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Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities?

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Abstract With rare exceptions, anuran larvae have traditionally been considered to occupy lower trophic levels in aquatic communities where they function as microphagous suspension feeders. This view is being challenged by studies showing that tadpoles with generalized morphology often function as macrophagous predators. Here, we review the literature concerning macrophagy by tadpoles and provide two additional examples involving generalized tadpoles. In the first, we demonstrate with laboratory and field experiments that wood frog (*Rana sylvatica*) tadpoles are major predators of macroinvertebrates in ponds. In the second, we show that green frog (*R. clamitans*) tadpoles can cause catastrophic reproductive failure of the wood frog via egg predation. These results and data from other studies challenge the assumption that generalized tadpoles function as filter-feeding omnivores, and question the general applicability of community organization models which assume that predation risk increases with pond permanence. We suggest that predation risk is greater in temporary ponds than in more permanent ponds for many organisms that are vulnerable to predation by tadpoles. This being so, a conditional model based upon interactions that are species-specific, life-stage-specific, and context-dependent may better explain community organization along hydrological gradients than models which assume that temporary ponds have few or no predators.

Key words Community organization · Hydrological gradients · Macrophagy · *Rana* · Predatory tadpoles

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Introduction

Anuran larvae are important elements of many freshwater communities and have been used extensively in ecological experiments that have examined crowding effects, resource competition, food web interactions, and the role of predators in mediating competitive interactions (Morin 1983; Wilbur 1984, 1987; Hairston 1989; Resetarits and Bernardo 1998). Tadpoles have also been used extensively in behavioral studies to understand how tradeoffs in foraging and antipredator behaviors affect community composition and structure along environmental gradients (Werner and McPeck 1994; Wellborn et al. 1996).

Except for a small percentage of anuran larvae that exhibit morphological, dietary, and niche specializations (e.g., Orton 1953; Crump 1983; Lannoo et al. 1987; Altig and Johnston 1989), ecologists have traditionally viewed tadpoles as being herbivores that occupy lower trophic levels in aquatic communities. More precisely, trophic experts have characterized most tadpoles as being omnivorous, microphagous suspension feeders (Wassersug 1975; Seale 1980; Duellman and Trueb 1986; Stebbins and Cohen 1995) since they possess labial teeth, keratinized jaw sheaths (beaks), buccopharyngeal gill filters and associated structures for suspension feeding, and highly elongated guts for processing bulk quantities of low-quality food (Wassersug 1980). Common food items of tadpoles that exhibit this generalized morphology include pollen, free and attached algae, particulate organic debris and associated microorganisms, microzooplankton, and periphyton (Seale and Beckvar 1980; Altig and Johnston 1989). In addition to suspension feeding, generalized tadpoles can process coarser material such as leaf fragments or coarse detritus by passing these directly into the esophagus.

Macroinvertebrates generally occur at low frequencies in the guts of tadpoles (e.g., Busack and Zug 1976; Diaz-Paniagua 1985, 1989), a finding which has led to the common assumption that generalized tadpoles do

not play significant roles as higher-level predators in aquatic communities. However, predation on macroinvertebrates may be more important than dietary studies suggest for two reasons. First, opportunistic predators that subsist as microphagous suspension feeders can reach much higher densities than strict carnivores of similar size. In this case even when per capita consumption of macroinvertebrates is low, the collective effect of tadpole predation can be significant. Second, tadpoles have rapid gut clearance rates that typically average <6–8 h when animals are fed ad libitum (Savage 1952; Calef 1973; Wassersug 1975). Because of rapid turnover rates, the frequency of prey in guts based on “snapshots” from preserved specimens may give a false impression of actual predation rates. Consider a hypothetical case in which tadpoles have average gut clearance rates of 6 h and occur at 1000 individuals m^{-2} of pond bottom (local tadpole densities in temporary ponds may exceed 2000–3000 individuals m^{-2} of pond bottom; Woodward 1982a; Biesterfeldt et al. 1993). A dietary analysis that yields only four benthic macroinvertebrates from a sample of 50 tadpoles is equivalent to weekly removal rates that exceed 2,000 invertebrates m^{-2} – an effect that could be ecologically significant in terms of organizing invertebrate communities or influencing prey population dynamics.

Although experimentation provides the most direct way to examine opportunistic predation by tadpoles on macroinvertebrates, we are unaware of any studies of this sort to date. Here, we use a combination of field observations and experiments to document two examples of macrophagy involving ranid tadpoles. We also summarize the existing literature on opportunistic predation by generalized tadpoles, and discuss some of the implications with regard to species interactions and community assembly along hydrological gradients. Our focus is on pond tadpoles with relatively unspecialized feeding niches and generalized morphology. These include most Type 4 tadpoles of Orton (1953) and encompass the majority of pond tadpoles. Representative forms in North America include the wood frog (*Rana sylvatica*), bullfrog (*R. catesbeiana*), American toad (*Bufo americanus*), and most other native species. We do not include stream-dwelling tadpoles with generalized morphology, primarily because of the scarcity of dietary studies on this group.

Methods

Experiment 1: wood frog predation on invertebrates in laboratory tanks

We conducted a 2×3 factorial experiment with ten replicates to determine whether wood frog tadpoles would prey upon soft-bodied benthic macroinvertebrates. The data gathered were useful in interpreting the results of a field experiment described below. The two factors were the presence or absence of tadpoles, and the type and size of prey (small chironomid larvae, large chironomid larvae, and large lumbricid oligochaetes). We netted live midge larvae from water-filled plastic wading pools that were placed in a

field for several months, then visually sorted animals into two size cohorts. Respective mean length (± 1 SE), body diameter, and dry mass for small larvae were 7.8 ± 0.26 mm, 0.51 ± 0.02 mm, and 0.37 ± 0.01 mg; respective values for large larvae were 11.58 ± 0.21 mm, 0.76 ± 0.03 mm, and 2.27 ± 0.15 mg; $n=20$ for each group. We collected lumbricid oligochaetes (respective mean length, body diameter, and dry mass = 75.2 mm \pm 5.9 mm, 1.60 ± 0.05 mm, and 18.1 ± 2.5 mg; $n=18$) from mud along the flooded margin of a local lake. These organisms rarely encounter tadpoles and are presumed to be insignificant natural prey; they were used to determine if tadpoles could physically handle relatively large, soft-bodied prey.

