

## Vision is not necessary for size-selective zooplanktivory in aquatic salamanders

MICHAEL J. LANNOO<sup>1</sup>

Department of Anatomy, Dalhousie University, Halifax, N.S., Canada B3H 4H7

Received October 1, 1986

LANNOO, M. J. 1986. Vision is not necessary for size-selective zooplanktivory in aquatic salamanders. *Can. J. Zool.* **64**: 1071–1075.

Vision is usually implicated as the sensory modality employed in size-selective zooplanktivory by aquatic vertebrates. I tested this generalization for nocturnally active salamanders by offering sighted and enucleated *Ambystoma maculatum* larvae a choice of large vs. small, or normally coloured vs. artificially darkened *Daphnia*, a natural prey. Salamanders in all treatments took the largest *Daphnia* and exhibited similar high feeding rates. There was no preference for artificially darkened *Daphnia*, as would be expected if visual cues predominate. Together these results indicate that vision is not exclusively responsible for size-selective predation by nocturnal salamanders. The often stated or implied assumption that size selectivity indicates visual predation in aquatic vertebrates should thus be questioned.

LANNOO, M. J. 1986. Vision is not necessary for size-selective zooplanktivory in aquatic salamanders. *Can. J. Zool.* **64**: 1071–1075.

Les vertébrés aquatiques utilisent ordinairement leur sens de la vue pour choisir des proies en fonction de la taille dans le zooplancton. J'ai mis cette théorie à l'épreuve chez des salamandres actives la nuit, en offrant un choix de petites ou de grosses proies ou un choix *Daphnia*, une proie naturelle, de couleurs normales ou de *Daphnia* colorées artificiellement à des larves rendues aveugles et des larves intactes d'*Ambystoma maculatum*. Dans toutes les expériences, les salamandres ont choisi les plus grosses daphnies et leur taux d'alimentation s'est avéré semblable et élevé dans tous les cas. Il n'y avait pas de préférence pour les daphnies plus foncées colorées artificiellement comme on devrait s'y attendre si les salamandres chassaient à vue. Ces résultats indiquent donc que la vision n'est pas exclusivement responsable de la prédation en fonction de la taille chez les salamandres nocturnes. La théorie souvent invoquée selon laquelle la sélectivité des proies suppose une prédation par chasse à vue chez les vertébrés aquatiques est remise en question.

[Traduit par la revue]

### Introduction

Aquatic vertebrates feed on zooplankton by one of two methods: they either take zooplankters individually and are size selective (normally taking the largest individuals available) or they filter feed and take a broad range of zooplankton sizes (Zaret 1980; Greene 1985). The former method is virtually always associated with diel activity patterns, the latter frequently with nocturnality.

Salamander larvae prey heavily on zooplankton (e.g., Dineen 1955; Lannoo and Bachmann 1984a), feeding on them individually and taking the largest animals available (Dodson and Dodson 1971; Branch and Altig 1981). It is commonly assumed that vision mediates this predation pattern (Anderson 1968; Dodson and Dodson 1971; Sprules 1972; Zaret 1980). However for this to be true salamanders should exhibit diel feeding patterns. This, in fact, is not the case. It is well known that many aquatic salamanders are nocturnal (e.g., Noble 1931; Anderson and Graham 1967; Joly and Caillère 1983). The exceptions are in areas where diel predators are scarce (Dodson and Dodson 1971; Sprules 1972) or where nocturnal predation is especially heavy (Holomuzki 1984).

How, then, do nocturnal salamanders detect zooplankton? Can salamanders be size selective if they cannot use vision? Or, conversely, if salamanders are size selective nocturnally, can the assumption be justified that size selection in diel populations is visually mediated?

If visual cues are essential, or even most important, to size-selective predation, three predictions should hold true for sighted salamanders feeding in light conditions compared with enucleated salamanders and dark conditions: (i) their feeding

rates should be higher (Peckarsky 1982), (ii) they should select larger prey (Dodson and Dodson 1971), and (iii) they should select darker, more visible prey (Sprules 1972). To test these predictions I offered sighted and enucleated larval *Ambystoma maculatum* in light or dark conditions a choice of large and small or normal and coloured *Daphnia* (a natural prey), and recorded prey type and number taken.

