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## Tailed frog tadpoles differentially alter their feeding behavior in response to non-visual cues from four predators

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**Abstract.** Tadpoles of the tailed frog (*Ascaphus truei*) are common in riffles within many small, high-gradient streams of the Pacific Northwest (United States and southern Canada), where they typically graze periphyton from exposed cobbles. We conducted field observations and experiments in Clearwater Creek, southwestern Washington, to determine if tadpoles would reduce their feeding activity (i.e., emergence from crevices to graze periphyton) in the presence of non-visual cues released from each of four aquatic predators: giant salamanders (*Dicamptodon* spp.), cutthroat trout (*Salmo clarki*), brook trout (*Salvelinus fontinalis*), and shorthead sculpin (*Cottus confusus*). In absence of predators, tadpoles usually emerged from under cobbles to feed at night (2000-0100 h), and spent the remainder of the 24-h interval hidden in crevices. In the presence of giant salamanders, cutthroat trout, and brook trout that were all confined within separate, in situ enclosures immediately upstream of tadpoles, tadpole activity was reduced two-, three-, and six-fold, respectively, compared with predator-free controls. In contrast, tadpoles appeared unable to detect upstream sculpins. Subsequent consumption experiments in the laboratory showed that salamanders, sculpins, and cutthroat trout all were capable of consuming tadpoles in both structurally simple and complex habitats. We hypothesize that the inability of tadpoles to detect predaceous sculpins may explain why tailed frog tadpoles are largely absent from lower-gradient streams where sculpins are often abundant.

**Key words:** amphibians, *Ascaphus truei*, *Dicamptodon*, giant salamanders, non-visual cues, predator-prey, tadpoles, tailed frog, sculpins, stream, trout.

In the presence of predators, prey species often exhibit antipredatory defenses such as decreased activity or mobility (Lawler 1989) and withdrawal into spatial refuges (Stein and Magnuson 1976, Sih et al. 1988, Rahel and Kolar 1990), prey behaviors that reduce predator encounter rates (Morse 1980, Sih 1987). Such behavioral adjustments, however, frequently come with a cost. For example, risk-balancing models (e.g., Lima 1985, Dill 1987) usually assume that prey attempt to balance the conflicting demands of acquiring adequate resources while minimizing predation risk. The basis for this trade-off is that the most resource-rich patches often contain the highest numbers of predators, whereas safe patches often comprise resource-poor environments for prey (Werner and Gilliam 1984, Ludwig and Rowe 1990). Several recent experimental studies have provided empirical support for this concept (e.g., Holomuzki 1986, Gilliam and Fraser 1987, Rahel and Kolar 1990).

Behavioral adjustments to predators necessitate that prey respond to reliable signals that advertise predator presence. There is accumulating evidence that dissolved chemicals emitted by aquatic predators are important non-visual sensory cues for prey (e.g., Phillips 1976, Peckarsky and Dodson 1980, Crowl and Covich 1990, Boudreau et al. 1993). The ability to detect predators chemically is particularly well developed in larval amphibians, which display a variety of evasive behaviors when exposed to chemicals from a large array of predaceous aquatic vertebrates and invertebrates (Kiseleva and Manteifel 1982, Petranka et al. 1987, Sih et al. 1992).

Recent experimental evidence suggests that prey response to chemicals emitted by predators is most pronounced in permanent aquatic habitats, such as perennial streams, where risk of predation may pose strong and pervasive selective pressures (Kats et al. 1988). So long as

effective predator detection systems operate, prey can exploit these resource-rich habitats with minimum risk (Petranka et al. 1987). For prey to persist within these habitats, however, they must detect and respond to cues emitted from each predator species that constitutes significant risk. This is a formidable challenge for amphibian prey because streams often contain many predators of widely different phylogenetic origins (Lee et al. 1980, Matthews and Heins 1987, Resetarits 1991).

In the Pacific Northwest, USA, tadpoles of the tailed frog (*Ascaphus truei* Stejneger) are common in high-gradient streams. Preliminary observations from an unreplicated 1990 field experiment in Clearwater Creek, Washington, suggested that tadpoles altered their feeding behavior in the presence of non-visual cues from giant salamanders (*Dicamptodon* spp.), a potential predator. Those observations prompted us to conduct a series of replicated experiments designed to quantify the effects of non-visual cues from several predators on the foraging behavior of *Ascaphus* tadpoles. Our objectives were to: (1) describe tadpole activity patterns that occur in the absence of predators; (2) describe the degree to which tadpole behavior is affected by non-visual cues from four common predator species occurring in the study area (giant salamanders, cutthroat and brook trout, and short-head sculpins); and (3) quantify the number of tadpoles these predators were capable of consuming in structurally simple and complex habitats. We show that tadpoles can detect non-visual cues emitted by three of these predators, and that each of these predators can consume large numbers of tadpoles.

