	Depth/Date	11/Feb	25/Feb	11/Mar
Temperature (°C)	Surface	28.60	27.60	28.20
	3.5 m	27.40	26.40	27.10
Dissolved oxygen (mg L ⁻¹)	Surface	5.80	10.82	12.60
	3.5 m	2.17	8.50	5.70
pH	Surface	7.06	6.03	7.02
	3.5 m	5.40	5.90	6.42
Conductivity (µS cm ⁻¹)	Surface	63.70	65.10	64.70
	3.5 m	65.90	63.30	65.10
Algal carbon (mg C L ⁻¹)	Euphotic zone	1.00	1.10	1.29

The nanoplankton fraction (≤20 µm) outnumbered the microplankton fraction (>20 µm) (Figure 3a). Overall, 121 taxa, belonging to nine classes, were identified: Chlorophyceae (50 taxa), Cyanobacteria (16 taxa), Zygnemaphyceae (20 taxa), Euglenophyceae (10 taxa), Bacillariophyceae (7 taxa), Cryptophyceae (7 taxa), Chrysophyceae (5 taxa), Dinophyceae (4 taxa), and Xanthophyceae (2 taxa). The first three classes were the most abundant in all sampling dates (Figure 3b), with greater contributions from small Chlorococcales such

as *Actinastrum aciculare* f. *minimum*, *Choricystis minor*, *C. Cyclindracea*, *Chlorella homosphaera*, *Monoraphidium minutum*, and *Scenedesmus elliptus*, in addition to *Synechococcus nidulans* and isolated cells of *Microcystis aeruginosa* (Cyanobacteria). *Cosmarium bioculatum* var. *depressum*, *C. sphagnicolum*, and *Closterium acutum* var. *variabile* were the zygne-maphyceans that most contributed to phytoplanktonic abundance. Of these taxa, only *A. aciculare* f. *minimum* and *Closterium acutum* var. *variabile* had sizes of > 20 μm.

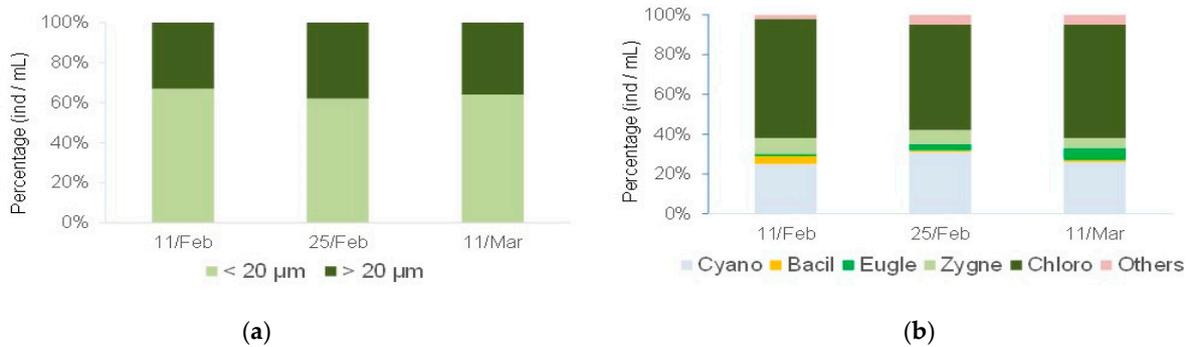


Figure 3. Phytoplankton size (a) and abundance of taxonomic groups (b) in the limnetic zone of the lake during the experimental period. Data are expressed as a percentage of algae density. Others = Cryptophyceae + Dinophyceae + Chrysophyceae + Xanthophyceae.

3.2. Experiment 2: Competition between *C. richardi* and *D. birgei* for Littoral Seston

Age-specific survival curves for *C. richardi* showed a tendency for increased survival of juveniles and young adults in both treatments, declining in the control (Cr−) from the 5th day, but only from the 10th day in the shared treatment with *D. birgei* (Cr+) (Figure 4a,b, respectively). Similarly, *D. birgei* also had better survival of juveniles and adults, which was higher in the control (Db−) compared to the shared treatment (Db+) during most of the experimental period (Figure 4c,d, respectively).

