Predation on microcrustaceans in evidence: the role of chaoborid larvae and fish in two shallow and small Neotropical reservoirs

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Abstract

This study was focused on the predation upon microcrustaceans by an invertebrate predator (chaoborid larvae), and vertebrate predators (fish), in two small reservoirs in southeastern Brazil, with and without macrophytes, in two climatic periods (dry and rainy seasons). *Chaoborus* larvae were sampled in the limnetic zone, as they are scarce in the littoral, and fish in both limnetic and littoral zones. Their diets were evaluated by the analysis of the crop (chaoborid) or stomach contents (fish). Chaoborid larvae consumed the dinoflagellate *Peridinium* sp. or other algae, rotifers, and planktonic microcrustaceans. The fish species that included microcrustaceans in their diets were juveniles caught in the littoral. Aquatic insects, plant fragments, and detritus were their major dietary items, microcrustaceans representing a minor item. Planktonic copepods contributed more to the diet of chaoborid larvae than planktonic cladocerans. Fish preyed on planktonic microcrustaceans, as well as on benthic and macrophyte-associated species. Microcrustaceans were not heavily preyed on by chaoborid larvae and fish in both reservoirs.

Key words: Chaoborus, cladocerans, copepods, diet, fish.

Introduction

The predation by invertebrate predators, primarily by *Chaoborus* larvae (Chaoboridae, Diptera) is high in tropical lentic ecosystems (Saunders and Lewis, 1988; Arcifa, 2000; Bezerra-Neto and Pinto-Coelho, 2002a; Pagano *et al.*, 2003; López and Roa, 2005; Castilho-Noll and Arcifa, 2007a, b). The zooplankton control by invertebrates lasts longer in low latitude lakes due to a longer growing season (Saunders *et al.*, 1999). The chaoborid larvae swallow the whole prey (Pastorok, 1980), and select prey whose size is smaller than the diameter of their mouth. Thus, late larval instars prey on larger organisms, such as microcrustaceans (Swift and Fedorenko, 1975; Moore and Gilbert, 1987; Arcifa, 2000).

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Zooplankton can be also preyed on by fish, although only a few species are truly planktivores in Brazilian water bodies, where other feeding guilds predominate (Araújo-Lima et al., 1995; Arcifa and Northcote, 1997). Early life stages of fish are the main vertebrate predators, although some small-sized species may include zooplankton in their diets (Maia-Barbosa and Matsumura-Tundisi, 1984; Arcifa et al., 1991; Ambrósio et al., 2001; Roche et al., 2005; Elmoor-Loureiro and Soares, 2010). Predation by juveniles can be large enough to cause the decline of the prey population, such as in the Amazonian Lago Grande, where the decrease of the cladoceran Daphnia gessneri has been attributed to predation by young Colossoma macropomum and turbidity (Carvalho, 1984). However, predation pressure by fish seems to be lower in the limnetic zone than in the littoral, especially in areas with macrophytes, where juveniles and adults of small species are more abundant (Meschiatti et al., 2000; Oliveira et al., 2001; Sánchez-Botero and Araújo-Lima, 2001; Meschiatti and Arcifa, 2002; Agostinho et al., 2003; Milani et al., 2010).

In shallow and small lentic water bodies, where the littoral and pelagic zones are close, including microcrustaceans, planktonic, benthic and macrophyte-associated species may be preyed on by fish. However, the distribution and abundance of predators and prey determine the predation pressure in the littoral and limnetic zones. Although some studies have shown that littoral macrophytes are avoided by planktonic species (e.g. Dorgelo and Heykoop, 1985; Meerhoff et al., 2006), the diel horizontal migration might be a prey strategy for escaping from predators in shallow temperate lakes (Lauridsen and Buenk, 1996; Burks et al., 2001; 2002). However, macrophytes can be a refuge for zooplankton since the densities of predators, such as fish and invertebrates, are low, as shown in a subtropical Uruguayan lake (Iglesias et al., 2007).

This study aimed at investigating the importance of predation on planktonic

and littoral species of microcrustaceans by invertebrate and vertebrate predators in two reservoirs in northwestern São Paulo State.