We examined prey survival using 15 cm \times 30 cm \times 8 cm (height) plastic containers that held 2 l of dechlorinated water. We arranged the 60 containers on a laboratory bench and aerated each using a feeder tube from a common aeration system. We used a randomized blocked design to assign treatments to containers, then haphazardly drew tadpoles from a common container to establish densities of 40 tadpoles per container (889 tadpoles m^{-2}) for the tadpole treatments. Blocks corresponded to the ten replicates positioned in sequence along the laboratory bench. Tadpoles used in the experiment (stages 25–32; Gosner 1960; mean wet mass = 0.35 ± 0.03 g; $n=22$) were collected from the field site described below. We fed tadpoles ad libitum (1.34 g of rabbit chow per box) for 1 day to acclimate tadpoles to laboratory conditions, then removed most food with a fine-mesh net immediately prior to adding prey. We followed the same protocol for control containers without tadpoles (1.34 g of food added, then removed immediately prior to adding prey) so that water was conditioned similarly.

At the start of the experiment we added 200 mg of powdered rabbit chow to all containers and either 15 chironomids or 8 oligochaetes to each container. The rabbit chow provided an alternative food source for tadpoles that was judged to be limiting based on previous laboratory experiments. After 2 days we filtered the contents of containers through a fine-mesh net and recorded the number of surviving prey. To verify that mortality of prey was due to tadpole predation, we conducted spot checks of containers for 45 min on day 2 by haphazardly moving about while searching for conspicuous feeding activity. We recorded any attacks or kills that were observed during this period.

Experiment 2: effects of tadpole addition in the field

Generalized tadpoles could potentially depress populations of pond invertebrates in a number of ways, the two most likely being via direct predation and by resource competition with invertebrates that scrape, suspension feed, or feed on detritus or other coarse particulate matter. To distinguish between effects due to predation and those due to competition, we conducted a short-term predator addition experiment. Our rationale was that the effects of direct predation should occur within several days of tadpole addition, but that other effects such as resource competition would take much longer to appear. The design involved sampling invertebrates in matched halves of ponds, adding tadpoles to randomly chosen halves, then resampling invertebrates after 5 days and 14 days. The response after 5 days was consider more critical in distinguishing predation effects, while the longer-term response was more likely to reflect additional factors such as adult choice of oviposition sites or competition.

We used eight seasonally ephemeral ponds (mean diameter 2.7 m; maximum depth <0.5 m) that were constructed 2 years prior to the experiment in a partially shaded forest tract in Madison Co., North Carolina. Macroorganisms that occupied the ponds within 1 year after construction included snails, crayfishes, salamanders (*Notophthalmus viridescens*, *Gyrinophilus porphyriticus*), wood frog tadpoles, and a variety of insects such as caddis flies, midges, mosquitoes, and odonates. The ponds dry in late summer and refill in late autumn.

We partitioned each dried pond bed in half in the autumn using a fence constructed of wooden posts, plastic clothesline, and clear plastic sheeting. We buried sheeting at the base of the fence and

staked the bottom to prevent tadpoles or invertebrates from trespassing. We contoured bottom sediments in each half with a rake to match halves as closely as possible with respect to size, shape, and depth. Ponds filled in November and contained a variety of invertebrates when the experiment was conducted in late April-early May.

In early March, we transferred all wood frog egg masses that were laid in the ponds to nearby 0.9-m-diameter plastic wading pools that contained pond water. We fed hatchlings that emerged in late March commercial rabbit pellets every 2–3 days so that tadpoles grew at rates similar to tadpoles in nearby ponds. On 28 April we sampled pond invertebrates in each pond half using a 15 cm × 15 cm fine-mesh net (mesh size = 0.35 mm) that was dragged nearly vertically about 1 cm deep through bottom sediments over a distance of 30 cm. This captured invertebrates in the bottom sediment along with zooplankton and insect larvae in the first 14 cm of the water column. We collected three subsamples from each pond half; these were pooled and preserved in 10% formalin.

Immediately after taking dredge samples, we randomly assigned treatments to pond halves and added 2000 tadpoles to halves that received tadpole treatments. Tadpoles used in the experiment were haphazardly drawn from the wading pools and assembled into lots of 2000; lots were then randomly assigned to the pond halves. Tadpole densities in ponds (approximately 700 tadpoles m⁻²) were below the median local density that occurs in natural breeding sites in the region (Biesterfeldt et al. 1993) and near the upper limit of average densities in ponds that we have sampled in western North Carolina (the average tadpole density on pond bottoms may exceed 900 tadpoles m⁻²; authors, unpublished work).

We resampled pond invertebrates after 5 days and 14 days in the same way. Samples were washed in a No. 25 US standard sieve (mesh diameter = 0.71 mm), hand-sorted, and preserved in 70% ethanol. Mesh size was not sufficient to prevent small invertebrates and the earliest instars of chironomids from passing through. We identified preserved specimens to taxonomic levels that were feasible given the large sample size ($n > 11,000$). To determine if there was evidence of size-selective predation, we haphazardly selected a subsample of 30 midges (the numerically dominant group) from each pooled sample and estimated mean volume using ocular micrometer measurements of length and width.

