Chaoborus diet in a tropical lake and predation of microcrustaceans in laboratory experiments.

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ABSTRACT: Chaoborus diet in a tropical lake and predation of microcrustaceans in laboratory experiments. The diet of Chaoborus brasiliensis has been evaluated in the crop contents of larvae I, II, III, and IV from Lake Monte Alegre. The dinophyte Peridinium was consumed by all instars, particularly by I, II and III. Larvae III and IV preyed on microcrustaceans on a larger scale, mainly cyclopoid copepods and Daphnia. In laboratory experiments, instars III and IV were offered pairs of prey in vessels under controlled temperature and light. Based on the experimental results prey items can be ranked: adult copepod › Bosmina › young Daphnia for instar III and Bosmina › young Daphnia › adult copepod for instar IV. Ingestion rates of instar III were lower than those of instar IV, whose feeding activity seemed to be restricted to a period of the day. Prey dimensions, especially body width, and predator mouth diameter were correlated.

Key-words: Bosmina, copepods, Daphnia, Chaoborus, feeding habits, Peridinium, predation experiments.

RESUMO: A dieta de Chaoborus em um lago tropical e a predação sobre microcrustáceos em experimentos de laboratório. A dieta de Chaoborus brasiliensis foi avaliada através da análise do conteúdo do papo das larvas I, II, III e IV coletadas no Lago Monte Alegre. A dinofícea Peridinium foi consumida por todos os estádios, principalmente pelo I, II e III. As larvas III e IV consumiram predominantemente microcrustáceos, principalmente copépodos e Daphnia. Em experimentos de laboratório, sob condições de luz e temperatura controladas, os estádios III e IV foram colocados em recipientes contendo pares de presas. A partir dos resultados destes experimentos, pôde-se estabelecer a seguinte ordem de preferência das presas: copépodo adulto › Bosmina › Daphnia jovem para o estádio III e Bosmina › Daphnia jovem › copépodo adulto para o estádio IV. A taxa de ingestão do estádio III foi menor do que a do estádio IV, cuja atividade alimentar parece estar restrita a um período do dia. O tamanho da presa, principalmente a largura do corpo, e o diâmetro da boca do predador foram correlacionados.

Palavras-chave: Bosmina, copépodos, Daphnia, Chaoborus, hábitos alimentares, Peridinium, experimentos de predação.

Introduction

Chaoborus larvae (Diptera, Chaoboridae) are known as voracious consumers of zooplankton. High predation rates are associated with a high assimilation efficiency, growth, and production, especially of instars III and IV (Cressa & Lewis, 1986; Lopez & Cressa, 1996; Bezerra-Neto, 2001), resulting in a strong impact on prey. Reproduction is continuous in the tropics (Lewis, 1979; Saunders & Lewis, 1988; Arcifa et al., 1992), therefore, crustacean populations can be controlled for a longer period in warm lakes than in temperate ones (Saunders et al., 1999). Thus, predation impact by invertebrates could be stronger during a longer period in the tropical zone compared to the temperate one.

The effects of Chaoborus predation on zooplankton dynamics and community structure have been investigated in the field (Saunders & Lewis, 1988; Arcifa et al., 1992; Arcifa, 2000; Bezerra-Neto, 2001), as well as in experiments (Spitze, 1991; Vonder Brink & Vanni, 1993; Fischer & Frost, 1997). Predation influences prey populations, affecting mostly: a) prey abundance, when high ingestion rates decrease its densities; b) size structure of prey, when predation is selective on particular size classes;

c) morphology, when prey with plain morphological structure is selected; d) behavior, when predation leads to prey migration.

Chaoborus has been identified as the main invertebrate predator in Lake Monte Alegre, reproducing continuously during the year, and attaining the highest abundance in summer, when peaks of 4 ind.l^{-1} were recorded (Arcifa et al., 1992; Arcifa & Meschiatti, 1993).

Studies on feeding habits of larvae in the lake revealed that they are omnivores (Arcifa, 2000). The dinophyte Peridinium was the main dietary item of the first two instars, its contribution decreasing in late instars, which preyed predominantly on Bosmina tubicen, followed by young Daphnia gessneri, copepods, and rotifers.

