Feeding behaviour of larval *Ambystoma mexicanum*

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Abstract. The Axolotl, *Ambystoma mexicanum*, endemic to the freshwater lakes, Xochimilco and Chalco in Mexico City, feeds on zooplankton during its larval stages. We evaluated the functional response over eight weeks of *A. mexicanum* fed different prey items found in its natural habitat (rotifers: *Brachionus havanaensis*, *B. calyciflorus*, *B. rubens* and *Plationus patulus*; cladocerans: *Moina macrocopa*, *Macrothrix triserialis*, *Alona glabra* and *Simocephalus vetulus*; and ostracods: *Heterocypris incongruens*). Zooplankton consumption by *A. mexicanum* varied in relation to the prey species and age of the larvae. Unlike oviparous fish larvae which often feed preferentially on rotifers in the first few weeks, *A. mexicanum* larvae fed more on cladocerans and ostracods. Among the cladocerans offered, larval *A. mexicanum* consumed higher numbers of *M. triserialis* and *M. macrocopa*. Feeding on the largest cladoceran tested, *S. vetulus*, increased after the fifth week. There was a consistent increase in the number of ostracods *Heterocypris incongruens*, consumed with age, from 4 to 169 prey per larva over eight weeks. The results are discussed with relation to the importance of zooplankton diet in conservation effort of this endangered species in Lake Xochimilco.

Keywords: Axolotl, cladocerans, feeding ecology, functional response, rotifers.

Introduction

The Axolotl, *Ambystoma mexicanum*, is native to Mexico, with a distribution restricted to just two freshwater lakes (Xochimilco and Chalco) in the southern part of Mexico City (Armstrong and Malacinski, 1989). It is the largest member of the family Ambystomatidae reaching up to 40 cm as adults. Unlike other paedomorphic amphibians, including those of the genus *Ambystoma*, *A. mexicanum* is incapable of reproduction after metamorphosis (Smith and Smith, 1971; Voss and Shaffer, 2000). Due to degradation of its natural lake environment, *A. mexicanum* is nearly on the brink of extinction (Zambrano et al., 2006) despite the advantages of paedomorphosis (Hanken, 1999; Stephan-Otto

and Ensástigue, 2001; Denoël et al., 2005). One of the reasons is that the physical, chemical and hydrological characteristics of its habitat, Lake Xochimilco, has changed with a 90% reduction in the lake area (Valiente et al., 2010). In order to maintain the water level in the lake, partly-treated domestic waste water is being added. Agricultural fertilizers and pesticides from the neighbouring floricultural fields also find their way into the lake (Contreras et al., 2009). The exotic fish *Oreochromis niloticus*, which also feeds on zooplankton, is abundant in this water body (Valiente et al., 2010). All these factors reduce the availability of zooplankton, which is the natural diet for larval *A. mexicanum* during the first few weeks after hatching (Voss and Shaffer, 2000).

Rotifers (about 70 species), cladocerans (10 species), and ostracods, are among the main components of the zooplankton communities of Lake Xochimilco (Nandini, Ramírez-García and Sarma, 2005). The most common genera among the rotifers are *Brachionus*, *Keratella*, *Polyarthra*, *Trichocerca*, *Filinia* and *Asplanchna*. Among the microcrustaceans, *Alona glabra*, *Ceriodaphnia dubia*, *Moina macrocopa* and ostracods are the most common taxa in the canals of Xochimilco. *Ambystoma mexicanum*

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feeds mainly by suction; it has a large buccal cavity with tiny teeth arranged in rows at the entrance of the oral cavity and a retractable tongue (Shaffer, 1989). Rotifers and cladocerans are better suited as prey for larval *Ambystoma mexicanum* in the first weeks of development, primarily due to their wide variety of shapes and sizes that easily fit the gape of the young larvae, as well as their slow swimming speed (<2 mm per second as compared to the 80 mm per second of copepods) which facilitates capture (Negrea, Botnariuc and Dumont, 1999; Nogrady, Wallace and Snell, 2005).

Information on the feeding behavior of a species, particularly during the larval stages where mortality is often the highest (Gerking, 1994; Zambrano et al., 2006), is important for both culture and conservation efforts. It has been shown that resource partitioning across larval stages favours the maintenance of facultative paedomorphosis (Denoël and Joly, 2001). Larval *A. mexicanum* in Xochimilco competes with larval *O. niloticus* for zooplankton but due to its poor eyesight (Hassinger, Anderson and Dalrymple, 1970) larval *A. mexicanum* could often be the weaker competitor.

