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Effects of allelochemicals released by vertebrates (fish, salamander and tadpole) on *Moina macrocopa* (Cladocera)

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ABSTRACT

We studied the survivorship (average lifespan, life expectancy at birth and generation time) and reproduction (gross and net reproductive rates, and the rate of population increase) of *Moina macrocopa*, a common cladoceran found in many freshwater bodies of Mexico. We used 3-conditioned-media obtained from (a) fish (*Poeciliopsis occidentalis*), (b) axolotl (*Ambystoma mexicanum*) and (c) frog tadpole (*Hyla eximia*). Standard life table demography experiments were done at laboratory temperature (22°C) on neonates from a single parthenogenetic female of *M. macrocopa* and fed *Chlorella* at $1.0x10^6$ cells ml^{-1}. Compared with survivorship variables, the age-specific reproduction of *M. macrocopa* was more dramatically influenced by the predator conditioned-medium. Compared with controls, there was a significant increase in the offspring production in all three treatments involving the vertebrate conditioned medium; the highest was observed in the tadpole conditioned medium while the lowest was with *Ambystoma*-conditioned medium. Average lifespan (ALS), gross (GRR) and net reproductive rates (NRR), generation time (GT) and the rate of population increase (*r*) were all significantly affected depending on the vertebrate-conditioned medium. For example, ALS was adversely affected due to *Ambystoma* while, it was stimulated due to fish-conditioned medium. Gross and net reproductive rates were lowest in control than in conditioned media from fish, frog tadpoles and axolotl. Generation time was lowest (6 days) in controls and in axolotl-conditioned medium but longer (9 days) in treatments containing fish or frog tadpole-conditioned medium. The three conditioned-media from the predators induced the differential changes in life traits of *M. macrocopa*. The effects of kairomones in *Ambystoma*-conditioned medium, however, than other two on the measured demographic variables of *M. macrocopa*.

Key words: Allelochemicals, axolotl (*Ambystoma mexicanum*), Cladocera, fish (*Poeciliopsis occidentalis*), frog tadpole (*Hyla eximia*) kairomone, life history, *Moina macrocopa*, Predation.

INTRODUCTION

Allelochemicals are substances that directly and indirectly mediate interactions in the aquatic system, particularly food-web related aspects (8,19). In last two decades, research on demographic variables of zooplankton and chemical communication has focused on prey-predator relationships (3,9). These chemical substances affects the life

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history traits in zooplankton (Ciliates: 37, Rotifers: 13, Cladocerans: 33 and Copepods: 17). Demographic and morphological responses to predators' cues have been reported in several zooplankton species, (24,29,31). The cues act as alarm signals, a common phenomenon among aquatic animals (31). Morphological responses are widely documented in cladocerans with hard carapace such as *Daphnia* (19,31). However, not all cladoceran species possess thick carapace (10). For example, members of *Moina* are composed of delicate and flexible carapace and thus not easy to record changes in their morphology when exposed to kairomones from the predators. It is also possible that for *Moina* most inducible defences lie in life-history changes. *Moina* responds quickly in its demographic variables due to changes in the ambient water including allelochemicals released by the predators (25).

Both vertebrates (fish spp.) and invertebrates (copepods and insect larvae) exert considerable predation pressure on cladocerans in natural waterbodies. Fishes, amphibians and aquatic birds largely influence the abundances and dynamics of many zooplankton species, including those of cladocerans in natural waters (6). Within the vertebrate predators, most information on the chemical cues comes from the fish (19). In freshwater ecosystems, other vertebrates that interact with the cladocerans are: salamanders and frogs and they play important role in controlling the abundance and diversity of cladocerans. However, the importance of chemical cues induced by amphibians has been examined only in few studies (16).

Among the tropical Cladocera, *Moina* is interesting due to its ability to tolerate high temperatures and to use the detrital diets (10). In addition in many Mexican waterbodies, species of *Moina* are more widely distributed, hence, can be expected to interact with vertebrate predators. For example, *Moina* is frequently found in Xochimilco Lake, where the axolotl is well distributed (2,23). Axolotl is also known to feed on many species of cladocerans and at times up to 150 individuals of *Moina macrocopa* per hour (5). Because *Moina* and axolotl coexist in Central Mexican waterbodies, apparently it recuperates its population densities despite predation threat from *Ambystoma* spp. In addition, larval frogs, salamanders and fishes together influence diversity and dynamics of cladocerans in Xochimilco (34). It is, however not known, if the cues induced by these three groups of vertebrates have similar influence on the demographic variables of their zooplankton prey.