Low densities of Bosmina and Daphnia coincided with high densities of Chaoborus in the lake in 1985/86 (Arcifa et al., 1992), leading the authors to hypothesize that Chaoborus predation was a key factor influencing the seasonal variation of some zooplankton populations. During 1998/99, Bosmina has virtually disappeared from the lake (Fileto, 2001), what has been ascribed to predation by Chaoborus and Hydracarina (Cassano et al., 2002). Taking into account those findings, experiments were set in the field (Castilho-Noll & Arcifa, 2007a) and in the laboratory, for testing Chaoborus influence on microcrustacean prey.

The aim of this study was to investigate the selectivity and ingestion rates of the predator Chaoborus brasiliensis - larvae III and IV - on some microcrustacean prey from Lake Monte Alegre. Laboratory experiments were performed and data on crop content of Chaoborus instars I to IV collected in the lake have been included as a basis for prey choice and for coupling field and laboratory.

Study Area

Lake Monte Alegre (21° 11'S, 47° 43'W) is located in southeastern Brazil, and formed in 1942 by damming Laureano Creek, which belongs to River Pardo basin. The region is characterized by a tropical climate, with a marked cool–dry season (May to September) and a warm–wet one (October to April). It is a small, eutrophic, shallow (area = 7 ha, Z max. = 5 m), warm discontinuous polymictic reservoir. The lack of manipulation of the dam, as the lake is used only for research and teaching, the surface outlet, the small size, the low flow of the creek, and winds of low velocity without constant direction contribute to its stability (Arcifa et al., 1990).

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

Materials and methods

Crop content of Chaoborus larvae

Larvae were collected biweekly after sunset, in Lake Monte Alegre, from December 1998 to November 1999. A hundred and twenty liters were pumped from the water column with a bilge pump (Model 34600-0000, Jabsco ITT Ind., Costa Mesa, California, U.S.A.), delivering 30 l.min^{-1}, and filtered through a 60 mm mesh net. The organisms were narcotized and fixed according to Haney & Hall (1973).

In the laboratory, larvae were measured for instar identification, under a stereomicroscope. Larvae were placed individually on a slide, the head being pulled with a needle, according to Arcifa (2000). Then, the gut, which was attached to the head, was cut in front of the crop, whose content was gently squeezed and evaluated with a microscope for prey identification and counting. Biomass of microcrustaceans were obtained from the formula found by Castilho-Noll and Arcifa (2007b). Biomass of the rotifers Keratella spp. and the dinophyte Peridinium was obtained from the literature on Lake Monte Alegre (Silva, 1989; Silva, 1995).

Preparation of the experiments

Preys were chosen based on the crop content evaluation of Chaoborus larvae from Lake Monte Alegre made by us and by Arcifa (2000). The experiments summarized in Table I were undertaken during the period from 28/X/98 to 31/X/2001 and the date of each experiment was dependent on prey availability in the lake.

One day before starting the experiments, Chaoborus larvae were collected in the lake with a 170 mm mesh net and placed in beakers with food (rotifers, copepods, and cladocerans). They were acclimated in a room with controlled temperature (23ºC) for 24 h (12 h dark:12 h dim light). Zooplankton samples were taken with a 60 mm mesh net, prey species were selected, counted, measured and placed in 60 ml beakers, with lake water filtered through glass fiber filters (0.45 mm). The

Table I: Conditions of each experiment.

