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Effect of water quality on the feeding ecology of axolotl *Ambystoma mexicanum*

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ABSTRACT

Ambystoma mexicanum*, a highly endangered species, is endemic to lake Xochimilco (Mexico City, Mexico) which currently is being negatively affected by the introduction of* Oreochromis niloticus *(Tilapia) and water pollution. During the first weeks of development, when mortality is the highest,* Ambystoma mexicanum *depends on a diet of zooplankton. The aim of this study was to check whether contamination levels in lake Xochimilco influence zooplankton consumption by similar size classes of* A. mexicanum *and* Oreochromis niloticus*. In this study, we analysed changes in the functional responses and prey preference* of A. mexicanum *and larval Tilapia in two media, one with filtered lake Xochimilco water and another one with reconstituted water. As prey we used cladocerans* (Moina macrocopa, Alona glabra, Macrothrix triserialis *and* Simocephalus vetulus) *and ostracods* (Heterocypris incongruens). *Zooplankton was offered in 5 different densities, 10, 20, 40, 80, 160 ind./mL. Prey consumption by* A. mexicanum *varied in relation to the species offered and age of the larvae. From the first week to the eighth week prey consumption by* A. mexicanum *increased by 57%. Our functional response tests showed that regardless of the prey type, prey consumption by* A. mexicanum *was lower in the contaminated water from lake Xochimilco. Among the zooplankton offered in the contaminated environment predators preferred smaller and slower moving microcrustaceans such as* Alona glabra *and* Heterocypris incongruens*. Furthermore,* O. niloticus *preferred prey such as* Moina macrocopa *and* Macrothrix triserialis *in the contaminated medium and was more voracious than the axolotl. Our results indicate that both water quality of the lake and the presence of the more resistant exotic fish adversely impact the survival of this endangered amphibian.*

Key words: Ambystoma mexicanum, Oreochromis niloticus, *invasive species*, *zooplankton*, *water pollution.*

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INTRODUCTION

Amphibians including axolotls are usually adversely affected by anthropogenic influences (Alford and Richards, 1999; Blaustein and Bancroft, 2007). Pollution and climate change are among the main factors that contribute to the loss of amphibian taxa globally (Rahel and Olden, 2008; Sinervo *et al.,* 2010). The consequences of pollution in ecological processes of amphibians are almost never evident. While the direct effects of pollution on growth and reproduction are easily measured, the more subtle effects on behaviour often are undocumented. For example, concentrations of nitrate-nitrogen at 3 mg L^{-1} for 96 h affect food consumption and mobility, resulting in severe weight loss and high mortality of amphibians (Rouse *et al.,* 1999). Raimondo *et al.* (1998) have found that the predatory activity decreases in larval amphibians (*Rana catesbeiana*) exposed to heavy metals. Currently, underwater aquatic ecosystems are strongly affected by pollution (Mahaney, 1994; Lefcort *et al.,* 1997), anthropogenically caused as a result of industry, agriculture and the introduction of alien species.

There are 31 species in the genus *Ambystoma,* of which 21 species are distributed in different habitats in Mexico. *Ambystoma mexicanum* is critically endangered, with very sparse populations in its native habitat, lake Xochimilco in Mexico City (www.iucnredlist.org) (Fig. 1). *Ambystoma mexicanum* is a neotenic amphibian measuring 25-30 cm when adult. These amphibians are mostly detritivores but adults can also feed on fish. Cannibalism has been observed in crowded colonies but is not often seen in nature (Wells, 2007). Since eggs are often deposited on the substrate, they suffer the adverse effects of exposure to pollutants from an early stage. In the developing embryonic stages *A. mexicanum* can be altered when embryos are exposed to contaminants through their uptake from the environment (Werner, 1986; Higginson and Ruxton, 2010).