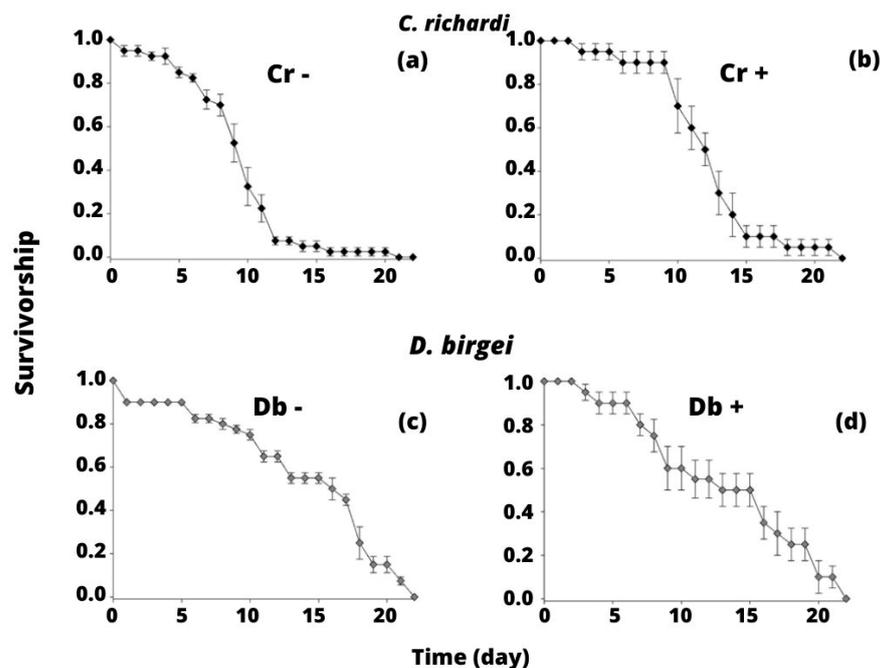


Figure 4. Survival curves at specific age (*lx*) of the species *C. richardi* (a,b) and *D. birgei* (c,d) grown in natural seston from the littoral zone alone (Cr−, Db−) and in association with each other (Cr+, Db+). Bars indicate the standard error of the mean based on the four replicates.

The age-specific fecundity curves of *C. richardi* showed that the age at first reproduction (day 4) and reproductive period (12 days) did not differ between treatments Cr− and Cr+ (Figure 5a,b, respectively), or between Db− and Db+ for *D. birgei* (day 3 and 21 days, respectively) (Figure 5c,d, respectively). Daily production peaks for both species indicated a greater number of neonates per female in shared treatments, Cr+ and Db+ (8 and 7 offspring female^{−1} day^{−1}, respectively) in relation to their respective controls, Cr− and Db− (5 and 6 offspring female^{−1} day^{−1}, respectively).