Experiment 1	
Date:	10-11/2/2000
Predator:	1 larvae III of C. brasiliensis in each beaker
Preys:	10 organisms of small D. gessneri (0.68 - 0.80 mm) and 10 organisms of B. tubicen (0.35 - 0.47 mm)
Experiment duration:	18 hours
Temperature:	23 °C
Experiment 2	
Date:	16-17/2/2000
Predator:	1 larvae III of C. brasiliensis in each beaker
Preys:	10 organisms of B. tubicen (0.35 - 0.47 mm) and 10 organisms of adult T. prasinus (0.47 - 0.61 mm)
Experiment duration:	18 hours
Temperature:	23 °C
Experiment 3	
Date:	28-29/10/1998
Predator:	1 larvae IV of C. brasiliensis in each beaker
Preys:	20 organisms of large D. gessneri (1.02 - 1.40 mm) and 20 organisms of adult T. prasinus (0.47 - 0.61 mm)
Experiment duration:	12 hours
Temperature:	23 °C
Experiment 4	
Date:	4-5/11/2000
Predator:	1 larvae IV of C. brasiliensis in each beaker
Preys:	20 organisms of small D. gessneri (0.68 - 0.80 mm) and 20 organisms of adult T. prasinus (0.47 - 0.61 mm)
Experiment duration:	12 hours
Temperature:	23 °C
Experiment 5	
Date:	12-13/2/2000
Predator:	1 larvae IV of C. brasiliensis in each beaker
Preys:	10 organisms of small D. gessneri (0.68 - 0.80 mm) and 10 organisms of B. tubicen (0.35 - 0.47 mm)
Experiment duration:	24 hours
Temperature:	23 °C
Experiment 6	
Date:	30-31/10/2001
Predator:	1 larvae IV of C. brasiliensis in each beaker
Preys:	10 organisms of large D. ambigua (0.90 - 1.22 mm) and 10 organisms of small D. ambigua (0.48 - 0.68 mm)
Experiment duration:	12 hours
Temperature:	23 °C

Footnotes: 1. The number of preys differed in the experiments as it was dependent on the abundance in the lake samples; 2. The experiment duration differed for instars, taking into account that larvae III spend more time in the water column of the lake than larvae IV (Arcifa, 1997), and can potentially feed for a longer period; 3. The experiment 5, with larva IV, lasted 24 h (12 h dark:12 h dim light) to test whether larva feeding was prolonged, resulting in higher ingestion rates green alga Scenedesmus spinosus (10^5 cells.ml^{-1}) was added for feeding prey. Four to eight replicates were prepared, depending on prey availability; one Chaoborus larva was added to each replicate. They were maintained in an environmental chamber, in the dark, at a constant temperature of 23ºC. The experimental time was designed based on the literature information that instars III and IV feed preferentially at night (Fedorenko, 1975; Swift, 1976). Because instar III stays longer in the water column than instar IV (Arcifa, 1997), the time of the experiments 1 and 2 was extended to 18 h. For instar IV the experiments lasted 12 h, except experiment 5 which lasted 24 h (12 h dark: 12 h dim light) to test whether larva feeding was prolonged, resulting in higher ingestion rates. Other details about prey number and duration of each experiment can be found in Table I.

At the end of the experiments, the animals of each beaker were narcotized and fixed (Haney & Hall, 1973). As the predator swallow the entire prey (Pastorok, 1981), all the remaining microcrustaceans in each replicate were considered survivors and were counted. These data were statistically compared by T-test for alternative hypothesis ($p < 0.05$), using the program Statistic 7.0.

The electivity index of Ivlev (1961, in Zaret, 1980) was used for evaluating predator preferences:

$$E = \frac{r - p}{r + p}$$

Where: E = electivity index

r = proportion of the food item at the beginning of the experiment

p = proportion of the food item at the end of the experiment

For E between -1 and 0, negative selectivity; for E between 0 and 1 the item had been selected.

Ingestion rates of larvae III and IV of Chaoborus were calculated by the following formula:

$$IR = \frac{Pi - Pf}{t}$$

Where: IR = ingestion rate

Pi = average number of prey at the beginning of the experiment

Pf = average number of prey at the end of the experiment.

t = time experiment (hours)

Daily ingestion rates were equal to the total prey consumed during the whole experimental period.

Results

Diet of Chaoborus instars I to IV in the lake

During the period of December 1998 to November 1999, the dinophyte Peridinium was the most important dietary item for instar I in the lake. Its contribution to the diet of instars II to IV decreased (Fig. 1), especially in biomass (Fig. 1b). Older instars included animal prey in their diets such as the rotifers Keratella spp., copepodites, adult copepods (Tropocyclops prasinus and Thermocyclops decipiens), and the cladoceran Daphnia gessneri. Nauplii was consumed in small proportion by instar II, whose favorite animal item were copepodites and rotifers. Adult copepods and cladocerans were mostly preyed on by late instars, which showed also some degree of cannibalism.

