

Changes in life-history parameters of cladoceran *Ceriodaphnia cornuta* (Sars, 1886) in the presence of *Chaoborus* larvae.

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ABSTRACT: Changes in life-history parameters of cladoceran *Ceriodaphnia cornuta* (Sars, 1886) in the presence of *Chaoborus* larvae. Studies of predation avoidance strategies are fundamental to the understanding of predator-prey relationships. We describe here life-history alterations of the cladoceran *Ceriodaphnia cornuta* in the presence of *Chaoborus* larvae (an important invertebrate predator in freshwater communities). Enclosures were placed in Namorados Dam, located in the semi arid region of Paraíba, Northeast Brazil. *C. cornuta* and *Chaoborus* samples were collected by vertical hauls using plankton net of 45mm pore size and 12 cm of diameter. We measured the body length of 240 *C. cornuta* individuals, with 120 individuals taken from samples where *Chaoborus* larvae were present in enclosures, and the remaining 120 from samples where the predator was absent. We also analyzed the development of spined and unspined forms (head and fornix spines) of *C. cornuta*, and the length of this spines. The presence of the predator influenced head spine presence. The length of head and fornix spines were also greater in the presence of invertebrate predator. Interestingly, in the presence of *Chaoborus* larvae, *C. cornuta* juveniles presented a significantly larger body size.

Key-words: Life-history, *Ceriodaphnia cornuta*, predator-prey relationships, *Chaoborus* larva, semi-arid ecosystem.

RESUMO: Alterações na história de vida do cladócer *Ceriodaphnia cornuta* (Sars, 1886) na presença da larva de *Chaoborus*. Estudos de estratégias anti-predação são fundamentais para o entendimento da relação predador-presa. O objetivo do presente trabalho foi descrever alterações na história de vida do cladócer *Ceriodaphnia cornuta* na presença da larva de *Chaoborus*, que é um importante predador em comunidades aquáticas dulcícolas. Limnocurrais foram introduzidos no açude dos Namorados, localizado no município de São João do Cariri – PB. As amostras de *C. cornuta* e *Chaoborus* foram coletadas através de arrastos verticais, usando uma rede de plâncton de 45mm de poro. Foram medidos 240 espécimes de *C. cornuta*, sendo 120 na ausência da larva de *Chaoborus*, e 120 na presença do predador nos limnocurrais estudados. A formação de espinho na cabeça e nos fórnices, bem como o comprimento destes espinhos na população de *C. cornuta* também foram analisados. A presença do predador causou influência na presença do espinho cefálico em *C. cornuta*. Tanto o espinho cefálico quanto o do fórnices também foram maiores na presença do predador invertebrado. Os jovens de *C. cornuta* apresentaram maior comprimento corporal na presença da larva de *Chaoborus*.

Palavras-chave: História de vida, *Ceriodaphnia cornuta*, relação predador-presa, *Chaoborus*, semi-árido paraibano.

Introduction

The ability to escape predation is one of the factors related to the ecological success of a species in a particular environment. Therefore, analysis of the interaction between invertebrate predators and their prey is fundamental to the understanding of the mechanisms by which the predators influence the structure of prey communities, as well as the behavior and morphology of individual prey species

(Williamson, 1983; Roche, 1990; Tollrian, 2000).

The majority of studies in aquatic environments analyzing the relationship between predator and prey have focused attention on *Daphnia* species, especially relating its morphological differences when influenced by predator *Chaoborus* larva (Krueger & Dodson, 1981; Schwartz, 1991; Tollrian, 1993; Luning, 1995; Repka et al., 1995).

Chaoborus (Diptera: Chaoboridae), is an important invertebrate predator in freshwater communities during its larval stage (Moore et al., 1994). These aquatic larvae are transparent and their antennae are transformed in the prehensile organ (Borror & De Long, 1969). Chaoborus larvae release a water soluble chemical (kairomones) which works as a chemical signal to many Daphnia species (Krueger & Dodson, 1981; Tollrian, 1990; Parejko & Dodson, 1991), inducing changes in the life-history of these cladocerans. Morphological alterations, i.e. neckteeth formation, seem to decrease the vulnerability of Daphnia to predation by Chaoborus. Concentration of kairomone released by Chaoborus is one of the factors related to the presence of neckteeth in juvenile instars of Daphnia pulex (Tollrian, 1993).

