

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 grandidieri*, *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 macrocopia* (Straus), *Pleuroxus aduncus* (Jurine), *Scapholeberis kingi* Sars, *Simocephalus serrulatus* (Müller); copepods: *Elaphoidella grandidieri* (Guerne 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 trans-

parent bottles using Bold's basal medium (Borowitzka and Borowitzka, 1988). The predator, *Hydra*, was isolated from a pond at Dolores Village, Tepotzotlán (State of Mexico) (19°43'34.41"N, 99°24'26.94"W), and was cultured in 10 L aquaria containing 8 L of EPA medium and was fed every three days using *Moina macrocopia* and *Ceriodaphnia dubia*.

Feeding behavior

We offered eight prey cladocerans (*Ceriodaphnia dubia*, *Daphnia pulex*, *Daphnia* cf. *mendotae*, *Macrothrix triserialis*, *Moina macrocopia*, *Pleuroxus aduncus*, *Scapholeberis kingi*, and *Simocephalus serrulatus*) to *Hydra*. 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 macrocopia*, *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

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

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

species). These experiments were conducted using ten replicates and at two temperatures (15°C and 25°C). After initiation and 2 h of feeding, the predators were removed and the uneaten prey individuals were fixed in 5% formalin. Later, the number of prey items left in the test jars was quantified and based on the difference between the initial and final prey density, we calculated the number consumed per predator. To calculate the food preference, we used the Manly's α index (Krebs, 1999).

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 macrocopia*. 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 0.5×10^6 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

(corr. coefficient=0.62) and positively related to the body size of the prey species. The prey ingestion and digestion times were not associated with the size of the prey. As for the survival of prey after being stung by *Hydra*, there were no significant differences in survival with relation to prey size. However, *Simocephalus* and *Pleuroxus* were eaten alive and the survival time corresponded to the total time that elapsed between capture and ingestion (Fig. 1). *Hydra* encountered *D. pulex* almost once every minute, while *Pleuroxus* was least encountered. All captured individuals were ingested and no prey items were rejected after being captured. The relation between the number killed and number encountered was highest for *Macrothrix* but lowest for *Pleuroxus* (Tab. 2).

Food preference

The trend in prey selection by *Hydra* was similar at both the temperature ranges tested (Fig. 2). Thus, regardless of temperature, *Diaphanosoma* and *Moina* were the most preferred items by *Hydra*, while all other prey species including copepods and rotifers (*Alona glabra*, *Daphnia* cf. *mendotae*, *Moina macrocopia*, *Scapholeberis kingi*, *Elaphoidella grandidieri*, *Brachionus rubens* and *Euchlanis dilatata*) were not positively selected.

Demography of *Daphnia* cf. *mendotae*

The age-specific survivorship curves of *D. cf. mendotae* subjected to different treatments containing allelochemicals showed reduction in survival when the highest number of predators (2 ind. mL^{-1}) was present in the test containers as compared to controls or those with lower numbers of *Hydra* (Fig. 3). Age specific reproductive curves of *D. cf. mendotae* also showed reduction in the number of offspring produced in the presence of *Hydra* at the highest density (2 ind. mL^{-1}). In the absence of (controls) or in lower concentrations of *Hydra*, the maximum number of offspring per female per day was about 3.5, while this was reduced to 1/3rd in treatments containing 2 individuals of *Hydra* mL^{-1} (Fig. 3). Information on the life

Tab. 2. Feeding behavior of the predator *Hydra* using different cladoceran species as prey. The number of prey encountered (E), attacked (A), captured (C), ingested (I) and killed (K) have been recorded, based on a total of 3 replicates containing one predator each.