Changes in feeding behaviour can be attributed to several aspects, such as changes in sensory abilities since it is known that contaminants (heavy metals) may interfere with the smell of aquatic organisms (Hara, 1982). Indirect effects are often more influential in the feeding ecology of species, even when direct effects are quantified indirect effects may result in unforeseen competitive interactions (Miller and Kerfoot, 1987). The contaminants or toxic substances may have important indirect effects on organisms with relation to their ecological settings, even if the direct effects are weak or undetectable (Lefcort *et al.,*

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1997; Pratt *et al.,* 1997; Bridges and Semlitsch, 2000). One of the potentially important effects of pollution is its influence on habitat changes (Treherne and Foster, 1981; Petranka *et al.,* 1987). Small amounts of contaminants that do not cause serious physiological effects may interfere with the food chain and thereby alter predator-prey and competitive interactions between prey species (Johnson *et al.,* 2012). Therefore, sub-lethal direct effects may be important in a cascade of indirect consequences.

Many lakes of central Mexico are contaminated as is the case of lake Xochimilco, the endemic habitat of the amphibian *A. mexicanum* (Smith and Smith, 1971). Water quality in the canals of the lake system is of poor quality because they are fed by partly treated wastewater, containing a large amount of inorganic and organic chemicals such as salts, heavy metals, essential-oil, fats, oils and industrial solvents (Carey and Bryant, 1995; Thomson *et al.,* 1999; Karraker *et al.,* 2008). Although contaminated, this system contains a few populations of amphibians (*Ambystoma mexicanum*), insects and fish (predators), mainly zooplankton and insect prey (Chaparro-Herrera *et al.,* 2011).

The replacement of a native predator by an exotic species may lead to changes in the structure of the community as a result of predation (Townsend, 2003), indirectly through the food interactions between prey (Hobbs and Huenneke, 1992; Kiesecker and Blaustein, 1998) or both (Beisner *et al.,* 2003). In recent years several invasive taxa have been recorded in Mexico. Tilapia (*Oreochromis* sp.) is among the most pernicious predators in aquatic systems and is now found commonly in a large majority of water bodies in Mexico (Zambrano *et al.,* 2010). Our previous observations indicate that *A. mexicanum* is a slow feeding species and thus could suffer in the presence of active predators such as Tilapia (Zambrano *et al.,* 2010).

Fig. 1. Larva of *Ambystoma mexicanum* in the 4th week of development.

While there is extensive literature on the toxic effects of pollutants on amphibian larvae, data to determine long-term effects on the dynamics of amphibian populations are fragmentary (Alford and Richards, 1999). Therefore, in this study we determined the effects of the (polluted) water present in the canals of Xochimilco through *ex-situ* experiments on food preference and functional response of larvae of *A. mexicanum*. We also conducted prey preference experiments on the invasive *Oreochromic niloticus* in order to compare its sensitivity under conditions similar to those for the endemic amphibian *A. mexicanum* in lake Xochimilco (Dominguez-Dominguez *et al.,* 2002, Chaparro-Herrera *et al.,* 2011;).

METHODS

Maintenance of *Ambystoma mexicanum*

Fertilised eggs (about 400 per breeding pair) of *A. mexicanum* were obtained from the Laboratory of Herpetology of the Faculty of Higher Studies Iztacala (National Autonomous University of Mexico), and were incubated at 15 to 18°C one photoperiod 12:12h L:D. The parents of the offspring of *A. mexicanum* had been kept under laboratory conditions for the previous ten years. It was impossible to get breeding pairs in the wild for two reasons: i) *A. mexicanum* is a protected species, and therefore it is not allowed to capture animals from lake Xochimilco; and ii) the density of population in the wild is less than 0.01 ind. m^{-2} (Chaparro-Herrera *et al.,* 2011).

