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“Fake prey”: planktonic ostracods negatively affect the predatory performance of *Chaoborus* larvae

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Previous laboratory experiments have indicated that *Chaoborus* larvae may be confused when exposed to a single prey species at a high density, resulting in decreased attack efficiency. Here, we hypothesized that a prey less vulnerable to *Chaoborus* larvae, such as *Physocypria schubarti* ostracods, could affect the predatory performance of *Chaoborus* on a more vulnerable prey, such as *Ceriodaphnia silvestrii* neonates. We predicted that fewer neonates would be ingested by *Chaoborus* larvae in the presence of ostracods at high densities due to the decreased attack efficiency caused by the confusion effect. This hypothesis was tested by combining predation assays and direct visual observations of live organisms. There was a significant decrease in the consumption of neonates when they were offered together with ostracods at high densities; however, this was not related to the ingestion of ostracods as an alternative prey or to decreased attack efficiency on neonates caused by the confusion. The energy wasted due to the numerous attacks on the ostracods (“fake prey”) possibly led the chaoborids to exhaustion, reducing their predatory performance on neonates. In ecological terms, high densities of ostracods in the water column may theoretically minimize the strong impact of *Chaoborus* sp. larvae on more vulnerable prey.

KEYWORDS: confusion effect; invertebrate predator; microcrustaceans; Chaoboridae

INTRODUCTION

The aquatic larvae of the dipteran *Chaoborus* are tactile predators capable of detecting vibrations produced by their prey’s swimming appendages, filtering apparatus or

jaws (Riessen *et al.*, 1984). Nevertheless, when facing zooplanktonic prey at very high densities, this predator may exhibit a decreased ability to detect the individual position of a target organism and to attack it due to the numerous

simultaneous vibrational signals from different directions, a “confusion effect” (Jensen and Larsson, 2002; Jeschke and Tollrian, 2007). In fact, some microcrustaceans seem to aggregate in swarms and/or groups as an antipredation strategy (Kvam and Kleiven, 1995; Ambler, 2002). Studying the confusion effect is not a simple task because there is no consensus on the best way to accurately measure it (Jensen and Larsson, 2002). Moreover, its influence on the predator’s functional responses may vary, resulting in models of different types (Jeschke and Tollrian, 2005). Despite these uncertainties, the reduction in predator attack efficiency when confronted with increasing prey densities has been used as an indicator of the confusion effect (Jeschke and Tollrian, 2007).

In Lake Jacaré, a natural tropical system in the Middle Rio Doce Valley in southeast Brazil, a dense population of the planktonic ostracod *Physocypria schubarti* with a peak of up to 650 individuals/L has coexisted with *Chaoborus* larvae (Pinto-Coelho *et al.*, 2008; Eurípedes *et al.*, 2009). Prey densities lower than this peak value were apparently related to a decrease in *Chaoborus* larvae attack efficiency in trials with the cladoceran *Daphnia obtusa* (Jeschke and Tollrian, 2007). Recently, laboratory experiments have demonstrated that although *P. schubarti* ostracods are recurrently attacked by *Chaoborus* larvae from Lake Jacaré, they are rarely preyed upon, even after 24 h of exposure to this invertebrate predator (Maroneze *et al.*, 2017). Indeed, preliminary crop analysis revealed that *P. schubarti* ostracods are not part of the local *Chaoborus* larvae diet, which is mainly composed of cladocerans and copepods.

Taken together, this information suggests that *Chaoborus* larvae should not have a strong impact on *P. schubarti* ostracods in the community of this tropical lake. Perhaps, the presence of this microcrustacean species in the water column has a negative effect on this tactile invertebrate predator. Locally, the numerous *P. schubarti* ostracods overlap spatially with other zooplanktonic prey species that are more vulnerable to *Chaoborus* predation, such as the cladocerans *Ceriodaphnia* and *Bosmina*. In theory, if *Chaoborus* larvae become confused due to the multiple vibrations emitted by the numerous *P. schubarti* individuals, its attack efficiency on other prey that swim among the ostracods could also decrease. The basis for this assumption is theoretical, so new studies are necessary to support it. Controlled experiments may be a good way to evaluate the idea that the presence of *P. schubarti* at high densities would affect the interaction between *Chaoborus* larvae and other prey that are more vulnerable to them.