### Study Site

Field collections and experiments were conducted in the Clearwater Creek basin approximately 10 km NE of Mt. St. Helens, Washington (~46°15'N, 122°15'W). Clearwater Creek and its tributaries were extensively disturbed by the 1980 eruptions of Mt. St. Helens, but aquatic communities have become reestablished in most parts of the basin (Hawkins 1988, Hawkins and Sedell 1990). The mainstem of Clearwater Creek (3rd order, 750 m elevation) has a mean gradient of about 4%. Several high-gradient (>15%) tributaries feed Clearwater Creek. Streambed substrates in the mainstem range from sand to large

cobbles. Substrates in the higher-gradient tributaries range from gravel to bedrock. See Hawkins (1988) for further details of the study area.

### Natural History of Study Organisms

#### Tailed frog

In the Clearwater Creek basin, the distribution of *Ascaphus truei* tadpoles is extremely patchy. Tadpoles reach densities as high as 28 individuals/m<sup>2</sup> in high-gradient, headwater (1st and 2nd order) tributaries. In contrast, tadpoles are sparse (0 to 0.5/m<sup>2</sup>) in the lower-gradient mainstem of Clearwater Creek (Hawkins et al. 1988, C. P. Hawkins unpublished data) and in other large (≥4th order) streams of the Pacific Northwest (see Nussbaum et al. 1983, Welsh 1990, Bury et al. 1991). Some have speculated that the near absence of *Ascaphus* tadpoles from larger streams is due to predation by trout (e.g., Putnam cited in Metter 1964, p. 194).

Adult frogs are carnivorous and feed on small invertebrates (Nussbaum et al. 1983), whereas tadpoles largely are herbivorous and consume periphyton (mostly diatoms; Metter 1964). Ventral flattening and the presence of a suctional oral disc allow tadpoles to preferentially inhabit surfaces of cobbles in swift water (e.g., ≥1 m/s, Hawkins et al. 1988). Tadpoles usually forage at night and hide under crevices during daylight hours (Altig and Brodie 1972).

Tadpoles take two or three years to complete development (Metter 1967) and attain individual size of about 1 g wet mass prior to metamorphosis. Because of their large individual size, tadpoles often represent >90% of total herbivore biomass in the streams they inhabit (Hawkins et al. 1988).

#### Predators

Several potential tadpole predators occur within the study area: giant salamanders (*Dicamptodon ensatus* and *D. copei*), red-legged frogs (*Rana aurora*), cutthroat trout (*Salmo clarki*), brook trout (*Salvelinus fontinalis*), shorthead sculpin (*Cottus confusus*), garter snakes (*Thamnophis sirtalis*), American dippers (*Cinclus mexicanus*), Pacific water shrews (*Sorex bendirei*), and raccoons (*Procyon lotor*). Extensive surveys made between 1984 and 1993 in over 15 streams within the basin revealed that giant salamanders, the two



FIG. 1. Photograph of twelve paired enclosures (dimensions: 103 cm length  $\times$  32.5 cm diameter) used to confine tailed frog tadpoles and their predators in Clearwater Creek. Arrow shows direction of flow. For each predator detection experiment (salamanders, trout, or sculpins), predators were placed in three of the six upstream enclosures; tadpoles were placed into each of the six downstream enclosures. Coarse mesh covers used to isolate predators in upstream enclosures have been removed. See text for additional details.

species of trout, and shorthead sculpins were the numerically most abundant predators (C. P. Hawkins, personal observation).