Material and Methods

Study area

Samplings were carried out in two small reservoirs, Pindorama and Onda Verde, located in northwestern São Paulo State, Brazil. The reservoirs are situated in rural areas and are used for irrigation. The sampling stations and some characteristics of the reservoirs and surroundings are presented in Table 1. Constructed in the 1970's, the Pindorama Reservoir is fed by three springs, one of them running through a sugar cane plantation, and is devoid of macrophytes. The Onda Verde Reservoir resulted from damming a tributary of São João Stream, in the 1960's. It is surrounded by riparian forest and citrus plantation, and it has stands of macrophytes (Eichhornia azurea, Salvinia auriculata, and some non-identified submerged species).

Table 1. Morphometric features, location andcharacteristics of the surroundings of Pindorama andOnda Verde reservoirs.

| | Reservoirs | | | | | |
|-----------------------------------|------------------------------|-------------------------------|--|--|--|--|
| Features | Pindorama | Onda Verde | | | | |
| Maximum depth (m) | 4.4 | 3.9 | | | | |
| Maximum length (m) | 315.6 | 255.4 | | | | |
| Maximum width (m) | 157.3 | 86.1 | | | | |
| Surface area (m ²) | 32795 | 11712 | | | | |
| Perimeter (m) | 849 | 658 | | | | |
| T | 21° 13' 31.4" S | 20° 33' 52" S | | | | |
| Location | 48°13'41.5" W | 49° 16' 15.8" W | | | | |
| Macrophytes | Absent | Present (floating and rooted) | | | | |
| Riparian forest | Covering part of the margins | Present in both margins | | | | |

The climate of the region is Tropical Hot and Rainy (Aw of Köppen), with a dry-cool season (April – September) and a rainy-warm one (October – March).

Sampling and Analysis

Predators were collected at the beginning of the rainy season (October 2009), which was denominated the dry season, and during the rainy season (March 2010), in both reservoirs.

Chaoborus larvae were collected at dusk in the limnetic zone through vertical hauls with a 65 μ m meshed net. The volume filtered by the net was calculated by the area of the net mouth and the height of the water column. Organisms were anesthetized with carbonated water and then fixed in 4% formaldehyde. Samples were not taken in the littoral zone, since previous samplings revealed the extremely low abundance of chaoborid larvae in that site. Zooplankton was studied in four periods in 2009 and the results will be presented elsewhere.

The larvae were measured under a stereomicroscope to identify the instars. Then, with a stylet, the head and part of the digestive tract were extracted and the crop content gently squeezed over a slide, according to Arcifa (2000). The content was examined under a microscope for identification and counting of prey. Instars were selected according to the sizes proposed for *Chaoborus brasiliensis* Theobald, as follows: instar I = (0.7-1.6 mm); instar II = (1.7-3.1 mm); instar III = (3.2-4.7 mm); instar IV = (4.8-7.9 mm).

Fish were collected in the limnetic zone using gillnets, 20 m long and 15 mm and 35 mm between knots, set at dusk for four hours. In the littoral zone, the methods were standardized by using a trawl net (5 m long, and a 3 mm meshed net), dip nets and sieves to catch juveniles and smaller species, during two hours in each reservoir, in each sampling period. Fish larvae were sampled by horizontal hauls, with an ichthyoplankton net, in the limnetic zone. Fish were fixed in 10% formalin and then conserved in 70% ethanol. Specimens have been deposited in the fish collection DZSJRP under identification numbers from 12989 to 13015.

After identification, fish were measured with a caliper (standard length) and dissected for the analysis of stomach contents under a stereomicroscope. The volume occupied by each food item was estimated, according to Hyslop (1980), relative to the total content of each stomach (100%). Although the diet of the whole fish fauna was evaluated, only the species which fed on microcrustaceans were included here.

Results

Abundance and diet of Chaoboridae larvae

In both reservoirs, densities of *Chaoborus* larvae were larger in the rainy season than in the dry season (Fig. 1). Algae contributed a larger proportion to the diet of chaoborid larvae in the Pindorama Reservoir, whereas microcrustaceans were more important for chaoborid in the Onda Verde Reservoir (Figs. 2, 3).

