

## OPINION

# What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats

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## SUMMARY

1. Understanding the trophic status of consumers in freshwater habitats is central to understanding their ecological roles and significance. Tadpoles are a diverse and abundant component of many freshwater habitats, yet we know relatively little about their feeding ecology and true trophic status compared with many other consumer groups. While many tadpole species are labelled herbivores or detritivores, there is surprisingly little evidence to support these trophic assignments.

2. Here we discuss shortcomings in our knowledge of the feeding ecology and trophic status of tadpoles and provide suggestions and examples of how we can more accurately quantify their trophic status and ecological significance.

3. Given the catastrophic amphibian declines that are ongoing in many regions of the planet, there is a sense of urgency regarding this information. Understanding the varied ecological roles of tadpoles will allow for more effective conservation of remaining populations, benefit captive breeding programmes, and allow for more accurate predictions of the ecological consequences of their losses.

*Keywords:* amphibian, assimilation, diet, feeding behaviour, omnivory

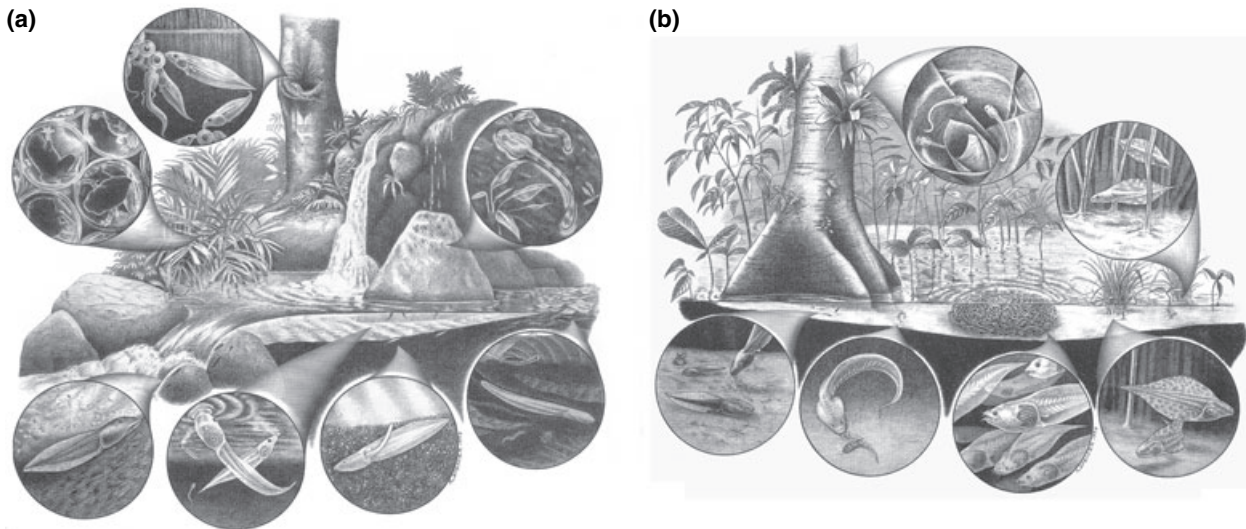
Amphibians are disappearing from the planet at an alarming rate (Stuart *et al.*, 2004; Lips *et al.*, 2005). Along with the inherent tragedy of this loss of biodiversity, there is the potential for a host of ecological effects that transcend amphibian populations and communities (e.g. Ranvestel *et al.*, 2004; Mendelson *et al.*, 2006; Whiles *et al.*, 2006). To predict the ecological consequences of the loss of amphibians, we must have a comprehensive understanding of their natural history and trophic interactions. Thus, we strongly concur with the call by Petranka & Kennedy (1999) for a re-evaluation and further study

of the functional roles and trophic status of generalised tadpoles, an abundant and diverse group of amphibians whose varied ecological roles remain surprisingly poorly understood.