### Methods

*Ambystoma maculatum* eggs and larvae were collected from Heart-shaped Pond in Halifax County, Nova Scotia, Canada (44°40' N, 93°40' W). Field-collected eggs were hatched in the laboratory. Larvae were raised on a mixture of live *Daphnia magna* and frozen brine shrimp (*Artemia salina*) and in accordance with guidelines set by the Canadian Council on Animal Care (1984). *Daphnia* were cultured in my laboratory from stocks maintained at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia.

A total of 40 *Ambystoma maculatum* larvae were tested. Laboratory-raised salamanders were kept on a 12:12 h light:dark cycle centered at 1400 at 21 ± 1° C. Field-collected larvae (SVL 21.0–26.0 mm) were tested within 24 h of capture and therefore not fed (test 1, below). Laboratory-raised larvae (SVL 10.5–13.0 mm) were not fed a minimum of 16 h before testing (tests 2, and 3, below). To remove competitive effects, only one larva per container was used in each experiment. Containers were rectangular and made of clear glass (10 × 8 × 6 cm, test 1) or opaque plastic (13.5 × 10 × 7 cm, tests 2 and 3). Glass containers were filled with 200 mL of aged tap water to a depth of approximately 25 mm; plastic containers were filled with 250 mL of water to a depth of approximately 20 mm. All salamanders were tested between 1000 and 1600 at 21 ± 1° C and were large enough to ingest the largest *Daphnia* offered to them. The "light" condition was normal laboratory fluorescent light, the "dark" condition was complete darkness in a photographic darkroom. Salamanders were allowed to acclimate to darkness for at least 20 min before testing began. I judged this acclimation time to be sufficient because in nature most salamanders in this population begin feeding each day at dusk or immediately

<sup>1</sup>Current address: Department of Anatomy, Faculty of Health Sciences, University of Ottawa, 451 Smyth Road, Ottawa, Ont., Canada K1H 8M5.

after darkness sets in. *Daphnia* concentrations offered to salamanders were within the range found in nature (Janssen 1980; Lannoo and Bachmann 1984b).

Salamanders were enucleated after first being anesthetized in 0.03% MS 222 (tricaine methanesulfonate). Enucleation was done with forceps and iridectomy scissors. The wounds were cauterized with a Hyrefractor cauterizing unit set at low voltage. Enucleated salamanders were tested a minimum of 24 h after surgery. Two of the 16 enucleated larvae did not subsequently feed and were excluded from the tests. During experiments in light conditions I made additional behavioural observations on both sighted and enucleated salamanders. These observations caused no visible disturbance to the animals. Parametric and nonparametric statistics were used, depending on whether data were distributed normally or nonnormally (Snedecor and Cochran 1967).

*Test 1: Sighted A. maculatum feeding on Daphnia in a range of sizes in light and dark conditions*

The following questions were addressed in this test: (i) Are salamanders feeding in light size selective? (ii) Are salamanders in dark size selective? (iii) Are there selectivity differences between salamanders feeding in light and dark conditions? (iv) Are there feeding-rate differences between salamanders feeding in light and dark conditions?

Twelve field-collected *A. maculatum* were tested, six each in light and dark conditions. One trial was conducted per salamander and all salamanders were tested simultaneously. Approximately 60 variously sized *Daphnia* (range, 0.8–2.4 mm carapace length) were placed in 12 containers. Containers were randomly assigned to light or dark conditions and salamanders were randomly assigned to containers. Salamanders fed for 30 min, after which they were immediately killed and preserved in 10% formalin (which did not cause regurgitation of stomach contents). *Daphnia* that had not been eaten remained in each container and were filtered from the water then killed and preserved in 10% formalin. Salamander stomachs were removed, opened, and ingested *Daphnia* were counted and their sizes were measured (carapace length) with a calibrated ocular micrometer. Likewise, *Daphnia* not ingested were counted and measured.

