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Feeding behaviour of larval *Ambystoma granulosum* (Amphibia: Caudata)

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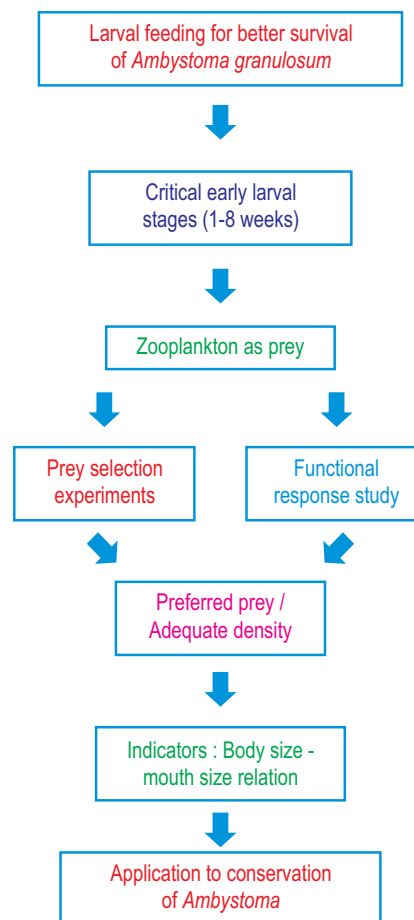
Abstract

Aim: Food availability during the early developmental stages of larval salamanders is a bottleneck for their successful breeding strategies and the conservation of amphibians. Zooplankton based diets allow salamander larvae to choose different prey types based on their size and energy gains. In this study, we quantified the patterns of prey selection and functional responses of *Ambystoma granulosum* during the larval stages (1 to 8 weeks).

Methodology: For the prey selection experiment, we offered a mixture of five crustacean zooplankton (*Alona glabra*, *Ceriodaphnia dubia*, *Heterocypris incongruens*, *Simocephalus vetulus* and *Daphnia pulex*). *A. glabra*, *C. dubia* and *H. incongruens* were used as prey for the functional response experiments.

Results: There was a direct and linear correlation between the larval length and the gape size during the study period. Prey selectivity by *A. granulosum* indicated a shift in choice of the crustacean species, where small-bodied items (e.g., *A. glabra*) were selected until the fifth week; during the later weeks, these were replaced by the larger *S. vetulus* and *D. pulex*. Functional response curves indicated that the pattern of prey consumption mainly corresponded to type II. *Ambystoma granulosum* offered *C. dubia* showed increased prey consumption with increasing larval age. However, when fed *A. glabra* the consumption increased until the sixth week but declined thereafter.

Interpretation: Studies on the feeding ecology of *A. granulosum* allowed us to understand the quantity and type of prey needed as the larvae grow. The highest prey biomass was consumed by *A. granulosum* only at the highest offered prey density. Since natural availability of prey in high levels are rare, larval *A. granulosum* possibly suffers from food deficiency and this in turn may lead to high mortality during early stages.



Introduction

The Family Ambystomatidae (Amphibia: Caudata) consists of *Ambystoma* (mole salamanders or axolotls) with 33 species distributed in the Nearctic region of which 17 are endemic to the central plateau of Mexico (Shaffer, 1984; Aguilar & Casas, 2009; Vitt & Caldwell, 2014). Many species of Mexican *Ambystoma* including *A. granulosum* Taylor, 1944 are neotenic, where adults retain juvenile characteristics due to a normal somatic development and delayed metamorphosis, giving them the advantage of reproducing in an aquatic environment (Shaffer, 1984; Gilbert, 2010; Johnson and Voss, 2013). *Ambystoma granulosum*, endemic to the State of Mexico, inhabits shallow waterbodies with narrow temperature range (14-18°C). Reproduction occurs during May to September. Ecologically, adult *A. granulosum* is a top predator and is capable of feeding on different prey items (Shaffer, 1989). However, during early larval stages, this salamander generally experiences heavy mortality in nature mainly due to a lack of appropriate diet, in addition to anthropogenic factors such as habitat degradation, contamination and the introduction of exotic species (e.g., carps) in their environment (Shaffer, 1989; Chaparro-Herrera *et al.*, 2013). Because of these reasons, this species has been rated as critically endangered by the International Union for Conservation of Nature (IUCN) and is protected by the national environmental laws (NOM-059-ECOL-2010, Secretariat of Environment and Natural Resources, 2010).