Tadpoles are found in a variety of freshwater habitats, and although they are most conspicuous in standing water habitats in temperate zones, tadpole assemblages can also be very abundant and diverse in lotic habitats in the tropics (e.g. Inger, Voris & Frogner, 1986; Whiles *et al.*, 2006). For example, densities of >50 individuals m<sup>-2</sup> have been reported from headwater streams in the Central American uplands (Lips, 1999; Ranvestel *et al.*, 2004). Where they are found, tadpoles show great morphological diversity, inhabit a wide variety of microhabitats, and most likely play a variety of ecological roles

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**Fig. 1** (a) Diorama depicting functional diversity of tadpoles associated with lotic habitats in the Neotropics. From the top right moving clockwise, species depicted are: *Thoropa miliaris*, a semiterrestrial grazer that lives in hygropetric habitats; *Cochranella granulosa*, a detritivore that burrows in deposits of organic materials; *Otophryne pyburni*, a psammonic detritivore; *Phasmahyla guttata*, a neustonic species with an umbelliform oral apparatus for feeding on the surface tension; *Hyla armata*, a suctorial species that grazes substrates in riffles and runs; *Eleutherodactylus ridens*, embryos of a direct developing species in litter accumulations at the axils of riparian plants, and; *Phrynohyas resinifitrix*, an omnivorous and oophagous species often found in tree holes. Original art by Kate Spencer, from Hoff *et al.* (1999). (b) Diorama depicting functional diversity of tadpoles associated with lentic habitats in the Neotropics. From the top middle moving clockwise, species depicted are: *Hyla bromeliacia*, a detritivore that lives in phytotelmata of bromeliads; *Hyla microcephala*, a midwater macrophagous tadpole; *Scinax staufferi*, a nektonic tadpole that scrapes biofilms and other materials from plants and inorganic substrates; *Rhinophrynus dorsalis*, a filter-feeder that swims in schools; *Leptodactylus pentadactylus*, an omnivore that often preys on smaller tadpoles, and; *Bufo marinus*, a benthic grazer.

(Altig & Johnston, 1989; Fig. 1). However, tadpoles are often overlooked and understudied relative to other consumer groups such as fishes and macroinvertebrates in freshwater ecosystems, and the true trophic status of many tadpole species remains unknown (Altig & Johnston, 1989; Pryor & Bjørndal, 2005a,b); basic information that is central to understanding their ecological significance and thus the consequences of their loss. A more accurate understanding of the nutritional ecology of tadpoles will also benefit captive breeding programmes, which appear to represent the last hope for many declining species (Mendelson *et al.*, 2006). Further, many amphibian declines have been linked to diseases such as chytridiomycosis and ranaviruses, and diet and feeding behaviours, particularly cannibalism and scavenging, could influence transmission and susceptibility.

The feeding and trophic relations of macrocarnivorous tadpoles that often engulf entire organisms (e.g. *Ceratophrys*, *Lepidobatrachus*, *Spea* spp.; see Crump, 1992) are relatively clear, and the diets of

suspension-feeders (e.g. microhylids, pipids and rhinophrynids) require a separate discussion. While addressing only the general feeding ecology of rasping tadpoles, which constitute the bulk of tadpole diversity, herein we counter the poorly supported consensus that tadpoles function consistently as herbivores, and we present a heuristic discussion of alternative ideas that is intended to catalyse much-needed and increasingly urgent research in this area of tadpole ecology.

Classical studies of tadpole diets can provide information on feeding behaviours and functional roles of tadpoles if sampling is carried out correctly, but these studies are often uninformative for assessing trophic status for four related reasons: (i) only ingested materials (e.g. gut contents) are assessed, usually at relatively low magnification, with no idea of relative digestibility; (ii) the complete taxonomic, calorific and nutrient compositions of consumed materials, and the nutritional needs of the tadpoles, are poorly known; (iii) sampling of comparative food sources from the environment is either not

performed or inadequate (e.g. too coarse-grained) and biased towards autotrophic materials and (iv) little is known about the behavioural feeding ecology of tadpoles (e.g. spatiotemporal patterns of foraging and biotic or abiotic factors that influence them). Investigators have been further thwarted by the lack of information on interspecific and ontogenetic changes in mouthpart operations and how the differences in tadpole mouthpart configurations afford selective feeding.