*Test 2: Sighted and enucleated A. maculatum feeding on large and small Daphnia in light and dark conditions*

The following questions were addressed in this test: (i) Is there a difference in sizes and total numbers of *Daphnia* ingested between the sighted–light treatment and the other treatments? (ii) Is there a difference in sizes and total numbers of *Daphnia* ingested between sighted–dark and enucleated–dark treatments (surgical control)? (iii) Is there a difference in sizes and total numbers of *Daphnia* ingested between enucleated–light and enucleated–dark treatments (control for diurnal differences in prey behaviour)?

The experimental design was a 2 × 2 factorial test comparing sighted and enucleated salamanders in light and dark conditions. Sixteen *A. maculatum* larvae, 4 per treatment, were used. Salamanders were each fed 20 large (2.0–2.4 mm carapace length) and 20 small (0.8–1.5 mm carapace length) *Daphnia*. Salamanders were tested in two trials, 20 min per trial. After each trial large and small *Daphnia* remaining were removed and counted; numbers ingested for each prey group were obtained by subtraction from 20 (original prey number). Totals for the two trials were added and these single numbers were used in the statistical analyses. To compare size selectivity between treatments, for each salamander numbers of large *Daphnia* ingested were divided by total numbers of *Daphnia* ingested (large plus small *Daphnia*) to create a size index. The greater the size index value the more large *Daphnia* were taken. This size index produces values between 0 and 1 and was used in the between-treatments statistical analyses. Results comparing size indices were tested using nonparametric Mann–Whitney *U*-tests.

I decided a priori to determine the effect of enucleation on feeding performance by comparing data from sighted–dark treatments with enucleated–dark treatments. To test for possible light–dark differences in *Daphnia* swimming or predator-avoidance behaviour, data from enucleated–light treatments were compared with enucleated–dark

treatments. In the statistical analyses for these control tests, data from enucleated–dark treated salamanders were used twice. While this procedure in a strict sense increases the chance of making a type II error (accepting a false hypothesis), because I decided to use these data a priori and because I collected all these data at about the same time, I felt that they could be used for both control tests with confidence.

*Test 3: Sighted and enucleated A. maculatum feeding on normally coloured and artificially darkened Daphnia in light conditions*

In this test prey-colour preferences and feeding rates were compared for sighted and enucleated salamanders. This test then addressed the role of vision in diel feeding in these salamanders.

Six sighted and six enucleated *A. maculatum* larvae were each allowed to feed for 20 min on 10 large (2.0–2.4 mm carapace length) normally coloured *Daphnia* and 10 large *Daphnia* kept overnight in a suspension of India ink particles. India ink has been frequently used to darken *Daphnia* in tests involving visual predation on zooplankton by fish (e.g., Zaret 1980). To the human eye ink-exposed *Daphnia* were considerably darker than normal *Daphnia* and appeared to behave normally. Because test 2 results showed no deleterious effects of enucleation surgery on feeding performance (see Results), no sham surgical controls were done. A colour index was calculated in the manner of the size index in test 2, by dividing numbers of ink-darkened *Daphnia* ingested by total *Daphnia* ingested. Nonparametric statistics were used in the analysis. Prey-colour preferences and feeding rates were compared for sighted and enucleated salamanders.

## Results

### Test 1

*Ambystoma maculatum* larvae in light conditions were size selective (Table 1, a). Salamanders in dark conditions were also size selective (Table 1, b). Salamanders in dark conditions took larger prey than those in light conditions but this difference was not significant when ingested prey sizes were corrected for available prey sizes (by subtracting mean size of prey available from prey ingested; Table 1, c). Feeding rates were nearly identical for salamanders in light and dark conditions both in terms of absolute numbers of prey ingested (Table 1, d) and percent available prey ingested (Table 1, e).