Experiments 1 and 2 - instar III as predator

Both cladocerans, Bosmina tubicen and small Daphnia gessneri, were preyed on by larvae III, decreasing significantly at the end of experiment 1 (Fig. 2a, Tab. II). Electivity index was higher for Bosmina than for small Daphnia (Fig. 3a).

When Bosmina tubicen and adult Tropocyclops prasinus were offered as prey, larvae III consumed the copepod, whose numbers decreased significantly at the end of experiment 2 (Fig. 2b, Tab. II); accordingly, copepod was selected by larvae (Fig. 3b).

Experiments 3, 4, 5, and 6 - instar IV as predator

When prey were adult copepod T. prasinus and large D. gessneri, larvae preyed on copepod, reducing significantly its density at the end of experiment 3 (Fig. 4a, Tab. II), with higher electivity index for the copepod (Fig. 5a). But when choices were T. prasinus and small D. gessneri, both prey were consumed and significantly reduced at the end of experiment 4 (Fig. 4b, Tab. II), with selectivity being higher for small Daphnia (Fig. 5b).

Compared to small D. gessneri, Bosmina tubicen was selectively preyed on (Fig. 4c), its density decreasing

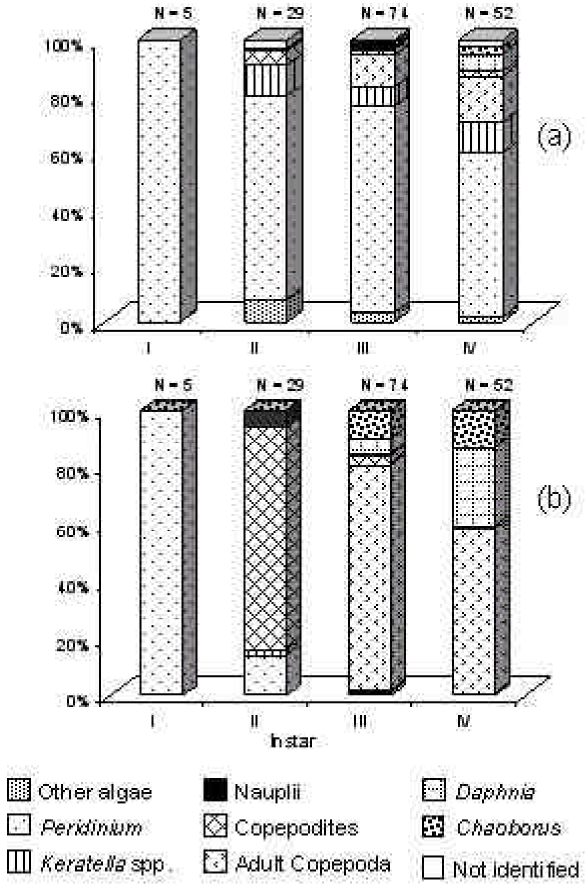

Figure 1: Proportion of food items in the crops of Chaoborus brasiliensis larvae I to IV, in number (a) and biomass (b) collected in the lake from December 1998 to November 1999. N= number of specimens analyzed.