Laboratory studies quantifying the number of zooplanktonic prey items consumed by larval axolotls in relation to the available food density reveal information which is helpful for its management and conservation (Dominguez-Dominguez, Nandini and Sarma, 2002). We tested the hypothesis that the feeding rates of larval *A. mexicanum* increase with age and that it is higher on larger sized microcrustacean prey than on rotifers as it has a large gape size since birth. The objective of this study was, to determine the rate of consumption of zooplanktonic prey (*Brachionus calyciflorus*, *B. havanaensis*, *B. rubens* and *Plationus patulus*), cladocerans (*Macrothrix triserialis*, *Simocephalus vetulus*, *Alona glabra* and *Moina macrocopa*) and the ostracod (*Heterocypris incongruens*) by the larval *A. mexicanum* during the first eight weeks following hatching. We also analyzed the gape size-body size relationship in relation to different ages of *A. mexicanum*.

Materials and methods

Maintenance of Ambystoma mexicanum

Fertilized eggs (about 400 from one breeding pair) of *Ambystoma mexicanum*, obtained from the Laboratory of Restoration Biology at the Institute of Biology of the National Autonomous University of Mexico were incubated at 15 to 18°C at a light: dark regime of 12 : 12 h. These individuals have been maintained under laboratory conditions for the past ten years. It was impossible to get breeding pairs from the wild because of two reasons; i) *A. mexicanum* is a protected species, therefore it is not permitted to capture animals from Lake Xochimilco and, ii) the population density in the wild is less than 0.01 ind. m^{-2}. About 3% of the eggs failed to hatch during the first week and nearly 40% of the hatched larvae died during the second week. All those that survived beyond this period were able to survive until the end the study period. We maintained the larvae using moderately hard water as the medium (EPA medium) which was prepared by dissolving 0.095 g NaHCO$_3$, 0.06 g CaSO$_4$, 0.06 g MgSO$_4$, and 0.002 g KCl in one litre of distilled water (Anon., 1985). Our personal observations indicate that hard water prevents the growth of fungus on the skin of the axolotl. The use of the same culture medium for the predator and the prey also helped avoid stress during the experiments. The larvae were placed in shallow transparent trays and were fed *ad libitum* on a mixture of rotifers and cladocerans.

Maintenance of zooplankton

The prey taxa, their sizes and the localities from where they were isolated are shown in table 1. All the zooplanktonic prey used in this study were cultured using EPA medium and the algal food *Scenedesmus acutus* or *Chlorella vulgaris* at a density of 0.5×10^6 to 1.0×10^6 cells ml^{-1}, respectively. The algal species were separately batch cultured using Bold's basal medium implemented by sodium bicarbonate (Borowitzka and Borowiztka, 1988). Log phase algae were harvested, centrifuged at 3000 rpm for 5 minutes, rinsed and resuspended in a small quantity of distilled water. The density of the algal stock culture was estimated using a Neubauer haemocytometer.

Functional response experiments

Functional response experiments were conducted at five food densities for each of the four species of rotifers (*B. calyciflorus*, *B. havanaensis*, *B. rubens* and *Plationus patulus*) and five species of microcrustaceans (cladocerans: *Alona glabra*, *Macrothrix triserialis*, *Moina macrocopa* and *Simocephalus vetulus*; ostracod: *Heterocypris incongruens*) with 4 replicates for each treatment (rotifer prey: 1, 2, 4, 6 and 8 ind. ml^{-1}, cladocerans and ostracods. 0.2, 0.4, 0.8, 1.6 and

Table 1. Length of the rotifers and microcrustaceans used in the experiments and the localities from which they were obtained.

| Species	Length (μm) (mean ± SE)	Localities
Brachionus calyciflorus	185 ± 12	Lake Xochimilco, Mexico City
B. havanaensis	120 ± 10	Lake Xochimilco, Mexico City
B. rubens	108 ± 2	Lake Xochimilco, Mexico City
Plationus patulus	150 ± 20	Lake Xochimilco, Mexico City
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