Of the approximately 400 eggs oviposited, around 75% hatched, but 40% of the hatched larvae died during the second week. The remaining individuals survived until the end of study period. Larvae were maintained in moderately hard water [Environmental Protection Agency (EPA) medium], which was prepared by dissolving 0.095 g of $NaHCO_3$, 0.06 g of $CaSO_4$, 0.06 g of $MgSO_4$, and 0.002 g KCl in 1 L of distilled water (EPA, 1985). Our observations indicate that hard water prevents the growth of fungus on the skin of the larvae of *A. mexicanum*. The use of culture medium for the predator and prey also helped to avoid stress during the experiments. The larvae were maintained in shallow transparent trays, and were fed *ad libitum* with a mixture of rotifers and cladocerans, before and after the experiments.

Maintenance of the larval fish *Oreochromis niloticus*

We obtained 400 newly hatched larvae from the laboratory of Aquaculture Environmental Education Center Acuexcomat, Mexico City. The larvae were maintained at room temperature of 18-22°C over a photoperiod of 12:12 h L:D. These organisms had been maintained in laboratory conditions for the previous 5 years but 10% of the larvae died during the first week. The remaining individuals survived until the study period ended. Larvae were

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maintained in the EPA medium. The other test conditions were similar to those described above.

Maintenance of zooplankton for food and experiments

The size of the prey and the locations where they were isolated are shown in Tab. 1. All zooplankton prey used in this study were grown using EPA medium and micro-algae *Chlorella vulgaris* and *Scenedesmus acutus* (at a density of 0.5 to 1.0×10^6 cells mL^{-1}, respectively) as food. Micro-algal species were grown separately in batches using Bold Basal medium supplemented with sodium bicarbonate (Borowitzka and Borowiztka, 1988). The microalgae were harvested in the exponential phase of their growth, centrifuging at 3000 rpm for 5 min; later they were rinsed and re-suspended in a small amount of distilled water. The micro-algal density was enumerated using a Neubauer hemocytometer.

Prey preference experiments

Experiments on prey preference were conducted in the laboratory every week for the first eight weeks. Experiments were carried out weekly to analyse the impact of water quality of lake Xochimilco on the preference and consumption of zooplankton by *A. mexicanum* and *O. niloticus*. We used freshly collected water from the lake which was to observe the effects of food quality on the ecology, and the water was filtered through a mesh of 20 µm. *A. mexicanum* or fish larvae were placed in clean water without food for 2 h prior to the experiments. The number of prey ingested was determined based on differences between the density of initial and final prey (Dominguez-Dominguez *et al.,* 2002). Zooplankton offered in preference experiments were cladocerans (*Moina macrocopa, Alona glabra, Macrothrix triserialis* and *Simocephalus vetulus*) and ostracods (*Heterocypris incongruens*). Consumption was estimated for each species based on the zooplankton left in the experimental vessels. Experiments were conducted in containers of 300 mL capacity, with the EPA medium as a control and with the filtered lake water. Three treatments were set up: i) food preference of *A. mexicanum* alone: two larvae were placed in 100 mL with 50 individuals of each prey; ii) food preference of *O. niloticus*: two larvae were placed in 100 mL of medium with 50 individuals of each prey; and iii) food preference of *A. mexicanum* and *O. niloticus* together: two larvae of each predator were placed together in 200 mL of medium with 100 individuals of each prey. We added two larvae per container in order to ensure adequate consumption of prey (Gliwicz and Wrzosek, 2008), and at the end of the experiment, prey consumption was expressed per larva. For each treatment, four replicates were set up. Manly's α was calculated for all the experiments. This index is derived on the basis of number of prey consumed in relation to that offered. Values of α greater than 1/m – where m is the number of prey species offered – indicates preference, less than 1/m indicates avoidance, and values same as 1/m indicate neither selection nor avoidance (Krebs, 1999).