### Test 2

All salamanders, sighted and enucleated, in light and dark conditions, fed similarly. Most important to the questions addressed in this test, there was no significant difference in size index between the sighted–light treatment and the other treatments (Table 2, a). Feeding rates were higher for animals in the sighted–light treatment, although these differences were not significant (Table 2, b).

There was no significant difference in size index between sighted–dark and enucleated–dark treatments (Table 3, a). Feeding rates were unexpectedly higher for enucleated than sighted salamanders (Table 3, b). These results indicate that enucleation surgery had no deleterious effects on feeding performance.

There was no significant difference between enucleated–light and enucleated–dark treatments in size index (Table 4, a) or feeding rate (Table 4, b). These results indicate no light–dark differences in salamander feeding performance due to diurnal differences in zooplankton swimming or predator avoidance behaviour.

### Test 3

Sighted and enucleated salamanders fed similarly on normally coloured and artificially darkened *Daphnia*. The most important result in terms of the questions addressed in this test was that both enucleated and sighted salamanders took coloured prey in the proportion that they were available (Table 5, a). Feeding

TAB  
lig  
Com  
Trea  
(a) I  
(b) I  
(c) I  
(d) I  
(e) I  
Nor  
avail  
ingest  
subtra  
rates t  
Daphn  
using  
less th  
↑Fed  
TAB  
larva  
condi  
(a) S  
(b) N  
Nor  
visual  
made u  
values,  
\*Fed  
rates  
signifi  
Th  
light  
to siz  
rates  
have  
they s  
1972)  
rates  
(Tabl  
avail  
colou

TABLE 1. Feeding performance of *Ambystoma maculatum* larvae in light and dark conditions fed *Daphnia* in a range of sizes (test 1)

Comparison: Treatment/Measure	n	$\bar{x} \pm SE$	P
(a) Light/Size			
Ingested	6	1.45 ± 0.02 mm	
Available	6	1.23 ± 0.01 mm	<0.0001*
(b) Dark/Size			
Ingested	6	1.63 ± 0.02 mm	
Available	6	1.33 ± 0.01 mm	0.003*
(c) Light vs. dark/Ingested-available			
Light	6	0.20 ± 0.04 mm	
Dark	6	0.32 ± 0.05 mm	0.20
(d) Light vs. dark/No. ingested†			
Light	6	25.3 ± 7.19	
Dark	6	25.5 ± 5.12	0.99
(e) Light vs. dark/% ingested†			
Light	6	37.2 ± 6.99	
Dark	6	33.9 ± 6.35	0.75

NOTE: Statistical comparisons *a* and *b* test *Daphnia* sizes ingested against *Daphnia* available in light and dark treatments, respectively. Test *c* compares sizes of *Daphnia* ingested in light and dark treatments after correcting for sizes of *Daphnia* available (by subtracting sizes of prey available from prey ingested). Tests *d* and *e* compare feeding rates between light and dark treatments in terms of number and percent of available *Daphnia* ingested. Means and standard errors are given; statistical comparisons were done using pooled *t*-tests (Snedecor and Cochran 1967). Asterisks indicate probability values less than 0.05.

†Feeding rates for a 30-min period.

TABLE 2. A comparison of the feeding performance of *A. maculatum* larvae with visual cues available to them (i.e., sighted animals in light conditions) to larvae unable to use vision (enucleated animals and dark conditions) feeding on large and small *Daphnia* (test 2)

Comparison	n	$\bar{x} \pm SE$ (range)	P
(a) Size index			
Sighted, light	4	0.78 (0.73–0.86)	
Enucleated or dark	12	0.76 (0.62–1.0)	>0.05
(b) Numbers ingested*			
Sighted, light	4	22.8 ± 5.9	
Enucleated or dark	12	14.9 ± 2.6	0.18

NOTE: Statistical test *a* compares size indices (formula in text) between visual and non-visual treatments; test *b* compares total numbers of *Daphnia* ingested. Comparisons were made using (a) Mann-Whitney *U*-tests and (b) pooled *t*-tests. In *a*, ranges are given for the values, which were not normally distributed.