3.2 ind. ml^{-1}). Adult zooplankton were used in the experiments. We used different densities of rotifers and microcrustaceans in the experiments since the former are more abundant in Lake Xochimilco than the latter. The functional response experiments were conducted weekly once for eight weeks, in 100 ml transparent jars containing 50 ml of EPA medium and for each prey species separately and at chosen concentrations. Larvae of *Ambystoma mexicanum* were separated from the culture tanks and starved for two hours before the experiments. We added two larvae per container in order to ensure prey consumption (Gliwicz and Wrzosek, 2008) and at the end of the experiment the prey consumption was expressed per larva. The larvae were allowed to feed for 60 minutes after which they were separated and unconsumed zooplanktonic items were enumerated. The difference between the initial and final densities of zooplankton was considered as the prey consumed by two individuals of *A. mexicanum*.

Although resource depletion during functional response tests is undesirable, we could not avoid it in this study because we did not observe the capture rate of the predator. We did observe less than 10% depletion in prey during the course of the experiment with rotifers in more than 85% of the trials; with the cladocerans and the ostracods there was 30% depletion in prey during the course of the experiment. Nevertheless, we did conduct the experiments over a period of only 60 minutes, just enough to observe consumer-dependent behaviour (Fussmann, 2008).

The differences between the values obtained in the consumption of the prey was analyzed using one way ANOVA (Sigma Plot 11).

Relationship between body size and gape width of A. mexicanum

To derive the relation between the body size of *A. mexicanum* with its gape size and to relate this to the prey items consumed, the following procedure was followed. We measured weekly the body size and mouth size of larval *A. mexicanum* during the first eight weeks using Nikon stereomicroscope (SMZ, 645) fitted with camera and later the data from the images were transformed to nearest μm using Helicon filter 4.26 image analyzer. Subsequently a linear regression was applied to analyze the relationship between body size and mouth size.
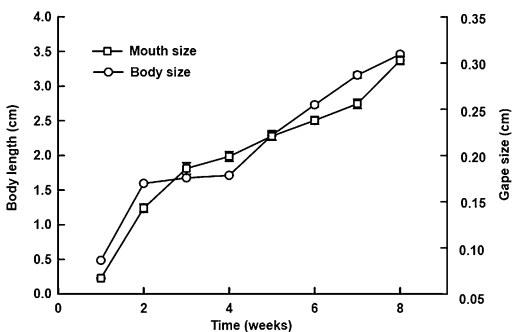
Figure 1. Body size and gape size in relation to age of *Ambystoma mexicanum* during the first eight weeks under an *ad libitum* feeding regime.

Results

The increase in body length and gape size during the experimental period of eight weeks in larval *Ambystoma mexicanum* is shown in fig. 1. The relationship between mouth size and body size of *A. mexicanum* was linear. There was a significant relationship between body length and gape size (fig. 2). In the first eight weeks following hatching, the larvae showed an increase in the gape size. There was a significant variation in the gape size among the individuals in a size range of 1.5 to 2.0 cm; thereafter this variability decreased considerably. However, the body length of *A. mexicanum* increased more notably during the fourth to fifth week (fig. 2).

Ambystoma mexicanum showed variations in feeding rates depending on the prey species and age of the larvae. Among the offered diets, rotifers were consumed in lower numbers

during the first week of the experiment, but were consumed more often at a density of 8 ind. ml^{-1} in the fourth week. *Plationus patulus* was consumed in very low numbers during the first week but consumption increased over the eight-week observational period (fig. 3). Among the rotifer prey, and *P. patulus* were the least consumed (<10 individuals per larva) while *B. rubens*, *B. havanaensis* and *B. calyciflorus*

were consumed in higher numbers ($P < 0.001$, three-way ANOVA, table 2).

Compared to rotifers, cladocerans were consumed in greater numbers by the larval *A. mexicanum* (fig. 4). They fed mostly on *M. triserialis* and *M. macrocopa* (consumption >70 individuals per larva). In the diet with *S. vetulus* consumption increased from 7 to 86 individuals during the eight weeks. More than 80% of the offered *M. triserialis* and *M. macrocopa* were consumed by *A. mexicanum*. On diets of either rotifers or cladocerans, we observed significant differences in prey consumption in relation to the prey type, prey density and age of the predator ($P < 0.001$, three-way ANOVA, table 2).