Another cladoceran group well documented is Bosmina species. They show alternation of different morphologies in time, in response to the presence of invertebrate predators (Black, 1980; Kerfoot, 1987; Chang & Hanazato, 2003).

Ceriodaphnia is also predated by Chaoborus larvae. Mumm (1997) and Pagano et al. (2003) studied Chaoborus predation on this cladoceran species. However, both these have not analyzed the induction of head spines in Ceriodaphnia cornuta by Chaoborus. C. cornuta shows a wide distribution in Brazil, and characteristically exhibit an oval body form and stooped head (El Moor-Loureiro, 1997).

In the present study, we describe life-history alterations of the cladoceran Ceriodaphnia cornuta under the influence of the invertebrate predator Chaoborus larva, at Namorados Dam, located in a semi arid region in Paraíba State – Brazil.

Materials and methods

Namorados Dam is located in São João do Cariri (07° 23' 04" S and 36° 48' 60" W), a semi arid region of Paraíba State, Northeast Brazil. This region is frequently subjected to extensive drought periods. The dam (Fig.1) has a maximum capacity of 2,118.980 m³, with a maximum depth of 5 m in the rainy season.

The presence of Chaoborus larvae in Namorados Dam have been reported by first time in this work. Furthermore, the only register for the presence of Chaoborus larvae in aquatic environments in Northeast Brazil was by Melo & Chacon (1976). Enclosures were placed in Namorados Dam on July 3, 2004 for other experiment. However, the register for the presence of Chaoborus larvae in this dam enabled the realization of this study. Six enclosures were placed in the dam on July 3, 2004, when occurred the first sampling and during a period when Chaoborus larvae were not observed. The second sampling was carried out one month later (August 3, 2004 - 30 days of experiment), when Chaoborus larvae were present. The diameter of the enclosures was 1.4 m and the depth 2.0m,



Figure 1: Namorado Dam in Caatinga region in São João do Cariri municipality (Photo: João Lugo 2007)

with an approximate volume of 3 m³. They were made of clear polyethylene plastic, suspended from a wooden frame floating on the surface, and were sealed at the bottom and open to the atmosphere at the top. All enclosures were filled with water from the Dam, to permit the maintenance of zooplanktonic densities, whilst also excluding fish.

Samples were collected by vertical hauls using a plankton net of 45mm pore size and preserved in 4% Formalin solution. One sample was collected from each enclosure, producing a total of twelve samples of zooplankton; six when predatory Chaoborus larvae were absent and six

samples when the larvae were present.

C. cornuta (Fig. 1 – A e B) and Chaoborus larvae were identified with reference to El Moor-Loureiro (1997) and Merritt & Cummins (1988), respectively.

In this study we analyzed the dimensions of head and fornix spines (Fig. 2 – A), and the length of these spines in the presence/absence of Chaoborus larvae. For this, we measured head and fornix spines of 120 *C. cornuta* individuals (60 from each treatment - larvae presence/absence), using a microscope – objective 40x, ocular 10x. Fornix spines are located on the bases of cladoceran antennae (Fig. 2 – A).

