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RESEARCH ARTICLE

Effects of vertebrate and invertebrate predators on the life history of *Daphnia similis* and *Moina macrocopa* (Crustacea: Cladocera)

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Abstract – Cladocerans serve as prey for several aquatic predators like fish and *Chaoborus* larvae. However, because different predators consume different sized prey, cladocerans may display differing life-history responses depending on predator type. Although most studies use the genus *Daphnia* to evaluate phenotypic plasticity in cladocerans, other genera might also respond to predator infochemicals. In this study, we compared life-history responses of *Daphnia similis* and *Moina macrocopa* to infochemicals released by a vertebrate (fish) and an invertebrate (*Chaoborus*) predator. As expected, some life-history parameters were altered depending on the type of predator. Overall, fish infochemicals increased the size at primipara, clutch size, net reproductive rate and longevity in both cladocerans. We argue that increased body lengths in the presence of fish promote bigger clutch sizes. Conversely, responses to *Chaoborus* were weaker, affecting only the net reproductive rates and longevity. Non-daphniid cladocerans may display similar responses to *Daphnia* when exposed to predators. However, as *Daphnia* is usually underrepresented in tropical lakes, studying other genera might offer new insights into predator-prey relationships and food webs in lake ecosystems.

Keywords: Zooplankton / chemical communication / tradeoff / predation

1 Introduction

Predator-prey relationships are among the most well-studied biological interactions in ecology. In many ecological systems, predators have a pervasive effect on the abundance, behavior and size structure of prey communities (Brooks and Dodson, 1965; Lima, 2002). However, prey usually do not act as passive food sources and may display adaptive changes to avoid being located, captured and ingested by predators. Many aquatic prey are able to determine the presence and identity of predators before encounters take place, through detection of chemical compounds released by predators as well as those of injured (and ingested) prey (Bronmark and Hansson, 2000; Ferrari *et al.*, 2010; Scherer and Smee, 2016). The early recognition of such infochemicals allows aquatic prey to display appropriate behavioral, morphological and life-history responses, which ultimately make prey less vulnerable to predation (Relyea, 2001; Laforsch and Tollrian, 2004; Gilbert, 2017).

In temperate lakes, pelagic food webs are usually dominated by spined, large-bodied cladocerans belonging to the genus *Daphnia* (Sarma *et al.*, 2005), conferring upon these organisms an important role in the transfer of energy from primary producers to top consumers. *Daphnia* may display several strategies to reduce the foraging success of both vertebrate (fish) and invertebrate (usually *Chaoborus* larvae) predators, through changes in the age and size at primipara, neonate body length, net reproductive rates, morphology and behavior (Boersma *et al.*, 1998; Laforsch and Tollrian, 2004; Tolardo *et al.*, 2016). However, the direction and magnitude of such changes might depend on the identity of consumers and their diet (Brett, 1992; Scherer and Smee, 2016), since vertebrate and invertebrate predators usually select for different prey size. Visual hunting fishes typically prefer large-bodied cladocerans like *Daphnia*, while *Chaoborus*

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larvae commonly feed on small-bodied cladocerans (Hanazato and Masayuki, 1989; Šorf *et al.*, 2014). Thus, the investment in somatic growth might be adjusted according to the dominant predator in order to increase the possibility of survival.

On the other hand, the pelagic region of tropical lakes is usually dominated by small-bodied genera like *Moina* and *Diaphanosoma* (Sarma *et al.*, 2005), which do not possess any helmet or caudal spines. The transparent and intrinsically small body size of most tropical cladocerans could be enough to avoid visual hunting predators, but the analysis of fish gut contents reveal that even small-bodied cladocerans may serve as a food source for visual hunting fishes (Elmoor-Loureiro and Soares, 2010). Additionally, a small body size could make small-bodied cladocerans more vulnerable to *Chaoborus* larvae. Compared to the genus *Daphnia*, fewer studies have evaluated how other cladocerans react to the presence of predators (*e.g.* Dawidowics *et al.*, 2010; Santangelo *et al.*, 2011; Gu *et al.*, 2017).