Field evidence of egg predation by ranid tadpoles

Studies of ecological interactions among North American *Rana* tadpoles have focused on resource competition even though the tadpoles of some species such as the wood frog and bullfrog are known egg predators on other anurans (Ehrlich 1979; Petranka et al. 1994). In eastern North America *R. catesbeiana*, *R. clamitans*, and *R. sylvatica* often co-occur locally, but partially segregate with respect to breeding sites (Werner and McPeck 1994; Wellborn et al. 1996). Optimal habitats are ephemeral ponds for the wood frog (*R. sylvatica*), fish-free semipermanent or permanent ponds for the green frog (*R. clamitans*), and permanent ponds with fish for the bullfrog (*R. catesbeiana*). The tendency for these and other anurans to sort out along hydrological gradients has been explained in terms of predator distributions, antipredator defenses of tadpoles, adult choice of oviposition sites, life-history constraints such as the minimum duration of the larval stage, and competitive interactions between tadpoles (Kats et al. 1988; Hopey and Petranka 1994; Werner and McPeck 1994; Wellborn et al. 1996). Here, we present field observations and data which suggest that egg predation may also play a role in excluding wood frogs from habitats with high densities of larger ranid tadpoles.

We examined predation on wood frog embryos by *R. clamitans* tadpoles at the Tulula Wetlands in Graham Co., western North Carolina. This site is a disturbed wetlands complex that is being used as a mitigation site and contains numerous ponds ranging from highly ephemeral puddles to permanent fish ponds. Ten large semipermanent to permanent ponds were constructed on the site in 1995–1996 and have since been used by *R. sylvatica* and *R. clami-*

tans for breeding. In 1997 we observed aggregates of overwintering *R. clamitans* tadpoles feeding on *R. sylvatica* eggs in two ponds with high densities of *R. clamitans* tadpoles.

To determine density effects and to verify what appeared to be mass mortality of embryos due to tadpole predation, we estimated densities of *R. clamitans* tadpoles and hatchling *R. sylvatica* in these and five other ponds (three constructed; two natural) that contained both species. We sampled ponds within 7–10 days after the wood frog hatch terminated using open-bottomed galvanized trash cans (bottom area = 0.11 m²; 20–64 samples per pond depending on pond size). These were pushed into the pond bottom at roughly equidistant points then dipnetted until five consecutive sweeps yielded no tadpoles. We used average catch to estimate tadpole densities of both species. We estimated embryonic survival for *R. sylvatica* using data on number of egg masses in ponds, mean number of eggs per mass based on direct counts of eggs in dissected masses (mean = 1006 eggs/mass; $n = 8$), pond surface area, and estimated number of hatchlings in ponds at the time of sampling. We used linear regression to examine relationships between densities of *R. clamitans* tadpoles in ponds and survival of *R. sylvatica* embryos. Other egg predators in the ponds included red-spotted newts (*Notophthalmus v. viridescens*) and *Ptilostomis* caddisflies. We rarely observed these feeding on *R. sylvatica* embryos during 4 years of study and considered both to be insignificant egg predators at this study site.

Statistical analyses

We analyzed data using SAS, version 6.09 (SAS Institute 1989). For the laboratory experiment we analyzed data with a General Linear Model procedure using ranked values because certain data sets violated the assumption of normality and could not be corrected using transformations. In the field experiment, we did not analyze snails, cladocerans, stoneflies, stratiomyid flies, and water boatmen individually because they occurred in fewer than three ponds. For the remaining taxa, and for all taxa pooled, we used a one-tailed signed rank test to compare densities of invertebrates in matched pond halves. We did not use paired *t*-tests because distributions of differences between pairs often grossly violated the assumption of normality. For all other analyses we used parametric tests.

Results

Experiment 1: wood frog predation on invertebrates in laboratory tanks

In the laboratory experiment, we observed tadpoles attacking, killing, and consuming both midges and oligochaetes. Large oligochaetes (often > 5 times the length of tadpoles) were bitten into pieces < 1 cm; these were consumed by either the attacker or nearby tadpoles. Chironomids were either swallowed whole or torn into pieces prior to being consumed. After 2 days prey survival differed significantly depending on presence of tadpoles ($F_{1,54} = 201.80$; $P < 0.0001$) and type of prey ($P = 0.02$). The interaction term was not significant ($P = 0.24$). Prey survival in the absence of tadpoles was > 98% in all prey treatments; in the presence of tadpoles mean survival varied from 24–54% among prey categories (Fig. 1). Pairwise comparisons of prey survival using a Tukey-Kramer test revealed that average survival was significantly lower for small chironomids compared to large oligochaetes. The comparison of small and large chironomids was marginally insignifi-

cant (power=0.36); however, the general trend among groups was for predation rates to decrease with increasing prey size (Fig. 1).

Experiment 2: effects of tadpole addition in the field

Chironomids (71%), copepods (16%), cladocerans (7%), and oligochaetes (4%) were the numerically dominant group among 11,505 invertebrates recovered from dredge samples (Table 1). Mean number of individuals in matched tadpole and control treatments did

not differ significantly for any taxon in samples taken immediately prior to adding tadpoles to ponds (signed rank test: range of *P*-values 0.19–0.74; Fig. 2), and the total number of invertebrates in tadpole versus control halves differed by only 1.5% (*P*=0.95). Five days after tadpole additions, total invertebrates in tadpole treatments were reduced to 49% of controls (signed rank test here and below; *P*=0.004), primarily because of lower densities of chironomid larvae (*P*=0.01). Average reduction in absolute numbers of chironomids was 1288 midges m⁻² of pond bottom based on estimates from dredge samples. The mean density of copepods in the tadpole treatment was significantly lower than controls after 5 days (*P*=0.04), while the difference for oligochaetes was near significance (*P*=0.09). The latter value suggests that oligochaetes were minor prey of tadpoles. Copepods and oligochaetes were both rare in samples on day 14 and neither comparison was significant. Densities of benthic, case-building caddisflies and mosquitoes that frequent the water column were not