While some studies have provided important information on components of tadpole feeding behaviours and diets, information on assimilation and nutritional ecology is mostly lacking. It is well established that dietary variables influence tadpole growth (e.g. Hegner, 1922; Steinwascher & Travis, 1983; Peterson & Boulton, 1999; Skelly & Golon, 2003), and sympatric species may differ in visible gut contents (Zhou, Zhang & He, 2005), which probably reflects different feeding sites or preferences. At the same time, we posit that the feeding habits and major energy and nutrient sources of typical rasping tadpoles in the field remain essentially unknown. Ingested material and that which is assimilated may differ substantially, as has been shown for numerous freshwater invertebrates (e.g. Cummins & Klug, 1979; Evans-White, Dodds & Whiles, 2003) and fishes (e.g. Bowen, Lutz & Ahlgren, 1995; Evans-White *et al.*, 2003) that have been traditionally considered herbivores or detritivores. What is often described as the consummatory diet of aquatic consumers may often serve only as a substrate and harvestable carrier for assimilated material such as microbes and protozoans, components that are often not properly assessed in analyses of gut contents. Knowing what tadpoles ingest can provide important insight into their functional roles (e.g. their contributions to the processing and transformations of basal resources such as changing particle sizes of organic materials through feeding and egestion), but this does not necessarily reflect their trophic status.

Examinations of tadpole feces have been used to assess tadpole diets (e.g. Pavignano, 1989), but these are also problematic as they produce a distorted image because this material obviously contains primarily what remains after digestion, and the contributions of these materials to diets are possibly inflated. Diatoms are particularly problematic because their silicon frustules, structures that are easily seen

and counted in these analyses, are very refractory in the environment. The presence of abundant empty frustules in tadpole guts does not necessarily show that they were ingested as live individuals. Among other kinds of studies (e.g. Cowie & Hedges, 1996), there is a need for investigations in which tadpoles are fed various types of viable diatoms. By comparing the number of empty frustules in the food source and the feces of tadpoles, we would gain insight into if and how diatoms are actually digested.

### Tadpoles as herbivores and detritivores

The dogma of tadpole herbivory probably stems from the frequent abundance of visible, algal-based items (i.e. green material) in their long guts, the successful rearing of tadpoles on plant-based materials, and the mechanics of the food-trapping structures designed for particle capture (e.g. Wassersug & Hoff, 1979). Three counter-arguments set the stage for further discussion: (i) most tadpoles are more likely omnivorous at best; (ii) tadpole diets show great temporal and spatial variation and (iii) contrary to the general concept that is also often incorrect for many other taxa, what tadpoles ingest (i.e. that which can be counted, measured and identified with standard techniques) is an improper proxy for what they actually assimilate.

Inexact definitions of food materials and semantic issues in the tadpole feeding literature compound problems, even though knowledge of the biology of the various food sources of tadpoles is just as important to our understanding of their ecological roles as is the biology of the tadpoles themselves. For example, 'periphyton' is often used to describe the prolific and complex communities that develop on submerged substrata, even though significant heterotrophic components are often present (Lock *et al.*, 1984). Hence, much of the 'periphyton' referred to in the tadpole feeding literature should be more accurately referred to as epilithon. 'Aufwuchs' and 'biofilm' are also better descriptors because the dominance of autotrophs is not implied. Bacterial and fungal constituents of these materials are seldom considered in the tadpole feeding literature, even though they may be equally or more important components in the epilithon in many systems, particularly those of more oligotrophic habitats (e.g. Stock & Ward, 1989; Hall, 1995; Hall & Meyer, 1998).

The dynamic nature of epilithic food resources that are available to tadpoles requires frequent and fine-grained sampling. Epilithon starts to form within hours of the entry of a new substrate into the water, and although they may look grossly similar, epilithic communities pass through succession rapidly and show great spatiotemporal variation relative to every factor in the environment (Lock *et al.*, 1984; Neely & Wetzel, 1997). Hence, sampling this material once in the field, or at the beginning or end of an experiment, usually will be inadequate for assessing food resource availability to tadpoles.