In this study, we evaluated how fish and *Chaoborus*-mediated water affect the life-history of two cladoceran species, *Daphnia similis* Claus, 1876 and *Moina macrocopa* (Strauss, 1820). *Daphnia similis* is usually found in temperate and subtropical lakes and ponds in the northern Hemisphere. On the other hand, *Moina macrocopa* inhabits lakes and temporary ponds worldwide. Although both species are largely used in ecotoxicological studies, only a few have assessed how predators affect their growth, reproduction and survival patterns (Gama-Flores *et al.*, 2013; La *et al.*, 2014; Tolardo *et al.*, 2016; Gu *et al.*, 2017). Because vertebrate and invertebrate predators select for different prey features, we expected contrasting changes in cladocerans exposed to different predators. We therefore sought to identify how *Daphnia similis* and *Moina macrocopa* react to the presence of fish or *Chaoborus* infochemicals, through assessment of changes in somatic growth, reproduction and lifespan.

2 Methods

2.1 Experimental design

A single clone of *Moina macrocopa* and a single clone of *Daphnia similis* were used throughout this study. The clone of *M. macrocopa* originated from a tropical puddle in Rio de Janeiro, Brazil (Elmoor-Loureiro *et al.*, 2010). This clone has previously been used to evaluate the effects of salinity and humic substances on a subset of life-history parameters (Suhett *et al.*, 2011). The clone of *D. similis* originated from a temperate region, although the exact location of its origin is unknown. This clone has previously been used to evaluate the effects of tilapia fish on a subset of life-history parameters (Tolardo *et al.*, 2016).

Clonal lineages of both species were established individually in aged tap water under high food conditions (10^5 cells mL^{-1} of *Scenedesmus* sp.) at 20 °C and a 16:8h light:dark cycle for several generations before the experiment. These conditions were used throughout the experiment described below.

The responses of *Moina* and *Daphnia* to fish and *Chaoborus*-mediated water were assessed by performing a life-table experiment. For each species, 30 randomly chosen neonates (< 24 h old) born from the second clutch of synchronized mothers were used to start the experiment. All experimental organisms were incubated individually in 40 mL of medium, either in a control, fish or *Chaoborus* treatment ($n = 10$ for each treatment and each species).

The predator-mediated water contained both predator kairomones and alarm signals from prey (Laforsch *et al.*, 2006). For the production of predator (fish or *Chaoborus*) treatments, groups of four *Gasterosteus aculeatus* Linnaeus, 1758 (three-spined sticklebacks, 3–4 cm in length) and 40 *Chaoborus obscuripes* (Wulp, 1859) larvae (third and fourth stages of development) were fed with 50 *Moina* and 50 *Daphnia* individuals every day and then allowed to excrete in 2 L of control water for 18 h (Santangelo *et al.*, 2010; Santangelo *et al.*, 2011). When feeding the predators, no algae were added to the medium. The medium used for all treatments was prepared on a daily basis and was filtered through 0.45 mm glass fiber filters (GF 50, Schleicher and Schuell, Germany). Additionally, in accordance with previous studies (Laforsch *et al.*, 2006; Santangelo *et al.*, 2010; Weiss *et al.*, 2012), we added $10\,\mathrm{mg \cdot L^{-1}}$ of ampicillin (AppliChem, Germany) to each medium to slow the decomposition of kairomones and alarm signals by bacteria. We assumed that the addition of ampicillin also reduced the abundance of predator-related bacteria, which could serve as an extra food source for the cladocerans (Maszczyk and Bartosiewicz, 2012). Ampicillin was also added to the control medium.

We monitored the experimental individuals until day 27, when all of the animals but *Daphnia* in fish-mediated water had died. Predator type and prey species were used as predictive variables, and life-table parameters were used as response variables. The assessed life-table parameters were age and size at primipara (when the first eggs appeared in the brood chamber), clutch size in the first three reproductive events, the net reproductive rate (R_o) and survival curves. The body length was measured from the top of the eye to the end of the carapace (the base of the tail spine in *D. similis*). For calculating the net reproductive rates, only data obtained until day 27 was used. Caudal spines in *D. similis* were not measured because a previous study using the same clone has demonstrated no changes in this parameter (Tolardo *et al.*, 2016).