In this context, we combined predation assays with direct visual observations of live organisms to answer the following questions: (i) Is the consumption of *Ceriodaphnia silvestrii* neonates by *Chaoborus* larvae decreased when they are offered together with *P. schubarti* ostracods? (ii) If so,

can this consumption decrease be related to a change in *Chaoborus* larvae attack efficiency? We hypothesized that high densities of *P. schubarti* ostracods would negatively affect the predatory performance of *Chaoborus* larvae on *C. silvestrii* neonates. Under this experimental condition, it was assumed that (i) fourth-instar *Chaoborus* larvae would ingest fewer *C. silvestrii* neonates after 24 h and (ii) there would be a decrease in the predator attack efficiency on these prey due to the confusion effect caused by the numerous *P. schubarti* ostracods.

METHOD

The animals came from a natural tropical lake in the middle Rio Doce valley in southeastern Brazil (19°48′38.8″ S 42°38′55.5″W—Lake Jacaré). Local environmental characteristics and species compositions may be found in other studies (Pinto-Coelho *et al.*, 2008; Brandão *et al.*, 2012; Barros *et al.*, 2013; Maia-Barbosa *et al.*, 2014). The zooplankton were collected through vertical hauls using a 45- μ m plankton net during July 2015. In the laboratory, the animals were kept separately in 1-L glass flasks with filtered lake water under controlled conditions at 25°C and a 12-h photoperiod. They were fed daily with microalgae, debris, rotifers and/or microcrustaceans obtained from the lake according to their specific requirements. To standardize the study conditions, animals with similar characteristics were taken from these laboratory cultures to be used in the experimental trials. We selected fourth-instar *Chaoborus* sp. larvae starved for 12 h, *P. schubarti* ostracods retained by a mesh of 0.3 mm and *C. silvestrii* neonates during the first 24 h of life. A pilot observation indicated that local fourth-instar *Chaoborus* larvae could have some difficulty in ingesting adult females of this cladoceran species, as *Chaoborus* are gape-limited predators (Moore and Gilbert, 1987; Arcifa, 2000). This explains why only *C. silvestrii* neonates in the first 24 h of life were used in the study. The selected organisms were monitored in two types of experiments: predation and observation tests.

Predation tests

Predation tests were designed to evaluate whether the consumption of *C. silvestrii* neonates by fourth-instar *Chaoborus* sp. larvae would decrease when these prey were offered together with *P. schubarti* ostracods. Groups of 5 *C. silvestrii* neonates were transferred to plastic bottles with 40 mL of filtered lake water. With the exception of the control group, in which the *C. silvestrii* neonates were offered alone, some of the plastic bottles received 5, 15 or 25 *P. schubarti* ostracods representing three different treatments with 125, 375 and 625

ostracods/L. In addition to the microcrustaceans, a single fourth-instar *Chaoborus* sp. larva was added per plastic bottle. Each experimental condition, including the control group, was replicated 15 times, resulting in the monitoring of 60 *Chaoborus* larvae, 300 *C. silvestrii* neonates and 675 *P. schubarti* ostracods. We also performed parallel tests with 15 replicates in which *P. schubarti* ostracods or *C. silvestrii* neonates were confined in plastic bottles free of predatory *Chaoborus* sp. larvae. All plastic bottles were kept under the same controlled conditions as were the laboratory cultures. After 24 h, the live microcrustaceans were counted to estimate the survival rate and the proportion of prey ingested by *Chaoborus* larvae. The percentages of neonates preyed upon were compared by one-way analysis of variance (ANOVA) followed by Tukey's multiple comparisons test (Statistica 6.0, $\alpha = 5\%$).