Functional response experiments

Functional response behaviour on two different prey (*M. macrocopa* and *H. incongruens*) of *A. mexicanum* was compared in EPA medium and water from lake Xochimilco. The functional response experiments were performed every week for the first eight weeks after hatching, at five prey densities for the two diets (*M. macrocopa* and *H. incongruens*: 10, 20, 40, 80 and 160 ind mL^{-1}) with four replicates (Chaparro-Herrera *et al.,* 2011). Adult zooplankton was used in the experiments. The media were placed in containers of 200 mL with 50 mL medium. We added the prey at the desired density to each container. Pre-starved larvae were added to the vessel. Experiments were conducted in diffuse fluorescent illumination at a temperature of 18±2°C. Axolotls were fed for a period of 1 h. Prey consumption was estimated based on the difference in initial and final prey density. The data were transformed using Michaelis-Menten constant where the line is a hyperbola similar to the consumption of *A. mexicanum*. We tested statistical differences in prey consumption using 3-way ANOVA.

RESULTS

In the analysis of preferences, microcrustaceans were used as prey. All these prey taxa coexist in lake Xochi-

Tab. 1. Microcrustaceans used in the experiments and location where taxa were obtained.

Species	Length (µm) (mean±SE)	Localities
Alona glabra	430±2	Lake Chapultepec, Mexico City
Macrothrix triserialis	770±15	Pond in Veracruz, Veracruz
Moina macrocopa	1310±20	Manuel Avila Camacho reservoir, Puebla
Simocephalus vetulus	2100±15	Pond in Veracruz, Veracruz
Heterocypris incongruens	930±13	Pond in Guanajuato, Guanajuato

SE, standard error.

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milco with *A. mexicanum*. The prey sizes ranged from 430 to 2100 mm (Tab. 1).

The behaviour of *A. mexicanum* and *O. niloticus* in terms of preference for microcrustacean diet offered over eight weeks showed distinct differences depending on the two different media, contaminated water (lake Xochimilco), or EPA medium (Fig. 2). In the first week, *A. mexicanum* manifested a low preference for microcustaceans, consuming only two species: *A. glabra* and *M. macrocopa* having a size of 430 and 1310 µm (Tab. 1), respectively, in the polluted environment. By comparison, Tilapia showed a preference for four of the five prey offered (*S. vetulus, M. macrocopa, M. triserialis* and *A. glabra*). In the eighth week, the final preference analysis of *A. mexicanum* in the contaminated environment indicated that it preferred two species: *M. macrocopa* and *M. triserialis*. Tilapia displayed a preference for *M. macrocopa, M. triserialis, S. vetulus* and *H. incongruens* at the end of the study.

In the controls (Fig. 2), an increase in the preferred types of prey was generally observed in the studied species, as was the case in the seventh-week behaviour of *A. mexicanum* control, which manifested a preference for four types (*M. macrocopa, S. vetulus, H. incongruens* and *M. triserialis*) of the five prey offered. Its counterpart in the contaminated environment showed a preference for two (*M. macrocopa* and *M. triserialis*) of the offered prey species. Regarding the preferences of the fish introduced into the environment, the control showed no preference for any of the five species (*M. macrocopa, M. triserialis, A. glabra, H. incrongruens* and *S. vetulus*), compared to the contaminated environment, where it preferred *A. glabra* and *S. vetulus.*

Prey consumption was higher in the control EPA medium than the contaminated lake water on either prey type, *M. macrocopa* or *H. incongruens* (Fig. 3). *A. mexicanum* showed a decrease of 73 and 74% in the consumption of *H. incongruens* (Fig. 3) and *M. macrocopa* (Fig. 3) respectively in the contaminated medium compared to control (EPA). In the diet of *H. incongruens* (Fig. 3) consumption increased from 25 to 78 individuals during the eight weeks. The axolotl showed significant differences in prey consumption in relation to prey type, prey density and age of the predator ($P<0.001$, three-way ANOVA) (Tab. 2) on both microcustaceans *M. macrocopa* and *H. incongruens* and in both test media, contaminated and control. Among the prey species offered, *A. mexicanum* consumed consistently higher numbers of *M. macrocopa,* particularly during the last weeks of the experimental period (Fig. 3). With age, the asymptote of consumption was also shifted to higher values, *i.e.* 9 to 78 during eight weeks. We observed, in general, greater consumption of microcrustaceans in controls (EPA). The maximum prey consumption of larvae *A. mexicanum* during the experimental period varied depending on prey taxa and test media (Fig. 3).