\*Feeding rates adjusted for a 30-min period.

rates were higher for sighted animals but this difference was not significant (Table 5, *b*).

### Discussion

Three predictions should have held true for sighted animals in light compared with other treatments if visual cues are important to size-selective predation in aquatic urodeles: (i) their feeding rates should have been higher (Peckarsky 1982), (ii) they should have selected larger prey (Dodson and Dodson 1971), and (iii) they should have selected the darker, more visible prey (Sprules 1972). The data here support none of these predictions. Feeding rates were similar whether salamanders used vision or not (Tables 1–5); salamanders always fed on the largest *Daphnia* available (Tables 1–4); and salamanders fed on normal and coloured prey in the ratio that they were available (Table 5).

TABLE 3. Results of control testing the effect of enucleation surgery on feeding performance (test 2): in this test sighted vs. enucleated *A. maculatum* larvae fed in dark conditions on large and small *Daphnia*

Comparison	n	$\bar{x} \pm SE$ (range)	P
(a) Size index			
Sighted, dark	4	0.82 (0.71–1.0)	
Enucleated, dark	4	0.79 (0.67–0.92)	>0.05
(b) Numbers ingested*			
Sighted, dark	4	9.0 ± 1.2	
Enucleated, dark	4	16.8 ± 6.6	0.29

NOTE: Statistical test *a* compares size indices of prey taken between sighted and enucleated salamanders; test *b* compares total numbers of *Daphnia* ingested for both groups. Comparisons were made using (a) Mann-Whitney *U*-tests and (b) pooled *t*-tests. In *a*, ranges are given for the values, which were not normally distributed.

\*Feeding rates adjusted for a 30-min period.

TABLE 4. Results of control testing for possible diurnal differences in *Daphnia* swimming or predator-avoidance behaviour that could affect salamander feeding performance (test 2): in this test enucleated salamanders fed in light and dark conditions on large vs. small *Daphnia*

Comparison	n	$\bar{x} \pm SE$ (range)	P
(a) Size index			
Nucleated, light	4	0.70 (0.62–0.75)	
Enucleated, dark	4	0.79 (0.67–0.92)	>0.05
(b) Numbers ingested*			
Enucleated, light	4	19.0 ± 3.3	
Enucleated, dark	4	16.8 ± 6.6	0.77

NOTE: Test *a* compares size indices between salamanders in light and dark treatments; comparison *b* tests total numbers of *Daphnia* ingested for both groups. Comparisons were made using (a) Mann-Whitney *U*-tests and (b) pooled *t*-tests. In *a*, ranges are given for the values, which were not normally distributed.

\*Feeding rates adjusted for a 30 min period.

TABLE 5. Results of a test designed to assess the role of prey visibility in prey detection and ingestion by *A. maculatum* larvae (test 3): in this test sighted and enucleated salamanders in light conditions were given a choice between normally coloured and artificially darkened *Daphnia*

Measure and treatment	n	$\bar{x} \pm SE$ (range)	P
(a) Colour index			
Sighted	6	0.45 (0.25–0.58)	
Enucleated	6	0.44 (0.33–0.57)	>0.05
(b) Numbers ingested*			
Sighted	6	9.5 ± 2.0	
Enucleated	6	6.0 ± 2.0	0.25

NOTE: Comparison *a* considers colour index (calculated similar to the size index; see text) between sighted and enucleated groups; test *b* considers numbers of *Daphnia* ingested. Comparisons were made using (a) Mann-Whitney *U*-tests or (b) pooled *t*-tests.

\*Feeding rates adjusted for a 30-min period.

From these results I conclude that not only is vision not being used in nocturnal feeding by these salamanders, but that vision may not be as important in diel feeding as initially suspected (Nicholas 1922; Anderson 1968; Dodson and Dodson 1971; Sprules 1972; Zaret 1980). This conclusion agrees with *Ambystoma* growth data collected by Detwiler and Copenhaver (1940) who observe, "...the absence of eyes or of light both fail to affect...growth, ...larvae feed just as well without eyes in the dark as they do in the light with eyes" (p. 245).