Although successful reproduction of *A. granulosum* is well-documented (Aguilar-Miguel *et al.*, 2009), the bottleneck of larval mortality still persists. This is because detailed knowledge on the food and feeding habits during the early larval stages is not known. In addition, studies from the gut contents of the field-collected specimens could not be done because that involves sacrificing individuals of critically endangered species, which is not permitted both legally and ethically. In addition, the age of the field-collected individuals is also difficult to determine.

Knowledge on the feeding behaviour of early larval stages is an important element for developing *ex situ* conservation strategies (Chaparro-Herrera *et al.*, 2011). Though it is known that larval salamanders feed on zooplankton, prey selection studies are too few to generalize for the genus *Ambystoma* (Viertel, 1992; O'Sullivan and Reynolds, 2004). Larval *Ambystoma* has also certain natural constraints such as reduced visual field, within which most zooplankton species do not naturally remain or pass through due to their low natural density (<500 ind/L) (Nandini *et al.*, 2005) and slow swimming speeds (<1 cm/s, cladocerans: Dodson and Frey, 2001). This low visual field strongly affects their prey selectivity patterns of salamanders (Chaparro-Herrera *et al.*, 2013). Even if a desired prey item is encountered, it must be available in adequate quantity so that it is energetically profitable for a predator to feed on (Lampert and Sommer, 2007). Since the amount of prey eaten

is a function of the quantity offered in the medium, most aquatic vertebrate predators show type II functional responses (Krebs, 1985). However, for most species of *Ambystoma* this information is not available.

The aim of this work was to quantify prey preference and functional responses of *A. granulosum* during their larval stages (8 weeks starting from birth).

Materials and Methods

The origin of *A. granulosum* for our study was from Chimaliapan, a Ramsar wetland in the State of Mexico. This species survives well and reproduces periodically in the Laboratory of Herpetology of our university, which donated us the fertilized eggs. They were maintained at $16 \pm 2^\circ \text{C}$ with a photoperiod of 12h:12h L:D using moderately hard water (the EPA medium). The EPA medium was prepared by dissolving $0.96 \text{ g l}^{-1} \text{ NaHCO}_3$, $0.6 \text{ g l}^{-1} \text{ CaSO}_4 \cdot 2\text{H}_2\text{O}$, $0.6 \text{ g l}^{-1} \text{ MgSO}_4$ and $0.04 \text{ g l}^{-1} \text{ KCl}$. The eggs hatched approximately after about 3 weeks. The newly hatched larvae were maintained in EPA medium (which also helps control fungal infections) and were fed ad libitum on a mixture of microcrustaceans (cladocerans and ostracods).

We cultured five species of crustacean zooplankton (*Alona glabra* Sars, 1861; *Ceriodaphnia dubia* Richard, 1894; *Heterocypris incongruens* Ramdohr, 1808; *Simocephalus vetulus* Müller, 1776 and *Daphnia pulex* Leydig, 1860) using EPA medium and the single celled green alga *Scenedesmus acutus* as the diet. Mass cultures of each these crustaceans were initiated with single parthenogenetic females. The zooplankton in mass culture tanks (2 l) received fresh algae daily at a density of $0.5 \times 10^6 \text{ cells ml}^{-1}$ and the medium was replaced every alternate day. The selection of the zooplankton species was based on their size and frequency with which they are found together with *A. granulosum* in its natural habitat, the Chimaliapan wetland (Garcia-Garcia *et al.*, 2012).