The response of cladocerans to changes in the life history variables (lifespan, population growth rates and generation times) are best quantified using life table demography method which facilitates evaluating the effects in an age specific manner (18,28). This study aimed to compare relative impacts of chemical cues from 3-vertebrate predators: fish (*Poeciliopsis occidentalis* (Baird and Girard)), salamander (*Ambystoma mexicanum* (Shaw & Nodder) and frog tadpole (*Hyla eximia* Baird) on the survivorship and reproductive patterns of *Moina macrocopa* (Straus).

MATERIALS AND METHODS

I. Source of organisms, culture and maintenance

The cladoceran *Moina macrocopa* was isolated from Xochimilco Lake, a perennial freshwater pond in the Mexican Central Valley. The tadpole population (*Hyla* *eximia*) was collected from a natural tropical waterbody, in the State of Veracruz, Mexico. The fish (*Poeciliopsis occidentalis*) was locally procured from a commercial source. The axolotl (*Ambystoma mexicanum*) (< 3-months old) were kindly supplied by the Vivarium Laboratory of our institute. For acclimation, the three vertebrate predators were kept in separate aquaria [each contained 20 L moderately hardwater water (EPA medium)]. The EPA medium was daily prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl 1.0 l distilled water (36). In fish aquarium, *Poeciliopsis occidentalis* (8 individuals of 25-30 mm length) were daily fed *ad libitum* using *Artemia nauplii*, *Moina macrocopa, Daphnia pulex* and occasional fresh oligochaete worms (*Tubifex*). In the aquarium with 10-12 tadpoles individuals of about 20-25 mm length) we offered a mixture of prey items [cladocerans and *Artemia* individuals and algae (*Chlorella vulgaris* and *Scenedesmus acutus*)]. *Ambystoma mexicanum* (about 80-90 mm length) was fed on live cricket (*Achaeta domestica*).

II. Predator-Conditioned medium

The vertebrate conditioned-medium was prepared on identical biomass basis. Thus, to produce predator-conditioned water, we separately placed 2 individuals of *Ambystoma mexicanum*, 8 of *Poecilopsis occidentalis* and 4 tadpoles (*Hyla eximia*) into glass jars (500 ml capacity) containing 250 ml EPA medium for 6.0 h. During this period, no food was added to jars. Thereafter the vertebrates were transferred to respective aquaria and the medium was filtered to remove excreta using Whatman GF/F filters of 0.47 µm pore diameter. We daily prepared the conditioned medium until the end of experimental period (3-weeks).

III. Cultivation of alga and cladocerans

Single celled-green alga *Chlorella vulgaris* (strain CL V-3, CICESE, Ensenada, Mexico) was used as the diet for cladoceran *Moina macrocopa*. The alga was batch-cultured in 2 L transparent bottles using Bold's basal medium supplemented with 0.5 mg L^{-1} of sodium bicarbonate every alternate day (3). Log phase *Chlorella* was harvested, centrifuged at 3000 rpm for 5 min, rinsed with distilled water and resuspended in small quantity of distilled water. The density of algal stock culture was estimated using a haemocytometer. To feed cladoceran stock cultures and for experiments we used one algal density ($1.0x10^6$ cells ml^{-1}).

Mass cultures of *M. macrocopa* were obtained starting with a single parthenogenetic individual to ensure same genetic characters. Cladocerans were mass cultured using EPA medium and were fed *Chlorella vulgaris* as food. The conditions for mass culture of cladocerans and for experiments were similar: pH: 7.5, laboratory temperature: 22±2°C, continuous, diffused fluorescent lighting. The algal food ($1x10^6$ cells ml^{-1}) and the medium were replenished daily. The cladocerans were cultured for many years in laboratory, before using them in experiments.