Among the prey species offered, *A. mexicanum* consumed consistently higher numbers of the ostracod *Heterocypris incongruens*, particularly during the last few weeks of experimental period (fig. 4). With increasing age, the asymptote of ostracod consumption was also shifted to higher values i.e., from 4 to 169 prey items during the eight weeks.

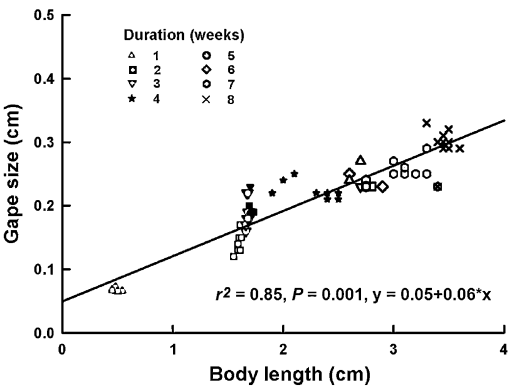We observed, in general, a greater consumption of larger zooplankton (>400 μm) but lower

Figure 2. Relationship between body length and gape size of *Ambystoma mexicanum* cultured for eight weeks under laboratory conditions.
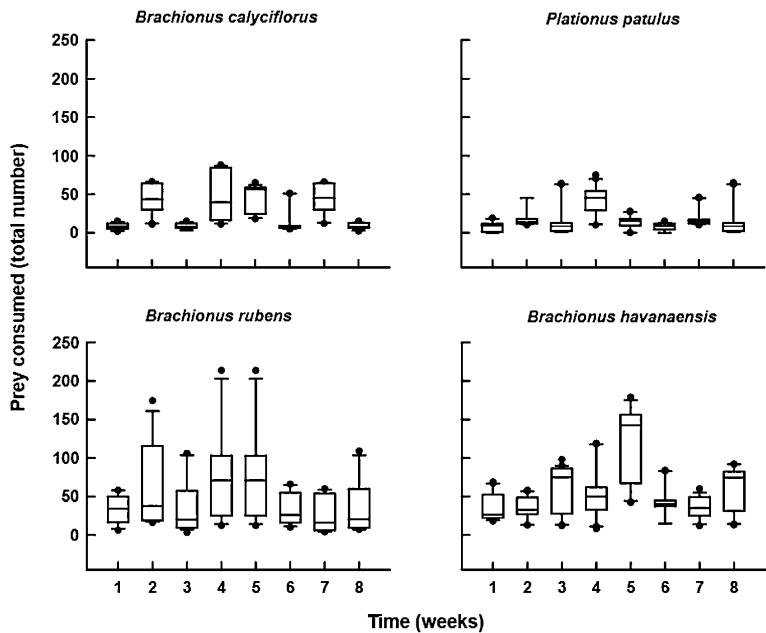

Figure 3. Functional response of *A. mexicanum* on rotifer diets during the first eight weeks. The prey species offered were a) *Brachionus calyciflorus*, b) *Plationus patulus*, c) *Brachionus rubens* and d) *Brachionus havanaensis*.

Table 2. Three way ANOVA on the prey consumption by *A. mexicanum* offered rotifers and microcrustaceans, during the first eight weeks of larval development. *DF* = degrees of freedom, *SS* = sum of squares, *MS* = mean square, *F* = *F*-ratio.

Effect	Rotifers					Cladocerans				
	SS	*DF*	*MS*	*F*	*P*	*SS*	*DF*	*MS*	*F*	*P*
Prey species	152 961	3	50 987	4456	<0.001	10 266	4	2567	3305	<0.001
Age	131 511	7	18 787	1642	<0.001	56 214	7	8031	10 340	<0.001
Concentration	222 850	4	55 712	4869	<0.001	791 888	4	197 972	254 900	<0.001
Species∗Age	113 561	21	5408	472	<0.001	55 045	28	1966	2531	<0.001
Species∗Concentration	90 863	12	7571	661	<0.001	6713	16	420	540	<0.001
Age∗Concentration	105 209	28	3758	328	<0.001	75 510	28	2697	3472	<0.001
Species∗Age∗ Concentration	117 885	84	1403	122	<0.001	58 101	112	519	668	<0.001
Error	5491	480	11.46			466	600	0.78		

rates for smaller prey such as rotifers. Smaller cladocerans such as *Alona glabra* (409 ± 5 μm) were consumed during the first week but later feeding shifted towards larger cladocerans.