The chlorophyte *Scenedesmus acutus* (University of Texas strain) was batch-cultured in 2 l transparent bottles using Bold's basal medium and supplemented every third day with 2 g of NaHCO_3 (Borowitzka and Borowitzka, 1988). The algal cultures received continuous aeration and fluorescent illumination. Log phase alga was concentrated by centrifugation at 3000 rpm for 5 min., rinsed and re-suspended in a small volume of distilled water. The concentrated alga was stored in a refrigerator until ready to use. The algal density was estimated using a haemocytometer.

The larval feeding studies were conducted using two different experiments: functional responses and prey selectivity. For both experiments the test conditions were similar: test volume, 50 ml present in 100 ml transparent jars; pH: 6.8-7.2; temperature: 16-18°C, continuous but diffuse fluorescent illumination; four replicates per treatment; each replicate with 2 pre-starved (for 2 h) larval *A. granulosum* of known age; feeding time in the test jars: 1 h.

Prey selectivity experiments were conducted weekly while the functional response studies were carried out every fortnight (from the second week onwards) for eight weeks. For prey selectivity tests, we introduced fifty individuals for each of the five prey species (*A. glabra*, *C. dubia*, *D. pulex*, *S. vetulus* and *H. incongruens*) into the test jars containing 50 ml medium using a Pasteur pipette under a stereomicroscope (Nikon SMZ645, Japan) and then we added two pre-starved larvae of *A. granulosum* of a chosen age. The predators were allowed to feed for 1 h after which they were separated from the prey and returned to culture tank while the uneaten prey individuals in each replicate were fixed in 4% formalin for later quantification. For each prey species, the difference in the final and initial prey number was considered as the number eaten by two predators and a mean number consumed per predator was derived. Controls containing only prey species were setup but since no reproduction occurred during the short feeding time, they were not used in the data analysis.

Functional response studies were conducted using three prey species separately (*A. glabra*, *C. dubia* and *H. incongruens*). Based on preliminary feeding trials, we tested the following prey densities: 0.2, 0.4, 0.8, 1.6 and 3.2 ind ml⁻¹. As in the prey selectivity studies, here also we used four replicates per treatment, each with two pre-starved larvae of known age.

The total length and gape size of ten larval *A. granulosum* were measured weekly for eight weeks using a stereomicroscope (Nikon SMZ645) and an electronic Vernier. Using an optical microscope (Nikon Eclipse E600) to 40, 100 and 200X and camera lucida (Nikon Y-RTD) we obtained the length and width of 30 prey individuals per species and derived dry weight of cladocerans (Dumont *et al.*, 1975; Watkins *et al.*, 2011). The dry weight of *H. incongruens*, was obtained by drying 30 individuals at 60 °C for 24 hours and then weighing in a microbalance CAHN-C33. From this, we calculated the maximum weekly prey consumption by *A. granulosum*.

Data from the prey preference studies were used to derive Manly's α (Manly, 1973). We quantified the type of functional response adjusting the consumption to Michaelis-Menten curve (Krebs, 1999; Sokal and Rohlf, 2009). The differences in the biomass consumed by the larval *Ambystoma* were evaluated using a two-way analysis of variance (ANOVA) and post hoc (Tukey) tests.

Results and Discussion

Data on the length, width and dry weight of the prey species used in this work are presented in Table 1. *Alona glabra* had the lowest biomass (0.85 µg per individual), while *S. vetulus* and *D. pulex* had nearly 30-times higher dry weight. There was a direct and linear correlation between the larval length and the gape size during the study period. During the eight weeks of this