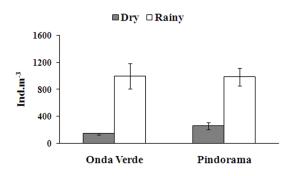


Figure 1. Mean densities (± SD) of larvae of *Chaoborus* sp. in the reservoirs, in the dry and rainy seasons.

The dinoflagellate *Peridinium* sp. and rotifers were part of the diet of all larval instars in the Pindorama Reservoir, particularly in the rainy season (Fig. 2). Instars III and IV fed on microcrustaceans in a larger proportion in the dry season (Fig. 2A) than in the rainy one (Fig. 2B). The copepods *Tropocyclops*

Nauplius

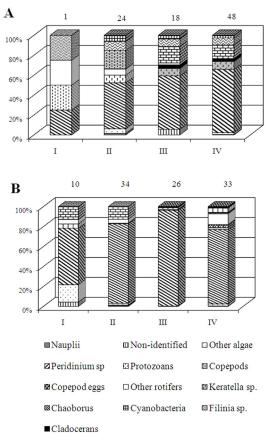


Figure 2. Relative abundance of food items of the four instars of *Chaoborus* sp., in the Pindorama Reservoir, in the dry (A) and rainy (B) seasons. Numbers on top of the bars are the individuals analyzed.

prasinus meridionalis Kiefer and *Thermocyclops decipiens* Kiefer contributed more to the diet than cladocerans, which were represented by *Daphnia laevis* Birge.

Food items differed in the Onda Verde Reservoir, where rotifers represented a major dietary item of all instars, microcrustaceans contributing a low proportion to the diet of the instars III and IV (Fig. 3A). In the rainy season, algae contributed a larger proportion to the diet of all larval instars and microcrustaceans to the diet of the instar IV (Fig. 3B). Both species of planktonic copepods were more consumed than cladocerans, which were mainly represented by *Ceriodaphnia cornuta cornuta* Sars. Animal items were more abundant in the dry season and algae in the rainy season.

Distribution and diet of fish

Young fish were found only in the

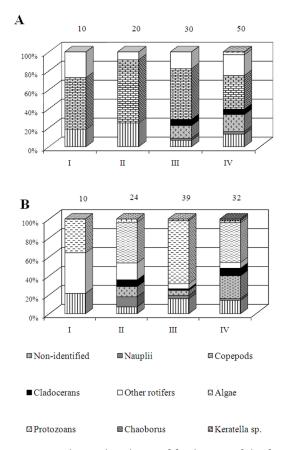


Figure 3. Relative abundance of food items of the four instars of *Chaoborus* sp., in the Onda Verde Reservoir, in the dry (A) and rainy (B) seasons. Numbers on top of the bars are the individuals analyzed.

littoral zone, especially within the macrophyte stands, when present as in Onda Verde. Fish larvae were not caught in the limnetic zone in either season.

Eleven species of fish were caught in the Pindorama Reservoir, Poecilia reticulata Peters and Oreochromis niloticus (Linnaeus) dominating in the dry season, and Cichla kelberi Kullander & Ferreira and Cichlasoma paranaense Kullander in the rainy season (Tab. 2). Terrestrial and aquatic insects and detritus (macerated material) were the major dietary items of all fish species. Young C. kelberi, C. paranaense, O. niloticus, Astyanax fasciatus (Cuvier), and P. reticulata included microcrustaceans in their diets (Tab. 3; Fig. 4). Planktonic copepods, the planktonic cladoceran Daphnia laevis, and the littoral species Macrothrix sp. and Simocephalus serrulatus (Koch) were included in the fish diet.