Observation tests

Observation tests were designed to verify a possible decrease in the *Chaoborus* larvae attack efficiency on *C. silvestrii* neonates when these prey were offered together with *P. schubarti* ostracods. Initially, groups of 5 *C. silvestrii* neonates were confined in Petri dishes (90 mm \times 15 mm) with 40 mL of filtered lake water. Then, groups of 25 *P. schubarti* ostracods were transferred to the dishes, simulating the condition under which the predation tests indicated a decreased consumption of neonates by chaoborids—625 ostracods/L. Lastly, a single fourth-instar *Chaoborus* sp. larva was transferred to each Petri dish. In the control group, only *C. silvestrii* neonates were offered to the *Chaoborus* larvae—0 ostracods/L. We replicated both experimental conditions 10 times, monitoring a total of 20 *Chaoborus* larvae, 100 *C. silvestrii* neonates and 250 *P. schubarti* ostracods. Animals confined in each Petri dish were visually observed for 30 min in an air-conditioned room with a temperature similar to that maintained in the laboratory cultures.

A *Chaoborus* sp. larva attack was considered as successful if it resulted in the microcrustacean ingestion (Pijanowska et al., 2006). This ambush predator usually

Table I: Final density of Physocypria schubarti (ostracods/L) after 24 h in the different treatments of the predation trials

	Treatment		
	125 ostracods/L	375 ostracods/L	625 ostracods/L
Mean	100.0	303.3	566.7
Minimum	50.0	250.0	500.0
Maximum	125.0	375.0	625.0

attacks prey when the distance between them is approximately 1 mm (Riessen et al., 1984). Therefore, only direct strikes toward prey close to the larva's body were considered an attack (Swift and Fedorenko, 1975). During the observations, the Petri dishes were superimposed on graph paper to assist in the estimation of this distance. In general, the attack is characterized by a sudden movement in which only the anterior portion of the larva's body moves toward the prey (Pastorak, 1980). The *Chaoborus* larvae attack efficiency on *C. silvestrii* neonates was estimated as the ratio between the number of successful attacks and the total number of attacks (Jeschke and Tollrian, 2007). The attack efficiency values obtained in the presence and absence of *P. schubarti* ostracods (0 and 625 ostracods/L) were compared through a *t*-test (Statistica 6.0, $\alpha = 5\%$).

RESULTS

Predation tests

After 24 h, the *Chaoborus* larvae did not effectively prey upon *P. schubarti* under any of the experimental conditions. Two ostracods were ingested only in the treatment in which they were at highest density, 625 ostracods/L. Although the consumption by *Chaoborus* larvae was extremely low, *P. schubarti* had a mortality rate between 9.3% and 20.0% in the different treatments. A mortality rate of 14.4% was also observed in the parallel test in which *P. schubarti* ostracods were confined in plastic bottles free of predatory *Chaoborus* larvae. It is important to emphasize that densities of *P. schubarti* remained high and distinct among the different treatments even with these mortality rates (Table I). Unlike the *P. schubarti* ostracods, the *C. silvestrii* neonates were strongly preyed upon by *Chaoborus* larvae (Fig. 1). In the control group, the percentage of *C. silvestrii* neonates consumed by *Chaoborus* larvae reached 81%. This proportion ranged from 59% to 84% in the treatments in which the *C. silvestrii* neonates were offered together with the *P. schubarti*. A significant decrease in the consumption of *C. silvestrii* neonates (22%) occurred exclusively in the treatment in which the ostracods were at the highest density (500–625 ostracods/L) ($F_{(3,56)} = 6.186$, $P = 0.001$) (Fig. 1). In the parallel test without the *Chaoborus* sp. larvae in the plastic bottles, the *C. silvestrii* neonates had a mean mortality rate of 2.7%.

Observation tests

The *Chaoborus* larvae attack efficiency on *C. silvestrii* neonates was similar under both experimental conditions.