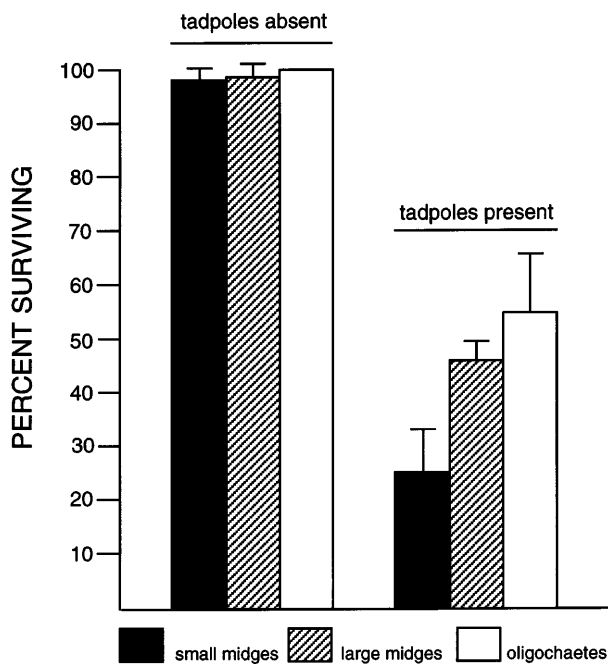
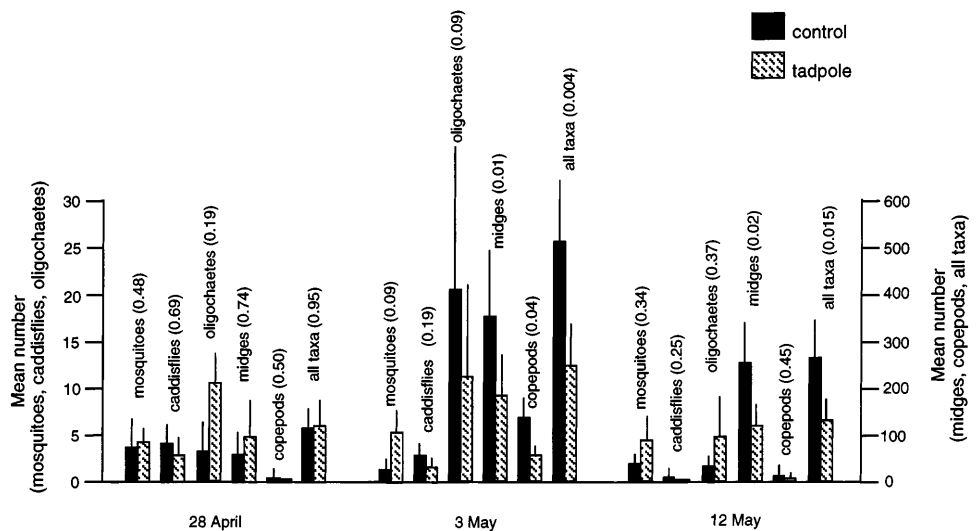


Fig. 1 Survival of midge larvae and oligochaetes after 2 days in laboratory containers with and without tadpoles. Bars are means + 1 SE

Table 1 Absolute and relative abundances of taxa collected in samples. Numbers reflect pooled data for all samples taken during the study

Taxon	Absolute number	Relative number
<i>Isonychia</i> sp. (caddisfly)	78	< 1%
<i>Platycentropus radiatus</i> (caddisfly)	39	< 1%
<i>Ptilostomis</i> sp. (caddisfly)	4	< 1%
Plecoptera (stonefly)	1	< 1%
<i>Lymnaea</i> (snail)	14	< 1%
Corixidae (water boatmen)	4	< 1%
Stratiomyidae (fly)	1	< 1%
<i>Aedes stictus</i> (mosquito)	189	1.6%
Oligochaeta (worms)	426	3.7%
Cladocera (water fleas)	768	6.7%
Copepoda (copepods)	1,822	15.8%
Chironomidae (midges)	8,159	70.9%
Total	11,505	

Fig. 2 Mean number of pond invertebrates recovered from dredge samples before (28 April) versus 5 days (3 May) and 14 days (12 May) after additions of tadpoles to ponds. Bars are means + 1 SE; *P*-values are for sign rank tests using the mean values for each pond half (*n*=8 ponds)



significantly reduced by the addition of tadpoles ($P > 0.05$).

Despite strong evidence of predation on soft-bodied benthic invertebrates, the absolute number of midges in samples increased after tadpole addition. This presumably reflects the fact that midges grew rapidly over the course of the experiment (four-fold increase in average body volume; Fig. 3) and were more likely to be trapped in sieves when samples were processed. The mean body size of midges did not differ significantly between treatments on any of the sample dates (paired t -test; $P > 0.36$; Fig. 3), suggesting that midge size did not strongly influence tadpole predation rates. Mean midge size in field samples were much smaller than those in the laboratory experiment, with the maximum average size (day 14) approximating the small size class used in the laboratory experiment.

Field evidence of egg predation by ranid tadpoles

We first observed green frog tadpoles eating *R. sylvatica* eggs shortly after the eggs were deposited. Within 2 weeks all egg masses had been consumed in Pond 1X (43 masses contained an estimated 43,258 embryos) and Pond 4X (15 masses containing an estimated 15,090 embryos). We did not capture any *R. sylvatica* hatchlings in can samples and did not observe *R. sylvatica* tadpoles in these ponds during the remainder of the field season. These data and observations indicate catastrophic mortality from tadpole predation.

Estimates of tadpole densities in seven ponds shared by *R. clamitans* and *R. sylvatica* indicate a strong inverse

relationship between green frog tadpole density and survival of wood frog embryos to hatching ($F_{1,6} = 23.17$, $P = 0.005$, $r^2 = 0.82$; Fig. 4). Our data and field observations suggest that ponds with green frog densities that exceed about 15 tadpoles m^{-2} act as population sinks for *R. sylvatica*; beyond this density embryonic mortality approximates 100%.