Giant salamanders, cutthroat trout, and shorthead sculpin ostensibly share a long evolutionary history with the tailed frog. *Dicamptodon* and shorthead sculpin have biogeographic ranges nearly identical to that of the tailed frog. Each is found in two major, disjunct regions: (1) the coastal mountains of northwestern North America, and (2) the inland mountains of eastern Oregon, Washington, Idaho, and western Montana (Metter 1968, Behler and King 1979, Lee et al. 1980, Leonard et al. 1993). Cutthroat trout have a wider geographic distribution but occur in all regions containing tailed frogs. Because a 100-m waterfall occurs in the lower part of Clearwater Creek, it is unclear whether cutthroat trout historically occupied sections of stream above this point or were later introduced. The brook trout is the only species in the study area that clearly has a limited (i.e., <100 yr) evolutionary history with the tailed frog. This trout species is native to eastern North America and was introduced into the study basin in the 1930s (C. Crisafulli, Mt. St. Helens National Monument, personal communication).

Densities of these four predators vary both longitudinally within basins and among habitat types (personal observation). Giant salamanders are most abundant in headwater tributaries and rare in the mainstem of Clearwater Creek; they are nearly equally abundant in riffles and pools. Trout are most abundant in the mainstem of the Clearwater, occur part way up some tributaries, but are absent from nearly all 1st-order and many 2nd-order sections. The two species of trout occur mainly in pools. Shorthead sculpins occur in the mainstem of the Clearwater and in lower-gradient sections of its tributaries. We have never found sculpins in sections with >10% gradient during the 10 yr we have been conducting surveys in the study area. Sculpins are most abundant in riffles, but also occur in pools.

## Methods

### *Field observations and experiments*

*General methods.*—To quantify diel periodicity of tadpoles in the absence of predators and to assess the response of tadpoles to non-visual cues from predators, we used in-stream enclosures, paired longitudinally end-to-end (Fig. 1). Enclosures were constructed of PVC pipe cut lengthwise (post-cut dimensions: 103 cm length  $\times$  32.5 cm diameter) and fitted with hardware cloth ends and covers (6.4 mm mesh) to allow water circulation and prevent animal escape. We used stream cobbles with natural amounts of periphyton to line the bottom of each enclosure. Cobbles provided refuge for animals, food (periphyton) for tadpoles, and ballasts for enclosures in the current. Average water depth and current velocity within enclosures were 12 cm and 12 cm/s, respectively. Enclosures were established in a single uniform riffle approximately 10 m wide and 30 m long within the mainstem of Clearwater Creek. Before beginning each experiment, we electroshocked and seined the entire riffle containing the enclosures and the adjacent upstream pool to remove all predators whose presence may have confounded response to experimental manipulations of predators.

Activity of tadpoles in the diel-periodicity and predator-cue experiments was determined by counting the number of individuals that were partially or completely visible on cobbles, on

enclosure sides (PVC), or on screens. Counts were later converted to percentages of the total number present in each enclosure. A diver's mask held to the water surface was used to facilitate underwater observations, and a portable spotlight was used to illuminate enclosures during nighttime observations. The spotlight was used for ~10–20 s per enclosure, and exposure to the spotlight did not appear to affect subsequent tadpole activity. For all statistical analyses conducted (see below) we set alpha to 0.05.

*Diel activity patterns.*—We quantified diel activity of tadpoles in the absence of predators during the summers (July and August) of 1991 and 1992. Fifteen tadpoles ( $30 \pm 5$  mm TL,  $\bar{x} \pm 1$  SD) were added to enclosures containing only periphyton-covered cobbles. Tadpole activity was quantified at 30-min to 4-h intervals, 32 different times, over this period.

*Predator detection experiments.*—Enclosures were also used during these two summers to conduct a series of separate 24-h experiments in which we tested tadpole response to the presence of brook and cutthroat trout (~200 mm TL), shorthead sculpins (~80 mm TL), and giant salamanders (~160 mm TL). For each experiment, one individual of each predator species was confined in each of three of the six upstream enclosures; the other three enclosures were used as controls. Fifteen tadpoles (total length: 25–30 mm) were placed in each of the six downstream enclosures (Fig. 1).

Release of fluorescein dye within each of the upstream enclosures was used to simulate downstream chemical flow fields. Dye thoroughly mixed before exiting the upstream enclosure, and nearly all the dye traveled directly into its paired downstream enclosure. Segregation of predators and prey in adjacent enclosures precluded the use of contact cues by tadpoles to detect upstream predators. Experiments were conducted 23–27 August 1991 (salamander and brook trout trials) and 21–25 July 1992 (cutthroat trout and shorthead sculpin trials), during summer baseflow.