Species	E	A	C	I	K	Feeding responses (probabilities)						
						A/E	C/A	I/E	I/A	I/C	I/K	K/E
<i>Scapholeberis kingi</i>	15	5	5	5	5	0.33	1	0.33	1	1	1	0.33
<i>Daphnia pulex</i>	43	11	5	5	11	0.26	0.45	0.12	0.45	1	0.45	0.26
<i>Moina macrocopia</i>	28	23	15	15	23	0.82	0.65	0.54	0.65	1	0.65	0.82
<i>Daphnia</i> cf. <i>mendotae</i>	23	13	6	6	13	0.57	0.46	0.26	0.46	1	0.46	0.57
<i>Simocephalus serrulatus</i>	21	4	4	4	4	0.19	1	0.19	1	1	1	0.19
<i>Ceriodaphnia dubia</i>	20	15	15	15	15	0.75	1	0.75	1	1	1	0.75
<i>Macrothrix triserialis</i>	19	16	16	16	16	0.84	1	0.84	1	1	1	0.84
<i>Pleuroxus aduncus</i>	13	1	1	1	1	0.08	1	0.08	1	1	1	0.08

history variables is presented in Fig. 4. Regardless of the treatment, the mean lifespan of *D. 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. 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. 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 canadensis* 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-

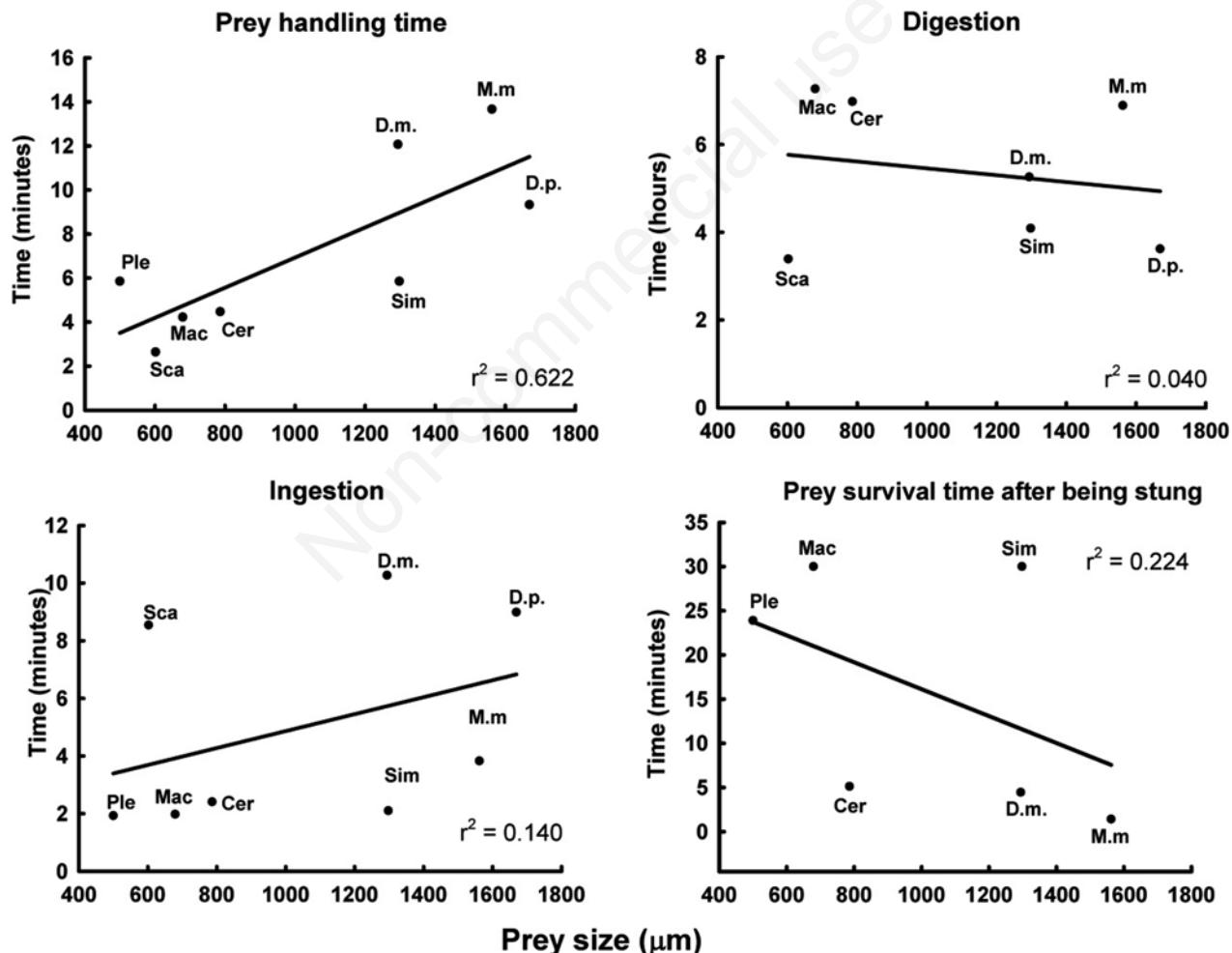


Fig. 1. Relation between prey handling time, digestion time, ingestion time and prey survival time (after being stung by *Hydra* sp.) and the cladoceran body size. Values are means of 3 replicates. Ple, *Pleuroxus* sp.; Mac, *Macrothrix* sp.; Cer, *Ceriodaphnia* sp; Sca, *Scapholeberis* sp.; D.m., *Daphnia* 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 d⁻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 d⁻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 daphniids. 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.*, daphniids) due to allelochemicals from the predators have also been reported (Lass and Spaak, 2003). However, each strategy is dependent on the predator type. Carapace spines were described as having first of all a functional-morphological significance (Fryer, 1974). For example, *Macrothrix* possesses many spines along the ventral margin of the carapace, which helps it to avoid predation by some invertebrates such as rotifers (*Asplanchnopus*) and polychaetes (*Aeolosoma*) (Sarma *et al.