Discussion

Evidence of macrophagous predation by generalized tadpoles

Our studies of ranid tadpoles demonstrate that generalized tadpoles can function both as omnivorous, microphagous suspension feeders and opportunistic, macrophagous predators. Our field studies are the first to provide experimental evidence of tadpole predation on benthic macroinvertebrates. *R. sylvatica* tadpoles appear to be selective predators that favor soft-bodied benthic invertebrates over nektonic forms or species with protective cases or shells. When attacking prey, a tadpole uses its finned tail to thrust forward before biting with the beak. Prey that are soft-bodied, relatively sedentary, and that are resting on firm substrates that allow tadpoles to effectively attack prey with their thrusting beaks appear to be most vulnerable to *R. sylvatica* predation. Harpacticoid copepods were common in our samples and the decrease in copepods following tadpole additions presumably reflects predation on these benthic forms. We suspect that tadpoles also feed on the eggs and hatchlings of a variety of other aquatic organisms such as odonates, snails, and caddis flies that are relatively invulnerable during later stages of development.

Our field data suggest that egg predation may also play a role in excluding wood frogs from habitats with high densities of larger ranid tadpoles. *R. clamitans* tadpoles can cause complete reproductive failure in *R. sylvatica* when densities of overwintering tadpoles are

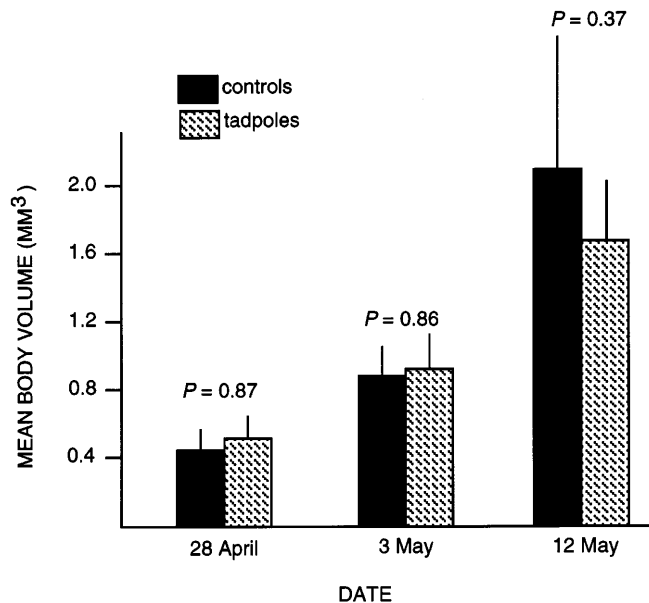


Fig. 3 Mean size of midge larvae for control and tadpole treatments. Tadpoles were added to ponds immediately after samples were taken on 28 April. Bars are means \pm 1 SE and P -values are for paired t -tests using the mean size of midges from each pond half

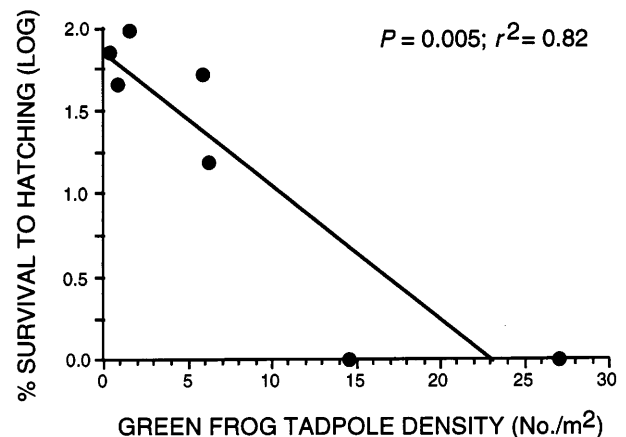


Fig. 4 Relationship between density of overwintering green frog tadpoles and embryonic survivorship of the wood frog

high. At the Tulula Wetlands, ponds with high densities of *R. clamitans* tadpoles act as population sinks that could influence the metapopulation dynamics of *R. sylvatica*. Although previous studies suggest that fish and invertebrate predation may exclude *R. sylvatica* from permanent ponds, our data indicate that tadpole predation by large ranids may also function similarly.

Predation by generalized tadpoles on other amphibians has been documented in eight families of anurans from both temperate and tropical regions of the world (Table 2). Although predation on embryos or hatchlings is most common, tadpoles of certain species prey on free-swimming tadpoles (e.g., Heyer et al. 1975; Kluge 1981; Peixoto and Gomes 1997) or metamorphosing individuals that are attempting to leave ponds (Wright 1931; Crump 1986, 1992). Both con- and heterospecific predation are well documented.

Invertebrates such as copepods, ostracods, cladocerans, rotifers, mosquito larvae, midge larvae, and other insects have been found in the guts of a taxonomically diverse array of anuran tadpoles (Table 2). These could reflect either scavenging or predation, and dietary studies alone cannot conclusively demonstrate predation. Our laboratory studies show that *R. sylvatica* tadpoles can easily kill and consume relatively large prey such as chironomids and oligochaetes, and observations by others have documented tadpoles preying on aquatic organisms such as insect larvae and crustaceans (e.g., Mulaik 1937; Blaustein and Margalit 1996). Thus, we assume that invertebrates found in tadpole guts frequently reflect predation rather than scavenging.

Protein and other high quality food resources such as lipids are often limiting in plant material commonly consumed by tadpoles and the inclusion of concentrated protein and lipid sources in the diet from animal matter can accelerate growth and development and increase size at metamorphosis (Nathan and James 1972; Steinwascher and Travis 1983; Pandian and Marian 1985; Crump 1992; Kupferberg 1997). Because generalized tadpoles have cornified beaks that are capable of piecing animal tissues, we see no design constraints that would limit tadpoles to herbivory or omnivorous microphagy. Selection should generally favor opportunistic predation, particularly on anuran embryos and hatchlings that may represent future competitors for scarce food resources.