| | Onda | Onda Vede | | Pindorama | |
|---|------|-----------|------|-----------|--|
| Family Cichlidae | D | R | D | R | |
| Cichla kelberi Kullander & Ferreira, 2006 | - | - | - | 558 | |
| Cichlasoma paranaense Kullander, 1983 | 52 | 13 | - | 26 | |
| Geophagus brasiliensis (Quoy & Gaimard, 1824) | - | - | 2 | - | |
| Oreochromis niloticus (Linnaeus, 1758) | 101 | 5 | 2630 | 3 | |
| Tilapia rendalli (Boulenger, 1897) | - | - | 1 | 1 | |
| Family Gymnotidae | | | | | |
| <i>Gymnotus pantanal</i> Fernandes <i>et al.</i> , 2005 | - | - | - | 1 | |
| Gymnotus sylvius Albert & Fernandes-Matioli, 1999 | 15 | - | - | - | |
| Family Poeciliidae | | | | | |
| Poecilia reticulata Peters, 1859 | 469 | 589 | 36 | 3 | |
| Family Loricariidae | | | | | |
| Hypostomus ancistroides (Ihering, 1911) | 33 | - | 4 | - | |
| Family Characidae | | | | | |
| Astyanax fasciatus (Cuvier, 1819) | - | - | 14 | - | |
| Astyanax sp. | 248 | 1 | - | - | |
| Oligosarcus pintoi Campos, 1945 | - | - | 1 | - | |
| Family Erithrinidae | | | | | |
| Hoplias malabaricus (Bloch, 1794) | 3 | 9 | 1 | 3 | |

Table 2. Fish species and number of individuals caught in Pindorama and Onda Verde reservoirs, in the dry (D) and rainy (R) seasons.

Table 3. Volume (%) and frequency of occurrence (% in parentheses) of the food items of fish caught in the Pindorama Reservoir. SL = range of standard length of the individuals; N = number of individuals analyzed; n = number of individuals with stomach contents.

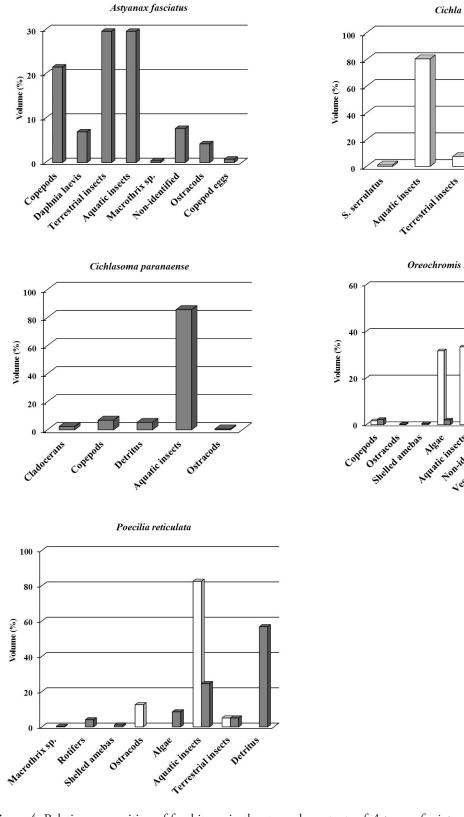
| | Astyanax fasciatus | Cichla kelberi | Cichlasoma paranaense Rainy | Oreochromis niloticus | | Poecilia reticulata | |
|---------------------|-----------------------|-------------------|-----------------------------------|-----------------------|----------|---------------------|-----------|
| Seasons | Dry | Rainy | | Dry | Rainy | Dry | Rainy |
| SL (cm) | 1.7-2.7 | 2.8-6.5 | 1.2-6.1 | 2.0-2.7 | 1.8-7.3 | 1.8-2.4 | 1.4-2.3 |
| Ν | 14 | 20 | 20 | 20 | 3 | 20 | 3 |
| n | 13 | 19 | 19 | 20 | 3 | 20 | 2 |
| Mites | | | | 3.0(5) | | | |
| Algae | | | | 2.0(10) | 31.5(33) | 8.5(15) | |
| Cladocerans | 7.3(30) | 1.0(5) | 2.3(5) | | | 0.2(5) | |
| Copepods | 21.5(46) | | 6.8(26) | 2.3(5) | 1.5(33) | | |
| Detritus | | | 5.4(5) | 32.7(35) | 34(33) | 56.7(60) | |
| Plant fragments | | | | 2.0(5) | | | |
| Aquatic insects | 29.4(30) | 80.5(94) | 85(89) | 47(45) | 33(33) | 24.5(30) | 82.5(100) |
| Terrestrial insects | 29.4(38) | 7.4(15) | | | | 5.0(5) | 5.0(100) |
| Non-identified | 7.5(7) | | | 10.0(10) | | | |
| Ostracods | 4.2(23) | 0.5(5) | 0.5(10) | 0.5(5) | | | 12.5(50) |
| Copepod eggs | 0.7(7) | | | | | | . , |
| Fish | | 10.5(15) | | | | | |
| Shelled amebas | | | | 0.5(5) | | 1.0 (5) | |