Some would argue that tadpoles are herbivores because they have a long gut, field-collected specimens often have green material in their guts, and reared individuals usually are fed plant-based materials (e.g. Alford, 1999). However, the long gut tract of tadpoles probably compensates for the weak to absent peristalsis (Naitoh *et al.*, 1990), and processing of plant materials that are fed to tadpoles typically involves modifications such that the materials no longer have the characteristics of natural plant material. In fact, many commercial foods that have been used in tadpole rearing contain animal tissues [e.g. Frog Brittle (Nasco Science, Fort Atkinson, Wisconsin, U.S.A.) and Tetramin® (Tetra Werke, Melle, Germany)]. The high propensity for plant-based foods to foul the water in rearing chambers and aquaria also demonstrates that they are excellent substrates for microbial and protozoan growth.

Rasping tadpoles can suspension feed under proper circumstances of particle abundance (e.g. Seale & Beckvar, 1980; Seale, 1982), and because of the obvious differences from attached or deposited benthic materials, phytoplankton presents a different feeding scenario. Phytoplankton has been postulated as an important food source in some studies. Johnson (1991) related growth of *Acris* tadpoles with phytoplankton abundance, but one must assign cause with caution. This correlation may well have been linked to simultaneous blooms of bacteria, protozoans and small metazoans (see Test & McCann, 1976) that would be more important within the benthic microhabitat of *Acris* tadpoles. Pryor (2003) found that bullfrog (*Rana catesbeiana*) tadpoles showed no growth over an 8-day period when fed three different species of algae, including two single-celled, planktonic species, although growth was evident in individuals fed *Anabaena flos-aquae*, a nitrogen-fixing

filamentous blue-green alga that is relatively high in protein.

Those species that do derive significant nutrition from autotrophic sources are probably assisted by gut flora. Pryor (2003) and Pryor & Bjorndal (2005a,b) recently described the mechanism and site of microbial fermentation in bullfrog tadpoles, the first description of gastrointestinal fermentation in amphibians. This important finding enhanced earlier ideas on symbionts in tadpole guts (e.g. Battaglini & Boni, 1967; Beebee & Wong, 1992; Lajmanovich, Emiliani & Peltzer, 2001). However, little is currently known about this digestive activity in tadpoles, and further research may show that it is of common occurrence.

As with other species that traditionally have been considered herbivorous, tadpoles that might be considered detritivores may gain most of their nutrition from non-autotrophic sources and should not be considered herbivores in any strict sense. Detritus is mostly composed of degraded plant materials, but this material often bears little resemblance to the original plant tissue in terms of its structure and nutritional content. Much of the nutritional value of detritus may stem more from associated microbes than the particles *per se* (e.g. Cummins & Klug, 1979; Bowen, 1980; Arsuffi & Suberkropp, 1986), and fungal biomass can account for 18–23% of the mass of leaf detritus in headwater streams (Methvin & Suberkropp, 2003). As such, tadpoles that ingest detritus should not be considered herbivores because they are more likely assimilating primarily microbes and associated extracellular materials, as has been demonstrated for many other freshwater detritivores (Cummins & Klug, 1979; Barlocher, 1985; Rossi, 1985; Graca, Maltby & Calow, 1993). As a recent example for tadpoles, stable C and N isotope analyses of centrolenid tadpoles and their presumed food source of fine benthic detritus in Panamanian streams indicated that these tadpoles were assimilating primarily microbes rather than the detritus they ingested (Hunte-Brown, 2006; Whiles *et al.*, 2006).

### Tadpoles as carnivores

Recent evidence suggests that generalised, rasping tadpoles incorporate a variety of animal materials into their diet, and cannibalism and scavenging are well documented for a variety of tadpole taxa (Crump,

1983, 1992). This labile, highly nutritious material can contribute disproportionately to growth and production of freshwater omnivores, even as a small component of the diet (e.g. omnivorous freshwater fish and invertebrates: Benke & Wallace, 1980; Evans-White *et al.*, 2003). As an example, a recent study of stonerollers (*Campostoma anomalum*), stream-dwelling minnows that are traditionally considered herbivores or omnivores, indicated that animal material (primarily invertebrates) that made up only about 6% of gut contents accounted for 21% of their production (Evans-White *et al.*, 2003). In one of the original analyses of the trophic basis of production of freshwater consumers, Benke & Wallace (1980) demonstrated that animal material accounted for about 80% of the production of a net-spinning caddisfly community, freshwater insects that were traditionally considered detritivores/omnivores. In the case of tadpoles, studies indicate that individuals that ingest animal material grow faster than those that do not (Crump, 1990; Heinen & Abdella, 2005), but quantitative information on the relative contributions of animal material to tadpole nutrition and production are still needed.