During the course of my light-condition experiments I observed three behavioural tendencies of salamanders feeding on *Daphnia* that provide further insights into these results. First, sighted animals oriented towards and approached prey up to approximately 3 to 4 cm (~1.5 to 2.0 body lengths) away (see also Hoff et al. 1985), whereas enucleated salamanders oriented towards and approached prey only within approximately 2 cm. Second, both sighted and enucleated salamanders ignored small prey and chose large over small prey when both were near. Thirdly, rectangular experimental enclosures caused prey to aggregate in corners (see also Bovbjerg 1975), where both sighted and enucleated salamanders fed most successfully.

From the first observation, it appears that vision plays a role in far-field prey detection by these animals, but in my experimental enclosures this did not translate into more prey, or more visible prey, being selected. Prey were taken in the near field and visual cues did not greatly affect this behaviour. This observation does indicate visual cues may become more important as prey density decreases and prey become less numerous and more difficult to find. The second observation, that both sighted and enucleated salamanders chose large over small *Daphnia*, confirms that in the near field, large prey are selected over small prey. This observation is, however, equivocal regarding which sensory systems are employed. The third observation suggests that enucleated salamanders are as good as sighted animals in locating prey aggregations. However, salamanders, like *Daphnia*, may simply be following container edges to their corners rather than following the *Daphnia* per se.

The conclusions I draw here about the potential unimportance of vision in salamander predation conflict with those of Nicholas (1922), who conducted experiments similar to mine. Nicholas fed sighted, enucleated, olfactory-deprived, and enucleated and olfactory-deprived *A. tigrinum* larvae earthworm pieces and concluded that visual cues are most important in prey detection, followed by olfactory cues, followed by mechanical cues. (Before Hetherington and Wake (1979) and Fritsch (1981) it was generally not known that caecilian and urodele amphibians have electroreceptors.) However, while laboratory *Ambystoma* will readily feed on worm pieces, liver pieces, frozen brine shrimp, and other dead prey, in the field they feed predominantly, if not exclusively, on live prey. The differences between Nicholas' results and mine probably reflect the fact that salamanders use different senses to feed on intact-alive vs. wounded or dead prey.

The role of olfaction in detecting zooplankton is also questionable. Salamanders tend to be "sit and wait" predators and take zooplankters individually (Anderson and Graham 1967; Hassinger et al. 1970; Branch and Altig 1981; Lannoo and Bachmann 1984b; Hoff et al. 1985). Because molecules diffuse through water slower than zooplankton usually swim, any scent given off by a zooplankter will often reach a stationary salamander after the zooplankter is past the salamander and out of striking distance (Peckarsky 1982). I ran a preliminary test examining the role of olfaction in zooplanktivory. I offered three enucleated *A. maculatum* larvae each 10 large and 10 small *Daphnia* that had been heat killed and then cooled to room temperature immediately before testing. This treatment eliminated all prey motion but presumably retained olfactory cues. Larvae were allowed to feed for 20 min and I recorded prey size and number ingested. Numbers of *Daphnia* ingested were greatly reduced; salamanders took a total of only six prey, a feeding rate 4.2 times lower than the feeding rates of animals in test 2, where live large and small *Daphnia* were prey. Keeping

in mind this small sample size, salamanders were also not size selective, taking three large and three small prey. These results suggest that olfaction alone is not sufficient for the observed feeding rates and size selection in salamanders. Indeed, Detwiler and Copenhaver (1940) found that *Ambystoma* larvae deprived of both eyes and nasal placodes as embryos responded by snapping at food and inanimate objects in motion. They state (p. 243), "We wish to emphasize the fact that in the absence of both eyes and the nasal placodes the larvae feed as well as do normal animals."