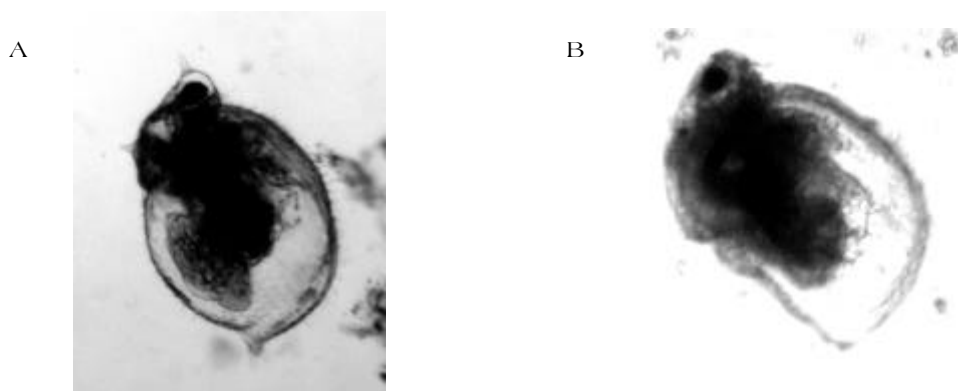


Figure 2: *Ceriodaphnia cornuta* (40x) showed a head and fornix spines (A) and one embryo; *Ceriodaphnia cornuta* (40x) without head spine (B).

The size structure of the *C. cornuta* population sampled from each enclosure was determined by measuring 20 *C. cornuta* individuals, producing a total sample size of 240 individuals (120 from each treatment – with/without larvae). Body length was measured from the top of the head to the end of the body, using a microscope (objective 10x, ocular 10x). The presence of eggs/embryos was also recorded. From each treatment (Chaoborus larvae presence/absence), the smallest females with eggs/embryos were considered primipara. Individuals smaller than this size were considered juveniles.

Water temperature and Chlorophyll-a concentration were determined from each enclosure in the first sampling (when Chaoborus larvae were not observed) and during the second sampling (one month later and when Chaoborus larvae were present in Namorados Dam). Water temperature was determined using a mercury thermometer. Chlorophyll-a was measured spectrophotometrically using the

method of Golterman et al. (1978), employing equations presented in Aleixo (1981) for calculations.

The non-parametric Mann-Whitney rank test was employed to evaluate differences in body length, head and fornix spine length, total density of zooplankton, and comparing any differences to the presence or absence of Chaoborus larvae. Ordinal data including head spine presence, life stage and the presence/absence of ovigerous females were analyzed by χ^2 test, associating these characteristics with presence or absence of the predator (Zar, 1999). All statistical analyses were conducted using Statistica for Windows, Statsoft (1998).

Results

The presence of the head spine in *C. cornuta* showed a significant association with the life-history stage of this cladoceran. The results revealed that

comparing the juveniles and adults of *C. cornuta* with the presence or absence of the spine (regardless of presence or absence of *Chaoborus* larvae), 89.04% of adults were spined, whilst 73.05% of juveniles have not presented a head spine ($c^2=78.89$; $df=1$; $p<0.01$; $N=240$) (Table I).

Head spine presence in *C. cornuta* also showed a significant association with the presence of *Chaoborus* larvae ($c^2=9.67$; $df=1$; $p<0.01$; $N=240$). In the absence of predator, 35.83% of *C. cornuta* specimens sampled showed head spines. However, in the presence of *Chaoborus* larvae 55.83% of organisms examined showed this spine (Table II). In addition, analyzing juveniles and adults separately, we observed that in the absence of predator, 24.18% of juveniles and 72.41% of adults of *C. cornuta* were head spined ($c^2=22.26$; $df=1$; $p<0.01$; $N=120$); but in the presence of *Chaoborus* larvae,

30.26% of juveniles and 100% of adults showed the head spine character ($c^2=54.96$; $df=1$; $p<0.01$; $N=120$) (Tabs. III and IV).

Chaoborus larvae also influenced the length of head spine in *C. cornuta*. This cladoceran exhibited a greater head spine length in the presence of *Chaoborus* larvae compared to when the larvae were absent ($U=1425$; $p<0.05$; $N=120$) (Fig. 3)

Presence of a fornix spine in *C. cornuta* did not show association with the life-history stage of this cladoceran in the presence or absence of *Chaoborus* larvae, because this spine was present as well as in all individuals analyzed (only 3 organisms did not show this spine). However, *Chaoborus* larvae influenced the length of this spine. *C. cornuta* exhibited a greater fornix spine length in the presence of *Chaoborus* larvae ($U=1165$; $p<0.01$; $N=120$) (Fig. 4).