Using stable isotope techniques, which account for assimilation rather than just ingestion, Schiesari (2004) examined tadpole diets in wetlands in Michigan and noted that *Rana catesbeiana*, *R. clamitans*, *R. pipiens* and *R. sylvatica* tadpoles consumed and assimilated substantial amounts of animal food, and suggested that larval *R. catesbeiana* were functioning as predators. Given that other comprehensive studies suggest bullfrog tadpoles are herbivores (e.g. Pryor & Bjornedal, 2005a,b), these observations underscore the potential for great spatiotemporal variation in tadpole diets and the clear need for further study. Hunte-Brown (2006) and Whiles *et al.* (2006) also used stable isotope techniques to examine the food web of an upland Panamanian stream and found that a variety of tadpoles in these systems, particularly *Rana warszewitschii* and *Colostethus* spp. had stable isotopic signatures that suggested they consumed some animal material; the difference between the  $\delta^{15}\text{N}$  of tadpoles and algal resources in this stream was much higher than the 2‰ fractionation per trophic step that is typical of these streams (Kilham & Pringle, 2000). Studies of tadpoles that account for ecological efficiencies (e.g. Benke & Wallace, 1980; Evans-White *et al.*, 2003), along with ingestion, will allow us to

quantitatively assess the potential importance of carnivory in tadpole nutrition.

### Tadpole feeding behaviour

Information on feeding behaviours is also central to understanding the ecological roles of tadpoles because feeding behaviour is often linked to functional roles (e.g. altering resource availability or quality for other consumers) and can result in both positive and negative interactions with other consumers. Detailed observations on feeding behaviours of tadpoles are still uncommon, although there is increasing evidence that tadpoles in many systems can act as ecosystem engineers that greatly modify resources and/or influence other consumers (Kupferberg, 1997; Flecker, Feifarek & Taylor, 1999; Ranvestel *et al.*, 2004; Whiles *et al.*, 2006).

Although interactions between freshwater grazers are often competitive, recent evidence from a neotropical stream suggests that, at least in some cases, tadpoles may facilitate other, smaller grazers. Using electric fences to experimentally exclude tadpoles from artificial substrates in a Panamanian stream, Ranvestel *et al.* (2004) found that grazing mayflies were significantly more abundant where tadpoles were allowed to feed. This pattern was attributed to feeding and bioturbation by tadpoles, which cleared organic and inorganic sediments from substrates and exposed underlying epilithon for mayflies to graze. This result provides intriguing evidence for myriad potential interactions that tadpoles may have with grazers and other consumer groups in freshwater habitats.

Kupferberg (1997) examined the influence of *Rana* and *Hyla* tadpoles on algae and grazing insects in a California stream and found that each had very different effects on ecosystem structure and function. For example, while *Rana* greatly increased algal biomass on stream rocks and increased primary production per unit area by 10%, *Hyla* reduced primary production per unit area by 18%. These responses were attributed to feeding activities of the tadpoles, not nutrient recycling. More importantly, significant differences in algal responses to the feeding activities of the two genera underscore the need for taxon-specific information on feeding behaviours and associated ecological effects, as taxa often lumped as 'grazers' or similar can have very different effects.

The ability of the tadpole gut to change structure relative to diet suggests that acceptable diets can vary considerably (e.g. Horiuchi & Koshida, 1989), and one would thus suspect that digestive enzymes are inducible. For example, *Bufo periglenes*, which is now presumed extinct, had relatively few, but large eggs and developed in what are considered oligotrophic pools based on the lack of autotrophic production (Crump, 1989). However, if these tadpoles fed from the microbial and fungal realm of organisms instead of the presumed autotrophic sources, the oligotrophic status of these habitats was irrelevant to the tadpoles. Because unfed *B. periglenes* tadpoles developed normally in laboratory tests and metamorphosed in similar time periods as fed tadpoles, Crump (1989) concluded that they could develop facultatively on only yolk reserves. This may be true to some degree, but this may also demonstrate the flexibility that tadpoles have to adopt alternative feeding strategies; the unfed tadpoles could have switched to microbial- protozoan food sources and perhaps never noticed the presumed lack of food. Common bacteria have generation times ranging from 11 to 75 min (Atlas, 1997) and could easily provide sufficient food, especially as fecal and excretory products built up and provided a growth medium between water changes.