IV. Experimental design

The life table demography tests using *M. macrocopa* were conducted in 100 ml medium present in 250 ml transparent jars. Treatments were replicated 5-times. Thus we used 20 test jars (3 types of conditioned medium + control) x 5 replicates) and into each jar we introduced a cohort of 10 neonates (10±2 h of age) of *M. macrocopa* (from clonal culture) under a streomicroscope using a Pasteur pipette. Following the initiation of life table demography experiments, we daily quantified the number of live test individuals and the number of offspring, if any, produced in each jar. Dead adults and any offspring produced were discarded. The experiments were terminated until the last individual of every cohort died (about 20 days).

Based on the data of survival of cohort and offspring produced, we derived selected life history variables: curves of age-specific survivorship, life expectancy and stable age, average lifespan, life expectancy at birth, gross and net reproductive rates, generation time and the rate of population increase. The following formulae were used (18):

l_x = Proportion of surviving to start of age x

m_x = Offspring produced per female at age x

Life expectancy at the start of age x: $e_x = \frac{T_x}{n_x}$

Where, T_x = Cumulative number of individuals from age x

n_x = Number of living individuals at the initiation of age x (days)

Proportion of each age class in stable age distribution: $C_x = \frac{w^{-x} \cdot l_x}{\sum_{i=0}^{\infty} w^{-x} \cdot lx}$

Where w = Maximum age observed

Gross reproductive rate = $\sum_{0}^{\infty} \cdot m_x$

Net reproductive rate $R_o = \sum_{0}^{\infty} l_x \cdot m_x$

Generation time: $T = \frac{\sum l_x \cdot m_x \cdot x}{R_o}$

Statistical analysis: The differences in the derived life history variables of *M. macrocopa* were statistically evaluated using the analysis of variance (ANOVA) and for multiple comparisons Tukey tests were carried out (SigmaPlot ver. 11, Systat Software, San Jose, CA).

RESULTS AND DISCUSSION

In all treatments, age-specific survivorship curves of *Moina macrocopa* showed increased mortality of cohort population after the first week. However, the survivorship reduced drastically in *Ambystoma*-conditioned medium compared to controls (Fig. 1). Age-specific life expectancy curves showed decreased survival with increasing age of

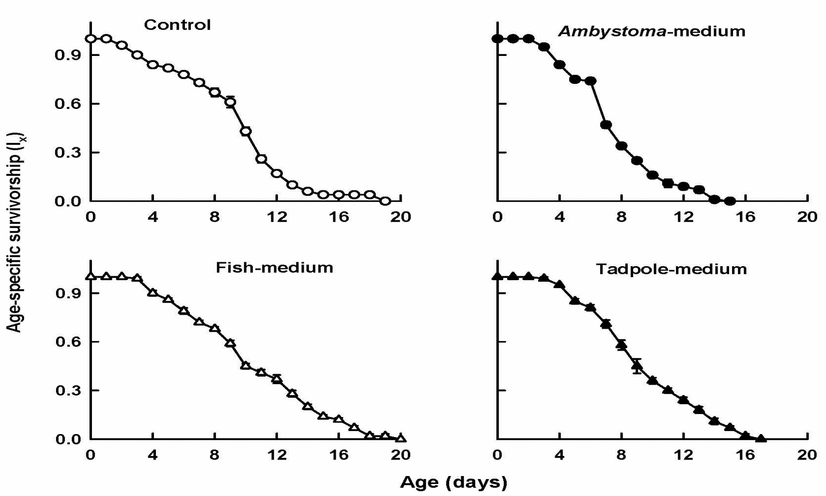

Figure 1. Age specific survivorship curves of *M. macrocopa* in controls and in treatments exposed to different vertebrate conditioned media. Data mean±SE based on 5 replicates (cohorts).