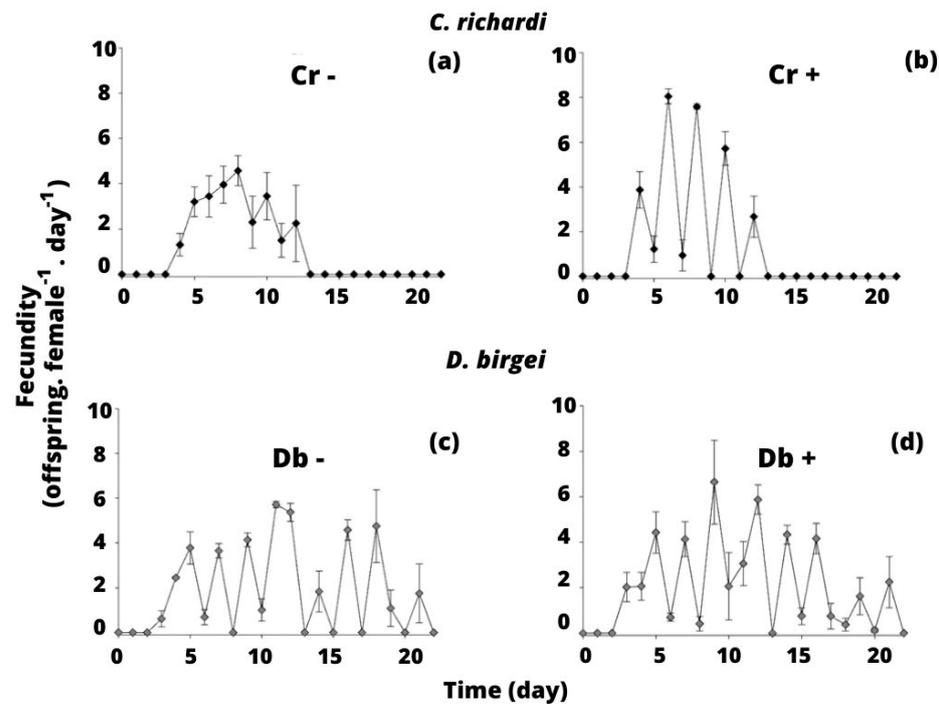


Figure 5. Fertility curves at specific age (*bx*) of the species *C. richardi* (a,b) and *D. birgei* (c,d) grown in natural seston from the littoral zone alone (Cr−, Db−) and in association with each other (Cr+, Db+). Bars indicate the standard error of the mean based on the four replicates.

The values of life table parameters of *C. richardi* and *D. birgei* recorded after the different treatments when alone (Cr−, Db−) and in association with each other (Cr+, Db+) are detailed in Table 3. In general, the life table parameters of *C. richardi* and *D. birgei* were not affected by the presence of each other. On the contrary, there was an increase in the values in Cr+ compared to Cr− regarding several parameters; this was significant, however, for only two parameters. Differences were not statistically significant for the parameters for Db− and Db+. Differences were also observed between the species in the controls (Cr− and Db−), with a better performance for *D. birgei* regarding several parameters (Table 3).

Physical and Chemical Factors, Algal Carbon, and Phytoplankton Composition and Size in the Lake during the Experimental Period

The physical and chemical factors and algal carbon concentration in the littoral zone of the lake are shown in Table 4. In the cool-dry season, there was low variation between values at the surface and at 1 m. pH values were recorded only at the beginning of the experiment due to problems with the pH meter. Turbidity values were not high and varied from 7.3 to 8.1 NTU, indicating a relatively low amount of suspended matter in this zone. Carbon concentrations varied from 0.96 to 1 mg C L^{−1} during the experimental period.

Table 3. Life table parameters: average lifespan (day), Grr—gross reproductive rate (offspring female⁻¹ lifetime⁻¹), R₀—net reproductive rate (offspring female⁻¹ lifetime⁻¹), G—generation time (day), r—population growth rate, and reproductive effort (R₀/reproductive period) of *C. richardi* and *D. birgei* alone (Cr−, Db−) and in association with each other (Cr+, Db+). Ns: non-significant ($p > 0.05$); n = 4 replicates.

Species	Average Lifespan	Gross Reproductive Rate	Net Reproductive Rate	Generation Time	Population Growth Rate	Reproductive Effort
Cr−	15.0 ± 1.4	26.0 ± 2.2	16.0 ± 1.5	7.0 ± 0.1	0.4 ± 0.01	2.1 ± 0.3
Cr+	16.0 ± 1.6	30.0 ± 1.7	25.3 ± 2.5	7.1 ± 0.1	0.5 ± 0.02	3.0 ± 0.2
<i>p</i>	ns	ns	0.02	ns	ns	0.01
Db−	21.0 ± 0.2	41.4 ± 2.4	25.4 ± 2.5	9.2 ± 0.2	0.4 ± 0.02	1.6 ± 0.1
Db+	19.0 ± 0.9	45.8 ± 5.2	25.9 ± 2.0	9.2 ± 0.5	0.5 ± 0.04	1.5 ± 0.1
<i>p</i>	ns	ns	ns	ns	ns	ns
Cr−	15.0 ± 1.4	26.0 ± 2.2	16.0 ± 1.5	7.0 ± 0.1	0.4 ± 0.01	2.1 ± 0.3
Db−	21.0 ± 0.2	41.4 ± 2.4	25.4 ± 2.5	9.2 ± 0.2	0.4 ± 0.02	1.6 ± 0.1
<i>p</i>	0.01	0.03	0.02	0.003	ns	ns

Table 4. Limnological factors at the surface and at 1 m and algal carbon in the littoral zone, recorded in the lake during the experimental period in July (cool-dry season).