Changes in tadpole feeding behaviour and growth responses probably signal a change in relative abundances of acceptable food items, and some behaviours present interesting signals beyond the actual acts. What conditions stimulate alternative behaviours and what is gained: digging feeding pits (=tadpole holes or nests; Black, 1971, 1974), feeding off the surfaces of other living tadpoles, feeding inverted at the surface film, feeding on the sides of research containers when abundant artificial food is available on the bottom, switching from rasping to suspension feeding, and avidly eating carrion? These changes in feeding behaviour often occur in situations where we might evaluate the abundance of food, but in reality they may be more related to food quality issues. Studies that focus on food quantity and quality (e.g. C/N ratios, caloric content) will provide much needed information on factors dictating tadpole feeding behaviours.

Using studies by Kupferberg (e.g. Kupferberg, Marks & Power, 1994), as an example, we know that tadpoles feed preferentially and perform differentially on specific food sources. Although these types of

studies can provide useful information, they often remove or reduce the choices that the tadpoles have, and what is deduced to be best for a given species of tadpole may only be the best of the choices presented. Further, indications that tadpoles grow better on periphyton than the macrophyte leaves on which the periphyton grow (Kupferberg *et al.*, 1994) is noteworthy, but in fact we do not know what components of the diet produced the enhanced response. Here again, subsequent studies that build on these results by quantifying food quality, assimilation, tadpole nutrition, and/or the trophic basis of tadpole production will illuminate mechanisms underlying feeding behaviour and growth responses.

### Future research needs

Our intention is to draw attention to and stimulate research on an increasingly critical gap in our knowledge of an important and imperiled group of consumers in freshwater habitats. Given the current situation of catastrophic declines, extirpations and extinctions, we feel a sense of urgency regarding our understanding, or lack thereof, of the feeding ecology and trophic status of tadpoles. Their losses can be expected to influence freshwater systems in many ways, but predicting the consequences and knowing what to look for is difficult without this basic information. We have tried to point out major perceived deficiencies in our current knowledge and, at the least, demonstrate that there is certainly no consensus regarding tadpole feeding ecology. Hence, for many tadpole taxa, we are currently left with the unsatisfactory designation of omnivore, with little quantitative information on the relative importance of the various food types.

A discussion of every way to attack the complex questions regarding tadpole feeding ecology is beyond our scope here, but some particularly promising approaches are worth mention. The meager and contradictory data on digestive enzymes (e.g. Kuntz, 1924; Altig *et al.*, 1975; Carroll, Seneviratne & Ruibal, 1991) need to be revisited with modern techniques. Additional studies on digestive ecophysiology (e.g. Toloza & Diamond, 1990; Beebe & Wong, 1992) in association with digestive facilitators would also greatly enhance our knowledge. Recent documentation of microbial fermentation in bullfrog tadpoles (Pryor, 2003; Pryor & Bjorndal, 2005a,b) supports

hypotheses regarding gut symbionts in tadpoles, and provides a foundation for similar, descriptive work of this nature on other taxa. Comparative studies of tadpoles that live in different habitats such as streams, ponds, tree holes and desert pools would also be illustrative. These habitats differ in the amount and kinds of food materials, and the duration of larval stages varies widely among them.

Stable isotope techniques (e.g. Peterson, 1999; Post, 2002) are promising for assessing trophic status of tadpoles because they reflect assimilation of materials over time rather than just ingestion at a given point in time, as is the case for gut content analyses. Recent investigations by Schiesari (2004); Hunte-Brown (2006) and Whiles *et al.* (2006) demonstrate the value of analyses of natural abundances of C and N isotopes in food resources and tadpoles for assessing tadpole trophic status. Enrichment studies, such as <sup>15</sup>N additions to ponds or streams (e.g. Hall, 1995; Hall, Peterson & Meyer, 1998; Raikow & Hamilton, 2001), are particularly promising as they serve as a tracer for food webs and allow for quantification of the role of consumers in nutrient cycling; enrichment studies in systems where tadpoles are diverse and abundant would provide valuable information on ecological roles.

