Effects of predation by Hydra (Cnidaria) on cladocerans (Crustacea: Cladocera)

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ABSTRACT

Planktonic cladocerans have evolved different strategies to avoid predation from vertebrates; these include changes in morphology, behavior, physiology, and/or life-history traits. However, littoral cladocerans are better adapted to avoid invertebrate predation particularly from insect larvae by evolving morphological and physiological adaptations. Nevertheless, this has not been proven for some littoral predators such as Hydra. In this study, we provide quantitative data on how Hydra affects its zooplankton prey. We studied the predation behavior on Alona glabra, Ceridodaphnia dubia, Daphnia pulex, Daphnia cf. mendotae, Diaphanosoma birgei, Macrothrix triserialis, Moina macrocopa, Pleuroxus aduncus, Scapholeberis kingi, Simocephalus serrulatus, Elaphoidella grandidiieri, Brachionus rubens and Euchlanis dilatata. We also tested the indirect effect of allelochemicals from Hydra on the demography of Daphnia cf. mendotae. Littoral cladocerans are specially adapted to resist nematocyst injection and discharge of toxic substances from Hydra. A significant decrease in the population growth rate of D. cf. mendotae from 0.21 to 0.125 d−1 was observed at Hydra densities of 2 ind. mL−1. The role of carapace thickness as an adaptive strategy of littoral cladocerans against Hydra predation is discussed.

Key words: Allelochemicals; invertebrate predation; nematocysts; predator-prey interactions; zooplankton.

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INTRODUCTION

Predation is one of the most important interactions in aquatic systems regulating distribution and abundance of aquatic species (Murdoch and Bence, 1987). Among the freshwater invertebrate predators in the littoral zone, Hydra is attached to substrates, such as macrophytes, dead leaves, stems, dead sticks and rocks (Massaro et al., 2013). Hydra has a wide geographical distribution and occurs on all continents except Antarctica (Jankowski et al., 2008). In spite of this wide distribution, it has received little attention from the ecologists. During the last 30 years Web of Science reports as many as 3000 papers on Hydra, yet <6% of them deal with ecological aspects; most of the articles are focused on biochemistry, cell biology, and genetic aspects. It is known that Hydra is a predator, but it could have much stronger influence on the prey than is thought because of its reproductive capacity, predation strategies and high longevity (>1 year) (Slobodkin and Bossert, 2010).

The preferred prey items of Hydra include many crustaceans, mainly cladocerans and copepods and some insect larvae and annelids (Massaro et al., 2013). The predator-prey interaction between Hydra and its prey could be direct or indirect. Direct interaction implies a physical encounter in which the predator kills the prey eliminating it from the system, while indirect interaction is regulated by chemical cues where the predator releases allelochemicals which are sensed by the prey or even a competitor, and thus modifies its behavior, morphology or life history traits (Harvell, 1990; Larsson and Dodson, 1993; Lass and Spaak, 2003). However, it is important to mention that these indirect responses of prey to allelochemicals from Hydra have not been adequately considered in the literature.

Zooplankton species that live in the littoral zone have evolved defense mechanisms as a result of long-term co-existence in the shallow weedy zones of water bodies with their predators (Åbjörnsson et al., 2004). Such mechanisms could involve, in the case of Hydra, reducing activation of nematocysts, some kind of immunity to the toxin or resistance to nematocyst penetration through the carapace thickness (Schwartz et al., 1983). The latter could be tested in prey species with strongly built carapaces such as Simocephalus and chydorids and with smoother ones like Daphnia, Diaphanosoma, and Moina (Dodson and Frey, 2001; Dumont and Negrea, 2002). There are several methods to study predator prey interactions (Greene, 1983; Krebs, 1985, 1999). These include observational approaches such as: i) feeding behavior where one can quantify number of occurrences of encounters, attacks, captures, and ingestions, as well as the time required for prey ingestion or digestion; experimental methods such as ii) feeding preferences; iii) functional and numerical responses; and iv) life table demography to compare the
survivorship and reproduction-related effects of allelochemicals from the predators on the prey.

In this study we: i) examined the vulnerability of cladocerans to Hydra predation; ii) related the cladoceran vulnerability to their habitat; and iii) explored the possibility that allelochemicals from Hydra had an influence on the life history traits of the cladoceran Daphnia cf. mendotae. This would increase our understanding of the role of Hydra in aquatic ecosystems. We hypothesize that in contrast to pelagic species, littoral ones would be less damaged by Hydra attack, and that allelochemicals from this cnidarian could have significant effects on the life history traits of its prey.