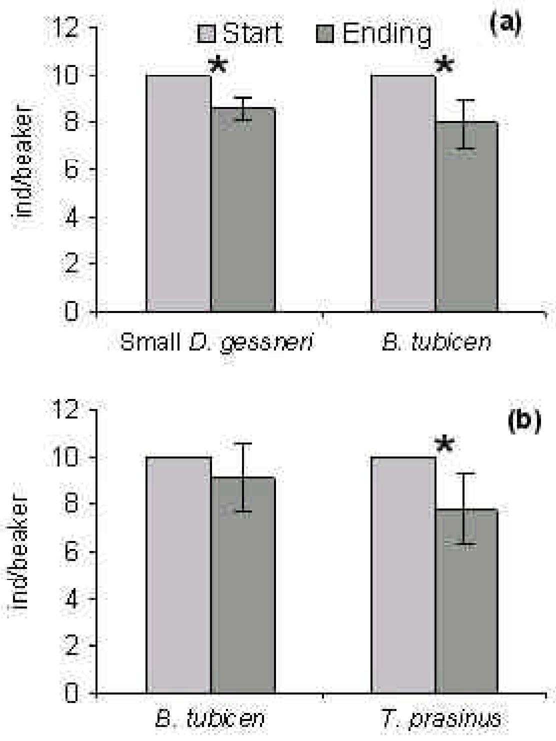

Figure 2: Number of prey at the beginning and its average number and standard deviation at the end of the Experiment 1 (a) and Experiment 2 (b) of C. brasiliensis larvae III. * Significant difference ($p < 0.05$).

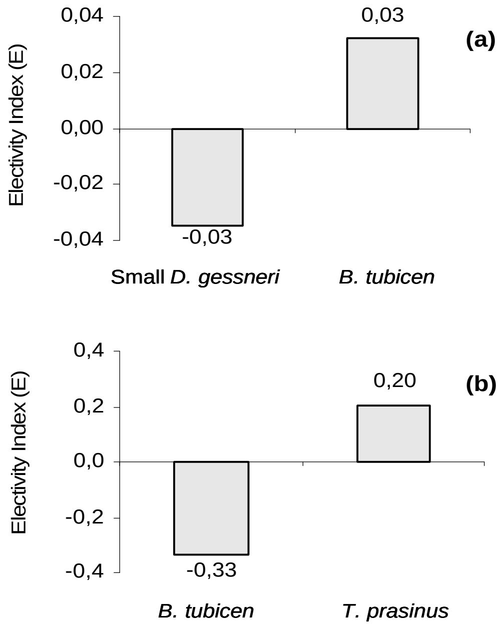

Figure 3: Electivity index of C. brasiliensis larvae III for each prey in Experiment 1 (a) and Experiment 2 (b).

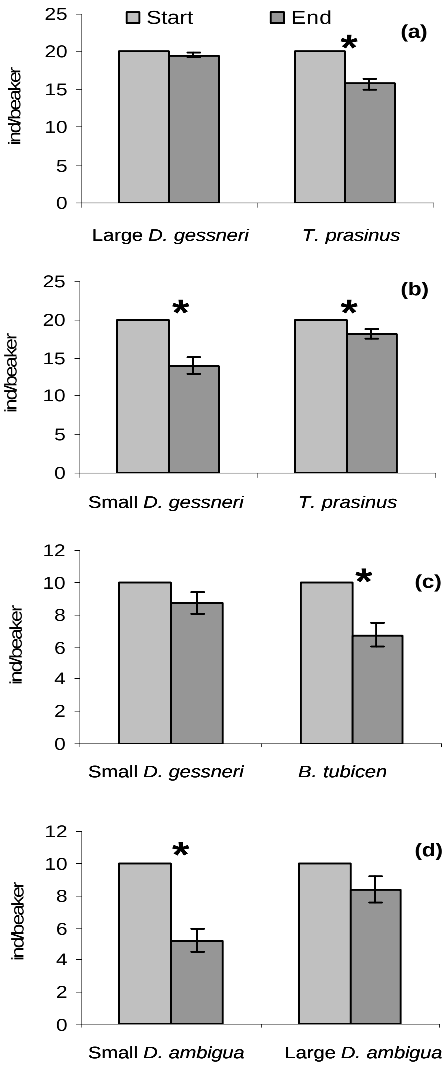

Figure 4: Number of prey at the beginning and its average number and standard deviation at the end of the Experiment 3 (a), Experiment 4 (b), Experiment 5 (c) and Experiment 6 (d) of C. brasiliensis larvae IV. * Significant difference ($p < 0.05$).

significantly at the end of experiment 5 (Fig. 5c, Tab. II).

Small Daphnia ambigua was preferentially preyed on by larvae IV in comparison to large individuals (Fig. 5d), which did not decrease significantly at the end of experiment 6 (Fig. 4d, Tab. II).