The mean values were 0.41 in the control without ostracods and 0.38 in the treatment with 625 ostracods/L ($t = 0.167$, $P = 0.868$) (Fig. 2). In total, the *Chaoborus* sp. larvae attacked the *C. silvestrii* neonates 30 times in the control group with 0 ostracods/L. On average, each single *Chaoborus* larva made three attack movements toward the *C. silvestrii* neonates over the 30 min. Of these, on average, one attack movement resulted in *C. silvestrii* neonate ingestion. When the *C. silvestrii* neonates were offered together with *P. schubarti* at 625 ostracods/L, they were attacked 31 times. In this treatment, the *Chaoborus* larvae also attacked the *P. schubarti* 113 times.

On average, each single *Chaoborus* sp. larva made 3.1 and 11.7 attack movements toward the *C. silvestrii* neonates and the *P. schubarti* ostracods, respectively, over the 30 min. Of these, on average, 0.8 attack movements resulted in *C. silvestrii* neonate ingestion. No *P. schubarti* were preyed upon by *Chaoborus* larvae under this experimental condition during the direct observation period.

DISCUSSION

Our 24-h predation tests demonstrated that the consumption of *C. silvestrii* neonates by *Chaoborus* larvae decreased by 22% when these prey were offered together with *P. schubarti* ostracods at the highest density, 500–625 ostracods/L. The decreased consumption in this treatment was not a consequence of the ingestion of *P. schubarti* as alternative prey as they were rarely preyed upon by *Chaoborus* larvae. These results have important ecological implications, especially for some zooplankton species population dynamics. They suggest that under certain circumstances, the presence of *P. schubarti* ostracods in the water column could minimize the impact of *Chaoborus* larvae predation on more vulnerable prey. Worldwide, this invertebrate predator plays a determinant role in the structure of several freshwater zooplankton communities; it can control the size of the prey population or even extinguish some species locally (Von Ende and Dempsey, 1981; Pinto-Coelho *et al.*, 2008; Arcifa *et al.*, 2015).

In Lake Jacaré, if the high densities of *P. schubarti* really affect the predatory performance of *Chaoborus* larvae on other prey, this negative effect is probably not constant, occurring only seasonally. Similar to other middle Rio Doce lakes, this environment is warm monomictic, so the zooplankton communities are strongly influenced by the mixing of the water column (Brandão *et al.*, 2012). Locally, *P. schubarti* increase in abundance when the water column is completely mixed (dry season). It was during this seasonal period that its population already reached the highest density peak recorded by the Brazilian Long Term Ecological Research Program (Site 4) (Eurípedes *et al.*, 2009). When Lake Jacaré is stratified during the rainy season, historical data from this biomonitoring program indicate a maximum number of 153 *P. schubarti* ostracods/L in the pelagic water column. This upper density threshold is within the range in which our experiments did not indicate a decrease in the *Chaoborus* larvae predatory performance on *C. silvestrii* neonates. For example, in the treatments with *P. schubarti* densities up to 375 individuals/L, the proportion of neonates ingested by *Chaoborus* larvae over 24 h ranged from 80% to 84%.

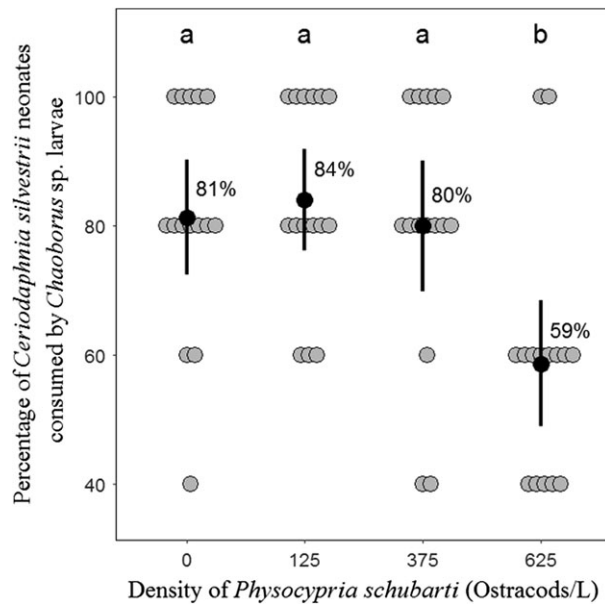


Fig. 1. Percentage of *Ceriodaphnia silvestrii* neonates consumed by *Chaoborus* larvae in the experimental trials with different densities of *Physocypria schubarti* ostracods (after 24 h). Means followed by the same letter are not significantly different from each other according to the Tukey test at 5% probability. Bars represent standard error.