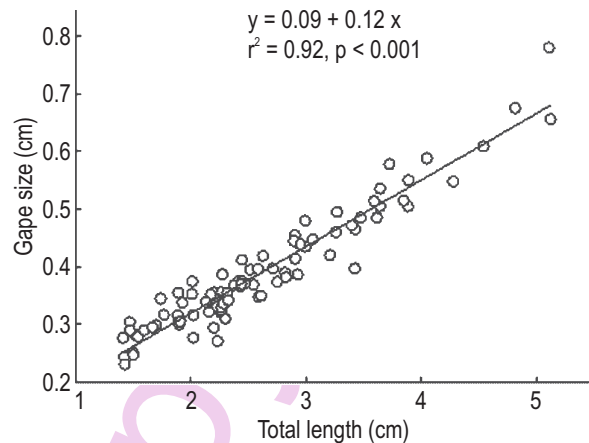


Fig. 1 : Relation between the total length (cm) and gape size (cm) of larval *A. granulosum* measured during eight weeks

study, the total length of the axolotl larvae increased from 11.13 to 37.65 mm while the gape size increased nearly proportionally (Fig. 1).

Prey selectivity by *A. granulosum* indicated a shift in a choice of crustaceans in the diet, based on the age of the larvae. Smaller prey items (e.g., *A. glabra*) were selected until the fifth week, and later, larger sized prey replaced these. On the other hand, *C. dubia* was positively selected only once during the experiments; mostly it was avoided. *Simocephalus vetulus* and *D. pulex* were frequently consumed by larval *A. granulosum* until the sixth week with a greater positive selection for *D. pulex* from the sixth week onwards (Fig. 2).

Functional response curves were fitted through Michaelis-Menten, which indicated that the pattern of prey consumption corresponded to type II response. The functional responses of *A. granulosum* fed *C. dubia* showed increased prey consumption with increasing larval age. However, when fed *A. glabra*, the consumption increased until the sixth week and declined thereafter. The consumption of *H. incongruens* decreased with increasing larval age (Fig. 3). The functional response data showed significant differences in relation to age of the larvae, prey items offered as well as their interaction (Table 2). In terms of biomass consumed (Fig. 4), it was evident that the prey consumption during the first five weeks of larvae was significantly lower (mean 0.76 mg per larva) than for other weeks (2.4 mg per larva). Larvae of 6-8 week-old mainly consumed *S. vetulus* and *D. pulex*. Notably, during latter weeks there was a greater increase in gape and total length of larval *A. granulosum*.

The prey species used in this work differed widely in terms of body length and dry weights. Compared to chydorids such as *Alona*, daphniids are much larger and carry higher biomass (Dumont *et al.*, 1975). *Heterocypris incongruens* used here is a parthenogenetic species and is a medium-sized ostracod