Factors	Depth/Date	04/Jul	13/Jul	22/Jul
Temperature (°C)	Surface	20.7	20.3	20.1
	1 m	20.7	20.3	20.1
Dissolved oxygen (mg L ⁻¹)	Surface	10.5	9.5	10.4
	1 m	10.5	9.4	9.8
pH	Surface	6.4	---	---
	1 m	6.4	---	---
Conductivity (μS cm ⁻¹)	Surface	54.0	55.0	54.6
	1 m	54.0	55.0	56.5
Turbidity (NTU)	Water column (0–1 m)	7.3	7.4	7.6
Algal carbon (mg C L ⁻¹)	Water column (0–1 m)	0.96	0.96	1.00

Nanoplankton ($\leq 20 \mu\text{m}$) once again dominated the phytoplankton in relation to the microplankton ($>20 \mu\text{m}$) (Figure 6a), in a similar proportion in comparison to the limnetic seston (~71%). In total, 102 taxa were identified in the littoral zone, belonging to nine classes: Chlorophyceae (42 taxa), Cyanobacteria (15 taxa), Zygnemaphyceae (11 taxa), Bacillariophyceae (9 taxa), Euglenophyceae (9 taxa), Cryptophyceae (6 taxa), Chrysophyceae (4 taxa), Dinophyceae (4 taxa), and Xanthophyceae (2 taxa). As observed in the seston samples from the limnetic zone, chlorophyceae was the class with the greatest contribution to phytoplanktonic abundance, followed by Cyanobacteria (4th and 13th day) and Chrysophyceae (22nd day; Figure 6b). In experiment 2, the largest contributors to phytoplanktonic abundance were small taxa of Chlorococcales observed during experiment 1. For Cyanobacteria, in addition to the isolated cells of *Microcystis aeruginosa*, *Cyanogranis ferruginea*, *Cyanodictyon imperfectum*, and *Coelosphaerium kuetzingianum* were also important. Regarding chrysophyceans, *Dinobryon divergens* and a small unicellular chrysophycean ($<20 \mu\text{m}$) were also important for phytoplanktonic abundance. In this study period, only *Cyanodictyon imperfectum*, *Coelosphaerium kuetzingianum*, and *Dinobryon divergens* had sizes of $>20 \mu\text{m}$.

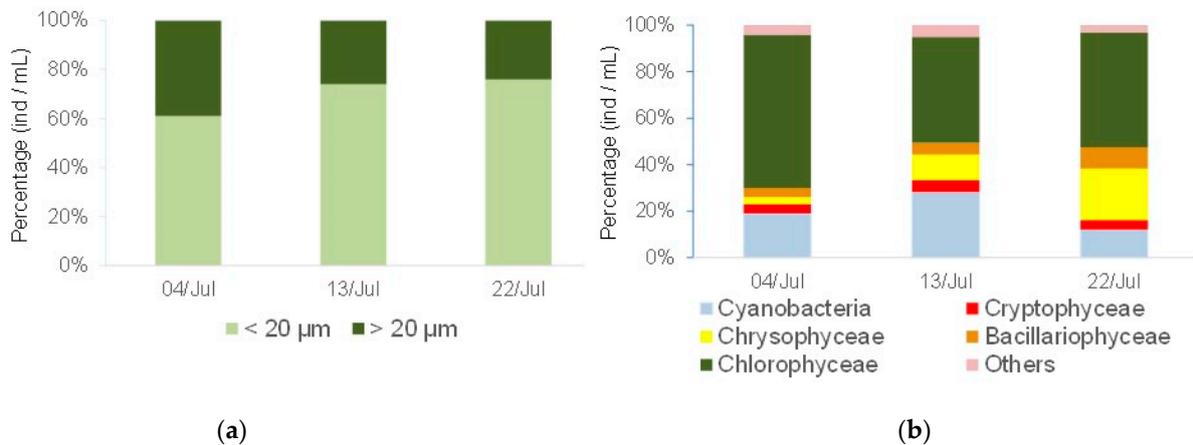


Figure 6. Phytoplankton size (a) and abundance of taxonomic groups (b) in the littoral zone of the lake during the experiment. Data are expressed as a percentage of algae density. Others = Dinophyceae + Xanthophyceae + Euglenophyceae + Zygnemaphyceae.

4. Discussion

4.1. Experiment 1: Competition between *C. richardi* and *D. gessneri* for Limnetic Seston

The relatively high concentrations of algal carbon during the experiment are within the limits reported for the warm–wet season (October–April) in the lake. In this season, algal carbon is generally high in the lake, reaching concentrations above 1 mg C L^{-1} and rarely decreasing to ca. 0.5 mg C L^{-1} [10]. The conditions indicated by the limnological factors were suitable for cladocerans in the experiments, since unfavorable conditions of the bottom layer were avoided.