Allocation of predator and no-predator treatments for each experiment was determined either randomly or by assigning every other enclosure to a predator treatment. The latter approach was used in 1992 experiments as a means of more effectively homogenizing the non-experimental effects of across chamber gradients that may have potentially confounded

our ability to detect tadpole responses to predator treatments (Hurlbert 1984). Tadpoles and predators were collected from nearby streams no more than 5 d before each experiment, and were held in situ with stream cobbles in 40-L coolers downstream of enclosures until experiments began. Predators were added to enclosures on the morning (0830–1100) of each evening's experiment. For experiments in which new predator species were tested on consecutive days, we replaced cobbles and scrubbed predator enclosures clean before new predators were added. Differences in tadpole activity between predator and no-predator treatments for each experiment were analyzed with a Student's *t*-test on log-transformed ( $x_i + 1$ ) counts of active tadpoles (Zar 1984).

Results from the diel activity observations were used to identify the 1–2 h time period tadpoles were most active and hence potentially most sensitive to the presence of predators. During this interval, we quantified tadpole activity in each enclosure in the same manner used to quantify tadpole diel activity.

Tadpole densities used in experiments (15/enclosure) were ~3× higher than the maximum mean density observed in the study area. We chose these densities to minimize random error associated with small sample sizes. High densities may have caused tadpoles to be more active than normal. However, all replicates contained equal numbers of animals, and differences in tadpole response between treatments and controls should therefore have been attributable solely to effects of predator/no-predator treatments.

#### *Laboratory consumption experiments*

We conducted two sets of laboratory experiments designed to determine (1) whether the three main types of the predators (salamanders, trout, and sculpins) were capable of consuming tadpoles and, if so (2) whether the three types of predators differed in the numbers of tadpoles consumed from both structurally simple and complex substrates. The experiments were also run over several weeks to mimic the predation pressure a tadpole might encounter during a substantial portion of its life cycle. For these experiments, we had too few experimental arenas and tadpoles to examine all four predators tested in the field for non-visual cues. Because

we were mainly interested in consumption of tadpoles by native predators, we used cutthroat trout and excluded brook trout from the experiments.

Experiments were conducted in six flow-through,  $3.6 \times 0.6$  m troughs at Utah State University that were supplied with non-chlorinated well water. Each chamber was divided with perforated plexiglass barriers into upstream control and downstream predator enclosures. Three of the enclosures were filled with pea gravel ( $\sim 5$  mm diameter) to simulate the substrate character of low-gradient benthic habitats and the other three with cobbles ( $\sim 150$  mm diameter) to simulate substrate character in higher-gradient reaches. Depth of water was maintained at  $\sim 10$  cm in the salamander and sculpin treatments to simulate riffle depths and at  $\sim 30$  cm in the trout troughs to simulate pool environments.

In the first experiment (10 September–30 October 1992), seven tadpoles were placed in each enclosure, and one individual of each predator was placed in separate pea gravel and cobble enclosures. Water temperature was held constant at  $10^\circ\text{C}$  to simulate spring and early summer conditions. After 50 d (500 degree days), the experiment was terminated and any remaining tadpoles were counted in the 12 enclosures. The second experiment (13 November–15 December) was similar in design to the first, except that (1) water temperature was held constant at  $16^\circ\text{C}$  to simulate late summer conditions, and (2) a dwindling pool of captive tadpoles forced us to use only four tadpoles per chamber. We also lost one of our experimental salamanders; we therefore replicated the sculpin treatment ( $n = 2$ ) in place of the salamander treatment. This experiment was terminated after 32 d (512 degree days), and surviving tadpoles were counted as in the first experiment.

Both experiments were conducted under a 12:12 h photoperiod. The approximately 500 degree-day experimental period represented about 23% of the annual degree days accrued in streams near the study area (Hawkins 1986). During the experiments, tadpoles were provided with periphyton-covered ceramic tiles ( $15.2 \times 15.2$  cm) as a food source. In the pea gravel enclosures, tiles were embedded so only tile surface was exposed; tadpoles had no opportunity to hide under tiles. Tiles were replaced with fresh ones whenever approximately  $\frac{1}{2}$  of the tile surface had been grazed.