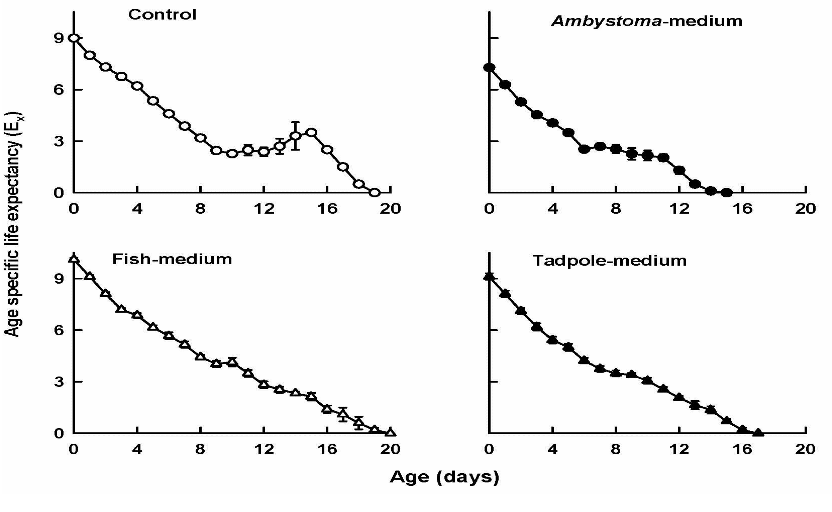

Figure 2. Age specific life expectancy curves of *M. macrocopa* in controls and in treatments exposed to different vertebrate conditioned media. Data mean±SE based on 5 replicates (cohorts).

cohort. However, in controls the survival was higher when the age of cohort population was 12-14 days (Fig. 2). Compared with survivorship variables, the age-specific reproduction of *M. macrocopa* was greatly influenced by the predator conditioned-medium. Compared with controls, there was a significant increase in the offspring production in all treatments involving the vertebrate conditioned medium; the highest was observed in the tadpole conditioned medium, while the lowest was with *Ambystoma*-conditioned medium (Fig. 3). In controls the offspring production was more or less continuous until the death of cohort, while, it was more fluctuating in vertebrate conditioned medium, especially in treatments containing tadpole kairomones. Stable age distribution curves were nearly similar in all treatments and the population obtained stable age equilibrium rapidly, within a week (Fig. 4).

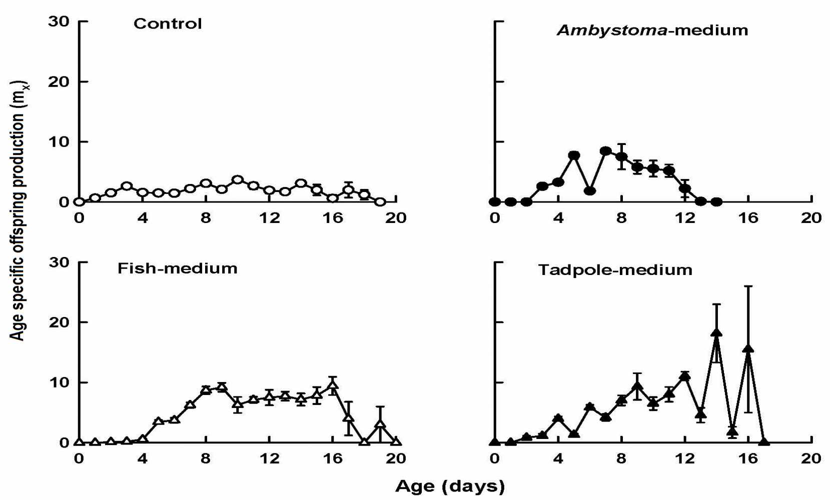

Figure 3. Age specific fecundity curves of *M. macrocopa* in controls and in treatments exposed to different vertebrate conditioned media. Data mean±SE based on 5 replicates (cohorts).

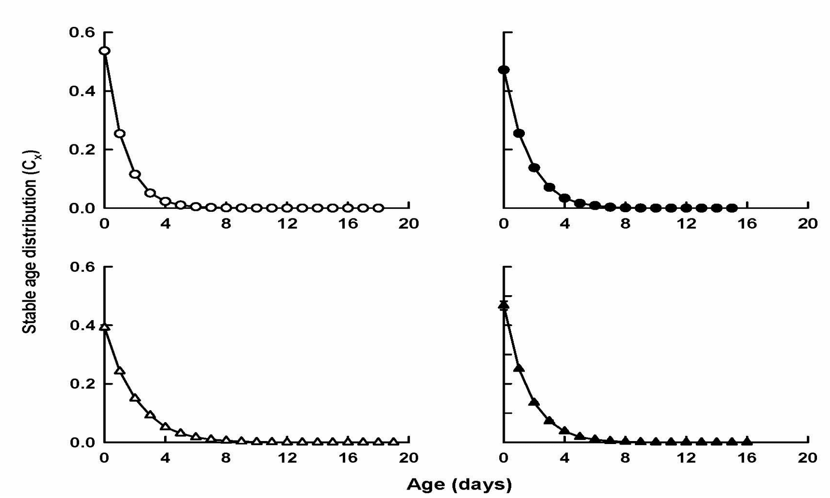

Figure 4. Stable age distribution curves of *M. macrocopa* in controls and in treatments exposed to different vertebrate conditioned media. Data mean±SE based on 5 replicates (cohorts).