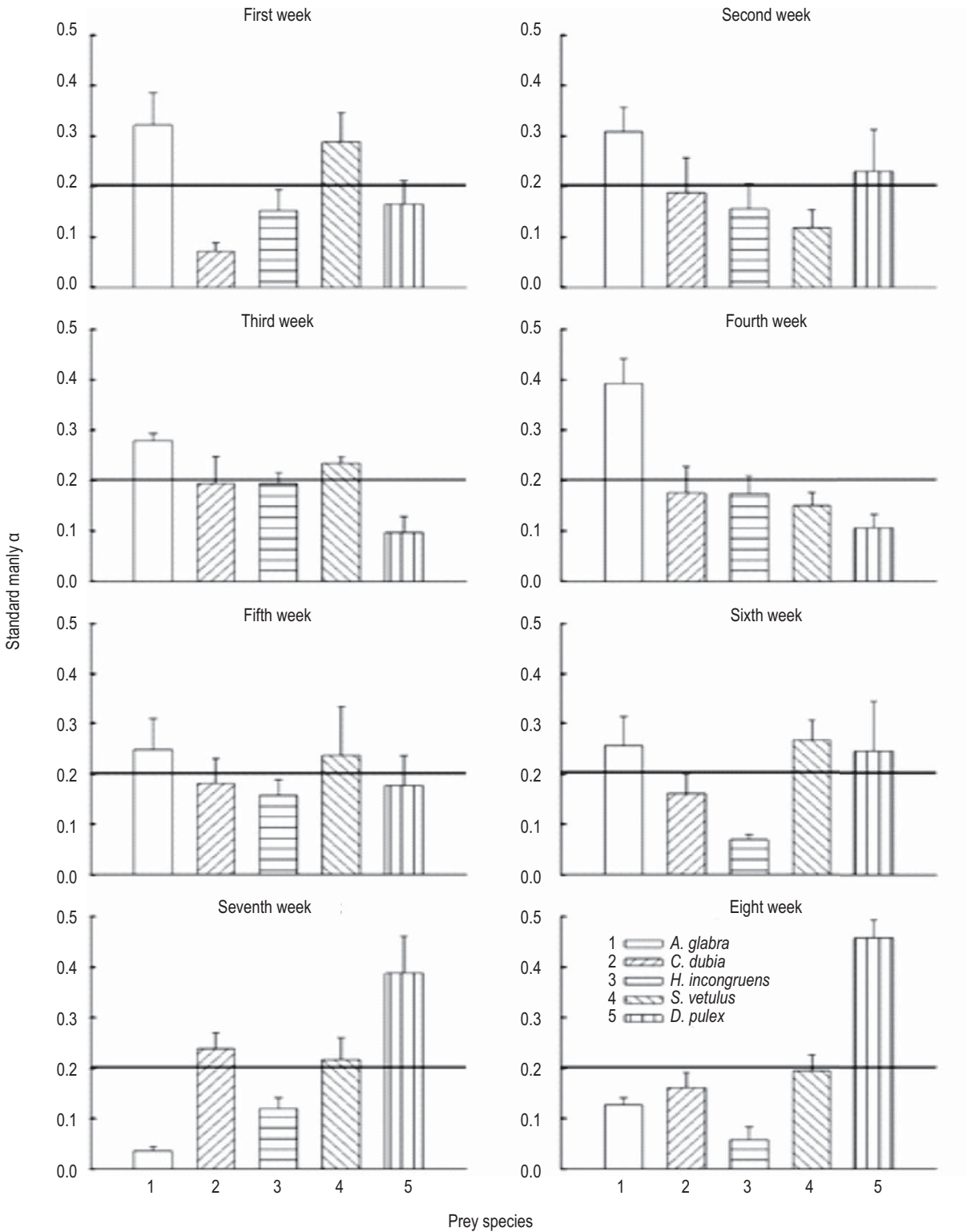


Fig. 2 : Prey selectivity (Manly's α) by the larval *Ambystoma granulosum* offered five crustacean prey species. For each week, data bars above the horizontal line shows preference for a given crustacean prey