Although more time consuming and expensive than stable isotope analyses, examination of polyunsaturated fatty acid profiles in food web components is also promising for assessing tadpole diets and trophic status. Like isotopic ratios, fatty acid markers can be used to link consumers to food resources, and they reflect assimilation over time. Fatty acid analyses have been successfully used to assess food web linkages in marine, lake and stream systems (Ahlgren *et al.*, 1997; Napolitano *et al.*, 1997, 1999; Muller-Navarra *et al.*, 2000; Stübing, Hagen & Schmidt, 2003; Sushchik *et al.*, 2003), and these analyses can provide detailed taxonomic information such as the specific types of algae that consumers assimilate (e.g. Parrish *et al.*, 1995; Napolitano *et al.*, 1997, 1999). Fatty acid analyses also give insight into the nutritional quality of various food sources.

Regardless of the specific techniques used, studies of tropical tadpole assemblages are most needed and would be of most value because taxonomic diversity, and thus presumably trophic diversity, is highest and declines are most widespread and catastrophic in the tropics. While detailed information on tadpole diets

and/or trophic status from any region is obviously a valuable contribution, there is clearly an urgent need in the tropics, where we are currently losing entire assemblages before knowing anything about their ecological roles.

### Acknowledgments

T. Halliday, C. Townsend and an anonymous reviewer provided valuable comments that greatly improved this manuscript. Parts of this effort were funded by National Science Foundation grant DEB #0234386.

### References

- Ahlgren G., Goedkoop W., Markensten H., Sonesten L. & Boberg M. (1997) Seasonal variations in food quality for pelagic and benthic invertebrates in Lake Erken – the role of fatty acids. *Freshwater Biology*, **38**, 555–570.
- Alford R.A. (1999) Ecology: resource use, competition, and predation. In: *Tadpoles: The Biology of Anuran Larvae* (Eds R.W. McDiarmid & R. Altig), pp. 240–278. University of Chicago Press, Chicago.
- Altig R. & Johnston G.F. (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs*, **3**, 81–109.
- Altig R., Kelly J.P., Wells M. & Phillips H. (1975) Digestive enzymes of seven species of anuran tadpoles. *Herpetologica*, **31**, 104–108.
- Arsuffi T.L. & Suberkropp K. (1986) Growth of two stream caddisflies (Trichoptera) on leaves colonized by different fungal species. *Journal of the North American Benthological Society*, **5**, 297–305.
- Atlas R.M. (1997) *Principles of Microbiology*. William C. Brown Publishers, Dubuque, IA.
- Barlocher F. (1985) The role of fungi in the nutrition of stream invertebrates. *Botanical Journal of the Linnean Society*, **91**, 83–94.
- Battaglini P. & Boni P. (1967) Indigenous microbial flora and the large intestine in tadpoles. *Experientia*, **23**, 950–951.
- Beebee T.J.C. & Wong L.-C. (1992) Leucine uptake by enterobacterial and algal members of larval anuran gut flora. *Comparative Biochemistry and Physiology*, **101B**, 527–530.
- Benke A.C. & Wallace J.B. (1980) Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology*, **61**, 108–118.
- Black J.H. (1971) The formation of tadpole holes. *Herpetological Review*, **3**, 7.