Ingestion rates

Average daily ingestion rates of instars III and IV were respectively 2.7 and 5.9 prey/Chaoborus/day (Tab. III). The ingestion rates cannot be statistically compared as the time differed among the experiments. However, it is possible that instar III has lower ingestion rates compared to instar IV.

Ingestion rates of instar IV obtained in experiment 5, which lasted 24 h, are not higher than those of the experiments 3, 4, and 6, which lasted 12 h (Tab. III), what could indicate that this instar prey on during part of a day.

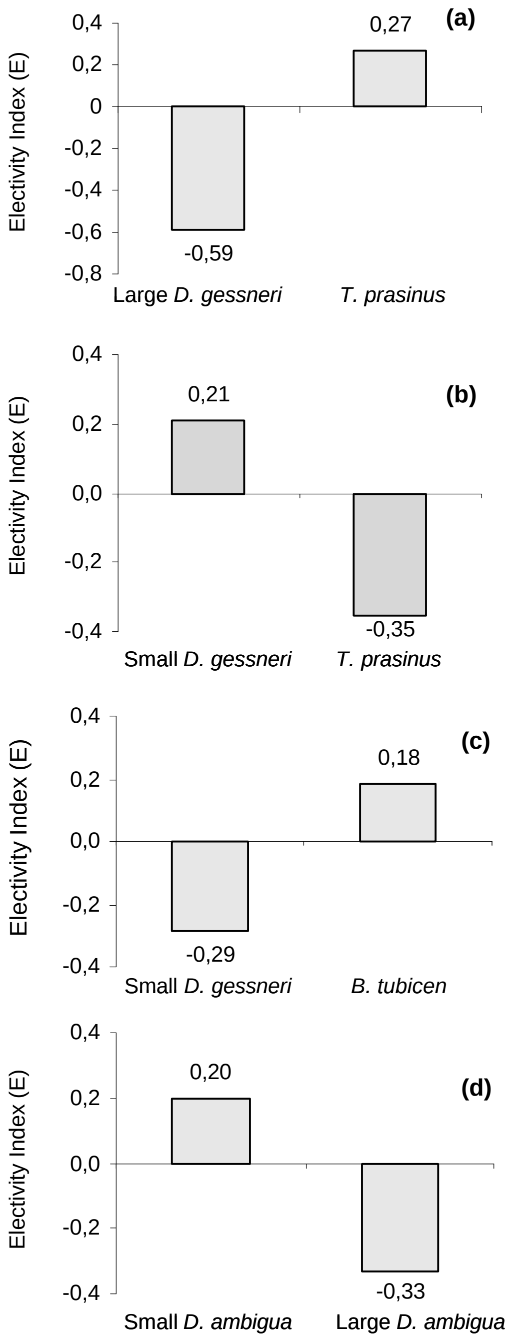

Figure 5: Electivity index of C. brasiliensis larvae IV for each prey in Experiment 3 (a), Experiment 4 (b), Experiment 5 (c) and Experiment 6 (d).

Table II: T-test for alternative hypothesis of prey average densities at the beginning and end of the experiments. * Significant values ($p < 0.05$). N= number of replicates.

	t	p	N
Experiment 1 (larvae III)			
Small D. gessneri (0.68 - 0.80 mm)	-6.26	‹0.001*	8
B. tubicen (0.35 - 0.47 mm)	-2.86	0.02*	8
Experiment 2 (larvae III)			
B. tubicen (0.35 - 0.47 mm)	-1.68	0.19	4
T. prasinus (0.47 - 0.61 mm)	-5.18	0.01*	4
Experiment 3 (larvae IV)			
Large D. gessneri (1.02 - 1.40 mm)	-2.01	0.08	8
T. prasinus (0.47 - 0.61 mm)	-10.58	‹ 0.001*	8
Experiment 4 (larvae IV)			
Small D. gessneri (0.68 - 0.80 mm)	-7.28	‹ 0.001*	8
T. prasinus (0.47 - 0.61 mm)	-3.92	0.006*	8
Experiment 5 (larvae IV)			
Small D. gessneri (0.68 - 0.80 mm)	-2.32	0.053	8
B. tubicen (0.35 - 0.47 mm)	-5.82	‹0.001*	8
Experiment 6 (larvae IV)			
Small D. ambigua (0.48 - 0.68 mm)	-6.11	0.004*	5
Large D. ambigua (0.90 - 1.22 mm)	-1.36	0.24	5

Table III: Average ingestion rates of larvae III and IV of Chaoborus brasiliensis in the experiments.