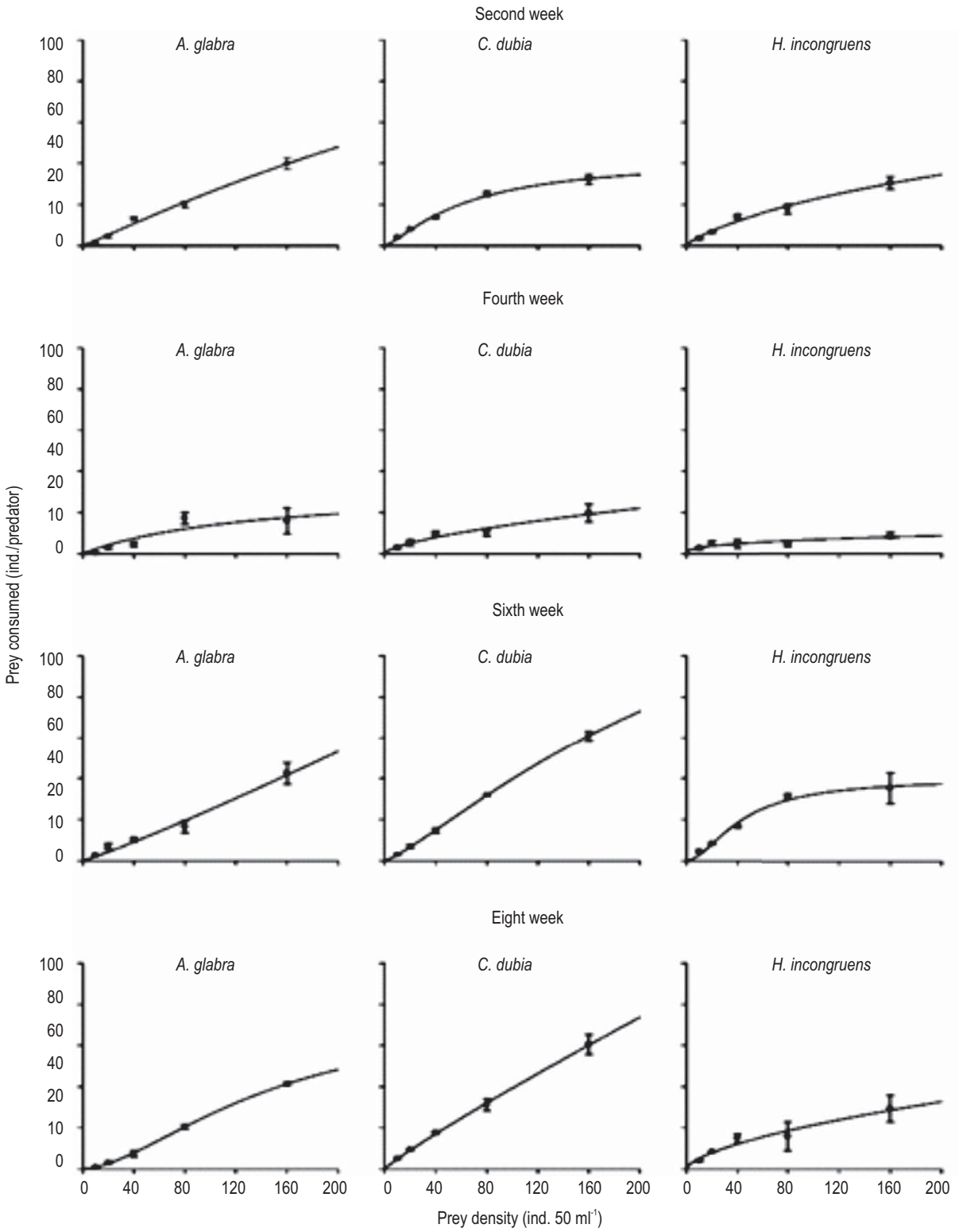


Fig. 3 : Functional response curves of *Ambystoma granulosum* on *Ceriodaphnia dubia*, *Alona glabra* and *Heterocypris incongruens*. Curves were drawn using Michaelis-Menten equation (see Material and Methods)

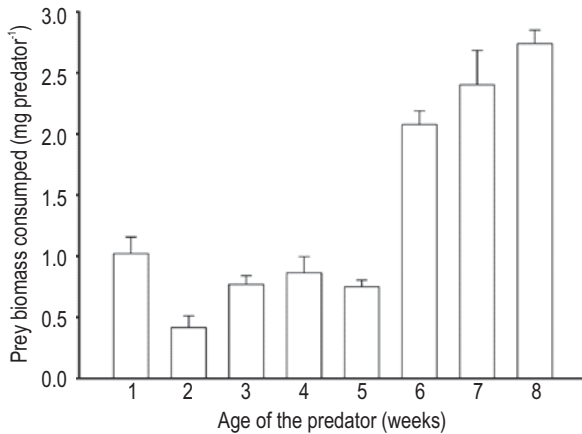


Fig. 4 : Prey biomass (mg/larva) consumed by *Ambystoma granuloseum* in relation to age (weeks). Data were based on prey selectivity experiments and expressed as the dry weight of the five zooplankton species