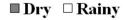
For the two species caught in both seasons, O. *niloticus* and P. *reticulata*, the number of dietary items was larger in the dry season than in the rainy one. Algae and aquatic insects were consumed in larger proportion in the rainy season by *O. niloticus* and *P. reticulata*,

Ostracods

Fish

Cichla kelberi

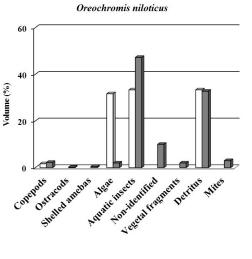


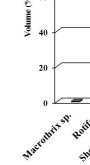


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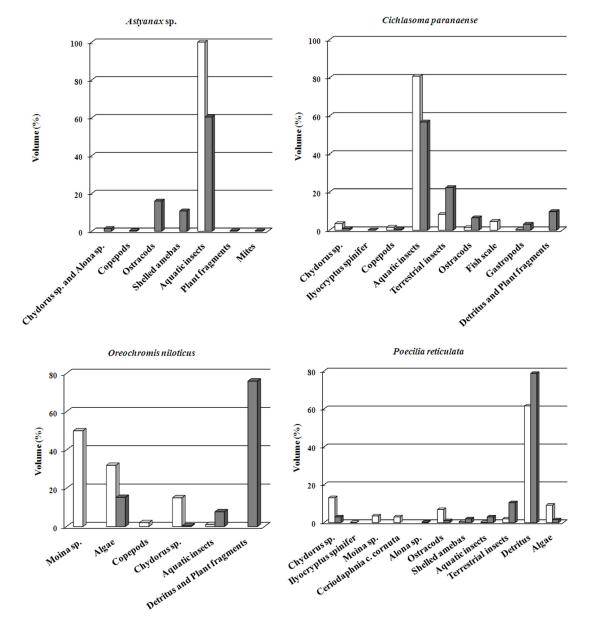
Figure 4. Relative composition of food items in the stomach contents of Astyanax fasciatus, Cichla kelberi, Cichlasoma paranaense, Oreochromis niloticus, and Poecilia reticulata, in the dry and rainy seasons in the Pindorama Reservoir.





respectively. Microcrustaceans (cladocerans and copepods) contributed *ca*. 0.2 to 9% to the diet of the fish fauna, except *A. fasciatus* that consumed a larger proportion of copepods (21.5 %) (Tab. 3).

Seven species of fish were recorded in the Onda Verde Reservoir, *Poecilia reticulata* and *Astyanax* sp. predominating in the dry season and *P. reticulata* in the rainy season (Tab. 2). Aquatic and terrestrial insects, detritus, and plant fragments were, in general, the main dietary items of fish. Four species fed on microcrustaceans, particularly young *O. niloticus* that consumed 65% of cladocerans, encompassing the planktonic *Moina* sp. (50%) and the macrophyte-associated *Chydorus* sp. (15%), in the rainy season (Tab. 4; Fig. 5). For the other fish species, the contribution of cladocerans and copepods to the diet was lower (~ 1.4 - 5%), except *P. reticulata* (19.7% of cladocerans in the rainy season; Tab. 4). The cladocerans ingested by the four fish species included the planktonic species *Ceriodaphnia cornuta cornuta* and *Moina* sp., and the



■ Dry 🗆 Rainy

Figure 5. Relative composition of food items in the stomach contents of *Astyanax* sp., *Cichlasoma paranaense*, *Oreochromis niloticus*, and *Poecilia reticulata*, in the dry and rainy seasons in the Onda Verde Reservoir.