	Prey	Daily IR (prey/Chaoborus/day)
Experiment 1 (larvae III)	Small D. gessneri	1.37 ± 0.74
	B. tubicen	2.0 ± 2.39
	Total	3.37 ± 2.1
Experiment 2 (larvae III)	B. tubicen	0.87 ± 1.5
	T. prasinus	2.25 ± 1.5
	Total	2.00 ± 2.16
	Average for larvae III	2.7 ± 2.2
Experiment 3 (larvae IV)	Large D. gessneri	0.62 ± 0.92
	T. prasinus	4.25 ± 2.05
	Total	4.87 ± 2.42
Experiment 4 (larvae IV)	Small D. gessneri	6.00 ± 3.38
	T. prasinus	1.87 ± 1.73
	Total	7.87 ± 4.12
Experiment 5 (larvae IV)	Small D. gessneri	1.25 ± 1.83
	B. tubicen	3.25 ± 1.98
	Total	4.5 ± 2.98
Experiment 6 (larvae IV)	Small D. ambigua	4.80 ± 2.49
	Large D. ambigua	1.60 ± 3.05
	Total	6.40 ± 3.29
	Average for larvae IV	5.9 ± 3.4

Table IV: Comparison of the relative contribution variation, in number, of food items between instars III and IV of Chaoborus brasiliensis in Lake Monte Alegre in two periods.

Prey	**Arcifa (2000) Period 1985/86**	**This paper Period 1998/99**
Peridinium	8 - 18 % *	60 - 70 % *
Bosmina	53 - 56 % *	0
Other Cladocera (mainly Daphnia)	2 - 12 % *	6 %
Copepoda	4 %	11 - 17 % *
Rotifera	4 %	7 - 10 % *
Chaoborus larvae	0	1 - 3 % *

* Range between instars III and IV

Discussion

Chaoborus brasiliensis is an important predator of zooplankton populations in Lake Monte Alegre as already reported (Arcifa, 2000; Arcifa et al. 1992, Castilho-Noll & Arcifa, 2007a). The increase in the diversity of dietary items along the instars observed in this study have been found by Arcifa (2000), as well as by other authors (Chimney et al., 1981; Hare & Carter, 1987; Irvine, 1997). As gape-limited predators, increasing body size and mouth diameter allow late instars to capture and ingest larger prey.

Comparing the diet of instars III and IV presented in this study with earlier data (Arcifa, 2000) several differences can be found, summarized in Table IV. The most noticeable differences between the data of both studies are the lack of Bosmina and the relative increase in the contribution of Peridinium to the diet of Chaoborus larvae III and IV in the present study. Bosmina was the predominant dietary item in 1985/86, when it was relatively abundant in the lake, reaching peaks of 60-90 ind.l^{-1} (Arcifa et al., 1992). Its density decreased drastically in 1998/99, this species virtually disappearing from the lake (Fileto, 2001). From 1985/86 to 1998/99, Bosmina lost the top rank in Chaoborus diet, increasing the contribution of Peridinium, copepods and rotifers. Cannibalism was also exhibited by late instars in 1998/99, that was not observed in the earlier period. Flexible feeding behavior of a plankton predator, with quick shifts from opportunistic to selective behavior, are adaptive responses to cope with zooplankton variations, inducing changes in prey composition and abundance (Pastorok, 1980a). Chaoborus has already shown this flexibility in Lake Monte Alegre, when the contribution of certain items, found in the predator crop content, such as copepods and Peridinium, increased during periods of low densities of the favorite prey, Bosmina (Arcifa, 2000).