The maximum prey consumption by larval *A. mexicanum* during the experimental period varied depending on the prey taxa (fig. 5). Among the rotifers *B. havanaensis* was consumed in highest numbers ($P < 0.001$, three-way ANOVA, table 2). However, as compared to crustacean diets, rotifers were consumed in much lower numbers. *Ambystoma mexicanum* showed in decreased order of maximal cladoceran prey: *M. triserialis* > *M. macrocopa* > *A. glabra* > *S. vetulus*. Among all the prey items offered *A. mexicanum* fed most on *H. incongruens*.

Discussion

Ambystoma mexicanum showed distinct changes in its feeding behavior with increasing larval age. It was quite evident that this predator did not consume high densities of rotifers during their larval stages. It consumed more cladocerans and ostracods from the first week onwards. Studies on other ambystomids, (i.e. *A. tigrinum*) also show that they prefer cladocerans (Gillis and Lauder, 1994). Larvae of fish or axolotl that have a large gape size generally prefer larger prey, particularly cladocerans (Caiola, Vargas and Sostoa, 2001). The gape size at hatching in the viviparous goodeidids, *Allotoca dugesi*

and *Ameca splendens*, as in *A. mexicanum*, were in the range of 400 to 800 μm; all of them showed a preference for cladocerans from birth (Dominguez-Dominguez, Nandini and Sarma, 2002; Peña-Aguado, Nandini and Sarma, 2009). It has been shown that while small individuals of the Alpine newt, *Mesotriton alpestris* and *Ambystoma tigrinum* feed on small sized prey, larger individuals can feed on both large and small prey (Denoël and Joly, 2001; Denoël, Whiteman and Wissinger, 2006). In this study we observed similar trends on a rotifer diet; when the axolotls were less than a month old they fed on rotifers but as they grew older they fed less on this prey type, although they never gave it up completely at any time during the study. The axolotls fed more on cladocerans from the first week onwards. It is quite possible that the predator did not invest in capturing the small (<200 μm) prey due to the low energetic returns from capturing rotifers in relation to cladocerans or ostracods (Juanes, 1994).