The realization that generalized tadpoles often function as macrophagous predators requires a reexamination of the ecological and evolutionary roles of tadpoles in aquatic systems. We discuss two of the most relevant issues in the next sections.

Species interactions, food web links, and community organization

Generalized tadpoles frequently have been used by community ecologists to examine species interactions and rules of community assembly. Studies primarily have been conducted in field enclosures or seminatural

outdoor tanks and run as black box experiments (Wilbur 1984; Hairston 1989; Gurevitch et al. 1992). The implicit assumptions in almost all of these studies are that tadpoles function as omnivorous grazers or suspension feeders, occupy lower trophic levels in experimental communities, and primarily interact either through exploitative competition for food resources (e.g., Morin 1983; Wilbur 1987) or interference mechanisms involving the transmission of growth inhibiting microorganisms (e.g., Griffiths et al. 1991). If these basic assumptions are false, then interactions that can occur among community members through both direct and indirect pathways are far more intricate and the causal mechanisms for experimental results are less certain.

Wilbur and Alford (1985) and Morin (1983) are two examples of many studies where tadpoles may have played dual roles as omnivorous filter-feeders and macrophagous predators. These studies examined tadpole interactions in seminatural communities established in metal tanks. In the former study, hatchling gray treefrogs (*Hyla chrysoscelis*) that were added to tanks containing larger tadpoles of the southern leopard frog (*Rana sphenoccephala*) had significantly lower premetamorphic survival than controls without *Rana*. Wilbur and Alford (1985) attributed the low survival of *H. chrysoscelis* to priority effects related to competition for food. Because tadpoles of *R. sphenoccephala* are known egg predators (Seale 1980) and can likely prey on hatchling tadpoles as well, we suggest that predation of *Rana* on hatchling *Hyla* may have contributed to the low survival of *Hyla*.

In the second example, Morin (1983) studied competitive interactions in tadpole communities by added hatchlings of six species to experimental tanks in accordance with the natural breeding phenology of the species. When predators were absent *Scaphiopus holbrooki* tended to dominate the assemblage, while *Hyla gratiosa* and *Pseudacris crucifer* had very low survival to metamorphosis. Morin logically attributed these patterns to superior competitive ability of *S. holbrooki* for limited food resources. However, two of the community members (*S. holbrooki*; *R. sphenoccephala*) are known anuran predators. Because tadpoles of *S. holbrooki* are capable of preying on eggs, tadpoles, and even large, metamorphosing conspecifics (Wright 1931; Ball 1936; Richmond 1947), this species may have preyed on *P. crucifer* – a relatively immobile species that would be vulnerable to attack. We also cannot rule out predation by large *R. sphenoccephala* tadpoles on *H. gratiosa* hatchlings. Thus, both resource competition and predation by tadpoles may have influenced community assembly. Our use of these examples is not intended to criticize the conclusions of these authors, but to encourage future researchers to more fully consider the potential significance of macrophagy by generalized tadpoles when designing experiments and interpreting results.

Interestingly, Woodward (1982b) is the only researcher who has considered tadpole predation in

Table 2 Examples of macrophagy by generalized tadpoles. Scientific names are given for all predators and prey that are amphibians (codes: *EGG* eggs, *HA* hatchlings, *TAD* free-swimming tadpoles, *INV* invertebrates, *CON* conspecifics). Codes for conditions reflect the experimental setting or data set that conclusions were derived

from (*G* analyses of gut contents, *L* laboratory observations or experiments, *S* seminatural experiments, *N* observations in natural habitats). Data for *Spea* are for instances where predation appears to be due primarily to noncannibalistic morphs