METHODS

Culturing Hydra and its prey

For the observations and the experiments, we isolated 13 prey species from a few waterbodies located in the State of Mexico (Tab. 1), that were later mass-cultured starting with a single parthenogenetic female; cladocerans: Alona glabra Sars, Ceriodaphnia dubia Richard, Daphnia pulex Leydig, Daphnia cf. mendotae Birge, Diaphanosoma birgei Korinek, Macrothrix triserialis (Brady), Moina macrocopa (Straus), Pleuroxus aduncus (Jurine), Scapholeberis kingi Sars, Simocephalus serrulatus (Müller); copepods: Elaphoidella grandidieri (Guine and Richard), and rotifers: Brachionus rubens Ehrenberg and Euchlanis dilatata Ehrenberg.

For mass cultures, as well as the experiments we used standard EPA medium, a medium that is frequently employed to culture rotifers and cladocerans (Weber, 1993). The EPA medium was prepared by dissolving 96 mg NaHCO₃, 60 mg CaSO₄, 60 mg mgSO₄, and 4 mg KCl in 1 L of distilled water. The prey species were all fed daily using the single-celled green alga Chlorella vulgaris at 0.5x10⁶ cells ml⁻¹. Alga was mass-cultured in 2 L trans투시터 corrected

Tab. 1. Water bodies from which different prey species were isolated.

<table>
<thead>
<tr>
<th>Species</th>
<th>Waterbody (Coordinates)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alona glabra</td>
<td>Xochimilco (19°17’17”N, 99°06’05”W)</td>
</tr>
<tr>
<td>Ceriodaphnia dubia</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
</tr>
<tr>
<td>Daphnia pulex</td>
<td>Xochimilco (19°17’17”N, 99°06’05”W)</td>
</tr>
<tr>
<td>Daphnia cf. mendotae</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
</tr>
<tr>
<td>Diaphanosoma birgei</td>
<td>Lirios (19°39’10”N, 99°13’14”W)</td>
</tr>
<tr>
<td>Macrothrix triserialis</td>
<td>Xochimilco (19°17’17”N, 99°06’05”W)</td>
</tr>
<tr>
<td>Moina macrocopa</td>
<td>Xochimilco (19°17’17”N, 99°06’05”W)</td>
</tr>
<tr>
<td>Pleuroxus aduncus</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
</tr>
<tr>
<td>Scapholeberis kingi</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
</tr>
<tr>
<td>Simocephalus serrulatus</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
</tr>
<tr>
<td>Elaphoidella grandidieri</td>
<td>Fish farm, Cuautla (18°49’28”N, 98°56’23”W)</td>
</tr>
<tr>
<td>Brachionus rubens</td>
<td>Xochimilco (19°17’17”N, 99°06’05”W)</td>
</tr>
<tr>
<td>Euchlanis dilatata</td>
<td>Presa Benito Juárez (19°41’22”N, 99°25’38”W)</td>
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</tbody>
</table>

The experiments were performed during a 45-min observational period in Petri dishes (50 mmx15 mm) containing 10 mL medium and one individual of Hydra and 10 individuals of the selected prey. For each prey species, we set up three replicates. For a given prey species, the feeding behavior of the predator (number and duration of prey encounter (e), attack (a), capture (C), ingestion (i) and the number killed (K)) was recorded (Greene, 1983). Based on these data, we obtained the handling time (duration from encounter through ingestion) and correlated it with the body size of the prey.

Food preference

For this experiment, we used the following prey: Alona glabra, Daphnia cf. mendotae, Diaphanosoma birgei, Macrothrix triserialis, Moina macrocopa, Scapholeberis kingi, Elaphoidella grandidieri, Brachionus rubens, and Euchlanis dilatata. Hydra was pre-starved for 24 h prior to the initiation of the experiments. All nine prey items were individually introduced into a Petri dish (50 mmx15 mm) containing 20 mL EPA medium and later two individuals of Hydra were placed into the same container. Cladocerans and copepods were introduced at 1.75 ind. mL⁻¹ (per species) and rotifers at 1.5 ind. mL⁻¹ (per
Demographic experiments using allelochemicals from Hydra