The two experiments were initially designed to be analyzed separately with the dependent variable being the difference in tadpole numbers between the downstream predator and upstream control treatments. Two analyses were planned: (1) a paired *t*-test to determine whether differences between control and treatment chambers ( $n = 6$ ) were greater than zero (i.e., the presence of predators reduced tadpole numbers), and (2) an unreplicated, balanced two-way ANOVA to determine whether the magnitude of difference between controls and treatments depended on predator species or substrate. For the latter analysis, the mean square error for the species  $\times$  substrate interaction would be used as an estimate of experimental error (Zar 1984). Because we had to alter the design of the second experiment after the loss of a predator, we pooled the observations from the two experiments prior to analysis and used multiple general linear hypothesis models to conduct an unbalanced, replicated ANOVA in place of the unreplicated two-way ANOVAs.

## Results

### *Field experiments*

*Diel feeding patterns.*—In the absence of upstream predators, tadpole activity was highest at night (Fig. 2). Peak activity ( $>40\%$  of tadpoles visible) occurred at  $\sim 2200$  h and gradually declined thereafter, whereas minimum activity ( $<5\%$  of tadpoles visible) occurred from 0430 to 1620. During times tadpoles were visible on exposed upper cobble surfaces, they consistently faced the current and were usually seen grazing periphyton. Of those tadpoles active at night, most ( $>75\%$ ) were found clinging to periphyton-covered cobbles, rather than on PVC enclosure sides and screens ( $<25\%$ ), which were largely devoid of periphyton. During daylight hours, tadpoles were almost always hidden from view on the undersides of cobbles; only rarely would even the tips of their tails be visible at this time.

### *Predator detection experiments*

The number of tadpoles emerging from crevices at night to feed differed strongly depending on predator species (Table 1). On 23 August 1991, presence of confined giant salamanders in upstream enclosures resulted in a significant

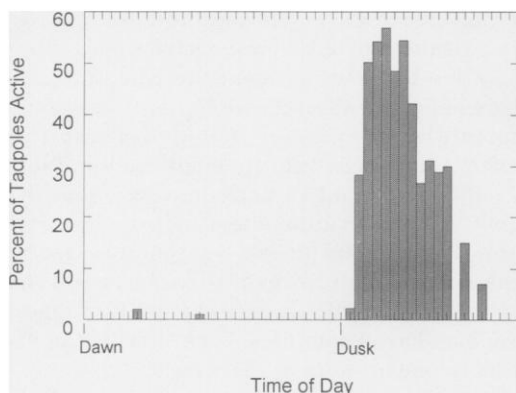


FIG. 2. Diel feeding periodicity of *Ascaphus truei* tadpoles. Activity was determined by counting the number of individuals that emerged from crevices under cobbles and were visible on periphyton-covered cobble surfaces, and expressing these as a percentage of the total number of tadpoles present. Tadpoles were not exposed to predators during any of these observations ( $n = 32$ ). Each increment on x-axis = 30 min.

two-fold reduction in tadpole activity compared with tadpoles in predator-free controls. During the following morning (24 August), we conducted a changeover experiment in which

salamanders were transferred to predator-free enclosures, and enclosures previously containing salamanders were cleaned (brushed and cobbles replaced) and left as predator-free controls. Tadpoles in both sets of downstream enclosures were left undisturbed. We conducted this follow-up experiment to confirm that differences in tadpole activity between predator and control treatments were attributable to salamander presence. That night we observed a complete reversal in tadpole response within the two sets of enclosures. Similar to the first night's observations, presence of salamanders resulted in a significant three-fold reduction in tadpole activity compared with predator-free controls (Table 1).

We also observed significant reductions in activity when tadpoles were exposed either to upstream cutthroat trout (three-fold reduction, 23 August 1992) or brook trout (six-fold reduction, 27 August 1991), compared with unexposed tadpoles (Table 1). In a follow-up experiment, we removed all brook trout immediately after tadpole counts were made in the main experiment (at 2125 h) and counted tadpoles again at 2240 h, approximately 1 h after trout were removed. Activity of tadpoles in enclo-

TABLE 1. Summary of field experiments involving tailed frog tadpole response to non-visual cues of upstream predators. Tadpole activity is expressed as percentages; significance determined using Student's  $t$ -test on  $\log(x_i + 1)$  counts of active tadpoles observed during each experiment.  $n = 3$ .