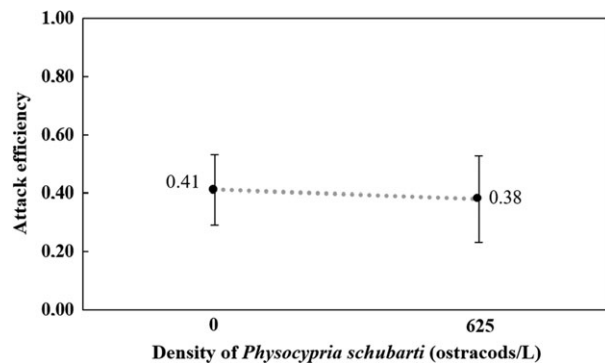


Fig. 2. Attack efficiency of *Chaoborus* larvae on *Ceriodaphnia silvestrii* neonates in experimental trials with and without the presence of ostracods. Bars represent standard error.

These values were similar to the percentage of *C. silvestrii* eaten by *Chaoborus* larvae in the control group without *P. schubarti* (81%).

Although we recorded a significantly decreased consumption of *C. silvestrii* neonates by *Chaoborus* sp. larvae when these prey were offered together with *P. schubarti* at the highest densities, 500–625 ostracods/L, this decrease does not seem to be related to the “confusion effect”. Under this circumstance, a decrease in the *Chaoborus* sp. larvae attack efficiency on *C. silvestrii* neonates was not observed. Moreover, the number of attacks that did or did not result in the ingestion of *C. silvestrii* neonates by this invertebrate predator were similar regardless of whether these prey were offered alone or together with *P. schubarti*. These results suggest that the ability of *Chaoborus* sp. larvae to detect and attack *C. silvestrii* neonates in our experiments was not negatively affected by the multiple vibrational stimuli from the numerous *P. schubarti* ostracods. Some authors presume that this invertebrate predator would be able to discriminate and select distinct prey according to their particular swimming vibrations before attacking (Pastorak, 1980; Winner and Greber, 1980). This idea is consistent with a previous study characterizing the signals emitted by distinct prey species of *Chaoborus* larvae (Kirk, 1985); however, it is inconsistent with another similar study (Giguère and Dill, 1979).

If the decreased consumption of *C. silvestrii* neonates by *Chaoborus* larvae was not caused either by the ingestion of *P. schubarti* as an alternative prey or by a decreased attack efficiency related to the confusion effect, what could explain this result? Based on our data, the question remains open; however, some evidence derived from the direct observation tests may help to refute or support possible mechanisms underlying this decrease in the predatory performance of the chaoborids. Since *Chaoborus* larvae are ambush predators, an encounter with the prey must occur before it attacks (Pastorak, 1980). The encounter occurs when the swimming prey approach the *Chaoborus* larvae, entering the strike zone (Riessen et al., 1984). When the *C. silvestrii* neonates were offered together with *P. schubarti* ostracods at the highest density, 625 ostracods/L, these cladocerans exhibited a peculiar behavior. As they approached the *Chaoborus* sp. larvae but were not close enough to be attacked, they suddenly changed their swimming behavior by moving in the opposite direction. This reaction was observed when the *Chaoborus* sp. larvae attacked a nearby ostracod shortly before the *C. silvestrii* neonates were about to enter its strike zone. Apparently, *C. silvestrii* detected the hydrodynamic disturbance caused by the sudden movement of the *Chaoborus* sp. larvae and immediately moved away.

Perhaps this reflects the behavior exhibited by some *Ceriodaphnia* species that swim rapidly after invertebrate predators attack them (Chang and Hanazato, 2003; Andrade and López, 2005).