2.2 Data analysis

Before analysis, all data were $\log_{10}$ transformed, except survival. After checking the requirements of normal distribution and homogeneity of variances using Shapiro–Wilks and Bartlett tests, the individual and interactive effects of predator type (control, fish or *Chaoborus*) and prey species (*M. macrocopa* or *D. similis*) were assessed by two-way ANOVA (age and size at primipara, and R_o) and two-way MANOVA (clutch size) in Statistica 7.0 software. When significant effects of predators were observed, paired comparisons with an analysis of contrast were performed as post hoc tests. Survival curves were compared using the Log-rank test in Prism 4.0 software. An overall comparison between treatments was carried out for each prey species, followed by pairwise comparisons. For pairwise comparisons, a corrected α was used, according to Bonferroni's procedure for multiple comparisons (corrected $\alpha = 0.05/3 = 0.017$).

Table 1. Two-way ANOVA and two-way MANOVA results for the effects of prey type (*Daphnia similis* and *Moina macrocopa*) and predator type (fish and *Chaoborus*) on life-history traits of cladocerans.

Two-way ANOVA	*d.f.*	MS	*F*	*P*
Age at primipara				
Prey	1	1.371	449.68	<**0.00001**
Predator	2	0.015	4.80	**0.013**
Prey*Predator	2	<0.001	0.08	0.923
Error	48	0.003		
Size at primipara				
Prey	1	0.436	853.00	<**0.00001**
Predator	2	0.012	23.00	<**0.00001**
Prey*Predator	2	<0.001	1.00	0.281
Error	47	<0.001		
Net reproductive rate				
Prey	1	0.706	24.23	**0.00001**
Predator	2	0.675	23.14	<**0.00001**
Prey*Predator	2	0.543	18.62	<**0.00001**
Error	49	0.029		
Two-way MANOVA	*d.f.*	Pillai's trace	*F*	*P*
Clutch size				
Prey	3	0.711	34.40	<**0.00001**
Predator	6	0.853	10.66	<**0.00001**
Prey*Predator	6	0.695	7.64	<**0.00001**

3 Results

All of the life-history parameters assessed were affected by prey, predator and/or the interaction among these factors (Tab. 1). The age and size at primipara were affected by prey and predator types. *Moina* reproduced at earlier ages and smaller body sizes when compared to *Daphnia*. In *Daphnia*, the presence of fish led to a decrease in the age at primipara, but to an increase in the size at primipara. Similarly, the presence of fish led to an increase in the size at primipara in *Moina* (Fig. 1a and b). The clutch sizes in the first three reproductive events were affected by prey, predator and their interaction (Tab. 1). Overall, the presence of fish led to an increase in the clutch sizes of *Moina* and *Daphnia* (Fig. 1c). The net reproductive rates were also affected by prey, predator and their interaction (Tab. 1). The presence of any predator led to an increase in the net reproductive rates of *Moina*. For *Daphnia*, fish led to an increase and *Chaoborus* led to a decrease in the net reproductive rate (Fig. 1d).

Survival curves were compared between the three treatments for each species. We observed different survival curves for *Moina* (Log-rank test, $P < 0.0001$) and *Daphnia* treatments (Log-rank test, $P = 0.0004$). However, pairwise comparisons showed different patterns for each prey species. For *Moina*, similar survival curves were observed for fish and *Chaoborus* treatments, where animals survived longer than under control conditions (Fig. 2a). For *Daphnia*, on the other hand, similar survival curves were observed for control and *Chaoborus* treatments, where animals survived less than under fish conditions. In the fish treatment, 80% of animals were alive by day 27, when the experiment was finished (Fig. 2b).

4 Discussion

When faced with the risk of predation, prey organisms are able to display likely adaptive changes in behavior, morphology and life-history, as demonstrated by some of our results. However, the direction and magnitude of such changes in cladocerans usually depend on the identity of prey and predators (Tolardo *et al.*, 2016; Gu *et al.*, 2017), as well as other variables such as light intensity (Effertz and von Elert, 2017), clonal lineage (Boersma *et al.*, 1998) and the history of the predator-prey interaction (Fisk *et al.*, 2007). In aquatic systems, vertebrate and invertebrate predators usually drive different, sometimes opposite responses in cladoceran prey (Brett, 1992). Although most studies use the genus *Daphnia* as a model organism to understand such adaptive changes in cladocerans, this study shows that other genera, such as the smaller-bodied *Moina*, may display similar responses to those commonly observed in *Daphnia*.