Table II: c^2 test ($c^2=9.67$; $df=1$; $p<0.01$; $N=240$), comparing "spined and unspined" head forms of *Ceriodaphnia cornuta*, in the presence or absence of *Chaoborus* larvae.

"Head spine" in <i>Ceriodaphnia cornuta</i>	<i>Chaoborus</i> larvae		
	absence	presence	Total
absence	77 (64.17%)	53 (44.17%)	130
presence	43 (35.83%)	67 (55.83%)	110
Total	120	120	240

Table III: c^2 test ($c^2=22.26$; $df=1$; $p<0.01$; $N=120$), comparing adults and juveniles with "spined and unspined" head forms of *Ceriodaphnia cornuta*, when the predator (*Chaoborus* larva) was absent.

"Head spine" in <i>Ceriodaphnia cornuta</i>	<i>Ceriodaphnia cornuta</i>		
	adults	juveniles	Total
absence	8 (27.59%)	69 (75.82%)	77
presence	21 (72.41%)	22 (24.18%)	43
Total	29	91	120

Table IV: c^2 test ($c^2=54.96$; $df=1$; $p<0.01$; $N=120$), comparing adults and juveniles with "spined and unspined" head forms of *Ceriodaphnia cornuta*, when the predator (*Chaoborus* larva) was present.

"Head spine" in <i>Ceriodaphnia cornuta</i>	<i>Ceriodaphnia cornuta</i>		
	adults	juveniles	Total
absence	0 (0%)	53 (69.74%)	53
presence	44 (100%)	23 (30.26%)	67
Total	44	76	120

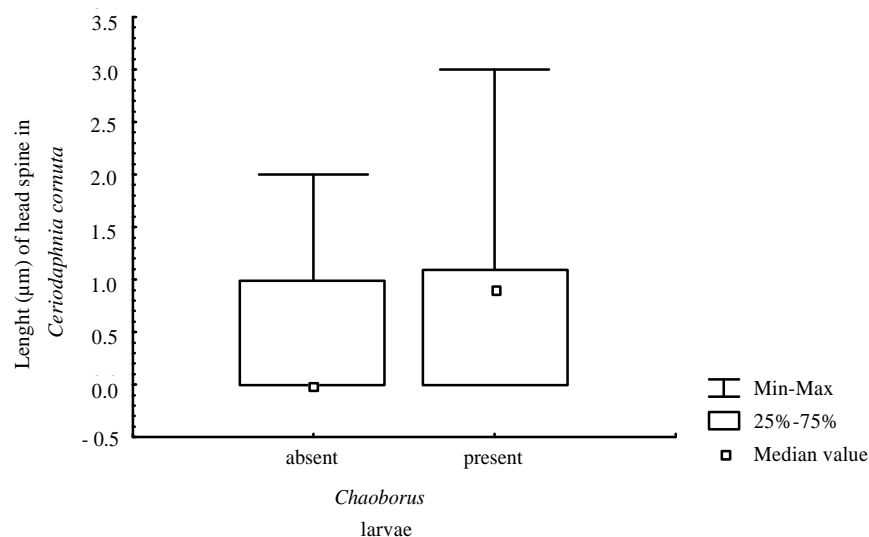


Figure 3: Mann-Whitney test ($U=1425$; $p<0.05$; $N=120$) to head spine length (μm) of *Ceriodaphnia cornuta* compared to presence or absence of the invertebrate predator (*Chaoborus* larva).