Theoretically, if the interactions described above occurred over the 24 h of the predation tests, the number of encounters between the *Chaoborus* larvae and *C. silvestrii* neonates may have decreased, contributing to the decreased consumption of this prey. At first, this reasoning seems plausible because the vulnerability of a zooplankton species to this invertebrate predator is related, among other factors, to the frequency of encounters between them (Pastorak, 1981). The encounter rate may be affected by the predator’s strike zone size and the prey’s body size, swimming speed and density (Giguère et al., 1982; Riessen et al., 1984; Tollrian, 1995). In the plastic bottles in which *P. schubarti* had a density of 625 individuals/L, these ostracods probably entered the *Chaoborus* larvae strike zone more often than did the *C. silvestrii* neonates. In addition to their higher density, they had a larger body size and apparently swam faster than *C. silvestrii* neonates. If most of the encounters between *Chaoborus* larvae and *P. schubarti* ostracods resulted in attacks, *C. silvestrii* neonates that were approaching the predator may have detected the hydrodynamic disturbance and moved away from the predator on several occasions. Despite being attractive, this perspective is weakened by the previously emphasized fact that the number of attacks toward the *C. silvestrii* neonates over the 30 min in the observation tests was not affected by the presence of *P. schubarti* ostracods. To support this perspective, the escape response of *C. silvestrii* neonates should have led to a lower encounter rate with *Chaoborus* larvae and hence fewer attacks.

Alternatively, another explanation for our results may be related to excessive energy expenditure and consequent physical exhaustion of the *Chaoborus* larvae after they have repeatedly and unsuccessfully attacked the ostracods. According to Giguère (Giguère, 1980), a *Chaoborus* larva spends approximately 0.57 mJ of energy during a strike movement. This value was estimated by monitoring *Chaoborus crystallinus* larvae of distinct instars at 21°C. If a microcrustacean such as a copepod is captured after 3–8 attack attempts, the energy expended would correspond to a small percentage of the prey’s energy content (up to 3.9%). Assuming a value of 0.57 mJ per attack movement and the total number of attacks in our observation tests, the following scenario of the energy expenditure of *Chaoborus* sp. larvae over 30 min may be inferred. The energy expenditure was 17.1 mJ in the control group with 30 attack attempts towards neonates and 82.1 mJ in the treatment with *P. schubarti* ostracods at the highest density with 31 and 113 attack

attempts towards neonates and ostracods, respectively. This increase of 79.2% in the energy expenditure occurred without any advantage for *Chaoborus* sp. larvae because no *P. schubarti* ostracods were ingested.

In this context, the numerous antagonistic interactions with the “fake prey” at the highest density may have seriously fatigued the *Chaoborus* larvae, causing an actual decrease in the total number of attacks toward the *C. silvestrii* neonates and/or in their attack efficiency. If true, note that, contrary to our initial idea, such decreased attack efficiency would be primarily related not to the confusion effect but to the fatigue of the larvae. Over the 30 min of the observation tests, we did not record exhausted larvae. A longer exposure time to the numerous *P. schubarti* ostracods may be necessary for *Chaoborus* larvae to become stressed. In the predation tests, as previously reported, the consumption of neonates by *Chaoborus* larvae did not decrease when the ostracod density was up to 375 individuals/L, even after 24 h. These results contradict what we have just suggested. However, in the treatments with lower *P. schubarti* density, the number of antagonistic interactions per time unit between *Chaoborus* larvae and these ostracods may not have been enough to reach the minimum threshold to cause the predator physical exhaustion. All these assumptions must be interpreted cautiously until more extensive empirical data support them. Finally, it is also important to mention that no information about the energy content of prey species from Lake Jacaré is available. Thus, it is still not possible to predict whether failed attack attempts toward *P. schubarti* ostracods are detrimental to *Chaoborus* larvae in energetic terms. This topic is a relevant research question to be answered in the future.