The survival profiles of *C. richardi* and *D. gessneri* can be classified as type II and III, respectively [40]. In populations with a type II curve, mortality is independent of age, while in type III, few organisms are able to pass through the most vulnerable stage shortly after birth. The advantage for organisms that have a type III survival pattern is that those individuals that are able to pass through the most vulnerable stage tend to have an increased chance of survival in the later stages.

The mortality increase of juveniles of *D. gessneri* at the beginning of the experiment indicates a greater vulnerability of the species in relation to the smaller species, *C. richardi*. Our results agree with several studies that report a greater sensitivity of juveniles with the increasing body size of the species [2,5,6,41]. In other studies with cladocerans of Lake Monte Alegre, there was already an indication of the greater sensitivity of young *D. gessneri* regarding limiting food [25], which resulted in lower rates of juvenile growth compared to *C. richardi* [42]. In addition, the low reproductive rates of *D. gessneri* fed seston in the present study agree with work by [43], who reported the low growth of this species in the seston of Lake Monte Alegre, although the quantity and quality of edible algae were favorable to cladocerans, particularly in summer. In another study, both the densities and growth rates of *D. gessneri* were affected by the food concentration, even before it was competitively suppressed by *C. richardi* [10].

The reduced average life span of *D. gessneri* in the shared treatment with *C. richardi* suggests that the species' survival was affected by the presence of the competitor. Starvation [44,45] and crowding [46] may explain this reduction. The low mortality and the large number of neonates produced by *C. richardi* daily may have been sufficient to cause fluctuations in the food supply, impairing the most vulnerable species, *D. gessneri*. Although the experiment was designed to maintain the food concentration by changing the medium daily, a reduction in the food amount may have occurred during a short period between changing the medium in consequence of the high reproductive rates of *C. richardi*.

The increase in population density in the same place increases competition for space, making exploitative competition for resources more intense [47]. In this type of interaction,

the species capable of using the same resources of the most vulnerable species wins the competition [48].

The reduced average lifespan of *D. gessneri* in the presence of *C. richardi* influenced its reproduction by a decrease in the reproductive period, and, consequently, a significant decrease in the gross reproductive rate. Food depletion for adults is reflected in a low fertility and birth rate, resulting in low density of offspring [24]. The food amount available to the mother is what determines the energy allocated for reproduction [17]. In addition, adults of large species tend to allocate less energy for somatic growth compared to small species, impairing reproduction when food is scarce [49].

In spite of the concentrations of sestonic algae carbon being theoretically non limiting ($\sim 1 \text{ mg C L}^{-1}$) during the experiment, above the incipient limiting level (between 0.1 and 0.2 mg C L^{-1}) and the threshold food concentration ($<0.025 \text{ mg C L}^{-1}$) reported for *D. gessneri* and *C. richardi* [42] and above that used (0.70 mg C L^{-1}) by [10], the seston components were not entirely edible to cladocerans. The total algae carbon in the lake is not suitable for cladocerans due to inedible phytoplankton, reducing the food available to these organisms [50]. In the present study, the maximum contribution of microplankton (40%) agrees with the above authors' findings. In laboratory experiments, large microplankton algae present in the seston of Lake Monte Alegre negatively influenced *D. gessneri* reproduction [50]. Despite the better quality of summer seston compared to winter seston in Lake Monte Alegre, it was still not the best food for promoting cladoceran growth [51].

Unlike *D. gessneri*, the life table parameters of *C. richardi* were not affected by the competitor. The superiority of *C. richardi* over *D. gessneri* agrees with experimental studies with the edible chlorophycean *Desmodesmus spinosus* [10,25]. The smaller species excluded the larger one in a few days of the experiment at low but not high food concentrations of the edible chlorophycean [10]. The results obtained in the present study may support the hypothesis of the smaller size, which supposes the capacity of a small species to suppress a large species and to survive in conditions of limiting resources [2]. Based on the results presented here, *C. richardi* can be considered an *r*-strategist due to its characteristics such as rapid embryonic development and high reproductive and growth rates, reaching high densities in a short time [17]. In addition, the results of this study could also be interpreted in the light of the r_{\max} hypothesis [18], where *Ceriodaphnia*, which had the highest intrinsic growth rate without food limitation, would be the most favored by seston conditions.