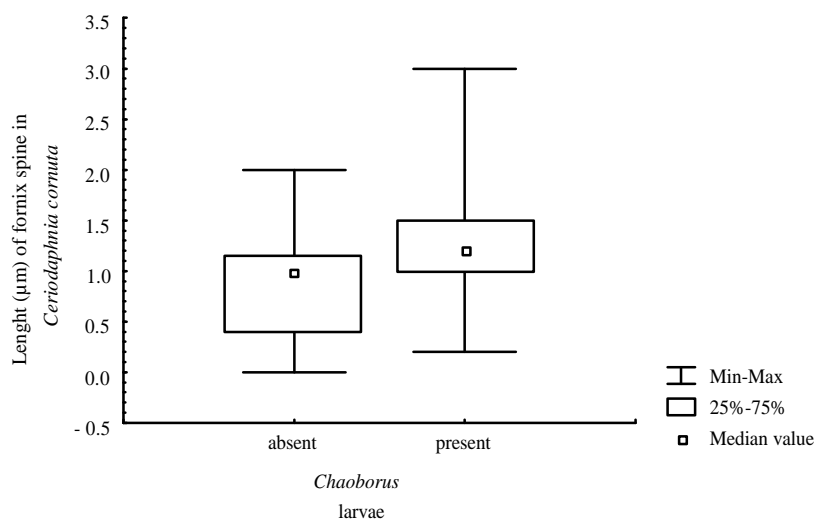


Figure 4: Mann-Whitney test ($U=1165$; $p<0.01$; $N=120$) to fornix spine length (μm) of *Ceriodaphnia cornuta* compared to presence or absence of the invertebrate predator (*Chaoborus* larva).

Body size of cladoceran *C. cornuta* (adults + juveniles) was significantly larger in the presence of *Chaoborus* larvae ($U=5512$; $p<0.01$; $N=240$) (Fig. 5). Moreover, when analyzing juveniles and adults of *C. cornuta* separately, the juvenile body size was significantly larger in the presence of the predator larvae ($U=2804$; $p<0.05$; $N=167$), but the adults body size were not significantly different ($U=539$; $p=0.37$; $N=73$). In the presence of *Chaoborus*, the size of *C. cornuta* juveniles ranged from 0.23 to 0.36 mm and the size of adults from 0.37 to 0.56 mm. In contrast, the body length of juveniles and adults ranged from 0.17 to 0.33 mm and 0.34 to 0.53 mm, respectively, when

the invertebrate predator was absent (Figs. 6 and 7).

Despite the higher number of ovigerous females compared to non-ovigerous females in *C. cornuta* population (regardless presence or absence of *Chaoborus* larvae) ($\chi^2= 5.18$; $df=1$; $p<0.05$; $N=240$), we noticed that in the absence of predator larvae, 17.50% of females are ovigerous whereas in the presence of *Chaoborus* larvae, 30% of females exhibited eggs/embryos (Tab. V).

During the first enclosures sampling, the mean chlorophyll-a concentration was 16.38 mg.l^{-1} ($N=6$). On the second sampling, carried out one month later, when *C. cornuta* individuals showed a greater body size, the

average chlorophyll-a concentration decreased to 2.8 mg.l⁻¹ (N=6). In addition, the total zooplankton density (Rotifera + Cladocera + Copepoda) did not show

significant differences between samples (Fig. 8). The water's temperature was 24.0 ± 0.0 °C during the first sample (N=6) and 25.5 ± 0.7 °C in the second sample (N=6).