The demographic experiments were conducted in jars with 50 mL of EPA medium containing 10 neonates of *Daphnia cf. mendotae* (<24 h) per jar, and at one of four densities of *Hydra* (0 (=control), 0.1, 0.2, and 2 ind. mL\(^{-1}\)). The *Hydra* population was fed using *Moina macrocopa*. Throughout the experimental period, the test jars contained both, the prey and the predator, but latter was separated from the former by a small mesh (70 µm pore size) placed inside the test jars so as to prevent the direct attack on the prey by *Hydra*. *Chlorella* at a concentration of 0.5x10^6 cells mL\(^{-1}\) was used as food for daphniids in the test jars. For each treatment we set up four replicates (cohorts). Daily we counted the number of original cohort alive and the number of neonates born, if any. Later, the dead individuals and neonates were discarded and the surviving adults were transferred to fresh jars containing appropriate test combinations. The experiments were discontinued when every individual of the original cohort had died. From the data on survival and reproduction, we derived standard demographic variables (mean lifespan, gross and net reproductive rates, generation time and the rate of population increase) following Krebs (1985).

RESULTS

Feeding behavior

The prey handling time by *Hydra* was significantly

<table>
<thead>
<tr>
<th>Species</th>
<th>E</th>
<th>A</th>
<th>C</th>
<th>I</th>
<th>K</th>
<th>Feeding responses (probabilities)</th>
<th>A/E</th>
<th>C/A</th>
<th>I/E</th>
<th>I/A</th>
<th>I/C</th>
<th>I/K</th>
<th>K/E</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Scapholeberis kingi</em></td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>0.33</td>
<td>1</td>
<td>0.33</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td><em>Daphnia pulex</em></td>
<td>43</td>
<td>11</td>
<td>5</td>
<td>5</td>
<td>11</td>
<td>0.26</td>
<td>0.45</td>
<td>0.12</td>
<td>0.45</td>
<td>1</td>
<td>0.45</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td><em>Moina macrocopa</em></td>
<td>28</td>
<td>23</td>
<td>15</td>
<td>15</td>
<td>23</td>
<td>0.82</td>
<td>0.65</td>
<td>0.54</td>
<td>0.65</td>
<td>1</td>
<td>0.65</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td><em>Daphnia cf. mendotae</em></td>
<td>23</td>
<td>13</td>
<td>6</td>
<td>6</td>
<td>13</td>
<td>0.57</td>
<td>0.46</td>
<td>0.26</td>
<td>0.46</td>
<td>1</td>
<td>0.46</td>
<td>0.57</td>
<td></td>
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<tr>
<td><em>Simocephalus serrulatus</em></td>
<td>21</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>0.19</td>
<td>1</td>
<td>0.19</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td><em>Ceriodaphnia dubia</em></td>
<td>20</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>0.75</td>
<td>1</td>
<td>0.75</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td><em>Macrothrix triserialis</em></td>
<td>19</td>
<td>16</td>
<td>16</td>
<td>16</td>
<td>16</td>
<td>0.84</td>
<td>1</td>
<td>0.84</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td><em>Pleuroxus aduncus</em></td>
<td>13</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.08</td>
<td>1</td>
<td>0.08</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.08</td>
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history variables is presented in Fig. 4. Regardless of the treatment, the mean lifespan of \( D. \text{ cf mendotae} \) varied from 14 to 17 days with significant differences in relation to the density of predators per jar. Gross reproductive rate and net reproductive rates decreased in the presence of 2 individuals of \( Hydra \) mL\(^{-1}\). At a predator density of 0.2 ind. mL\(^{-1}\), only the net reproductive rate showed a significant decrease. Generation time of \( D. \text{ cf. mendotae} \) varied little (12-13 days) among treatments. Tukey tests showed significant differences between treatments containing 0.1 ind. mL\(^{-1}\) and 2 ind. mL\(^{-1}\) of predators. The rate of population increase per day \((r)\) of \( D. \text{ cf. mendotae} \) varied from 0.12 to 0.21 per day. The \( r \) of this cladoceran species decreased significantly (\( P<0.05 \), ANOVA) with increasing density of \( Hydra \) in test jars.

**DISCUSSION**

Our study demonstrated that \( Hydra \) had different effects on the zooplankton species tested here. Elliot *et al.* (1997) have noted that \( Hydra \) is a potential predator that can greatly reduce zooplankton communities and some vertebrates in juvenile stages. The impact caused by \( Hydra \) to its prey species depends on the density in which the predator occurs in nature. Few studies report the abundance of \( Hydra \) in nature. There are some works (Griffing, 1965; Dvorak and Best, 1982) which reported high abundances but only mentioning as fishnets covered by \( Hydra \) or high percentage of \( Hydra \) in \( Nitella \).