DISCUSSION

In the present study we observed that the feeding behaviour of *A. mexicanum* was influenced by water quality to a greater extent than that of Tilapia. Water quality in the canals of the lake system is poor since wastewater is used to fill it (Carey and Bryant, 1995; Thomson *et al.,* 1999; Karraker *et al.,* 2008). The adverse effects of this water quality was evident in the functional response tests where prey consumption was about 70% lower in lake water of lake Xochimilco as compared to the controls. These changes in consumption behaviour may be due to changes in sensory abilities since it is known that pollutants interfere with the smell, and probably therefore with how the feeding behaviour of aquatic organisms (Hara, 1982) *A. mexicanum* larvae respond to chemical signals. In the prey preference studies we observed that one week old *A. mexicanum* preferred only *A. glabra* in contaminated lake water but *A. glabra*, *M. macrocopa* and *H. incongruens* in the controls. *A. glabra* is preferred mainly because of its small size and slow movements that make

Tab. 2. Three-way ANOVA test on the prey consumption by *A. mexicanum* offered micro-crustaceans in two media (pollution and control), during the first eight weeks of larval development.

Source of variation	Prey species									
	Heterocypris incongruens					*Moina macrocopa*				
	DF	SS	MS	F	P	DF	SS	MS	F	P
A	1	64638	64638	2662	<0.001	1	64638	64638	2662	<0.001
B	7	142909	20415	840	<0.001	7	142909	20415	840	<0.001
C	4	883433	220858	9095	<0.001	4	883433	220858	9095	<0.001
Interaction of A × B	7	33278	4754	195	<0.001	7	33278	4754	195	<0.001
Interaction of A × C	4	45545	11386	468	<0.001	4	45545	11386	468	<0.001
Interaction of B × C	28	131006	4678	192	<0.001	28	131006	4678	192	<0.001
Interaction of A × B × C	28	27701	989	40	<0.001	28	27701	989	40	<0.001
Error	240	5827	24			240	5827	24		

SS, sum of squares; DF, degrees of freedom; MS, mean square; F, F-ratio; A, media; B, larval age; C, prey concentration.