CONCLUSION

Since the 1980s, the ecological interaction between *Chaoborus* larvae and planktonic microcrustaceans has been investigated by different authors (Pastorak, 1980; Hanazato and Yasuno, 1989; Castilho-Noll and Arcifa, 2007; Pujoni *et al.*, 2016). Our laboratory tests provide new information on this topic. They suggest that high densities of a prey with low vulnerability to *Chaoborus* larvae, such as *P. schubarti* ostracods, negatively affect its predatory performance on a prey with high vulnerability, such as *C. silvestrii* neonates. The decreased consumption of *C. silvestrii* neonates by *Chaoborus* larvae was not caused by the ingestion of the *P. schubarti* as an alternative prey. It was also not related to decreased *Chaoborus* sp. larvae attack efficiency on the *C. silvestrii*—a “confusion effect”. Under these circumstances, the excessive energy expenditure due to the wasted attacks

toward the ostracods, “fake prey”, may have led the *Chaoborus* larvae to temporary physical exhaustion, reducing their predatory performance on neonates. Due to the inherent limitations of experimental research, the results of laboratory tests may not be identical to those obtained in the field environment (Jeschke and Tollrian, 2005). Nevertheless, our experiments illustrate that the interactions between zooplankton species can be quite complex. They also show that studying such interactions, even under artificial conditions, may be an important way to improve our knowledge of zooplankton population dynamics in nature.

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REFERENCES

- Ambler, J. W. (2002) Zooplankton swarms: characteristics, proximal cues and proposed advantages. *Hydrobiologia*, **480**, 155–164.
- Andrade, A. and López, C. (2005) Predatory interactions between *Thermocyclops decipiens* Kiefer (Cyclopoida: Copepoda) and two small cladocerans: behavior and prey post-encounter vulnerability. *J. Limnol.*, **41**, 153–159.
- Arcifa, M. S. (2000) Feeding habits of Chaoboridae larvae in a tropical Brazilian reservoir. *Braz. J. Biol.*, **60**, 591–597.
- Arcifa, M. S., Ferreira, T. C. S., Fileto, C., Castilho-Noll, M. S. M., Bunioto, T. C. and Minto, W. J. (2015) A long-term study on crustacean plankton of a shallow tropical lake: the role of invertebrate predation. *J. Limnol.*, **74**, 606–617.