Although not significant, the increased survival of *C. richardi* in association with *D. gessneri*, as well as better reproductive performance, indicated by fecundity curves and reproductive rates, seem to be indicative of facilitation. A similar result was found in an experiment where the population growth rate of *C. richardi* was significantly higher in the presence of *D. gessneri* in non-limiting food concentration conditions [10]. Facilitation between different species, difficult to identify in the field, is easily detected in laboratory studies [22]. It can occur when food is not limiting and/or when organisms have distinct diets [4], such as when small cladocerans feed on semi-digested fecal particles [22]. Facilitation is more likely to occur between species that compete for different resources ([23]. The factors that would explain the facilitation effect of the presence of *Daphnia* for *Ceriodaphnia* are still unknown.

Some studies conducted with natural food have reported competitive interactions between *Ceriodaphnia* and *Daphnia*, with results varying between species but indicating the competitive superiority of the smaller species in conditions of resource limitation, while *Daphnia* was superior in non-limiting food conditions [2,5,6,24]. Neill [2] based the conclusions on the sensitivity of juveniles of *Daphnia* to resource depletion, while Lynch [5] considered the different foraging methods for each species and the changes in the phytoplankton community as responsible for the variation. Lynch [5] also found that young *Ceriodaphnia* consumed a much higher proportion of diatoms and delicate flagellates than *Daphnia*, which is more specialized in capturing small particles. The age of competing organisms and the variation in resources were the main factors discussed by [24] to explain their results. For Romanovsky and Feniova [6], the ability of *Ceriodaphnia*

to control substantial food portions and to produce large broods would hardly lead to its exclusion, even in situations where *Daphnia* was competitively superior.

Although both *C. richardi* and *D. gessneri* anticipated the first reproduction in shared treatments, only the former achieved high reproductive rates as a result of its early maturation. A similar situation occurred in the competition experiments with *Daphnia obtusa* and its congeners: *D. magna*, *D. pulex*, and *D. longispina* [7]. *D. obtusa* had anticipated the first reproduction; thus, the shortest development time and a shorter interval between clutches in the presence of the competitors allowed this species to reach a larger population size, suppressing the growth of competitors.

Many species of cladocerans, dominant in the limnetic zones of tropical lakes, tend to reach maturity in a few days (≤ 3 days) [52]. Early maturation not only contributes to greater fertility, but also gives the species a competitive advantage over other species, including the larger ones, under limiting food conditions [17]. These characteristics found in *C. richardi* may explain its numerical dominance, with an increase in the lake over approximately two decades [53]. On the other hand, late maturation in *D. gessneri* cannot be considered only as a disadvantage in the environment, since the species occurs throughout the year in Lake Monte Alegre, despite in lower densities in some periods [10,53]. Delayed maturation may allow the populations of cladocerans to preserve their limited resources, enabling population recovery when more favorable conditions return [52].

4.2. Experiment 2: Competition between *C. richardi* and *D. birgei* for Littoral Seston

The relatively high algal concentrations and low turbidity values found in this study have previously been reported in the littoral zone of this lake [39]. The limnological conditions of the littoral zone were favorable to cladocerans.

The survival profiles of *C. richardi* and *D. birgei* can be classified as type I (high survival of juveniles), with a tendency for type II (constant mortality) in the treatments Cr+ (shared treatment) and Db− (alone), starting in the second half of the experiment. The survival increase of juveniles of *C. richardi* in the presence of *D. birgei* may be related to facilitation, while the second species performed better alone, at least in its early developmental stages.

Theoretically, the food resources of the littoral zone, in terms of quantity and quality, were not limiting during the experiment. The relatively high concentration of algal carbon during the experiment (~ 1 mg C L⁻¹) was again above the incipient limiting level (between 0.1 and 0.2 mg C L⁻¹) and the threshold food concentration (< 0.025 mg C L⁻¹) for lake cladocerans, including *C. richardi* [42]. However, *C. richardi* did not have the same reproductive performance with the littoral seston compared to that of the limnetic zone (experiment 1), with lower reproductive rates with all treatments.

In spite of the similarity of seston characteristics in the littoral and limnetic zones in terms of quantity and quality (predominance of chlorophytes), with a relatively high proportion of edible algae, the use of other food resources, such as bacteria and debris, which are more abundant in this zone, but not evaluated in the present study, may have influenced the reproduction of *C. richardi*. However, bacteria and debris have low nutritional values [22] and could influence the life history parameters of cladocerans [52].