(Fernandez et al., 2016). All the tested prey species co-occur in nature with *A. granuloseum* (García-García et al., 2012). Confirmation of the feeding of axolotls on zooplankton in nature can be confirmed by two generally accepted methods: gut contents of field-collected specimens and offering a known density of prey species for a specific period and quantifying the uneaten prey items. The former could not be performed since *A. granuloseum* is a critically endangered species. Therefore we used the latter method. As in many other species of salamanders, there exists a linear relation between the larval length and gape size of *A. granuloseum*. This relation suggests an isometric growth during the first eight weeks of larval stages. Petránka (1989) also reported a similar relation for other species of axolotls. Chaparro-Herrera et al. (2011) have shown that larvae of *Ambystoma mexicanum* with a total length of 3.5 cm had a gape size of about 0.26 cm. In this work, for larval *A. granuloseum* of comparable body length, the gape was much higher (0.51 cm) suggesting that this species can feed on much larger prey as compared to *A. mexicanum*.

Ambystoma granuloseum showed distinct changes in the feeding behaviour with increasing larval age. The inclusion of larger prey items as they age is not limited to *A. granuloseum* alone. Many other ambystomids (e.g. *A. tigrinum*, *A. mexicanum*, *A. ordinarium*) also feed on larger cladocerans with increasing larval size. Similarly, *A. granuloseum* here predominantly consumed cladocerans but ostracods were nearly avoided. This is also similar to the previous studies which showed positive selection of cladocerans over other crustacean prey (Gillis and Lauder, 1994; Chaparro-Herrera et al., 2011; Ruiz-Martínez et al., 2014). Larval amphibians and fish that have a larger gape size at birth generally prefer larger prey (Caiola et al., 2001).

This is possibly the reason why *A. granuloseum* consumed more *A. glabra* during the first week itself and later as larvae grow,

the diet included other larger prey items such as *S. vetulus* and *D. pulex* at and after 6 weeks. It has been shown that while small individuals of the Alpine newt, *Mesotriton alpestris* and *A. tigrinum* feed on small sized prey, the larger individuals feed on both large and small prey (Denoël and Joly, 2001; Denoël et al., 2006). In this study we observed similar trends; when the larvae of *A. granuloseum* were less than a month old, they fed *A. glabra* and as they grew older they fed larger prey but still included the smaller cladocerans.

The gape size at hatching in the viviparous goodeid fish, *Allotoca dugesi* and *Ameca splendens*, as in the axolotl, *A. granuloseum*, were in the range of 360 to 2200 μm ; all of them showed a preference for cladocerans from birth (Dominguez-Dominguez et al., 2002; Peña-Aguado et al., 2009). Cladocerans are considered a good diet throughout the life cycle of neotenic ambystomatids (Ruiz-Martínez et al., 2014) due to their nutritional quality and abundance in freshwater ecosystems in which axolotls inhabit (Dodson and Frey, 2001). Since the cladoceran diversity is also high in shallow waterbodies in which *A. granuloseum* inhabits (Viertel, 1992; García-García et al., 2012), this would permit the axolotls to choose their prey in the environment.