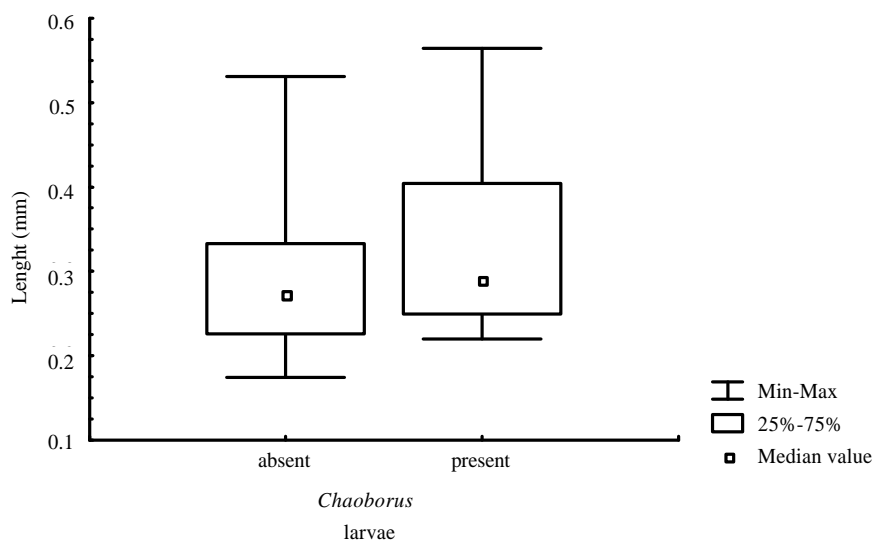


Figure 5: Mann-Whitney test (U=5512; p<0.01; N=240) to body length (mm) of Ceriodaphnia cornuta (adults + juveniles) compared to presence or absence of the invertebrate predator (Chaoborus larva).

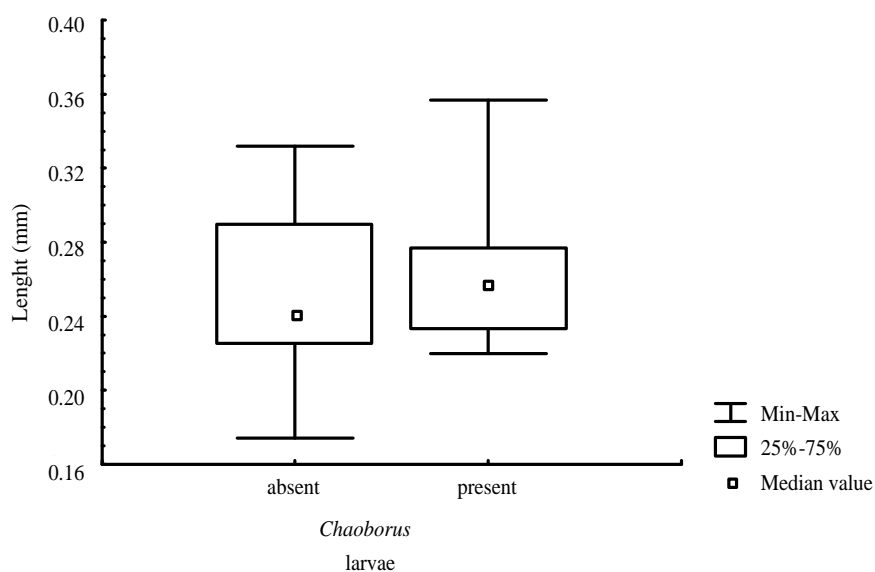


Figure 6: Mann-Whitney test (U=2803.5; p<0.05; N=167) to body length (mm) of Ceriodaphnia cornuta juveniles compared to presence or absence of the invertebrate predator (Chaoborus larva).

Table V: χ^2 test ($\chi^2= 5.18$; df=1; p<0.05; N=240), comparing the presence of ovigerous females in the presence or absence of Chaoborus larvae.

Chaoborus larvae	Ovigerous females		Total
	absence	presence	
absence	99 (82.50%)	21 (17.50%)	120
presence	84 (70%)	36 (30%)	120
Total	183	57	240