C. richardi did not show any preference for the limnetic or littoral zone (edge and middle of macrophytes) of Lake Monte Alegre, but its growth rate was higher when cultivated in the littoral seston (middle of macrophytes) [39], contrary to what was observed in the present study. The difference between the results obtained may be related to the experimental design, where the organisms were grown individually [39] and at the population level (this study). In this study, the daily reduction in the food amount caused by intraspecific competition, in addition to the possible use of resources with a lower nutritional value, may have affected the reproduction of *C. richardi*.

There is no evidence of competition between *C. richardi* and *D. birgei* for the littoral seston. On the contrary, the species seem to have benefited, after the initial stages, from the presence of each other, especially *C. richardi*. The results suggest that mutualism [20]

between the two cladocerans is asymmetric, with one species having more advantages than the other regarding the positive relationship.

The foraging efficiency of *Ceriodaphnia* [54] and the ability to feed on small particles [5,55] are also common features of the genus *Diaphanosoma* [56]. In addition, the early age at first reproduction, the short time of embryonic development and the relatively large clutches are characteristics shared by both *Diaphanosoma* [57,58] and *Ceriodaphnia* [58].

Although the threshold food concentration (TFC) for *D. birgei* is unknown, the species showed through its reproductive rates that the TFC may be even lower than that found for the species *D. gessneri* and *C. richardi*. In experiments with a chlorophycean, at very low concentrations, *D. birgei* was the only one able to reproduce compared to *C. richardi* and *D. gessneri*, even experiencing the effects of competition with them [25].

Diaphanosoma is known as an efficient filter feeder that consumes sources other than phytoplankton, such as debris, mainly nanoparticles [56]. In Lake Monte Alegre, *D. birgei*, when feeding on the limnetic seston, was able to grow and reproduce, but its performance was better when edible chlorophyceans were added to the seston [43] or with seston from the middle of macrophytes [39]. All developmental stages of *Diaphanosoma* can survive under food deficiency [56], making it similar to *Ceriodaphnia* in terms of survival and reproduction. The efficiency in the use of resources by *C. richardi* and *D. birgei* was not tested in this study, but both cladocerans appear seem to be equally efficient in the use of sestonic resources. Species with rapid embryonic development and high reproductive rates are considered *r*-strategists [17], the case of both cladocerans.

However, *D. birgei* does not have the same performance as *C. richardi* in Lake Monte Alegre [59], suggesting that it is more influenced by factors other than food in the environment. It is possible that *C. richardi* is less sensitive to biotic and/or abiotic factors in the lake than *D. birgei* due to its reproductive and behavioral strategies [53], resulting in a higher density [59]. Another fact to consider is that *D. birgei* is preyed on by the main invertebrate predator, *Chaoborus* larvae, which consumes young and adult individuals at higher rates than *C. richardi*, influencing its population dynamics in the lake [60].

5. Conclusions

Ceriodaphnia richardi was superior to *Daphnia gessneri* in experiment 1, with the limnetic seston, affecting the survival and reproductive parameters of the inferior species. Although the contribution of edible nanoplanktonic algae to the limnetic seston was high, the presence of microplanktonic algae might have interfered with the filtration of *D. gessneri*. There are indications of facilitation in the interaction between *C. richardi* and *D. gessneri*, favoring the first species. The superiority of *C. richardi* reflects the success of this species in the lake, whose abundance has increased over the years. The superiority of *C. richardi* over *D. gessneri* supports the “small body size hypothesis” and “ r_{\max} hypothesis”.

There is no evidence of competition between *Ceriodaphnia richardi* and *Diaphanosoma birgei* for the seston from the littoral zone, which is dominated by a nanoplanktonic fraction. The species *C. richardi* and *D. birgei* seem to have benefited from the presence of each other in experiment 2, where increases in the values of some life table parameters were observed, especially in relation to *C. richardi*. Both species are small sized and *r*-strategists; therefore, as the strategies are similar, one species was not superior to the other, in addition to both benefiting from the presence of the competitor.

The results suggest that the seston of the littoral and limnetic zones, regarding quantity and quality, does not always lead to competition between cladoceran species. This implies that competition between cladoceran species may not be as prevalent in the environment, as it was observed under experimental laboratory conditions with limited food. In the environment, food concentrations are not always limiting and the species with a greater ability to exploit it outperforms the others. Thus, fluctuations in population abundance and spatial distribution can be influenced by other factors, including invertebrate predation and temperature.

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