Predator	Date	Time of observation (h)	% Tadpoles active ( $\bar{x} \pm 1$ SD)				
			Predator	No predator	$t$	$p$	
<b>Giant salamander</b>							
a. Main experiment	23 Aug 1991	2117	31.1 $\pm$ 10.2	64.7 $\pm$ 24.0	3.87	0.018	
b. Changeover experiment <sup>a</sup>	24 Aug 1991	2230	20.0 $\pm$ 11.5	64.4 $\pm$ 15.4	4.19	0.014	
<b>Brook trout</b>							
a. Main experiment	27 Aug 1991	2125	8.9 $\pm$ 10.2	53.3 $\pm$ 6.7	3.70	0.021	
b. Predator removal experiment <sup>b</sup>	27 Aug 1991	2240	37.8 $\pm$ 10.2	42.2 $\pm$ 7.7	0.62	0.568 NS	
<b>Cutthroat trout</b>							
	23 July 1992	2200	13.3 $\pm$ 11.16	44.4 $\pm$ 6.7	3.83	0.019	
<b>Shorthead sculpin</b>							
a. Main experiment	21 July 1992	2205	68.7 $\pm$ 14.0	71.0 $\pm$ 10.1	0.26	0.810 NS	
b. Density augmentation							
1. Moderate	21 July 1992	2305	40.0 $\pm$ 20.0	49.0 $\pm$ 17.1	0.66	0.544 NS	
2. High	25 July 1992	2200	42.3 $\pm$ 16.6	35.7 $\pm$ 7.5	-0.52	0.632 NS	

<sup>a</sup> Salamanders introduced into previously predator-free enclosures so that these 'no-predator treatments' became 'predator treatments,' and 'predator treatments' formerly exposed to salamanders became 'no-predator treatments.' See text for further details.

<sup>b</sup> Brook trout removed from predator enclosures. Tadpole activity was re-examined 1 h after this manipulation, and activity in enclosures initially lacking predators ('no-predator' treatments) was compared with enclosures in which trout were removed (formerly 'predator' treatments). See text for further details.

TABLE 2. Analysis of variance for pooled results from the two laboratory consumption experiments. The analysis was based on the difference in survivorship between the upstream control (predator-free) chamber and the downstream treatment (predator) chambers.

Source	SS	df	MS	F	p
Species	8.762	2	4.381	2.670	0.148
Species × substrate	8.727	2	4.364	2.660	0.149
Experiment	4.762	1	4.762	2.902	0.139
Error	9.844	6	1.641		

tures formerly containing brook trout increased from 9 to 38% ( $p < 0.05$ ), and reached activity levels similar to those observed in control enclosures ( $p > 0.05$ , Table 1).

The presence of upstream shorthead sculpins at a density of one fish per enclosure caused no significant reduction in tadpole activity. To determine whether the lack of response by tadpoles may have been caused by low dose associated with the small body mass of sculpins, we conducted two subsequent experiments with increased densities of sculpins (2 per enclosure, immediately following main experiment on 21 July, and 5 per enclosure on 25 July). Design of these follow-up experiments was identical to the main experiment except that increased numbers of sculpins were used. As in the main experiment, we observed no significant differences in tadpole activity between predator and no-predator treatments (Table 1), in spite of density augmentation.

Laboratory consumption experiments

At the end of the laboratory consumption experiments, tadpole survivorship was significantly higher in the upstream predator-free enclosures than in the downstream predator enclosures ( $t = 8.07$ ,  $df = 11$ ,  $p < 0.001$ ). At the end of Experiment I, over 90% of tadpoles survived in the control enclosures, whereas only about 50% of tadpoles survived in the salamander treatment, 45% in the sculpin treatment, and about 20% in the trout treatment (Fig. 3A). At the end of Experiment II, about 80% of the tadpoles survived in the control enclosures, whereas only 12.5% survived in the trout enclosure, and none survived in either of the four sculpin

enclosures (Fig. 3B). No significant differences in consumption rate were detected among predator species or experiment, nor did substrate type appear to affect the ability of predators to capture tadpole prey (i.e., no significant species effect nor species × substrate interaction, Table 2). It is important to note, however, that the ability to detect differences in tadpole survivorship among treatments was compromised by the low statistical power of our experiment. The near significant F-values ( $p$  about 0.15) suggest we may have committed Type II statistical errors in one or more of these tests.