Factors other than vision may correlate positively with prey body size, such as mechanical water disturbances prey make as they swim (e.g., Gerritsen and Strickler 1977) and electrical field changes around prey due to their muscle contractions, and may be sensed by salamanders. Scharrer (1932), Gorner et al. (1984), and Elepfandt (1982, 1984) have shown that neuromasts, and Himstedt et al. (1982) have shown that ampullary organs, are used by amphibians to detect prey. It is possible that these lateral line systems, either singly or in combination, are used by nocturnal salamanders to detect zooplankton.

By suggesting that lateral line organs are being used by nocturnal salamanders to detect zooplankton I do not wish to diminish the importance of vision and olfaction in detecting other prey types or for determining other behaviours. While salamanders feed predominantly on zooplankton (Dineen 1955; Freda 1983) and exhibit a specialized floating behavior to do so (Anderson and Graham 1967; Branch and Altig 1981; Lannoo and Bachmann 1984b), they also feed on snails, oligochaetes (Dodson and Dodson 1971; Brophy 1980; Lannoo and Bachmann 1984a), and amphibian eggs (Grusser-Cornehls and Himstedt 1976) for which olfactory and visual cues would likely be most important (Joly and Caillère 1983). In addition, aquatic adults exhibit other behaviours such as courtship and mating that probably depend on vision and olfaction (e.g., Halliday and Sweatman 1976). However, to generalize, given the numerical and volumetric predominance of zooplankton and other small prey found in the stomachs of salamander larvae and the salamander tendency towards nocturnality, it may well be that visual and olfactory cues are of secondary importance to prey detection in these animals.

#### Acknowledgements

The Anatomy Department at Dalhousie University kindly provided me with the laboratory space, darkroom, and word processing equipment used during this project. R. Wassersug, J. Holomuzki, and D. Rowe thoughtfully reviewed earlier drafts of this manuscript. This study was supported by a Sigma Xi Grant-in-Aid of Research and an NSERC grant to R. Wassersug.

- ANDERSON, J. D. 1968. A comparison of the food habits of *Ambystoma macrodactylum sigillatum*, *Ambystoma macrodactylum croceum*, and *Ambystoma tigrinum californiense*. *Herpetologica*, 24: 273-284.
- ANDERSON, J. D., and R. E. GRAHAM. 1967. Vertical migration and stratification of larval *Ambystoma*. *Copeia*, 1967: 371-374.
- BOVBJERG, R. V. 1975. Dispersal and dispersion of pond snails in an experimental environment varying to three factors singly and in combination. *Physiol. Zool.* 48: 203-215.
- BRANCH, L., and R. A. ALTIG. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. *Copeia*, 1981: 870-873.
- BROPHY, T. E. 1980. Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. *J. Herpetol.* 14: 1-6.
- CANADIAN COUNCIL ON ANIMAL CARE. 1984. Guide to the care and use of experimental animals. Canadian Council on Animal Care, Ottawa, Ont.