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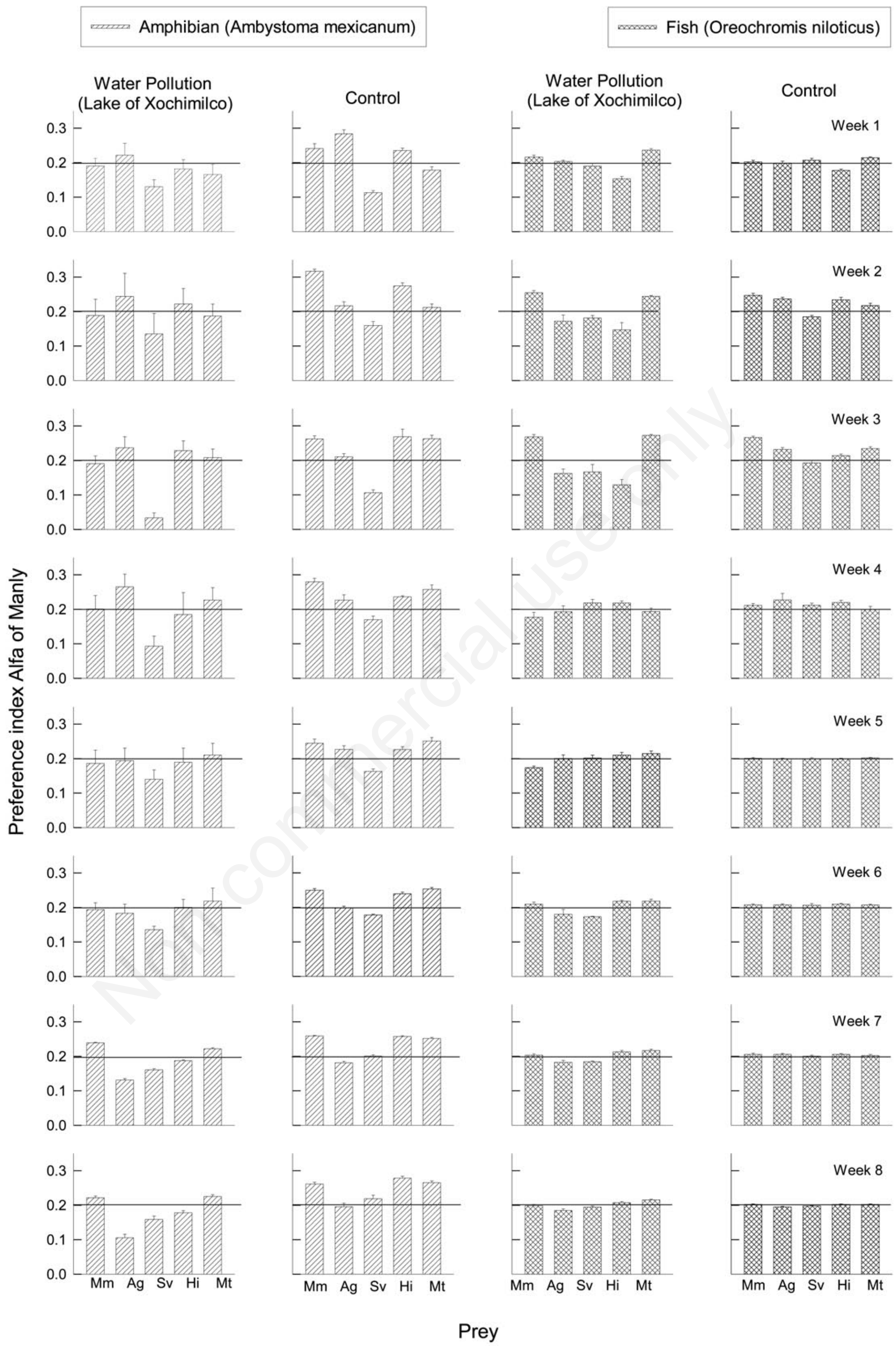

Fig. 2. Food preference (<0.2 Alpha Manly) of *Ambystoma mexicanum* compared to its competitor – *Oreochromis niloticus* (Tilapia) – introduced into contaminated media (water of lake Xochimilco) and moderately hard water control in the first eight weeks with five species of prey. Mm=*Moina macrocopa*; Ag=*Alona glabra*; Sv=*Simocephalus vetulus*; Hi=*Heterocypris incongruens*; Mt=*Macrothrix triserialis*. Values are expressed as means±standard error based on four replicates.