Predator taxa	Prey type	Prey taxa	Conditions	Source
Bufo				
<i>Bufo arenarum</i>	EGG	CON	N	Crump 1992
<i>B. bufo</i>	INV	Arthropods	G	Diaz-Paniagua 1989
<i>B. bufo</i>	EGG	<i>B. calamita</i>	N, S	Banks and Beebee 1987
<i>B. calamita</i>	INV	Rotifers	G	Diaz-Paniagua 1985
<i>B. calamita</i>	EGG	CON	N, S	Banks and Beebee 1987
<i>B. viridis</i>	INV	Mosquitoes	S	Blaustein and Margalit 1996
Dendrobatidae				
<i>Dendrobates auratus</i>	TAD	<i>D. auratus</i>	N	Duellman and Trueb 1986; Crump 1992
Discoglossidae				
<i>Discoglossus pictus</i>	INV	Arthropods	G	Diaz-Paniagua 1985
Hylidae				
<i>Hyla geographica</i>	EGG	CON; <i>Osteocephalus</i> spp.	L	Magnusson and Hero 1991
<i>H. granosa</i>	EGG	<i>H. geographica</i>	L	Magnusson and Hero 1991
<i>H. meridionalis</i>	INV	Rotifers; arthropods	G	Diaz-Paniagua 1985
<i>H. minuta</i>	TAD	CON; <i>Physalaemus</i> sp.	L	Peixoto and Gomes 1997
<i>H. pseudopuma</i>	EGG; HA	CON	L, N	Crump 1983
<i>H. rosenbergi</i>	EGG; TAD	CON	N	Kluge 1981
<i>Litoria alboguttata</i>	EGG; HA	<i>Bufo marinus</i>	L	Crossland and Alford 1998
<i>L. bicolor</i>	EGG	<i>B. marinus</i>	L	Crossland and Alford 1998
<i>L. infrafrenata</i>	EGG; HA	<i>B. marinus</i>	L	Crossland and Alford 1998
<i>L. nigrofrenata</i>	EGG	<i>B. marinus</i>	L	Crossland and Alford 1998
<i>L. rubella</i>	EGG	<i>B. marinus</i>	L	Crossland and Alford 1998
<i>Osteocephalus taurinus</i>	EGG	<i>Hyla</i> ; <i>Osteocephalus</i> spp.	L, N	Magnusson and Hero 1991
<i>Osteopilus septentrionalis</i>	TAD	CON	L	Crump 1986
<i>Phyllomedusa bicolor</i>	EGG	<i>H. geographica</i>	L	Magnusson and Hero 1991
<i>P. vaillanti</i>	EGG	<i>H. geographica</i>	L	Magnusson and Hero 1991
Leptodactylidae				
<i>Leptodactylus knudseni</i>	EGG	CON; other anurans	N	Hero and Galatti 1990
<i>L. knudseni</i>	EGG	<i>Hyla</i> ; <i>Osteocephalus</i> spp.	L, N	Magnusson and Hero 1991
<i>L. pentadactylus</i>	INV; HA	<i>B. marinus</i> ; <i>H. rosenbergi</i> ; <i>Physalaemus pustulosus</i> ; <i>Smilisca phaeota</i> ; mosquitoes	L	Heyer et al. 1975
<i>L. pentadactylus</i>	EGG; TAD	<i>H. rosenbergi</i>	L, N	Kluge 1981
<i>L. rhodomystax</i>	EGG	<i>H. geographica</i>	L	Magnusson and Hero 1991
<i>Physalaemus pustulosus</i>	EGG; TAD	<i>H. rosenbergi</i>	N	Kluge 1981
<i>Pleurodema nebulosa</i>	TAD	CON	N	Cei 1979
Myobatrachidae				
<i>Lechriodus fletcheri</i>	INV; TAD	Mosquitoes	S	Pimm and Kitching 1987
<i>L. fletcheri</i>	TAD	CON	L	Martin 1967
<i>Limnodynastes ornatus</i>	EGG; HA	<i>Bufo marinus</i>	L	Crossland and Alford 1998
Pelobatidae				
<i>Pelobates cultripes</i>	INV	Ostracods; arthropods; rotifers	G	Busack and Zug 1976
<i>P. cultripes</i>	INV	Arthropods; rotifers	G	Diaz-Paniagua 1985
<i>P. cultripes</i>	EGG	<i>B. calamita</i>	L, N	Tejedo 1991
<i>Scaphiopus holbrookii</i>	INV; EGG	Ostracods; CON	G, N	Richmond 1947
<i>S. holbrookii</i>	TAD	CON	N	Ball 1936
<i>S. holbrookii</i>	TAD	CON	L	Wright 1931
<i>S. hurteri</i>	TAD	CON	L	Bragg 1964
<i>Spea bombifrons</i>	TAD	<i>Scaphiopus couchi</i>	L, N	Bragg 1964
<i>S. bombifrons</i>	TAD	CON	L	Bragg 1964
<i>S. bombifrons</i>	TAD	<i>Bufo cognatus</i>	N	Bragg 1940
<i>S. multiplicata</i>	INV	Anostracan shrimp	L	Pfennig 1990
<i>S. multiplicata</i>	TAD	<i>Rana pipiens</i>	S	Woodward 1982b
Pelodytidae				
<i>Pelodytes punctatus</i>	EGG	<i>B. calamita</i>	L, N	Tejedo 1991
<i>P. punctatus</i>	INV	Arthropods	G	Diaz-Panagua 1989

Table 2 (Contd.)

Predator taxa	Prey type	Prey taxa	Conditions	Source
Ranidae				
<i>Hoplobatrachus occipitalis</i>	TAD	CON	N	Boll et al. 1998
<i>Pyxicephalus adspersus</i>	TAD	CON	N	Grobler 1972
<i>Rana catesbeiana</i>	EGG; HA	<i>R. blairi</i>	L	Ehrlich 1979
<i>R. clamitans</i>	EGG	<i>R. sylvatica</i>	N	This study
<i>R. perezi</i>	INV	Arthropods	G	Diaz-Paniagua 1985
<i>R. sylvatica</i>	EGG; HA	<i>Bufo americanus</i>	N, S	Petranka et al. 1994
<i>R. sylvatica</i>	EGG; HA	CON	L, N	Petranka and Thomas 1995
<i>R. sylvatica</i>	EGG	<i>Ambystoma maculatum</i>	N, S	Petranka et al. 1998
<i>R. sylvatica</i>	INV	Chironomids; oligochaetes; copepods	L; N	This study
<i>R. temporaria</i>	EGG	<i>Bufo calamita</i>	N, S	Banks and Beebee 1987
<i>R. temporaria</i>	EGG	<i>B. calamita</i> ; <i>Bombina variegata</i> ; <i>Hyla arborea</i>	S	Heusser 1970
<i>R. temporaria</i>	INV	Insects, cladocerans	G	Savage 1961
<i>R. tigrina</i>	TAD	CON	L	McCann 1932
<i>R. sphenocephala</i>	EGG	<i>R. pipiens</i> / <i>R. blairi</i>	N	Seale 1980

studies of experimental tadpole communities. He concluded that tadpoles of *Spea multiplicatus* ate all *R. pipiens* within 2–3 days after 7-day-old *Rana* tadpoles were added to field enclosures. Although some cannibalistic *Spea* morphs likely occurred at low frequencies in these experimental populations, the catastrophic mortality of tadpoles that occurred within 2–3 days of *Rana* addition strongly suggests that noncannibalistic morphs with generalized morphology were the major source of mortality.