| | Astyanax sp. | | Cichlasoma paranaense | | Oreochromis niloticus | | Poecilia reticulata | |
|---------------------|--------------|----------|-----------------------|-----------|-----------------------|-----------|---------------------|-----------|
| Seasons | Dry | Rainy | Dry | Rainy | Dry | Rainy | Dry | Rainy |
| SL (cm) | 2.13-4.49 | 4.46 | 1.60-4.70 | 2.56-8.18 | 1.93-4.25 | 2.57-3.28 | 1.80- 3.03 | 1.93-2.46 |
| Ν | 20 | 1 | 20 | 13 | 20 | 5 | 20 | 20 |
| Ν | 20 | 1 | 20 | 13 | 20 | 5 | 20 | 20 |
| Mites | 0.2(5) | | | | | | | |
| Algae | | | | | 15.2(30) | 32.0(60) | 1.5(5) | 9.1(30) |
| Cladocerans | 1.5(15) | | 0.9(25) | 3.4(46) | 0.3(10) | 65.0(80) | 4.5(20) | 19.7(45) |
| Copepods | 0.3(5) | | 0.5(5) | 1.5(23) | | 2.0(20) | | |
| Detritus | | | 9.5(10) | | 69.5(75) | | 78.7(85) | 61.5(75) |
| Fish scale | | | | 4.6(23) | | | | |
| Plant fragments | 0.2(5) | | 0.2(5) | | 6.7(25) | | | |
| Gastropods | | | 3.1(15) | 0.4(23) | | | | |
| Aquatic insects | 57(75) | 100(100) | 56.8(40) | 80.4(100) | 8.2(15) | 1.0(20) | 3.0(5) | 0.3(5) |
| Terrestrial insects | 14.2(35) | | 22.4(25) | 8.3(23) | | | 10.5(15) | 1.9(25) |
| Ostracods | 16.0(50) | | 6.5(10) | 1.4(30) | | | 1.0(15) | 6.9(35) |
| Shelled amebas | 10.6(40) | | | | | | 2.0(20) | 0.6(5) |

Table 4. Volume (%) and frequency of occurrence (% in parentheses) of the food items of fish caught in the Onda Verde Reservoir. SL = range of standard length of the individuals; N = number of individuals analyzed; n = number of individuals with stomach contents.

macrophyte-associated *Alona* sp., *Chydorus* sp., and *Ilyocryptus spinifer* Herrick (Fig. 5).

Discussion

Diet of Chaoboridae larvae

The highest densities of *Chaoborus* sp. in the rainy-warm season have been also observed in the tropical Lake Monte Alegre, where the decline of some cladoceran species was related with increased densities of chaoborid larvae (Arcifa *et al.*, 1992).

The larger contribution of algae to the chaoborid diet in the Pindorama Reservoir, in comparison to the Onda Verde Reservoir, might be related to the fact that its algae biomass is high (Câmara, 2011). Shift in food items from one season to another, observed here, could be a way to maximize the exploitation of fluctuating resources. The use of alternative food items by chaoborid larvae, in the seasons, agrees with findings in the Brazilian Lake Monte Alegre (Arcifa, 2000).

The major contribution of *Peridinium* sp. to the diet of chaoborid larvae in Pindorama points to the omnivorous habit of chaoborid larvae, which is in accordance with data from other lakes (Hare and Carter, 1987; Moore et al. 1994; Arcifa, 2000). Owing to the small size of *Peridinium* sp., however, its contribution in biomass is low (Castilho-Noll and Arcifa, 2007a). The vulnerability of rotifers to predation by Chaoborus depends on several aspects such as the lorica texture, body length, and type of swimming movement (Moore and Gilbert, 1987). A few species of rotifers were preyed on by the larvae among the 14 species present in the plankton (J. Abra, personal communication), with preference for Keratella sp. as observed by other authors (Bezerra-Neto and Pinto-Coelho, 2002b; Castilho-Noll and Arcifa, 2007a, b). Apparently, the presence of spines does not prevent the predation of Keratella by chaoborid larvae, which is favored by its high densities in Pindorama (J. Abra, personal communication) and its low escape ability. The low consumption of nauplii by Chaoborus larvae observed in this study, as well as in others (López and Roa, 2005; Castilho-Noll and Arcifa, 2007a, b) may result from an underestimated number owing to their quick digestion (Fedorenko, 1975; Moore, 1988).