Hershey and Dodson (1987) quantified the natural densities of \( Hydra \) and reported as many as 10 individuals of \( Hydra \) for every cm of a substratum. Much earlier, Ar-

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**Fig. 1.** Relation between prey handling time, digestion time, ingestion time and prey survival time (after being stung by \( Hydra \) sp.) and the cladoceran body size. Values are means of 3 replicates. Ple, *Pleuroxus* sp.; Mac, *Macrothrix* sp.; Cer, *Ceriodyaphnia* sp.; Sca, *Scapholeberis* sp.; D.m., *Daphnia* cf. *mendotae*; D.p., *Daphnia pulex*; M.m, *Moina macrocopa*; Sim, *Simocephalus* sp. The \( r^2 \) values for each regression are shown.
mitage and Capper (1976) also reported Hydra mean densities of up to 19 ind. m⁻³. This implies that Hydra can occasionally reach very high densities in a small volume and therefore its impact may have been underestimated under these conditions. For example, if we consider that one single Hydra from a density of 19 ind. m⁻³ could consume an average of 24 prey items day⁻¹ (authors’ personal observations), then they deplete the prey by about 456 ind. m⁻³ day⁻¹. This is a significant number of prey consumed by an invertebrate predator, as has been reported also in another cnidarian Craspedacusta by Davis (1955), where this jellyfish consumed about 400-500 zooplankton m⁻³ day⁻¹. Davis (1955) even remarked that with this capacity of predation, Craspedacusta could compete with planktivorous fish for food. Besides, Dodson and Cooper (1983) showed that when jellyfish reached densities of about 30 ind. m⁻³, their preferred prey (zooplankton) disappeared from the system. These studies suggest that the importance of predation by cnidarian predators can be much greater than is generally thought (Jankowski et al., 2005).

The nature, including the morphology, of prey items seems to be important for Hydra predation. In this study we demonstrated that Hydra was able to kill as many as 23 individuals of Moina or about 10 daphnids. However, only 1 individual of Pleuroxus was killed during the 45-min observational period. There are possibly several factors responsible for this. For example, prey species may have different strategies to avoid predation; these include changes in morphology, behavior, and life history variables (Macháček, 1991; Walsh et al., 2006). For the prey used in this study, some strategies against predation, such as change in size and in various life history variables are already documented (Dodson, 1974; Burks et al., 2000). The elongation or presence of spines on species of Daphnia, Ceriodaphnia, and Macrothrix avoids predation by some invertebrate predators (Havel, 1985; Tollrian and Harvell, 1999; Nandini and Sarma, 2005). Changes in the behavior (e.g., Scapholeberis) and shift in the age at first reproduction (e.g., daphnids) due to allelochemicals from the predators have also been reported (Lass and Spaak, 2001). However, each strategy is dependent on the predator type. Carapace spines were described as having first order tactile or non-visual predators (Zaret, 1980; Macháček, 1991).

In this study, even the larger species such as Moina were equally vulnerable, perhaps because larger the prey, greater was the encounter probability. This means that at least for this kind of sessile predators, size is not the main constraint in prey selection but possibly other characteristics are involved. The natural habitat (pelagic vs littoral) of the prey cladoceran could be one of the factors responsible for these observed differences in vulnerability to Hydra. For example, both Moina and Diaphanosoma are pelagic species that need to avoid visual predators most of the time. So, these prey species spend their energy to evolve strategies that would help them avoid predation such as reducing body size and age at maturation, increasing clutch size, and strategies to reduce visibility or increase speed in the water column (Gliwicz, 2003; Chapparro-Herrera et al., 2011, 2013). Therefore, the development of a more robust exoskeleton is very unlikely in pelagic species because it im-