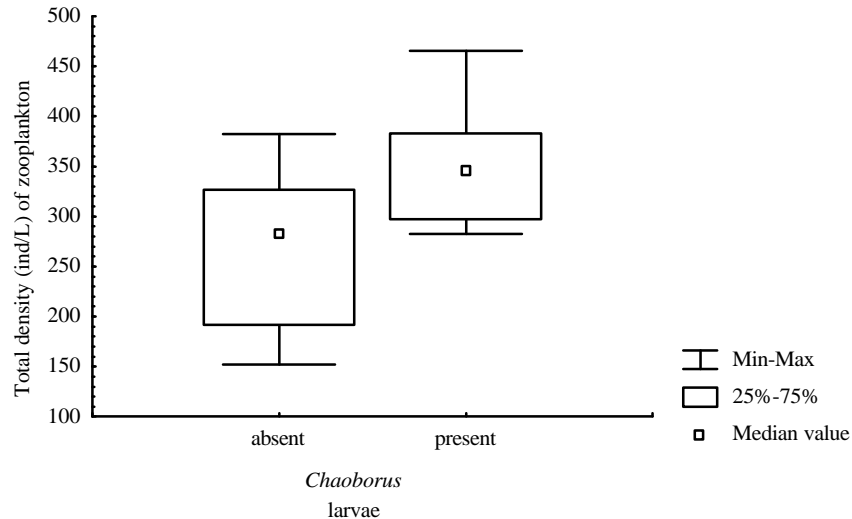


Figure 8: Mann-Whitney test ($U=8$; $p=0.11$; $N=12$) comparing the total zooplankton density to presence or absence of *Chaoborus* larvae.

Discussion

Head spine presence in *C. cornuta* showed a significant association with the presence of *Chaoborus* larvae. The length of head and fornix spines were also greater in the presence of the invertebrate predator. Repka et al. (1995), observed that the presence of neckteeth protected *Daphnia pulex* from *Chaoborus* predation and that small changes in the prey's morphology could affect its susceptibility to invertebrate predation. Morphological adaptations among zooplanktonic organisms are energetically expensive (Schwartz, 1991). Thus, when the predation risk is low it is uneconomic to display a costly predation avoidance strategy (Scheffer, 1997). Tollrian (2000) found lower predation rates in neckteeth morph daphnids than in typical morphs.

Our results showed that head spine presence was more common in adults than in juveniles. Although, the presence of predatory larvae was shown to increase the frequency of this character in both adults and juveniles. Moreover, the number of *C. cornuta* individuals with a head spine was higher when compared to other aquatic environments *Chaoborus*-free of semi arid region of Brazil (personal observation). In this study, among 120 individuals analyzed in absence of *Chaoborus* larvae (first sample), 43 individuals of *C. cornuta* showed the presence of this character (Tab. II). Therefore, it is possible that this effect has been stronger in this environment and weaker in other semi-arid dams in the

region, because in the first sample *Chaoborus* larvae could be already present, but in densities so low to be detected in the samples.

The observed bigger body size of *C. cornuta* in the second sample could be induced by the presence of *Chaoborus* larvae. Crispim (1998) also registered increases in body spines in *Daphnia* in the presence of an invertebrate predator, the cyclopod copepod *Acanthocyclops robustus*.

The water's temperature, another factor that could direct or indirectly influence in a differentiated way growth of *C. cornuta* (Goss & Bunting, 1983), showed a little variation in the enclosures studied.

Based on body size of *C. cornuta* juveniles, we suggest that the females of this cladoceran produced neonates with a greater body size in the presence of *Chaoborus* larvae, as registered by Crispim (1998) when in the presence of *A. robustus*, females produced less and bigger eggs, resulting in bigger neonates. In *Daphnia* populations, the size of brood can be influenced by body size of adults females (Tessier & Consolatti, 1989); by food availability or vertebrate and invertebrate predator influence (Gliwicz & Boavida, 1996).

All effects mentioned in this study were probably caused by the presence of the predator. We did not analyse the impact of predation by *Chaoborus* larvae, and this question needs to be addressed in further studies, in "in vitro" experiments. However, Pagano et al. (2003), using mesocosm experiments noticed that *Chaoborus*

predation had a strong negative impact on *Diaphanosoma excisum*, *Moina micrura* and *Ceriodaphnia cornuta*, favouring small herbivores (Rotifera and nauplii). Mumm (1997) observed that the effect of *Chaoborus* on the abundance of cladocerans is body size dependent but is also dependent on different prey species. Larger species like *Daphnia longispina* and small cladocerans (*Chydorus*) were not affected by predator presence to the same degree as smaller prey species such as *Ceriodaphnia* and *Diaphanosoma*.

In conclusion, presence of a "head spine" in *C. cornuta*, as well as the length of head spine and fornix spines, appears to be influenced by the presence of an invertebrate predator. Moreover, the increasing in body size of *C. cornuta* appears to be another strategy induced by the presence of *Chaoborus* larvae.

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