The preference for copepods in comparison to cladocerans, in the Pindorama Reservoir, was probably related to their smaller size than the limnetic cladoceran Daphnia laevis. A dominant cladoceran during most of the study, it has a large body size (maximum 1.64 mm), individuals larger than 0.70 mm predominating in the population. Therefore, only juveniles are preyed on by the chaoborid larvae, agreeing with data from the Lake Monte Alegre (Arcifa, 2000; Castilho-Noll and Arcifa, 2007b). These authors report that only young Daphnia gessneri and D. ambigua (length 0.48) - 0.80 mm) were preved on by the instars III and IV. The copepod prey, Thermocyclops decipiens and Tropocyclops prasinus meridionalis, are smaller than cladocerans (0.40 - 0.84 mm), and as they have spineless bodies they can be more easily ingested. They contribute a larger biomass to the diet of Chaoborus larvae (Castilho-Noll and Arcifa, 2007a) than smaller organisms, such as *Peridinium* sp. and rotifers.

Similarly to findings in Pindorama, the contribution of copepods prevailed in Onda Verde. The predominance of Ceriodaphnia cornuta cornuta, among the cladocerans, in the chaoborid diet could be favored by its suitable size (0.18 - 0.46 mm) and the dominance in the plankton. Contrasting results have been found regarding predation on C. cornuta by chaoborid larvae. López and Roa (2005) report a positive selection of C. cornuta by chaoborid fourth instar in a Venezuelan lake, whereas Arcifa (2000) found, in a Brazilian lake, a low proportion of *C. cornuta* in the diet of Chaoborus, which selected Bosmina tubicen Brehm, even during a high peak of C. cornuta in the lake. The presence of lateral spines in *C*. cornuta may lower the ingestion by Chaoborus, despite the adequate size placing Ceriodaphnia as a potential prey (Mumm, 1997; Pagano et al., 2003).

Although the contribution of planktonic cladocerans to the diet of chaoborid larvae was relatively low in Onda Verde (maximum 6.5%) we may suppose that the effect on the population dynamics can be significant. Castilho-Noll and Arcifa (2007a) reported that the contribution of *Daphnia gessneri* to the diet of instar IV, that has not exceeded 10%, was sufficient to cause a significant

higher mortality rate and lower population growth rate in the treatment with chaoborid larvae than in the *Chaoborus* - free treatment in mesocosm experiments. On the other hand, despite a larger proportion of copepods than cladocerans in the chaoborid diet, their population dynamics has not been influenced by predation. According to the authors, one of the reasons could be a larger production of eggs that results in higher recruitment, reducing the effects of predation, the same way we suppose happened here with *Thermocyclops decipiens* and *Tropocyclops prasinus meridionalis*, as they produced a high number of eggs.

A wider amplitude of food items with the inclusion of microcrustaceans, mostly in the diet of instars III and IV of *Chaoborus* in the reservoirs, can favor their biomass growth. The diversification of food items in the last instars can contribute to increasing the allocation of energy to body mass, as the biomass production is largest in the late instar (Bezerra-Neto and Pinto-Coelho, 2002c). As the predator mouth diameter and the maximum width, height, or diameter of the prey are related (Arcifa, 2000), and larger larvae can consume larger prey, last instars were benefited by the extra energy provided by larger items, in both reservoirs.

Summarizing the overall diet, in Pindorama the food items of chaoborid instars can be ranked Peridinium > rotifers > protozoans and Peridinium > rotifers > copepods > cladocerans, respectively for the instars I-II and III-IV, in both seasons (except for the instar I, in the dry season, where rotifers > *Peridinium* and protozoans). In Onda Verde, the diet was more diversified and varied in the seasons. Rotifers predominated in the diet of early instars in the dry season, whereas a larger number of items occurred in the rainy season, in the following order of importance - algae > rotifers > copepods > cladocerans. There was a shift in the diet of the instars III and IV, the items following this order - rotifers > copepods > cladocerans in the dry season, and algae > copepods > cladocerans and rotifers, in the rainy season.

Nauplius

Of the thirteen fish species recorded, three are exotic (*Oreochromis niloticus, Tilapia rendalli* and *Poecilia reticulata*) and one was introduced from the Amazon Basin (*Cichla kelberi*). The other species belong to the Upper Paraná River basin (Casatti *et al.*, 2009), except *Gymnotus pantanal* described from the Pantanal Matogrossense, the Paraguay River and Guaporé, Bolivia (Fernandes *et al.*, 2005).