As we predicted, the presence of fish or *Chaoborus* infochemicals drove some likely adaptive changes in the life history of both prey species. However, for all variable responses but the survival curve in *M. macrocopa*, fish and *Chaoborus* predators determined different responses, varying from no effects to stimulation or inhibition. For example, *Chaoborus* infochemicals had no effect on the age at primipara in both cladocerans used in this study. However, an increase in the age at primipara of *Daphnia* has been observed in the presence of *Chaoborus* infochemicals, because resources are allocated preferentially in somatic growth to prevent predation (Tollrian, 1995). On the other hand, the risk of predation by fish reduced the age at primipara in *D. similis*, corroborating earlier observations for this species (Tolardo *et al.*, 2016) and other daphniids (*e.g.* Pauwels *et al.*, 2010). Reproducing at earlier ages may decrease the risk of predation before reproduction can take place. Contrasting to *D. similis* in this study, the age at primipara in *M. macrocopa* was not affected by fish, suggesting that this trait is not so plastic in *M. macrocopa*. It might be argued that maturation already occurs extremely early (~3 days old at 24 °C) in the genus *Moina* (Santangelo *et al.*, 2008; Suhett *et al.*, 2011).

Daphnia and *Moina* usually display reduced size at primipara or no changes in this parameter in the presence of fish (Pauwels *et al.*, 2010; Santangelo *et al.*, 2010; Gu *et al.*, 2017). Increased size at primipara in the presence of fish-mediated water, as we observed in *D. similis* and *M. macrocopa*, is unexpected because larger body sizes make cladocerans more visible to visual hunting fishes (Brooks and Dodson, 1965; Hanazato and Masayuki, 1989). However, increased body lengths have been observed before in *Daphnia exilis* Herrick, 1895 exposed to fish mediated-water (Carter *et al.*, 2013). It has been argued that some *Daphnia*, under the threat of fish, might grow faster during juvenile stages and then invest in high reproductive effort and fast clutch release once maturity is achieved (Carter *et al.*, 2013; Tolardo *et al.*, 2016). It is possible that *M. macrocopa* displayed similar strategies in the presence of fish. The longer body size of *M. macrocopa* in the presence of fish might have allowed the higher reproductive effort and possibly faster clutch releases. Similarly, the congeneric *Moina micrura* (Kurz, 1874) releases consecutive clutches at earlier ages in the presence of fish