- Barros, C. F. Z., Santos, A. M. M. and Barbosa, F. A. R. (2013) Phytoplankton diversity in the middle Rio Doce lake system of southeastern Brazil. *Acta Bot. Bras.*, **27**, 327–346.
- Brandão, L. P. M., Fajardo, T., Eskinazi-Sant’anna, E., Brito, S. and Maia-Barbosa, P. M. (2012) Fluctuations of the population of *Daphnia laevis* Birge 1878: a six-year study in a tropical lake. *Braz. J. Biol.*, **72**, 479–487.
- Castilho-Noll, M. S. M. and Arcifa, M. S. (2007) Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake. *Aquat. Ecol.*, **41**, 587–598.
- Chang, K. H. and Hanazato, T. (2003) Vulnerability of cladoceran species to predation by the copepod *Mesocyclops leuckarti*: laboratory observations on the behavioural interactions between predator and prey. *Freshwater Biol.*, **48**, 476–484.
- Eurípedes, D. C., Brito, S. L., Mendendez, R. M. and Maia-Barbosa, P. M. (2009) Fluctuation of *Physocypria schubarti* (Podocopida, Ostracoda) in the limnetic region of Lake Jacaré (Middle Rio Doce, MG): a seven-year study. Proceedings of the XII Brazilian Limnology Congress (in Portuguese).
- Giguère, L. A. and Dill, L. M. (1979) The predatory response of *Chaoborus* larvae to acoustic stimuli, and the acoustic characteristics of their prey. *Zeitschrift für Tierpsychologie*, **50**, 113–123.
- Giguère, L. A. (1980) Metabolic expenditures in *Chaoborus* larvae. *Limnol. Oceanogr.*, **25**, 922–928.
- Giguère, L. A., Delâge, A., Dill, L. M. and Gerritsen, J. (1982) Predicting encounter rates for zooplankton: a model assuming a cylindrical encounter field. *Can. J. Fish. Aquat. Sci.*, **39**, 237–242.
- Hanazato, T. and Yasuno, M. (1989) Zooplankton community structure driven by vertebrate and invertebrate predators. *Oecologia*, **81**, 450–458.
- Jensen, K. H. and Larsson, P. (2002) Predator evasion in *Daphnia*: the adaptive value of aggregation associated with attack abatement. *Oecologia*, **132**, 461–467.
- Jeschke, J. M. and Tollrian, R. (2005) Effects of predator confusion on functional responses. *Oikos*, **111**, 547–555.
- Jeschke, J. M. and Tollrian, R. (2007) Prey swarming: which predators become confused and why? *Anim. Behav.*, **74**, 387–393.
- Kvam, O. V. and Kleiven, O. T. (1995) Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. *Hydrobiologia*, **307**, 177–184.
- Kirk, K. L. (1985) Water flows produced by *Daphnia* and *Diaptomus*: implications for prey selection by mechanosensory predators. *Limnol. Oceanogr.*, **30**, 679–686.
- Maia-Barbosa, P. M., Menendez, R., Pujoni, D. G. F., Brito, S. L., Aoki, A. and Barbosa, F. A. R. (2014) Zooplankton (Copepoda, Rotifera, Cladocera and Protozoa: Amoeba Testacea) from natural lakes of the middle Rio Doce basin, Minas Gerais, Brazil. *Biota Neotrop.*, **14**, 1–20.
- Maroneze, D. M., Pujoni, D. G. F. and Maia-Barbosa, P. M. (2017) Akinesis in *Physocypria schubarti* Farkas, 1958 (Podocopida, Cyprididae) does not fully explain its low consumption by predatory *Chaoborus* larvae in a Brazilian lake. *Crustaceana*, **90**, 297–310.
- Moore, M. V. and Gilbert, J. J. (1987) Age-specific *Chaoborus* predation on rotifer prey. *Freshwater Biol.*, **17**, 223–236.
- Pastorak, R. A. (1980) Selection of prey by *Chaoborus* larvae: a review and new evidence for behavioral flexibility. In Kerfoot, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, pp. 538–554.
- Pastorak, R. A. (1981) Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology*, **62**, 1311–1324.
- Pijanowska, J., Dawidowicz, P. and Weider, L. J. (2006) Predator-induced escape response in *Daphnia*. *Arch. Hydrobiol.*, **167**, 77–87.
- Pinto-Coelho, R. M. P., Bezerra-Neto, J. F., Miranda, F., Mota, T. G., Resck, R., Santos, A. M., Maia-Barbosa, P. M., Mello, N. et al (2008) The inverted trophic cascade in tropical plankton communities: impacts of exotic fish in the Middle Rio Doce lake district, Minas Gerais, Brazil. *Braz. J. Biol.*, **68**, 1025–1037.
- Pujoni, D. G. F., Maia-Barbosa, P. M., Barbosa, F. A. R., Fragozo-Jr, C. R. and Van Nes, E. H. (2016) Effects of food web complexity on top-down control in tropical lakes. *Ecol. Modell.*, **320**, 358–365.
- Riessen, H. P., O’Brien, W. J. and Loveless, B. (1984) An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. *Ecology*, **65**, 514–522.
- Swift, M. C. and Fedorenko, A. Y. (1975) Some aspects of prey capture by *Chaoborus* larvae. *Limnol. Oceanogr.*, **20**, 418–425.
- Tollrian, R. (1995) *Chaoborus crystallinus* predation on *Daphnia pulex*: can induced morphological changes balance effects of body size on vulnerability? *Oecologia*, **101**, 151–155.
- Von Ende, C. N. and Dempsey, D. O. (1981) Apparent exclusion of the cladoceran *Bosmina longirostris* by invertebrate predator *Chaoborus americanus*. *Am. Midl. Nat.*, **105**, 240–248.
- Winner, W. and Greber, J. S. (1980) Prey selection by *Chaoborus punctipennis* under laboratory conditions. *Hydrobiologia*, **68**, 231–233.