Among the four species of rotifers tested, *A. mexicanum* consumed *Brachionus havanaensis* in higher numbers. This suggests that the rotifer body size did not affect their capturability by larval *A. mexicanum*. *B. calyciflorus* was the largest rotifer tested compared to *B. havanaensis*. *Brachionus havanaensis* swims faster than *B. calyciflorus*, which probably increases the encounter rates and consequently the capture success. In blind invertebrate predators the velocities of prey movement increases encounter
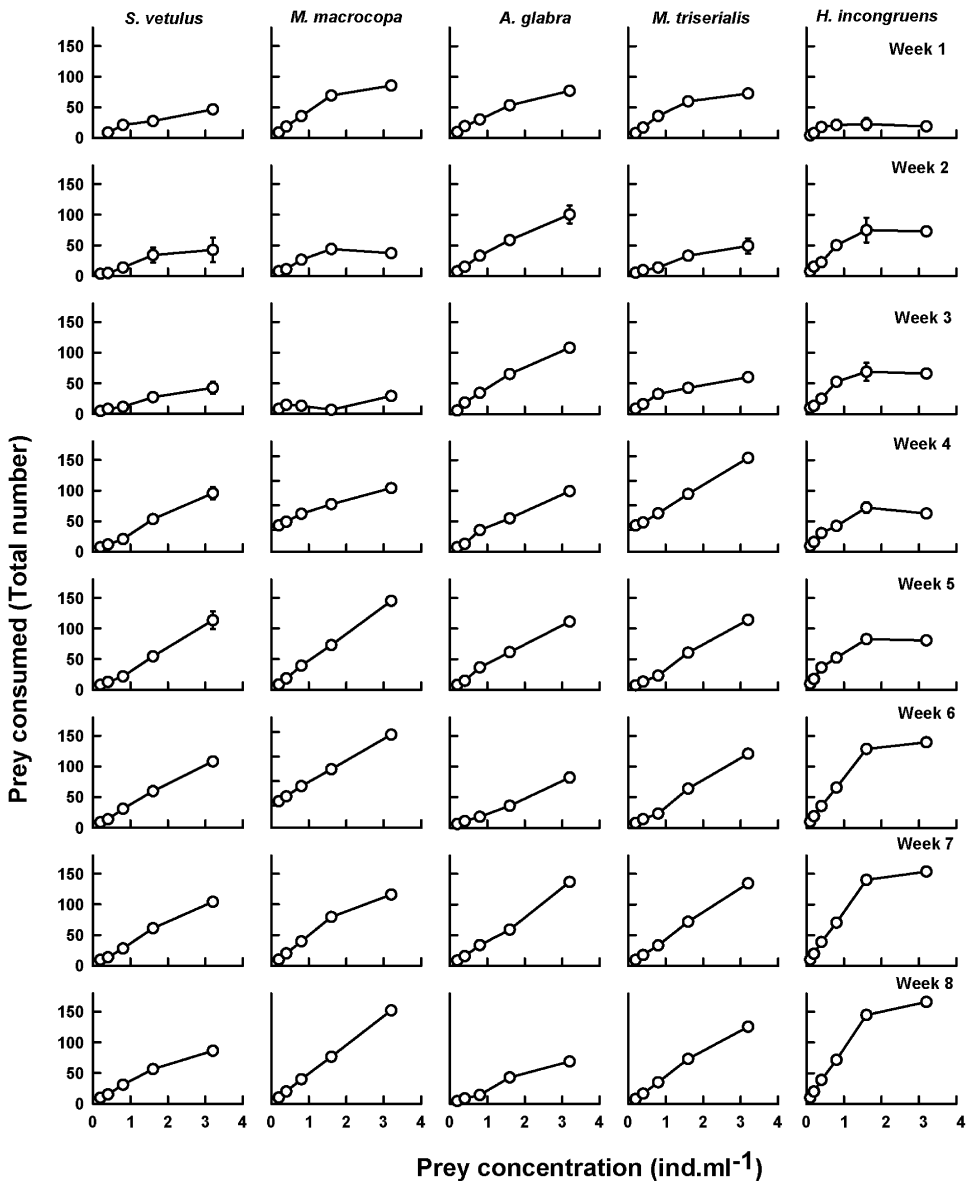
Figure 4. Functional response of *A. mexicanum* on microcrustacean diets during the first eight weeks (means ± SE based on four replicates).

rates significantly (Sarma, 1993; Iyer and Rao, 1996). This has also been observed in visual predators (Zaret, 1980), including *Ambystoma mexicanum Brachionus havanaensis* is also one of the most common species of rotifers in the canals of Xochimilco where *A. mexicanum* is endemic (Nandini, Ramírez-García and Sarma, 2005).

Although large prey imply higher energy costs in capture by *A. mexicanum* compared to lower swimming rates of rotifers, capturing cladocerans such as *Moina macrocopa* is more profitable energetically. Larvae of several fish species, particularly the large ones of viviparous taxa such as *Ameca splendens* (Peña-Aguado, Nandini and Sarma, 2009) and *Allo-*
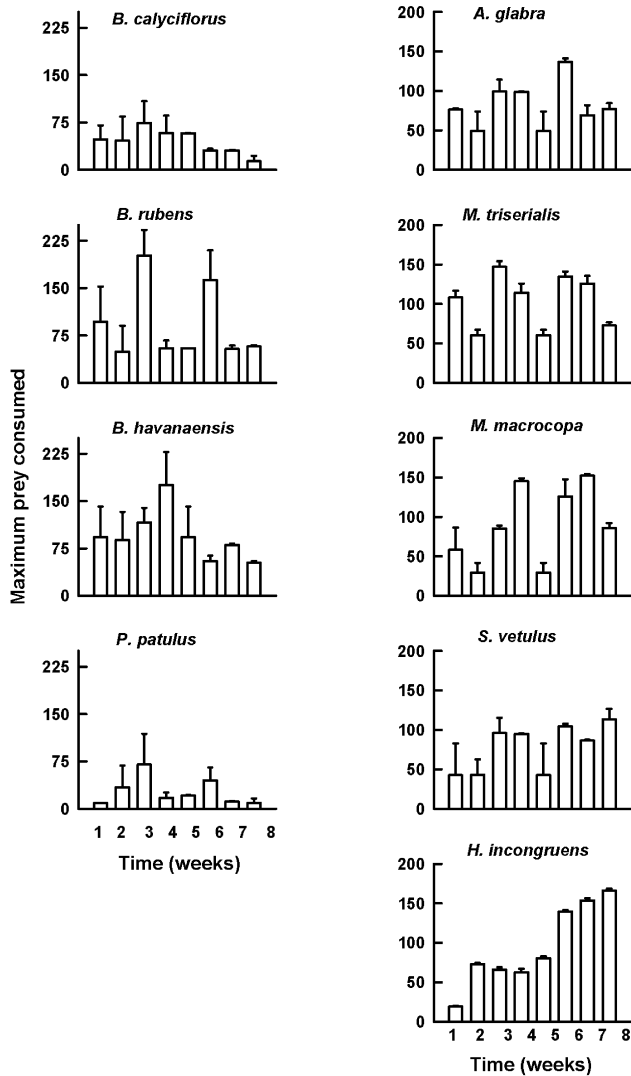
Figure 5. Maximal weekly prey consumption of *A. mexicanum* on different zooplankton diets (means ± SE based on four replicates).