Discussion

Our consumption experiments showed that giant salamanders, cutthroat trout, and short-head sculpins were all capable of consuming *Ascaphus truei* tadpoles when available, and showed that predation could significantly reduce tadpole numbers over an approximately 500 degree-day period. The three species tested represented predator groups with a wide range of foraging modes (sensu Cooper et al. 1985)—i.e., sedentary ‘ambush’ predators (shorthead sculpins), ‘stalkers’ (giant salamanders), and mobile ‘cruising’ predators (trout)—yet all species irrespective of foraging mode could capture, handle, and ingest tadpoles inhabiting both structurally simple and complex habitats. That giant salamanders and trout consumed tailed frog tadpoles was not surprising, because large-bodied aquatic vertebrates have historically been considered important predators of larval amphibians (e.g., Morin 1983, Semlitsch and Gibbons 1988, Fauth 1990, Resetarits 1991). The consumption rates of shorthead sculpins on tad-

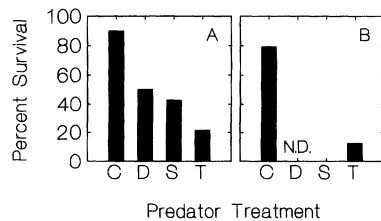


FIG. 3. Percent survivorship of tadpoles during (A) 50- and (B) 32-d exposures to different predators in laboratory streams. Codes are: C = control, D = giant salamander, S = sculpin, and T = trout. No data were available for the salamander treatment in the second experiment (=N.D.).



poles were surprising, given that sculpins are considerably smaller than trout and salamanders, and were only about twice as large as the tadpoles used in these experiments.

These consumption rates may be substantially higher or lower than those occurring in the field. The lab streams were smaller in size and had lower substrate complexity than that of natural streams. Both of these factors could have contributed to overestimates of the consumption that would actually occur under natural conditions. In contrast, consumption rates may have been underestimated in Experiment I for sculpins because of an unanticipated experimental artifact. For example, we noticed that in the pea gravel enclosures, tadpoles aggregated on the vertical sidewalls of the chamber near the waterline and as far away from the top of the gravel as possible. This behavior may have greatly reduced consumption by sculpins, which in this experiment appeared sluggish because of the low temperature (10°C). The larger salamanders and free-swimming trout were more active than sculpins at this temperature and could easily reach these tadpoles. During Experiment II, we observed sculpins actively stalking and pursuing tadpoles, which also were more active at the warmer temperature (16°C).

If we assume consumption rates are reasonable estimates for those occurring in natural streams and extrapolate these estimates over a year, individual salamanders, trout, and sculpins could consume at least 28 to 48 tadpoles annually. Considering that the combined densities of these predators may exceed two individuals/m<sup>2</sup>, and that tadpole densities range from 0 to 28/m<sup>2</sup>, these predators appear capable of eliminating all tadpoles from streams we have surveyed.

Tadpole feeding activity appears to be reduced by a non-visual, chemical cue released by three of the four predators examined. Two lines of evidence support the hypothesis that the primary signal advertising predator presence was a chemical cue. First, tactile (i.e., contact) cues were not possible because predators and tadpoles were confined in separate enclosures. Second, the combination of cobbles within enclosures and the double layer of hardware cloth separating predator and downstream tadpole enclosures made it highly unlikely tadpoles could detect predators visually. Furthermore, the most probable source of chemicals

perceived by tadpoles were external secretions (e.g., epithelial mucus) or excretory products (e.g., urine) emitted by predators rather than chemicals resulting from recent predation. Because predators were unfed for several days before experiments, it is unlikely that tadpoles reduced their activity in response to upstream chemical cues from recently ingested prey (e.g., alarm substance, see Pfeiffer 1962) or from a combination of compounds released by predators and ingested prey (Crowl and Covich 1990, Alexander and Covich 1991).

Because trout and salamanders in upstream enclosures caused large reductions in activity of tadpoles on exposed cobbles, the presence of these predators in nature may translate into substantial reductions in food intake by tadpoles. Periphyton in streams is most abundant on sunlit, upper surfaces of cobbles, where risk of tadpole predation by salamanders and trout is also likely to be high. Skelly (1992) showed that confined *Ambystoma* salamanders caused reductions in time spent in food-rich patches, increases in time spent within refuges, and consequently decreased growth by *Hyla* tadpoles. Considering the magnitude by which trout and salamanders depressed feeding by *Ascaphus*, it seems likely that *Ascaphus* tadpoles may also suffer reduced fitness from indirect (i.e., non-lethal) predator encounters.