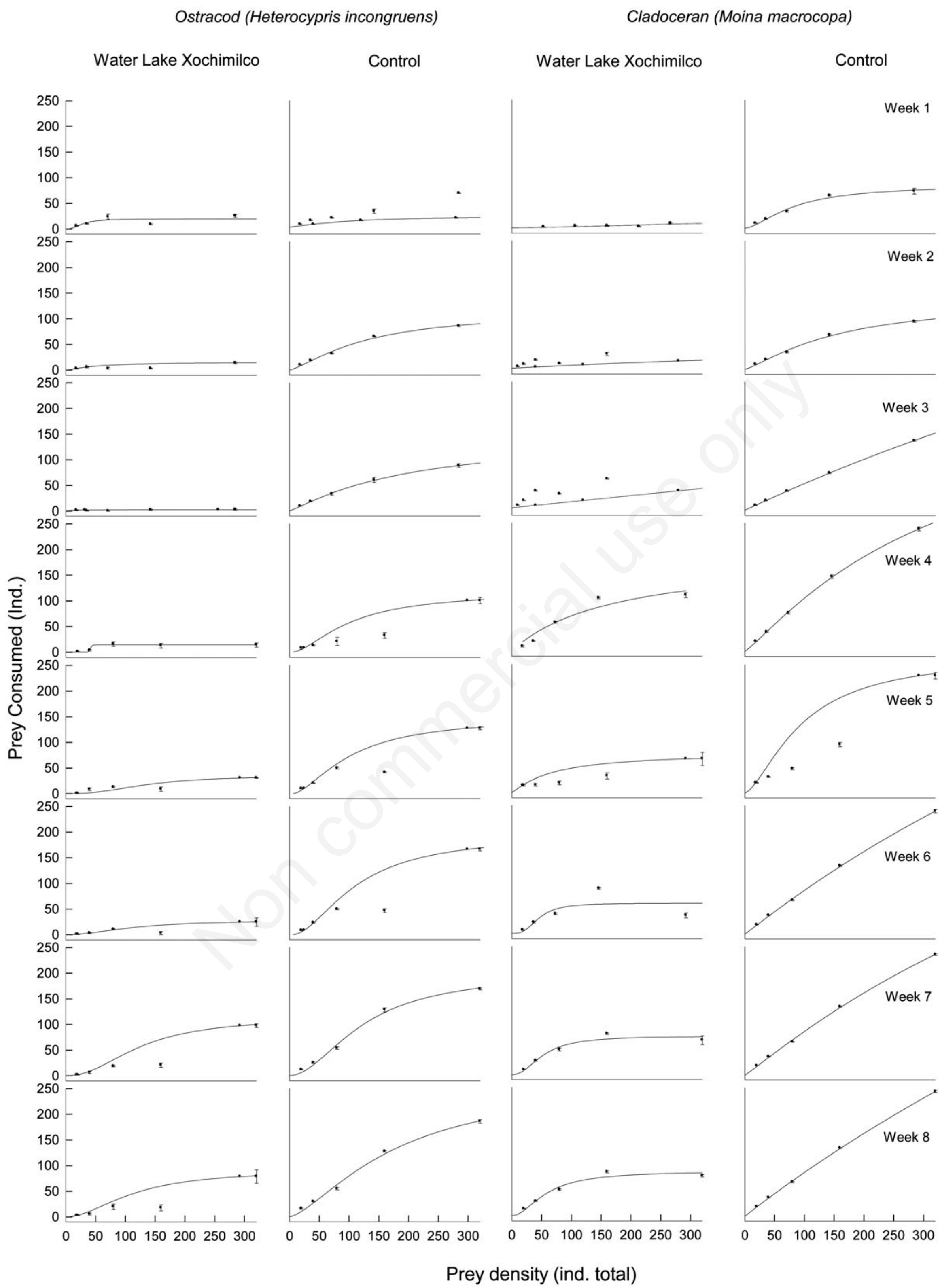

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Fig. 3. Functional response of *A. mexicanum* with diet microcrustaceans *Heterocypris incongruens* (ostracod) and *Moina macrocopa* (cladoceran) in a polluted environment (water of lake Xochimilco) and moderately hard water control in the first eight weeks. Values are expressed as means±standard error based on four replicates.

it an easy prey. Raimondo *et al.* (1998) found impaired antipredatory behaviour in bullfrog tadpoles exposed to heavy metals.

The presence of a more resistant invasive species is another major problem in conservation efforts for *A. mexicanum*. The prey preference patterns for *O. niloticus* in lake Xochimilco water was not markedly different than in controls; on the other hand, *A. mexicanum* showed a preference for a greater variety of prey in uncontaminated water. In preference experiments we found that small amounts of contaminants that do not cause physiological effects may interfere with the behaviour and thereby alter predator-prey and competitive interactions between species (Peterson *et al.,* 2011). Contaminants, especially heavy metals, can change the outcome of competitive interactions (Clements *et al.,* 1992; Landis *et al.,* 1997; Pratt *et al.,* 1997). Our results clearly show that the adverse effects of contaminants on feeding behaviour are greater on the endemic amphibian than on the exotic fish species.