Data on the selected life history variables are presented in Table 1. Average lifespan, gross and net reproductive rates, generation time as well as the rate of population increase were all significantly affected due to the vertebrate condition medium ($p<0.001$, ANOVA). Regardless of treatment, the average lifespan of *M. macrocopa* varied from 8 to 11 days, the shortest being in *Ambystoma*-conditioned medium and the longest for fish kairomones. Gross and net reproductive rates were lowest in controls compared with the conditioned media from fish or frog tadpoles. Lowest generation time (6 days) was observed in controls and in axolotl-conditioned medium, while it was significantly longer (ca. 9 days) in treatments containing of fish or frog tadpole-conditioned medium. Compared with controls, *M. macrocopa* in all three kairomones treatments showed significantly lower population growth rates.

Table 1. Demographic variables of *M. macrocopa* in controls and treatments exposed to different conditioned media

Variable	Control	Ambystoma	Fish	Tadpole
ALS	$9.49\pm0.11^{a,e}$	7.78 ± 0.15^{b}	10.61 ± 0.10^{c}	$9.62\pm0.19^{d,e}$
GRR	35.67 ± 1.36^{a}	$50.32\pm1.40^{a,d}$	$92.18\pm3.04^{c,d}$	$89.9\pm7.56^{b,d}$
NRR	16.41 ± 0.29^{a}	22.10 ± 0.61^{b}	37.43 ± 0.71^{c}	33.06 ± 0.55^{d}
GT	$6.42\pm0.08^{a,e}$	$6.15\pm0.16^{b,e}$	9.32 ± 0.21^{c}	8.08 ± 0.17^{d}
R	0.75 ± 0.02^{a}	$0.62\pm0.01^{b,e}$	0.48 ± 0.02^{c}	$0.62\pm0.03^{d,e}$

ALS: Average lifespan (days), GRR: Gross reproductive rate (offspring/female), R_0: Survival-weighted offspring/female), T: Generation time (days) and r : Rate of population increase per day. Data show the mean ± standard error based on 5 replicates. For each variable, data carrying similar alphabet are not statistically significant ($p>0.05$, Tukey test).

In aquatic ecosystems, allelochemicals mediate directly and indirectly the food-web related interactions (16,19). In freshwater ecosystems, zooplankters can detect potential predators owing to the kairomones exuded by the predators (4,10). It has been postulated that this latent alarm signal is a common phenomenon among aquatic animals, as well as an important source of information about predation risk for a wide range of prey taxa (31). Cladocerans in general and *Moina* in particular, are well-suited to test the effect of kairomones on the demographic responses due to their early maturity, high reproductive output and predominantly parthenogenetic mode of reproduction (25,28). *Moina* is among the few cladocerans with shorter generation times and higher population growth rates (21). It is also evident from this work that demographic variables of *Moina macrocopa* were influenced by the kairomones from the three aquatic vertebrate predators chosen here. Exposure to the vertebrate-conditioned medium for 6 h resulted in significant effects on survivorship and reproductive variables of *M. macrocopa*. In natural waters, different aquatic vertebrates such as fish, frog tadpoles and to a lesser extent axolotls feed on cladocerans including *Moina* (5). Therefore, species of cladocerans may have evolved defence strategies such as changes in the reproduction and body size to reduce the impact of predation pressure from vertebrates (38).

Morphological defenses in *Moina* are ineffective because this genus does not possess spines on the carapace and is undefended because it is not hard, hence, vulnerable to vertebrate predation (25). Very large or very small body size can sometimes help to escape predation (26) depending on the predator size; however, *M. macrocopa* used in this study was of intermediate size (body length ca. 1100 µm) and therefore it is easily captured by fish (11), salamanders (5) and frog tadpoles (20). Since most of these works dealt with direct predation rather than an indirect effect via kairomones, it is often difficult to separate these influences based on field samples where both these processes occur simultaneously. Laboratory experiments have unequivocally proved that indirect effects via kairomones are as important as direct predation effects in assessing the total impact of predators on the life history characteristics of prey species (24). For example, it has been shown that allelochemicals released by fish and *Chaoborus* cause shifts in the life history of *Daphnia hyaline* (32). It is known that cladocerans treated with fish-conditioned water reproduce early and at a smaller size and exhibit a greater reproductive investment compared with control.