- DETWILER, S. R., and W. M. COPENHAVER. 1940. The growth and pigmentary responses of eyeless *Amblystoma* embryos reared in light and in darkness. *Anat. Rec.* 76: 241-257.
- DINEEN, C. F. 1955. Food habits of the larval tiger salamander (*Amblystoma tigrinum*). *Proc. Indiana Acad. Sci.* 65: 231-233.
- DODSON, S. T., and V. E. DODSON. 1971. The diet of *Amblystoma tigrinum* larvae from western Colorado. *Copeia*, 1971: 614-624.
- ELEPFANDT, A. 1982. Accuracy of taxis water response to water waves in the clawed toad (*Xenopus laevis* Daudin) with intact or with lesioned lateral line system. *J. Comp. Physiol.* 148: 535-545.
- . 1984. The role of ventral lateral line organs in water wave localization in the clawed toad (*Xenopus laevis*). *J. Comp. Physiol.* 154: 773-780.
- FREDA, J. 1983. Diet of larval *Amblystoma maculatum* in New Jersey. *J. Herpetol.* 17: 177-179.
- FRITZSCH, B. 1981. The pattern of lateral line afferents in urodeles. A horseradish peroxidase study. *Cell Tissue Res.* 218: 581-594.
- GERRITSEN, J., and J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.* 34: 73-82.
- GORNER, P., P. MOLLER, and W. WEBER. 1984. Lateral-line input and stimulus localization in the African clawed toad, *Xenopus* sp. *J. Exp. Biol.* 108: 315-328.
- GREENE, C. H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. *J. Plankton Res.* 7: 35-40.
- GRUSSER-CORNEHLS, U., and W. HIMSTEDT. 1976. The urodele visual system. In *The amphibian visual system: a multidisciplinary approach*. Edited by K. V. Fite. Academic Press, New York. pp. 203-266.
- HALLIDAY, T. R., and H. P. SWEATMAN. 1976. To breathe or not to breathe; the newt's problem. *Anim. Behav.* 24: 551-561.
- HASSINGER, D. D., J. D. ANDERSON and G. H. DALRYMPLE. 1970. The early life history and ecology of *Amblystoma tigrinum* and *Amblystoma opacum* in New Jersey. *Am. Midl. Nat.* 84: 474-495.
- HETHERINGTON, T. E., and M. H. WAKE. 1979. The lateral line system in larval *Ichthyophis* (Amphibia: Gymnophiona). *Zoomorphologie*, 93: 209-225.
- HIMSTEDT, W., KOPP, J. and W. SCHMIDT. 1982. Electroreception guides feeding behavior in amphibians. *Naturwissenschaften*, 69: 552.
- HOFF, K. S., M. J. LANNOO, and R. J. WASSERSUG. 1985. Kinematics of midwater prey capture by *Amblystoma* (Caudata: Amblystomatidae) larvae. *Copeia*, 1985: 247-251.
- HOLOMUZKI, J. 1984. Influence of invertebrate predation on diel patterns of habitat use by larval salamanders. Abstracts of the Joint Meeting, American Society of Ichthyologists and Herpetologists, Society for the Study of Amphibians and Reptiles, Herpetologists' League, Norman, OK.
- JANSSEN, J. 1980. Alewives (*Alosa pseudoharengus*) and ciscos (*Coregonus artedii*) as selective and nonselective predators. In *Evolution and ecology of zooplankton communities*. Edited by W. C. Kerfoot. University Press of New England, Hanover, NH, and London, England. pp. 580-586.
- JOLY, P., and L. CAILLÈRE. 1983. Smelling behaviour of urodele amphibians in an aquatic environment: study in *Pleurodeles waltl*. *Acta Zool. (Stockholm)*, 64: 169-175.
- LANNOO, M. J., and M. D. BACHMANN. 1984a. Aspects of cannibalistic morphs in a population of *Amblystoma t. tigrinum* larvae. *Am. Midl. Nat.* 112: 103-109.
- . 1984b. On floatation and air breathing in *Amblystoma tigrinum* larvae: stimuli for and the relationship between these behaviors. *Can. J. Zool.* 62: 15-18.
- NICHOLAS, J. S. 1922. The reactions of *Amblystoma tigrinum* to olfactory stimuli. *J. Exp. Zool.* 35: 257-281.
- NOBLE, B. K. 1931. *The biology of the Amphibia*. McGraw-Hill, New York.
- PECKARSKY, B. L. 1982. Aquatic insect predator-prey relations. *BioScience*, 32: 261-266.
- SCHARRER, E. 1932. Experiments on the function of the lateral-line organs in the larvae of *Amblystoma punctatum*. *J. Exp. Zool.* 61: 109-114.
- SNEDECOR, G. W., and W. G. COCHRAN. 1967. *Statistical methods*. 6th ed. Iowa State University Press, Ames.
- SPRULES, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology*, 53: 375-386.
- ZARET, T. M. 1980. *Predation and freshwater communities*. Yale University Press, New Haven and London.