Young fish and adults of smaller species can use the littoral zone, particularly the macrophyte stands, as refuge against piscivorous fish (Roche and Rocha, 2005), and the early stages also use these habitats for development (Esguícero and Arcifa, 2010). Therefore, predation by fish on microcrustaceans is potentially higher in the littoral than in the limnetic zone.

The large contribution of aquatic insects to the diet of fish in this study has also been found in other Brazilian water bodies (*e.g.* Meschiatti *et al.*, 2000; Oliveira *et al.*, 2001; Meschiatti and Arcifa, 2002). Microcrustaceans were a minor dietary item here as in most Brazilian water bodies, where planktivorous fish are usually absent in the limnetic zone (Araújo-Lima *et al.*, 1995; Arcifa and Northcote, 1997), microcrustaceans being preyed on by young fish or smaller species, especially in littoral areas of the water bodies.

Astyanax fasciatus was an exception regarding microcrustacean predation, in Pindorama, as the contribution of microcrustaceans, particularly copepods, was large. In general, A. fasciatus feeds mostly on insects and algae, but microcrustaceans can be a major item in some water bodies. In the Americana Reservoir, planktonic cladocerans, such as Bosmina, Diaphanosoma, Daphnia, and Moina were commonly ingested by juveniles and adults of A. fasciatus (Arcifa et al., 1991). Copepods and cladocerans were major dietary items of both young and adult of this species in the Broa Reservoir (Maia-Barbosa and Matsumura-Tundisi, 1984). Although in Pindorama Daphnia laevis was consumed by A. fasciatus, the density of the cladoceran was low in the littoral zone, what may have contributed

to the larger proportion of copepods in the diet of *A. fasciatus*. A lower contribution of microcrustaceans than aquatic insects to the diet of *Astyanax* sp. in Onda Verde was probably related to the higher abundance of insects within the macrophyte stands.

The ingestion of littoral cladocerans such as *Chydorus*, *Alona*, and *Ilyocryptus* by young *Cichlasoma paranaense*, *Oreochromis niloticus*, and *Poecilia reticulata* is probably related to the way they forage in the littoral zone. These cladocerans have specializations to live at the bottom or in the middle of the vegetation, such as appendages and spines that allow scraping the food and moving around in these environments (Souza and Elmoor-Loureiro, 2008).

There is ontogenetic variation in the diet of *Cichla kelberi* in Pindorama Reservoir, the juveniles having a more diversified diet than the piscivorous adult fish, which included mainly aquatic insects and a low number of the large-sized littoral cladoceran *Simocephalus serrulatus*. The same variation has been reported for *C. ocellaris* in the Lake Monte Alegre, where juveniles fed on aquatic insects and secondarily on zooplankton and fish (Arcifa and Meschiatti, 1993).

The low number of planktivorous fish species in Brazilian water bodies leads to the prevalence of *Chaoborus* predation on zooplankton in the limnetic zone. In some lakes the increased predation by *Chaoborus* is caused by the introduction of a piscivorous fish, evidencing a top-down effect. In lakes of the Rio Doce Valley, the introduction of the cichlid *Cichla* cf. *ocellaris* and the characid *Pygocentrus nattereri* caused the extinction of native fish species, favoring the increase of chaoborid larvae, with the consequent disappearance of several cladoceran species (Pinto-Coelho *et al.*, 2008).

Conclusion

littoral microcrustaceans are preyed on by fish nearshore, and planktonic species by Chaoborus larvae in the limnetic zone. Predation by chaoborid larvae on microcrustaceans is lower than on other items, such as Peridinium sp. and rotifers, while aquatic insects, plant fragments and detritus are more consumed by fish. Fish species selected larger prey, such as aquatic insects, whereas the smaller microcrustaceans represented a minor dietary item. Chaoborus preferred smaller prey, such as Peridinium sp., rotifers, protozoans, copepods, and juveniles of large cladocerans. Although predation on microcrustaceans is not heavy, the extension of its influence on the population dynamics is still unknown in the reservoirs.

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