Experimental ecologists have made little progress in understanding how opportunistic predation by generalized tadpoles affects community structure in natural systems. Experimental studies of the wood frog (*R. sylvatica*) in the southern Appalachians provide the most compelling evidence that macrophagous tadpoles can potentially function as keystone predators in organizing pond communities. Wood frog tadpoles are both suspension feeders and opportunistic predators. Like many species that inhabit ephemeral ponds, the tadpoles often reach high densities, have high activity levels, and form large feeding aggregates (Wassersug 1973). Wood frog tadpoles cannibalize the eggs of late breeders (Petranka and Thomas 1995) and will readily consume the eggs of American toads (*Bufo americanus*), gray treefrogs (*Hyla chrysoscelis*), and other anurans that cooccur locally (Petranka et al. 1994). The tadpoles are major predators on spotted salamander (*Ambystoma maculatum*) embryos, and in some cases may nearly eliminate this top predator from vernal ponds (Petranka et al. 1998). As demonstrated here, the tadpoles also prey upon soft-bodied benthic invertebrates. These documented food web links coupled with the potential for wood frog tadpoles to compete with other anurans as suspension feeders—reflect the complex ecological roles that macrophagous tadpoles can potentially have in organizing pond communities both through top-down and bottom-up effects. Wood frog tadpoles, for example, could adversely affect spotted salamanders by consuming embryos, by competing directly for inverte-

brate prey such as chironomid larvae, or by reducing zooplankton levels by filter-feeding on phytoplankton. Our data suggest that wood frog tadpoles function both as keystone predators and microphagous suspension feeders in small ephemeral ponds in the southern Appalachians.

Freshwater habitat gradients revisited

Seasonal hydroperiod affects both alpha and beta diversity in freshwater ponds. Changes in biotic and abiotic parameters along the gradient from highly ephemeral to permanent ponds play a key role in shaping organismal behaviors and life history traits, limiting the adaptive responses of aquatic organisms, and restricting the distribution of species and communities to a subset of the gradient (e.g., Heyer et al. 1975; Woodward 1983; Kats et al. 1988; Semlitsch 1988; Skelly 1995, 1997; Smith and Van Buskirk 1995; Hecnar and M'Closkey 1996; Wellborn et al. 1996). Seasonally ephemeral ponds have been portrayed as having few or no predators, while semipermanent and permanent ponds have high loads of predatory insects and fishes, respectively, which can limit species distributions along the gradient (Wellborn et al. 1996; Skelly 1997). The tradeoffs between selection for rapid growth and development rates versus antipredator behaviors is viewed as a critical driving force that shapes life history traits and behaviors and organizes communities along the gradient.

The view that ephemeral ponds have few or no predators is based on the assumption that generalized tadpoles are not macrophagous predators. In reality, ephemeral ponds may pose extreme predation risk to certain occupants because high tadpole densities, intense competition for food resources, time constraints associated with living in temporary habitats, and the low nutritional value of plant matter favor opportunistic predation by tadpoles. Thus, it is not surprising that most species that are egg predators (Table 2), cannibals

(Crump 1983, 1992; Pfennig 1990; Pfennig et al. 1993), specialized carnivores (Blair 1976; Ruibal and Thomas 1988), or that have been found to have relatively high occurrences of macroinvertebrates in their guts (Table 2) inhabit temporary ponds.

We believe that a less stereotypic view of the relationship between predation risk and pond permanence will lead to a more comprehensive understanding of community organization along hydrological gradients. Much depends on local conditions and species-specific interactions, and the rules of assembly may not be as straightforward as we once thought. At the Tulula Wetlands, for example, American toads almost never oviposit in ephemeral ponds with high densities of wood frog tadpoles. These are high-risk sites where egg and hatchling predation is usually catastrophic (Petranka et al. 1994). Adult toads actively avoid sites with wood frog tadpoles and typically use either road side puddles that are not used as breeding sites by *R. sylvatica*, or semi-permanent ponds where green frog tadpoles eliminate wood frogs via egg predation. With respect to American toads, semipermanent ponds usually offer less risk than ephemeral ponds with *R. sylvatica* – the reverse of that typically portrayed for freshwater hydrological gradients. The same may apply for a variety of aquatic organisms that are vulnerable to tadpole predation. Woodward (1982b), for example, concluded that *R. pipiens* is restricted to more permanent ponds because of tadpole predation by ephemeral pond tadpoles. Similarly, Blaustein and Margalit (1996) found that mosquito larvae may suffer heavy predation from tadpoles that hatch in small pools prior to their arrival of ovipositing mosquitoes.

We view spatiotemporal patterns along hydrological gradients as being complex, dynamic, and often unpredictable. For a given species such as the American toad or a midge, predator gradients may reverse from year to year depending on predator population dynamics and breeding success. We see the landscape as an ever changing mosaic where predation risk varies in complex spatial and temporal patterns, particularly in fish-free ponds. Generalized tadpoles that function as opportunistic predators are an important part of the predation risk landscape, and the boom-and-bust reproductive patterns and local extinction events that characterize many anuran species (Hecnar and M'Closkey 1996; Semlitsch et al. 1996) contribute much to spatiotemporal variability in predation risk. This unpredictability may explain in part why many aquatic organisms with biphasic life cycles assess predation risk and choose oviposition sites opportunistically (Resetarits and Wilbur 1989; Petranka and Fakhoury 1991; Petranka et al. 1994), and why aquatic forms often show strong behavioral flexibility with respect to predator avoidance. Although the traditional predator gradient model clearly is helpful in explaining many patterns along hydrological gradients (e.g., Skelly 1995, 1997; Smith and Van Buskirk 1995; Wellborn et al. 1996), it also obscures the complexity of predator-prey interactions by treating tadpoles as microphagous omnivores and by ignoring

the high predation risk associated with predatory tadpoles that inhabit temporary ponds.

Although herpetologists and amphibian biologists have long been aware of dietary specializations and macrophagy by tadpoles, too many members of the scientific community who fall outside this realm have stereotypic views of tadpoles as being “herbivores” or strict microphagous suspension feeders. Clearly, the time has arrived for a more realistic view of the functional roles of generalized tadpoles in aquatic systems. Tadpoles show much diversity in feeding niches, and future studies likely will reveal that many generalized species play dual roles as both microphagous suspension feeders and macrophagous predators. We encourage researchers to reconsider the long-held notion that tadpoles are “herbivores” and to reevaluate the mechanisms by which generalized tadpoles organize communities, drive life history evolution, and generate patterns of biodiversity across the landscape.

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