Actual consequences of predator chemical cues on prey fitness may depend upon temporal variation of signals emitted by mobile predators, and time lags between predator movement from profitable food patches for prey and resumption of prey activity in these dangerous habitats (Petranka et al. 1987). Results of the brook trout removal experiment suggest that the time lag between predator absence and tadpole recovery of activity on exposed cobbles was extremely short (i.e., <1.0 h). This interval is a fraction of the time reported (up to 3 d) for larval *Ambystoma* salamanders to recover from chemicals emitted by predaceous fish (Petranka et al. 1987). Rapid recovery of *Ascaphus truei* tadpoles in the present study may be due to high current velocities within tadpole habitats (i.e., torrential riffles) and correspondingly high exchange rates of dissolved chemicals in these environments. Fast-flowing, turbulent streams may greatly reduce residual 'chemical ghosts' of dispersed predators perceived by prey compared with slow-flowing habitats. Such rapid

behavioral adjustments that reduce unnecessary time spent in refuges can provide tadpoles with greater opportunities for feeding and growth, and accelerated metamorphosis (Wilbur 1980, Skelly 1992).

*Ascaphus* tadpoles were sensitive to chemicals from a broad taxonomic range of predaceous vertebrates found in streams. One plausible explanation for this result is that tadpoles respond to a generalized predator signal that is largely independent of predator phylogeny. This idea is supported by the fact that tadpoles responded strongly to brook trout, an introduced species with only limited evolutionary history with *Ascaphus truei*. In this case, tadpoles may have responded to a chemical signal characteristic of all trout. Others have hypothesized that responses to predator chemicals by amphibian prey appear generalized (Kats et al. 1988, Lawler 1989), traits that ostensibly provide prey with an ability to respond to a full phylogenetic range of potential predators. However, this hypothesis does not account for tadpole insensitivity to shorthead sculpins. The lack of response to sculpins implies either an extremely limited tadpole-sculpin coevolutionary history or that sculpins have evolved a way to limit or mask release of chemicals potentially perceived by tadpoles. Differential sensitivity of prey to non-visual cues from several predators is apparently not restricted to tadpoles. In a lab study, Malmqvist (1992) reported that several stream-dwelling insects were sensitive to chemical cues emitted by some predators, but could not detect sculpins non-visually (but see Kohler and McPeck 1989).

Of the four common predators in Clearwater Creek and surrounding basins, only shorthead sculpins exhibit basin-wide, complementary distributions with tailed frog tadpoles. Tadpoles reach high densities in small, high-gradient tributaries, where they co-occur with giant salamanders and a few trout, but are virtually absent in the mainstem of Clearwater Creek where sculpins are the numerically most abundant vertebrate predator (C. P. Hawkins, unpublished data).

Why do tadpoles and sculpins exhibit this complementarity? One hypothesis is that tadpoles and sculpins simply require different habitat conditions (e.g., differences in temperature, current, substrate, etc.), and these species evolved in isolation. If this is the case, one rea-

son why tadpoles have not evolved sensory defenses against sculpins is that sculpins constitute no risk and thus represent an innocuous selective pressure. This hypothesis is supported by studies that suggest only amphibian species at great risk from predators (i.e., showing high spatial overlap) display strong antipredatory responses (Kats et al. 1988, Lawler 1989).

A second hypothesis for this pattern is that the two species did evolve together, and that predation by sculpins is a strong ecological force that largely eliminates tadpoles from streams inhabited by this sculpin. In this sense, tadpoles do not co-occur with sculpins because they have not evolved an effective means to detect this "stealth" predator. This hypothesis is supported by the following lines of evidence. Maximum temperatures in the mainstem Clearwater are nearly optimal (16°C) for tadpole growth (Claussen 1973), and periphyton biomass (the primary food of tadpoles) is often substantially higher here than in smaller tributaries where tadpoles are most abundant (personal observation). Furthermore, the current velocities and substrates present in the mainstem appear capable of supporting higher tadpole densities based on tadpole-habitat associations observed in smaller tributaries (Hawkins et al. 1988). Finally, sculpins appear to be physically excluded from high-gradient, headwater streams, presumably because these small, benthic fish cannot swim past waterfalls ( $\geq 3$  m) that are common in small mountain streams. Because *Ascaphus* tadpoles can cling to and climb smooth vertical rocks, these streams may serve as refugia for tadpoles and thereby allow regional coexistence of the two species. We plan to test these hypotheses by conducting a series of transplant experiments in which we will measure tadpole foraging activity, growth, and mortality in different types of stream reaches within the Clearwater drainage, in both the presence and absence of sculpins and other predators.

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