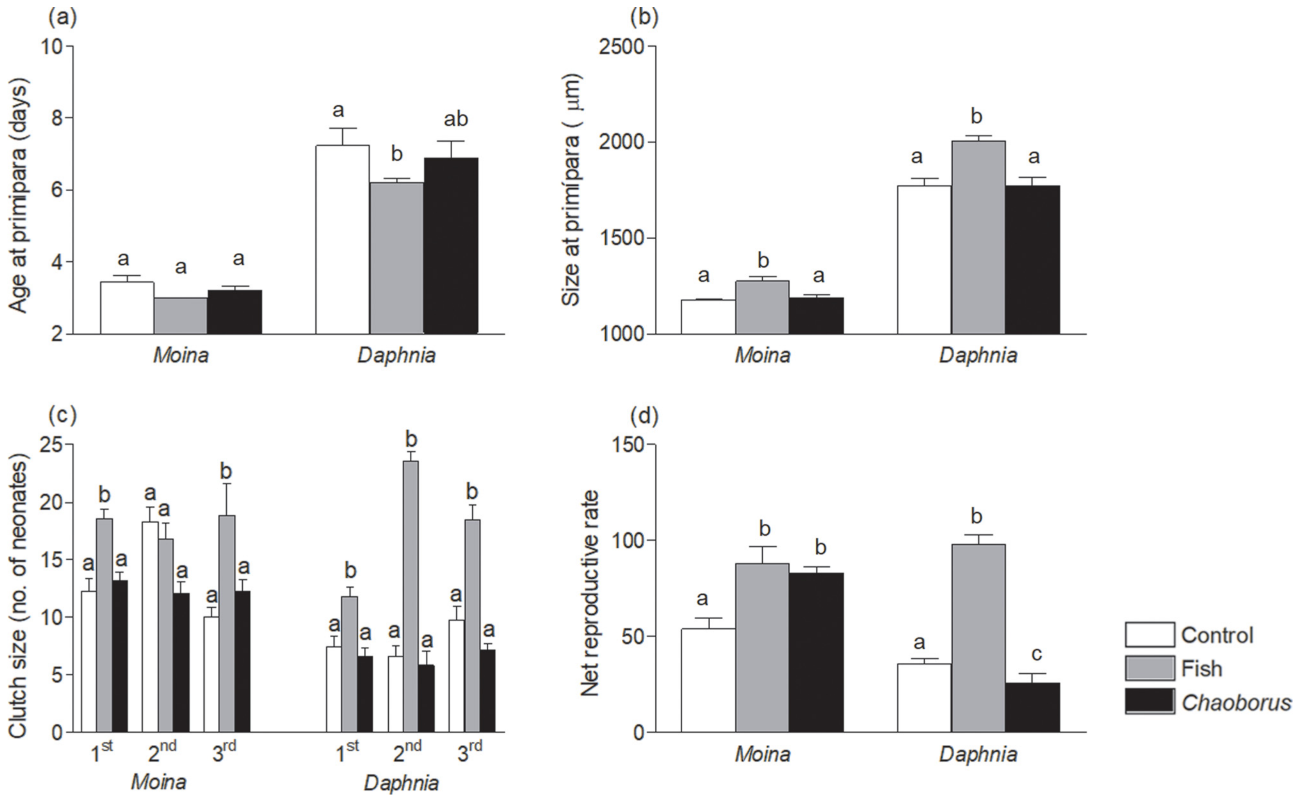


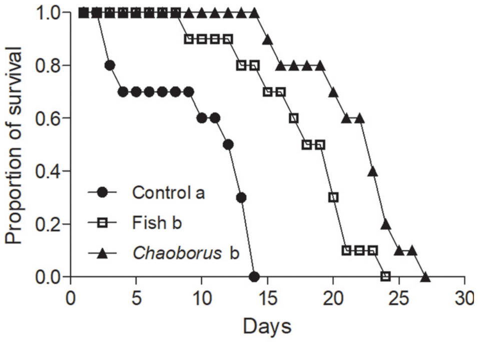
Fig. 1. Life-history parameters (mean + 1 SE) of two cladocerans (*Moina macrocopa* and *Daphnia similis*) in the absence of predators (white bars), in the presence of fish-mediated water (gray bars) and in the presence of *Chaoborus*-mediated water (black bars). (a) Age at primipara, (b) size at primipara, (c) clutch-specific size, and (d) net reproductive rate. Different letters above bars denote significant differences within each prey type and reproductive event after an analysis of contrast.

(Santangelo *et al.*, 2010). On the other hand, *Chaoborus*-mediated water was not capable of increasing the size at primipara in *D. similis*, contrasting to patterns observed in some other daphniids (Brett, 1992; Tollrian, 1995). For *M. macrocopa*, it is possible that the smaller body size would not benefit from any increase as a defense against *Chaoborus* predation because *Moina* is already too small, as previously suggested for *Moina micrura* (Santangelo *et al.*, 2011).

Clutch sizes were clearly affected by fish-mediated water in *D. similis* and *M. macrocopa*, also corroborating earlier studies (Santangelo *et al.*, 2011; Tolardo *et al.*, 2016; Gu *et al.*, 2017). The investment in bigger clutches under the threat of fish might ensure that some offspring will survive predation. This pattern is more evidenced when the net reproductive rates are compared between fish and control conditions. *Chaoborus*-mediated water, on the other hand, did not clearly affect the clutch sizes in the first three reproductive events, in either cladoceran prey. Our results on clutch sizes differ from some previous studies, in which the presence of *Chaoborus* led to a decrease in the clutch size of *Daphnia* (Luning, 1992). However, when we consider the net reproductive rates, some different patterns emerge. The presence of *Chaoborus* led to a decrease in this parameter in *D. similis*, but to an increase in *M. macrocopa*.