toca dugesi (Dominguez, Nandini and Sarma, 2002) show a highly preferential consumption of *Moina macrocopa* compared to other cladocerans such as *Alona glabra*, *Ceriodaphnia dubia* or *Daphnia pulex*. The movement of *Moina*, in particular, renders it more visible, making it one of the most highly consumed taxa by several tropical fish species (Zaret, 1980).

Among the cladocerans, the most consumed prey was *Macrothrix triserialis*, which has spines on its carapace that serves as protection against invertebrate predation (Smirnov, 1992; Nandini and Sarma, 2005). It is possible that the consumption of *M. triserialis* was high due to the shared benthic habitat of the predator and the prey. It has been shown that *Ambystoma mabeei* also prefers large littoral cladocerans such as *Simocephalus* (McCoy and Savitsky, 2004). This observation was also supported by the fact that *A. mexicanum* consumed the littoral ostracod *Heterocypris incongruens* in highest numbers from the first week onwards. There

are very few studies on the use of ostracods as prey for fish or amphibian larvae, but our study clearly showed that these microcrustaceans are important components of the axolotls' diet.

Ambystoma mexicanum has rudimentary teeth, which are only designed to capture food but not to tear or chew it (Fenske, Köhler and Kretzschmar, 1995). The size range of microcrustaceans, from 500 to 4000 μm, is well adapted to the gape size of axolotls in the first weeks because they swallow their food whole. The axolotl is not an active hunter; its feeding behaviour is more like that of a sit-and-wait predator. Larvae of *A. mexicanum* are also mostly benthic; they rarely swim up the water column for feeding (Duhon, 1989). These traits are disadvantageous to *A. mexicanum* as compared to the active and voracious fish larvae. Previous studies indicate that the young of viviparous fish often prefer cladocerans from the first week of birth as compared to those of oviparous fish, (Nandini and Sarma, 2000; Peña-Aguado, Nandini and Sarma, 2009).

Several studies on the zooplankton community of ponds inhabited by salamanders (*Ambystoma tigrinum*, Dodson and Dodson, 1971) show that these often have a very low density and diversity of microcrustaceans. Feeding studies on the alpine newts (*Mesotriton alpestris*) do not indicate they are capable of feeding so efficiently on copepods so as to reduce their population densities to nearly negligible levels (Schabetsberger and Jersabek, 2004). A later study by Schabetsberger et al. (2006) indicates that fish rather than amphibians are often responsible for a dramatic shift in the zooplankton community structure. The former feed selectively on large copepods and cladocerans, thereby reducing the interference and exploitative competition faced by small cladocerans and rotifers (Hurtado-Bocanegra, Nandini and Sarma, 2002) which increase in density and diversity. Our study clearly indicates that *A. mexicanum* is threatened by the introduction of Tilapia in the canals of Xochimilco, directly since the fish are capable of damaging the

eggs and larvae of the axolotls and indirectly by tilting the community structure in favor of rotifers (Gill, 2003; Nandini, Ramírez-García and Sarma, 2005), the least preferred prey of *A. mexicanum*.

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