The exact duration for conditioning medium to obtain kairomones is not known. Different studies have shown that a 24 h period is considered as more commonly used. However, laboratory studies show that kairomones from the predators can be secreted into medium in a much shorter duration and yet with marked influence on the life history parameters of prey. For example, it is known that the duration as short as 2 h for producing conditioned medium of tadpoles of *Hyla plicata* has a significant effect on the population growth rates of the rotifer *Plationus patulus* (30). In the present study we produced the conditioned medium after exposure to the three predators for 6 h in each case and the kairomones so liberated into the medium produced strongly effects the demographic variables of *M. macrocopa*. There is also some indication that excessively starved predators release little or no kairomones (35). The duration of 6 hours chosen here for the producing conditioned-medium is far less than that considered as strong-starvation period such as point of no return, which may be for several months for aquatic vertebrates including fish (14).

Among the life history variables related to survivorship and reproduction, the latter are generally more sensitive to changes in the ambient water than the former (15). In the present study both these sets of variables were affected by the kairomones from all the three vertebrates. An increased alertness triggered by the presence of kairomones has been shown to decrease predation success on cladocerans (7). Prey may be able to distinguish among predator types (35) and hence produce different behavioural responses. It is clear from this study that the three predators had the capacity to induce differential changes in life traits of *M. macrocopa*. A comparison of the effects of kairomones from the three different vertebrates showed no clear trend in relation to the demographic variables in controls. However, it appeared that *Ambystoma*-conditioned medium was least effective in producing demographic changes in *M. macrocopa*.

The relative impacts of the kairomones from the three predators showed that effects of fish conditioned medium on the tested cladocerans differed significantly from those of the amphibians. It appears that in nature fish probably has far greater influence on its cladocerans prey than axolotl or frog tadpoles. This seems reasonable to speculate since during their lifetime the zooplankton prey are in contact with fish for longer duration than amphibians which frequently move out of water for terrestrial mode of life. In addition, in nature, of these three vertebrate predators, fish exerts more intensive predation pressure on cladocerans. Thus, *Moina* considered as a preferential diet by the fish (22) is more related from the point of view of predator-prey interactions. In the present work *M. macrocopa* responded more rapidly to waterborne kairomones of *Poeciliopsis* than those from the tadpole or axolotl. Thus zooplankton may have adapted a strategy to respond more rapidly to predators with which they share an environment throughout their lifespan than those which spend only a part of their lifespan.

Alternatively, the relative strength of kairomones secreted by three different vertebrate predators too may have to play a role in differently affecting the life history variables of *Moina*. We did not quantify the kairomones from the conditioned-medium. Since we obtained conditioned medium based on similar biomass considerations of the predators, it appears that the chemical nature of kairomone from each predator was also possibly responsible for the observed effects on the demography and survivorship of *Moina*. Fish kairomones are generally low molecular weight (500 Da), non-volatile and anionic compounds, highly water soluble and are resistant to extreme pH and temperature variations (1). Amphibians produce diverse bioactive peptides in their skins. These are secreted in to the medium and act as kairomones. Both fish and amphibians produce chemical cues which are water soluble and are highly resistant to temperature. For example, tadpole kairomones do not lose their activity when boiled or frozen (12). Thus though the chemical nature of kairomones from fish and amphibians is roughly documented, the kairomone chemical nature is yet not fully known.

CONCLUSIONS

Data presented here suggest that several demographic characteristics of *Moina macrocopa* are modified in response to water borne chemical signals released by the three vertebrate predators (fish, salamander or tadpoles). The life history variables of *M. macrocopa*, related to both survivorship and reproduction were affected by the kairomones. By comparing the impacts of kairomones from three predators, it became evident that the effects of fish conditioned medium on the tested cladoceran species differed significantly from those of amphibians. Thus it appears, that in nature fish probably has far greater influence on its cladocerans prey than axolotl or frog tadpoles. However, further studies are still needed with diverse genera of cladocerans.

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