*, 2004; Nandini and Sarma, 2004, 2005). However, this defense strategy was not effective against *Hydra* predation. In our study *Macrothrix* showed the highest probability of being killed after an encounter with *Hydra* (K/E=0.84). It has been observed that prey species with elongated spines such as *Brachionus havanaensis* and *Brachionus macracanthus* offer protection against predation.

tion by the predatory rotifer *Asplanchna* because it cannot ingest them (Nandini *et al.*, 2003). In this work, *Macrothrix* was easily ingested by *Hydra*, probably because cnidarians possess flexible tissues so that the spines of the prey do not damage them (Anderson, 2001).

The body size of the prey is yet another aspect that has received considerable attention in predator-prey interactions. It has been mentioned that the body size is crucial in prey selection by both invertebrate and vertebrate predators (Dodson, 1974). Many studies have shown that zooplankton species under predation threat reduce their body size and are thus less vulnerable to visual predators, but more vulnerable to 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-

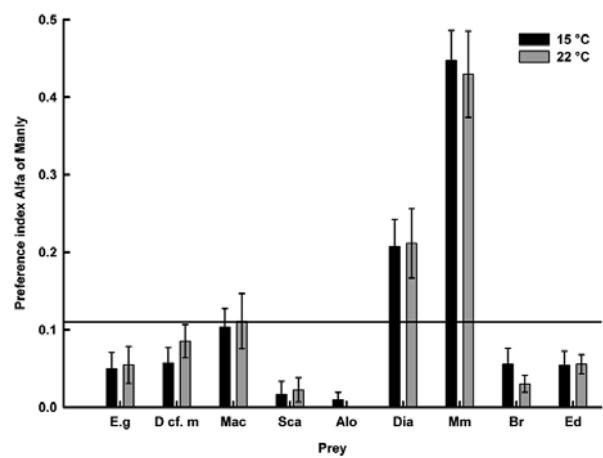


Fig. 2. Food preference (>0.11, Manly's α) by *Hydra* on different prey species: E.g., *Elaphoidella grandidieri*; D cf. m, *Daphnia* cf. *mendotae*; Mac, *Macrothrix triserialis*; Sca, *Scapholeberis kingi*; Alo, *Alona glabra*; Dia, *Diaphanosoma birgei*; Mm, *Moina macrocopa*; Br, *Brachionus rubens*; Ed, *Euchlanis dilatata*. The mean values \pm SE based on 10 replicates are shown.

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 *Simcephalus*, 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.

