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

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 · Macrophyphy · Rana · Predatory tadpoles

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 McPeek 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 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). 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 lumbriculid 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 lumbriculid oligochaetes (respective mean length, body diameter, and dry mass = 75.2 mm ± 5.9 mm, 1.60 ± 1.05 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 × 30 cm × 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, caddisflies, salamanders (Notophthalmus viridescens, Gyrinophila 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