Prey dimension influences Chaoborus predation, with smaller items being replaced by larger ones in the diet of late instars (Lewis, 1977; Arcifa, 2000). In Lake Monte Alegre, smaller items, such as copepodites and nauplii, decreased or disappeared from the diet of instars III and IV.

Based on instar III consumption and electivity indexes determined in the experiments of this study, prey can be ranked: adult copepod › Bosmina › young Daphnia. For instar IV the rank order is: Bosmina › young Daphnia › adult copepod. The preferences of instar III agree with the items found in the crop contents in 1998/99, except Bosmina. Larvae III preference for copepods in the experiments prevailed over Bosmina, the main prey in the past, whereas larvae IV preference for Bosmina in the experiments matched that found in the lake in 1985/86 (Arcifa, 2000).

Among the prey offered in the experiments, the lowest electivity index was recorded for large adult Daphnia gessneri (-0.59), and thus, prey was selected by dimensions, particularly body width. This was also evident when small Daphnia ambigua was positively selected, contrasting with the negative selection of the large ones. In trials where the two largest prey -experiments 3 and 6, with two large Daphnia species- were paired off with smaller prey, the large Daphnia were always negatively selected.

Body width of prey found in the crop contents and experiments, reported by M.H.L. Silva (unpublished), varied from 0.165 to 0.220 mm and were within Chaoborus mouth diameter (0.17-0.25 and 0.25-0.30

mm, respectively for instars III and IV), except large Daphnia (0.485 mm). Relationship between Chaoborus mouth diameter and prey body width has been found in Lake Monte Alegre (Arcifa, 2000), as previously reported by Moore & Gilbert (1987), who argued that width is more important than length as rigid prey is swallowed long-wise.

Ingestion rates observed in this study for small Daphnia gessneri and D. ambigua (6-30% ingested prey/day) were near the range found by Allan (1973) for Daphnia parvula (12-23% ingested prey/day). Lower rates have been recorded for copepods (9-21% ingested prey/day), which were above values found by Roth (1971, in Pastorok, 1980b) for Tropocyclops prasinus (1.9% ingested prey/day).

Generally, late instars ingest more prey than the instars I and II (Lewis, 1977; Pastorok, 1980b), and instar IV responds for about three quarters of growth and food consumption of Chaoborus larval stage (Elser et al., 1987). It is possible that instar IV can be responsible for a larger predation impact on crustacean plankton populations in Lake Monte Alegre as the contribution of microcrustaceans to its diet is higher and there is indication of higher ingestion rates, compared to instar III.

Our experimental data in the laboratory and those from mesocosms in the lake (Castilho-Noll & Arcifa, 2007a; Perticarrari, 2005) indicated that Daphnia gessneri and Bosmina tubicen populations seem to be the most affected by high predation pressure in Lake Monte Alegre. Population dynamics of Daphnia in mesocosms was influenced by invertebrate predation (Castilho-Noll & Arcifa, 2007a). In mesocosms set in the lake for evaluating diel vertical migration Bosmina tubicen increased, reaching up to 100 ind.l^{-1}, after Chaoborus disappearance, whereas in the treatment with predator the cladoceran densities never exceeded 2 ind.l^{-1} (Perticarrari, 2005). Ingestion rates of B. tubicen in the 1985/86 should be very high as up to 17 individuals have been found in the crop of one larva III (Arcifa, 2000). Predation by Chaoborus and Hydracarina could be a strong reason for Bosmina decline in Lake Monte Alegre (Cassano et al., 2002), as reported for other lakes regarding Chaoborus predation (Elser et al., 1987).

Although copepods are an important item in the diet of Chaoborus, mainly larva III, in this study, their populations were not affected in a mesocosm experiment as densities of prey and predator did not correlate and mortality rates were not higher in the presence of the predator compared with the predator-free treatment (Castilho-Noll & Arcifa, 2007a). The authors suggested that high fecundity, relatively low egg development time, and lower predation on egg-bearing females could account for the lower predation impact on copepods. Moreover, reverse diel migration seems to be adopted by cyclopoid copepods in the lake to cope with predation, although they show a high plasticity, changing behavior very quickly, sometimes stopping migration (Perticarrari, 2005; Perticarrari et al., 2004).

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