![Fig. 2. Food preference (>0.11, Manly’s α) by Hydra on different prey species: E.g, Elaphoidella grandidieri; D cf. m, Daphnia cf. mendota; Mac, Macrothrix triserialis; Sca, Scapholeberis kingi; Alo, Alona glabra; Dia, Diaphanosoma birgei; Mm, Moina macrocopa; Br, Brachionus rubens; Ed, Euchlanis dilatata. The mean values ±SE based on 10 replicates are shown.](image-url)
plies additional costs associated with increased weight during swimming (Schwartz and Hebert, 1989). Hence cladoceran species with thick carapace are more common in the littoral or benthic regions (Dodson and Frey, 2001) where they face non-visual predators. These non-visual predators such as cnidarians, turbellarians and some insect larvae have hunting strategies necessitating the manipulation of the prey items such as injecting toxic substances and sucking the internal contents (Hampton and Gilbert, 2001; Dumont, et al., 2014). Therefore, littoral prey can be expected to develop stronger and thicker carapace possibly at the cost of strong antenna muscles or other structures associated with swimming (Korovchinsky, 1992). Because of this reason, most littoral species are associated with substratum and do not necessarily swim fast or continuously in order to remain in the water column. This is evident in Chydoridae (Smirnov, 1974), for example the chydorid Anchistropus is the only predator of Hydra perhaps because of its immunity to attacks by nematocysts due to its thick carapace (Van Damme and Dumont, 2009). We would expect a similar immunity from other genera of chydorids, and this was demonstrated in this study where Pleuroxus was less vulnerable to Hydra. This is also applicable to Simoccephalus, which develops thicker carapace in order to avoid invertebrate predation (Schwartz and Hebert, 1989) and which showed little vulnerability also to Hydra predation in our study. Thus, it is expected that predation by Hydra affects populations of pelagic prey reaching the littoral regions of waterbodies, either for food or shelter than the species adapted to live in these habitats.

**Fig. 3.** Age-specific survivorship (closed circles) and fecundity (open triangles) curves of Daphnia cf. mendotae at indirect presence (allelochemicals) of Hydra at four concentrations: control, Hydra 0.1 ind.mL⁻¹, Hydra 0.2 ind.mL⁻¹ and Hydra 2 ind.mL⁻¹. The mean values ±SE are shown.
In addition to these morphological strategies, the prey species may also show changes in their life history (survivorship and reproduction-related adaptions) as a result of perceiving the allelochemicals released by the predators (Gama-Flores et al., 2003; Lass and Spaak 2003; García et al., 2007). Here we quantified the effect of allelochemicals from *Hydra* on the life history variables of *Daphnia cf. mendotae*, with which it co-occurs. Evidently daphniid survival was not strongly affected by allelochemicals from *Hydra*; however fertility was severely re-

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**Fig. 4.** Demographic variables (mean life span, gross reproductive rate, net reproductive rate, generation time and rate of population increase) of *Daphnia cf. mendotae* at indirect presence (allelochemicals) of *Hydra* under four concentrations: control, *Hydra* 0.1 ind.mL^{-1}, *Hydra* 0.2 ind.mL^{-1} and *Hydra* 2 ind.mL^{-1}. The mean values ±SE are shown.
duced as result of the presence of the predator, especially in the treatment containing 2 ind. mL⁻¹ of Hydra. For a number of invertebrates including zooplankton, survivorship is generally less affected due to stress than reproductive parameters (Kammenga and Laskowski, 2000). In addition, it is known that the allelochemicals of Hydra are considered as allomones where the chemical substances released by the predator cause a negative effect on prey, perhaps due to toxic characteristics, without necessarily causing a change in the morphology nor affecting the predator itself (Sher et al., 2005).

Macháček (1991) and Stibor and Lüning (1994) suggest that a reduction, due to allelochemicals from predators, in growth rates could favor reproduction. We observed that allelochemicals from Hydra affected both survivorship and reproduction of D. cf. mendotae. These data agree with Weider and Pijanowska (1993) who suggested that life history traits of daphnids prey are flexible depending on the source of allelochemicals (vertebrate vs invertebrate predators). The allelochemicals released by Hydra may be exerting a toxic effect on daphnids which explains the decrease in the fitness of the population. The allelochemicals released by Hydra may also bring certain morphological changes in the litoral prey such as thickening of the carapace, which has already been reported as a successful strategy against certain invertebrate predators (Laforsch et al., 2004; Rabus et al., 2013).

CONCLUSIONS

In conclusion, our data showed that Hydra can exert direct and indirect effects on its prey and more so for the pelagic taxa, that reach from time to time close to the littoral zones in search of either food or as shelter from predators. Therefore in ponds where Hydra is present, the pelagic cladoceran genera such as Diaphanosoma, Daphnia, and Moina, may have reduced survival and reproductive put. Our results suggest that chydorids should be the most abundant group in ponds where Hydra is abundant. Further studies are still needed to test these relationships under natural conditions.

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REFERENCES


Sarma SSS, Dumont HJ, Nandini S, 2004. Interactions between the anomopod cladocerans Ceriodaphnia dubia, C. cornuta, Simocephalus vetulus and S. serrulatus, the aphanoneurid worm Aeolosoma sp., and the fish Skiaia lerna: predation or competition, or both? Hydrobiologia 526:147-156.