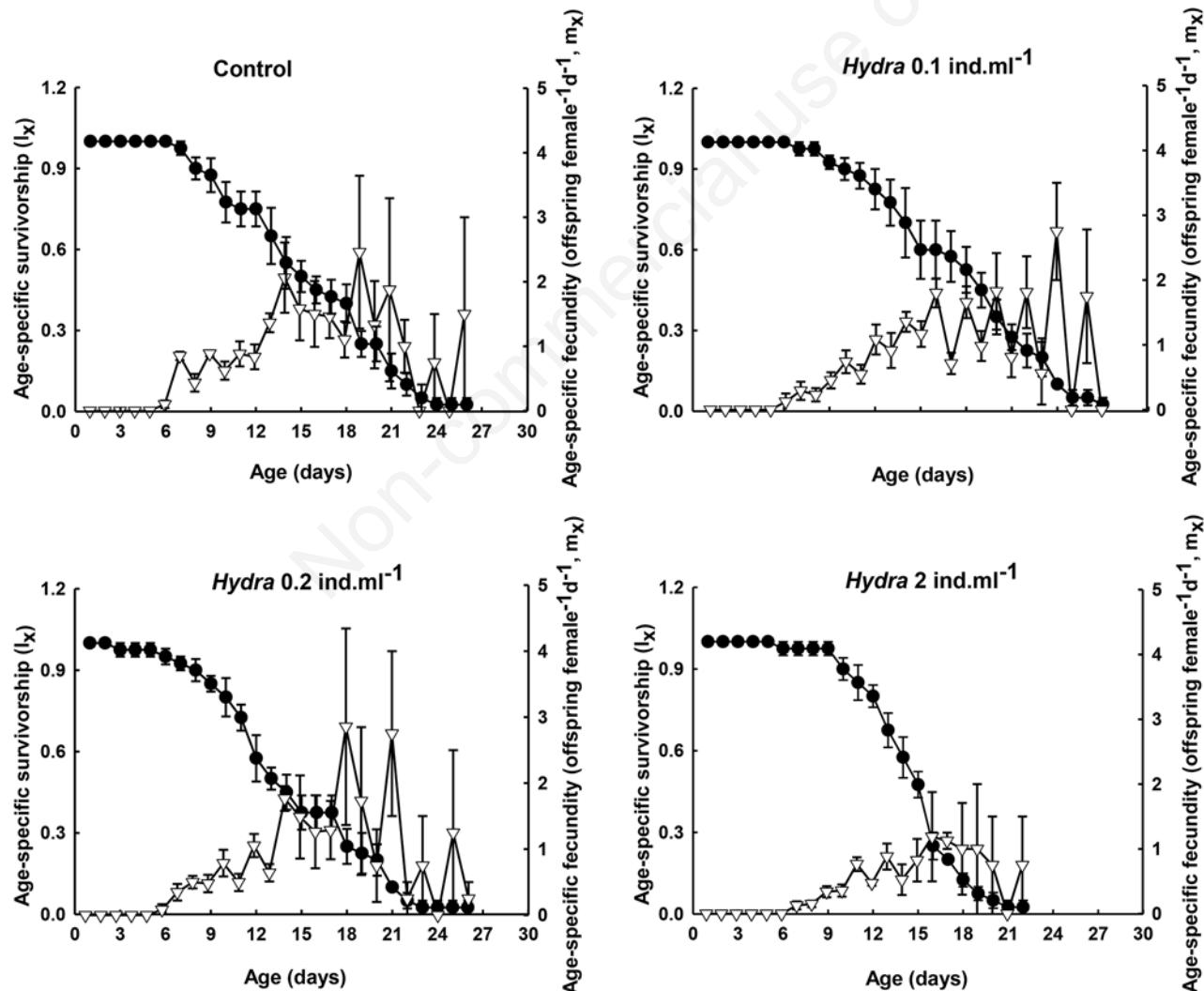


Fig. 3. Age-specific survivorship (closed circles) and fecundity (open triangles) curves of *Daphnia* cf. *mendotae* at indirect presence (allelochemicals) of *Hydra* at four concentrations: control, *Hydra* 0.1 ind.ml^{-1} , *Hydra* 0.2 ind.ml^{-1} and *Hydra* 2 ind.ml^{-1} . The mean values $\pm \text{SE}$ 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; Gar-