The higher net reproductive rate in *M. macrocopa* under the threat of *Chaoborus* might be explained by its longer survival and continued reproduction when compared to control conditions. Since increasing the body length might not be sufficient to protect small-bodied cladocerans against *Chaoborus* (Santangelo *et al.*, 2011), investing in reproduction might be an alternative strategy, similar to what happens in cladocerans exposed to fish infochemicals. Conversely, *D. similis* displayed a reduced net reproductive rate in the presence of *Chaoborus*, in spite of having no different survival curves when compared to control conditions. Reduced net reproductive rates in *Daphnia* are sometimes associated to larger neonates (Tollrian, 1995), which are born less vulnerable to *Chaoborus* predation. Resource allocation shifts from somatic growth to reproduction are usually observed under the threat of fish, and the opposite trend might occur under the threat of *Chaoborus* (Stibor and Luning, 1994).

As mentioned above, the survival curves differed between control and predator treatments, and the responses to predators varied between prey species. Both predators extended the lifespan in *M. macrocopa* and fish had a similar effect on *D. similis*. These results differ from previous ones showing a decrease in the lifespan of cladocerans exposed to fish kairomones (*e.g.* Dawidowics *et al.*, 2010). The potential presence of fish-associated bacterial food in fish-conditioned water may benefit cladocerans (Maszczyk and Bartosiewicz, 2012). However, as ampicillin was added to our media, we rule out this hypothesis. Although not tested in this study, an alternative reason explaining the enhanced lifespan of cladocerans in the presence of predators would be the production of heat shock proteins. It is recognized that predators may induce the production of heat shock proteins in


(a) *Moina*

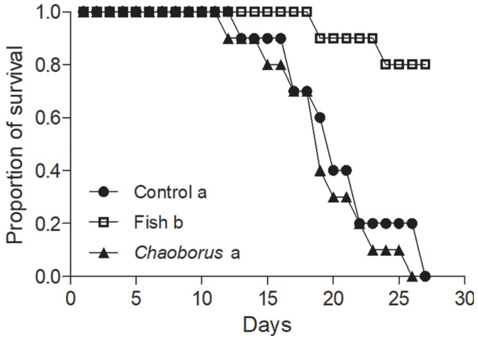

(b) *Daphnia*

Fig. 2. Survival curves of *Moina macrocopa* and *Daphnia similis* neonates over time in the absence or presence of predators (fish or *Chaoborus*). Different letters in predator treatments denote significantly different survival curves after a Log-rank test.

Daphnia (Pauwels *et al.*, 2005), and that those proteins contribute to expand the lifespan of *Daphnia* (and other organisms) by protecting the cells against the accumulation of damaged proteins (Schumpert *et al.*, 2014).

Most of the life-history parameters measured in this study responded positively to the presence of fish-mediated water, implying that positive correlations among some of the life-history traits exist. However, it is worth noting that some unmeasured tradeoffs might exist. For example, *M. macrocopa* may display reduced moving rates in the presence of fish infochemicals, suggesting a tradeoff between life history and behavior changes under the threat of predation (Gu *et al.*, 2017). *Daphnia* may become more vulnerable to parasites as a consequence of increasing the rate of development when exposed to predator infochemicals (Allen and Little, 2011). Likewise, the immune system of *Daphnia* might be negatively affected by fish, especially under high food levels (Pauwels *et al.*, 2010). Additionally, the risk of predation by fish might reduce the feeding rates of *Daphnia* (Pestana *et al.*, 2010), and larger clutches are sometimes associated to smaller neonate body lengths in *Daphnia* and *Moina* (Boersma *et al.*, 1998; Santangelo *et al.*, 2011).

In conclusion, some similar responses exist between *Daphnia* and other cladocerans exposed to vertebrate and invertebrate predators. However, evaluating how non-*Daphnia* cladocerans react to predators might offer new insights into predator-prey relationships and food webs in lake ecosystems, especially under different evolutionary backgrounds. For example, relatively recent studies have found additional defenses in *Daphnia* against myriad predators (Petrusek *et al.*, 2009; Rabus *et al.*, 2013). This approach might be especially important in the tropics where large-bodied *Daphnia* is not common (Sarma *et al.*, 2005). Finally, fish and *Chaoborus* infochemicals might drive similar changes in some life-story parameters of cladocerans, as observed in *M. macrocopa* for the net reproductive rates and survival curves.

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