Further, this study showed that chydorid species such as *A. glabra* are essential for *A. granuloseum* larvae during the first six weeks of hatching, which is the critical period for larval survival (Zambrano et al., 2003). These results agree with those reported in Chaparro-Herrera et al., (2013) where *Ambystoma mexicanum* preferred chydorids. However, unlike *A. mexicanum*, *A. granuloseum* did not prefer ostracods. The consumption of higher biomass by feeding on larger cladocerans (*S. vetulus* and *D. pulex*) in the diet of *A. granuloseum* beyond the 6 weeks of age indicates an ontogenetic shift in the prey selection to meet high energy requirements (Prieto and Atencio, 2008). The lack of preference for *Heterocypris incongruens* in this study was possibly due to near absence of ostracods in natural ponds in which *A. granuloseum* occurs. In Chimaliapan wetlands, *A. granuloseum* naturally occurs with *C. dubia*, *S. vetulus* and *D. pulex* (García-García et al., 2012) which are possibly the preferred food for ambystomatid larvae (McCoy and Savitzky, 2004; Chaparro-Herrera et al., 2011) as also observed here. Larval *A. granuloseum* did not invest its energy in capturing the ostracods due to the low energetic returns since the ostracod shell is resistant to digestion by the larval fish and amphibians (Juanes and Conover, 1994). In addition, *A. granuloseum* has rudimentary teeth, which are only designed to capture food but not to tear or chew it and thus they swallow their food whole (Fenske et al., 1995). Swallowing ostracods whole may not result in higher energy gain since the shell contains low calorific value (Benoy et al., 2002).

Studies on the feeding ecology of *A. granuloseum* allow us to understand the quantity and type of prey needed as the larvae

Table 1 : Morphometry (length and width in μm) and dry weight of zooplankton prey used in the experiments. Shown are the mean \pm standard error based on 30 individuals per species

Prey species	Length (μm)	Width (μm)	Individual dry weight (μg)
<i>Alona glabra</i>	361 \pm 2	249 \pm 1	0.85
<i>Ceriodaphnia dubia</i>	834 \pm 4	617 \pm 4	7
<i>Heterocypris incongruens</i>	610 \pm 2	369 \pm 2	24
<i>Simocephalus vetulus</i>	1570 \pm 17	1046 \pm 15	26
<i>Daphnia pulex</i>	2161 \pm 28	1186 \pm 18	26

Table 2 : Results of two-way ANOVA performed on prey items consumed by *Ambystoma granulosum* in relation larval age, zooplankton species type and their interaction. DF: degrees of freedom, SS: sum of squares, MS: mean square, F: F-ratio, P: probability

Source of variation	DF	SS	MS	F	P
Larval age (weeks A)	3	564929	188309	12	<0.001
Prey items (B)	2	2061215	1030607	65.8	<0.001
Interaction of A & B	6	370749	61791	3.9	0.007
Residual	24	376004	15666		

grow. Changes in the feeding behaviour of *A. granulosum* in this work were analyzed using prey selectivity and the functional response experiments (Van Der Meer and Ens, 1997). As in many other previous studies, the larval *A. granulosum* continued to consume higher prey quantity with increasing age. Functional response analyses showed a type II curve. Type II curves show an increase in prey consumption with increasing availability of prey items in the medium until a certain level beyond which prey consumption tapers off (Trexler *et al.*, 1988). The type II curves are common in aquatic vertebrate predators including *A. mexicanum* (Chaparro-Herrera *et al.*, 2011). Gill and Hart (1994) and Juanes and Conover (1994) state that aquatic predators select prey that would contribute to higher energy gain. In addition, while choosing the prey type, the predators must incur low energy loss during capture and with high rates of capture success (Gill and Hart, 1994; Juanes and Conover, 1994). This trend was also evident here in the functional response experiment where during early stages, *A. granulosum* fed *A. glabra* and later on, as they grew, the larvae shifted to larger prey such as *D. pulex*.

The predators consumed prey items in terms of biomass, from <0.5 to >2.5 mg ind⁻¹, depending on the larval age. This quantity is much lower than fish of comparable age (Juanes and Conover, 1994). This is related to the behaviour of *A. granulosum*, which is a passive hunter. In nature too, *A. granulosum* as a predator spends less time in actively foraging on prey items. In addition, the highest prey biomass was consumed only at the highest offered prey density. Natural availability of such high prey levels are rare. This suggests that larval *A. granulosum* suffers food deficiency in nature, especially in Chimaliapan wetlands, where the rotifers dominate over crustaceans (García-García *et al.*, 2012).

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