Contaminants also interfere with development. *A. mexicanum* over eight weeks showed a decrease in consumption both in food preference tests and the functional response experiments. Several studies indicate that consumption rates of predators are significantly lower in contaminated media (Lefcort *et al.,* 1999). Since pollutants also cause increased metabolic costs (Rowe *et al.,* 1998), this combination can be more detrimental for *A. mexicanum* as it would result in lower growth rates and a lack of nutrients for the necessary metabolism.

There are reports of developmental abnormalities in amphibians when cultured on contaminated waters. For example, Rowe *et al.* (1998) mentions that bullfrog tadpoles living in contaminated areas have oral deformities resulting in lower grazing capacity. Although we did not observe such deformities, we found the feeding rates to be lower. Nitrate levels in Xochimilco can be expected to be higher as the lake receives partly treated wastewaters. Newly hatched larvae of the salamanders are more susceptible to nitrate (Rouse *et al.,* 1999). It is possible that the reduced feeding rates we observed were due to the development of methemoglobinemia (Hecnar, 1995). Indeed, methemoglobin reduces activity in amphibians, including feeding activity.

Zooplankton populations, the main food of the larvae of *A. mexicanum* in the early weeks of development, have been strongly affected by the presence of the exotic, introduced fish *Oreochromis niloticus* because they are susceptible to fish predation. Our observations of high densities of small (<300 µm) zooplankton, principally rotifers and a paucity of large (>1000 µm) zooplankton such as cladocerans in lake Xochimilco (Nandini *et al.*, 2005) are in accordance with the published literature on fish predation effects on plankton communities (Gliwicz, 2003). While rotifer populations are more resistant to these changes (Sarma *et al.,* 2001; Ramirez-Perez *et al.,* 2004), they are not the preferred prey of axolotls (Chaparro-Herrera *et al.*, 2011). The above is just a small part of all the problems that exist for future reintroduction in lake Xochimilco. Many factors have to be taken into account, such as the effect of each pollutant, turbidity, field studies at the site of the lake, direct effect of the species introduced, *etc*. Having summed up all the factors affecting larval *A. mexicanum*, it is evident that a management plan is urgently required which has to deal with these factors prior to the reintroduction of this species into lake Xochimilco.

Introduced fish are known for their ability to proliferate rapidly (Denöel *et al.*, 2005; Capps *et al.,* 2009; Purcell *et al.,* 2012), and to reduce zooplankton abundance in lakes and ponds (Sullivan, 2010). As Tilapia grow, their foraging strategies change from visual feeding, focusing almost exclusively on zooplankton (Lu *et al.,* 2009; Lisney and Hawryshyn, 2010; Sabbah *et al.,* 2012). The results obtained in this study indicate that consumption rates of Tilapia are higher than *Ambystoma*. Shepherd and Mills (1996) estimated that during times of high zooplankton biomass [>100 mg/L dry mass (DM)], introduced fish at age 0 consumed more cladocerans. Corroborating the above, our results show higher consumption of large cladocerans such as *M. macrocopa* and *M. triserialis*, regardless of water quality. It has been well documented that the overall size structure of zooplankton is smaller in lakes dominated by fish populations (Iglesias *et al.,* 2011). The same is true for lake Xochimilco where small zooplankton dominate in terms of numbers and biomass (Enriquez-García *et al.,* 2009). In the case of *A. mexicanum*, on the other hand, the same results show a disadvantage in consumption in the contaminated medium, a medium originally inhabited by amphibians.

CONCLUSIONS

There have been many studies on the conservation and reintroduction of endangered species but few have taken into account their ecology or provided in-depth analyses of their habitat. Our work clearly indicates that contamination levels and the presence of high densities of the exotic *O. niloticus* in lake Xochimilco are among the important factors that can adversely affect *A. mexicanum* populations. Both factors need to be controlled for with the aim of conserving this endemic and endangered amphibian.

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