cía *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-

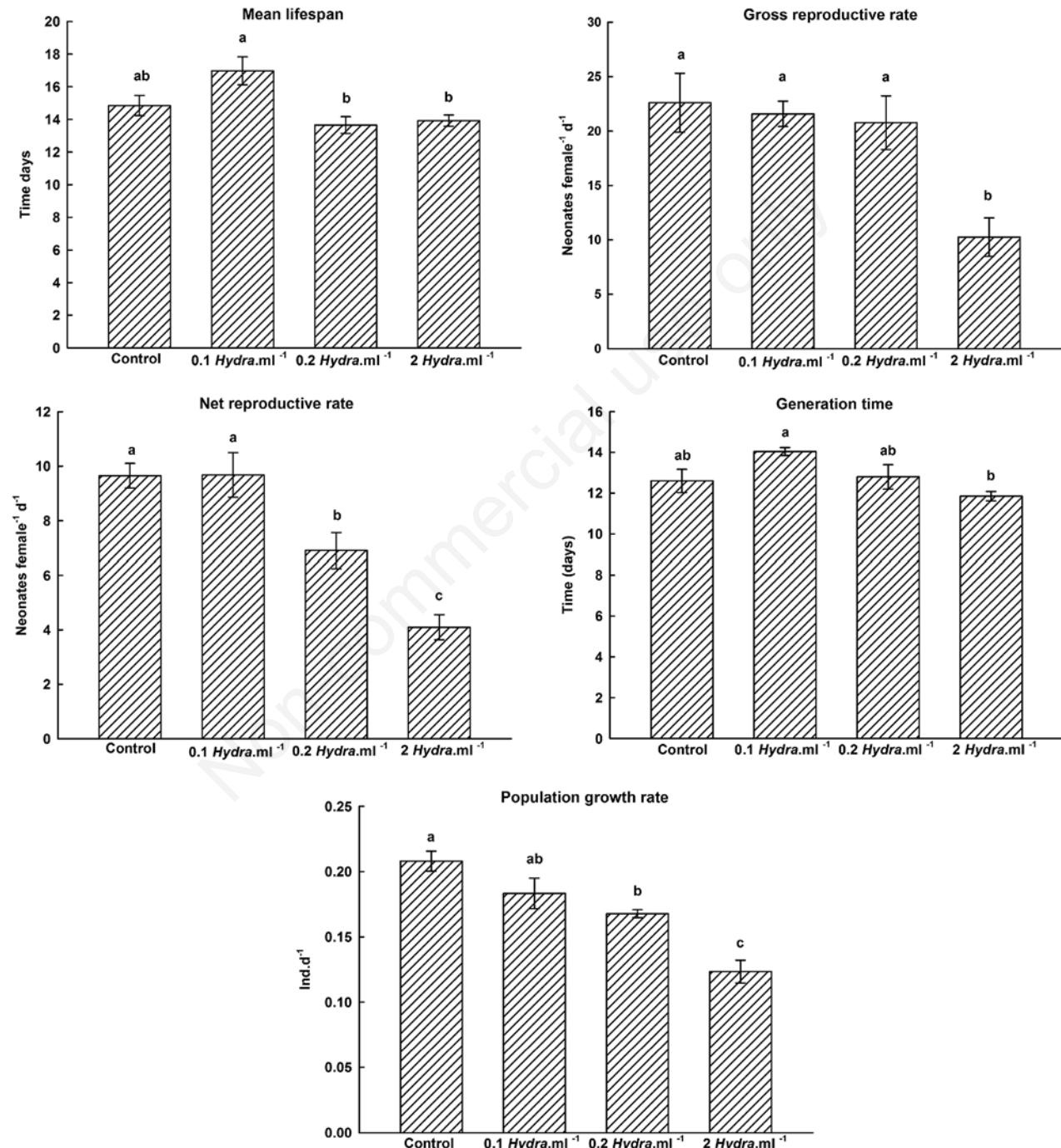


Fig. 4. Demographic variables (mean life span, gross reproductive rate, net reproductive rate, generation time and rate of population increase) of *Daphnia cf. mendotae* at indirect presence (allelochemicals) of *Hydra* under four concentrations: control, *Hydra* 0.1 ind. mL^{-1} , *Hydra* 0.2 ind. mL^{-1} and *Hydra* 2 ind. mL^{-1} . The mean values $\pm \text{SE}$ 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 daphniid 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 daphniids which explains the decrease in the fitness of the population. The allelochemicals released by *Hydra* may also bring certain morphological changes in the littoral 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 rate. 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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