- Black J.H. (1974) Tadpoles nests in Oklahoma. *Oklahoma Geology Notes*, **3**, 105.
- Bowen S.H. (1980) Detrital nonprotein amino acids are the key to rapid growth in *Tilapia* in Lake Valencia, Venezuela. *Science*, **207**, 1216–1218.
- Bowen S.H., Lutz E.V. & Ahlgren M.O. (1995) Dietary-protein and energy as determinants of food quality – trophic strategies compared. *Ecology*, **76**, 899–907.
- Carroll E.J. Jr, Seneviratne A.M. & Ruibal R. (1991) Gastric pepsin in an anuran larvae. *Development, Growth and Differentiation*, **33**, 499–507.
- Cowie G.L. & Hedges J.I. (1996) Digestion and alteration of the biochemical constituents of a diatom (*Thalassiosira weissflogii*) ingested by an herbivorous zooplankton (*Calanus pacificus*). *Limnology and Oceanography*, **41**, 581–594.
- Crump M.L. (1983) Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. *American Naturalist*, **121**, 281–287.
- Crump M.L. (1989) Life-history consequences of feeding versus non-feeding in a facultatively non-feeding toad larva. *Oecologia*, **78**, 486–489.
- Crump M.L. (1990) Possible enhancement of growth in tadpoles through cannibalism. *Copeia*, **1990**, 560–564.
- Crump M.L. (1992) Cannibalism in amphibians. In: *Cannibalism. Ecology and Evolution Among Diverse Taxa* (Eds M.A. Elgar & B.J. Crespi), pp. 256–276. Oxford University Press, Oxford.
- Cummins K.W. & Klug M.J. (1979) Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, **10**, 147–172.
- Evans-White M.A., Dodds W.K. & Whiles M.R. (2003) Ecosystem significance of crayfishes and stonerollers in a prairie stream: functional differences between co-occurring omnivores. *Journal of the North American Benthological Society*, **22**, 423–441.
- Flecker A.S., Feifarek B.P. & Taylor B.W. (1999) Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. *Copeia*, **1999**, 495–500.
- Graca M.A.S., Maltby L. & Calow P. (1993) Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. *Oecologia*, **93**, 139–144.
- Hall R.O. Jr (1995) Use of a stable carbon-isotope addition to trace bacterial carbon through a stream food-web. *Journal of the North American Benthological Society*, **14**, 269–277.
- Hall R.O. Jr & Meyer J.L. (1998) The trophic significance of bacteria in a detritus-based stream food web. *Ecology*, **79**, 1995–2012.
- Hall R.O. Jr, Peterson B.J. & Meyer J.L. (1998) Testing a nitrogen-cycling model of a forest stream by using a nitrogen-15 tracer addition. *Ecosystems*, **1**, 283–298.
- Hegner R.W. (1922) The effects of changes in diet on the incidence, distribution and numbers of certain intestinal Protozoa of frog and toad tadpoles. *Journal of Parasitology*, **9**, 51–67.
- Heinen J.T. & Abdella J.A. (2005) On the advantages of putative cannibalism in American toad tadpoles (*Bufo a. americanus*): is it active or passive and why? *American Midland Naturalist*, **153**, 338–347.
- Hoff K.S., Blaustein A.R., McDiarmid R.W. & Altig R. (1999) Behaviour: interactions and their consequences. In: *Tadpoles: The Biology of Anuran Larvae* (Eds R.W. McDiarmid & R. Altig), pp. 215–239. University of Chicago Press, Chicago.
- Horiuchi S. & Koshida Y. (1989) Effects of foodstuffs on intestinal length in larvae of *Rhacophorus arboreus* (Anura: Rhacophoridae). *Zoological Science*, **6**, 321–328.
- Hunte-Brown M.E. (2006) The effects of extirpation of frogs on the trophic structure in tropical montane streams in Panama. PhD Dissertation, Drexel University, Philadelphia, Pennsylvania.
- Inger R.F., Voris H.K. & Frogner K.J. (1986) Organization of a community of tadpoles in rain forest streams in Borneo. *Journal of Tropical Ecology*, **2**, 193–205.
- Johnson L.M. (1991) Growth and development of larval northern cricket frogs (*Acris crepitans*) in relation to phytoplankton abundance. *Freshwater Biology*, **25**, 51–59.
- Kilham S.S. & Pringle C.M. (2000) Food webs in two neotropical stream systems as revealed by stable isotope ratios. *Verhandlungen Internationale Vereinigung für Limnologie*, **27**, 1768–1775.
- Kuntz A. (1924) Anatomical and physiological changes in the digestive system during metamorphosis in *Rana pipiens* and *Ambystoma tigrinum*. *Journal of Morphology*, **38**, 581–598.
- Kupferberg S.J. (1997) Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biology*, **37**, 427–439.
- Kupferberg S.J., Marks J.C. & Power M.E. (1994) Effects of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life-history traits. *Copeia*, **1994**, 446–457.
- Lajmanovich R.C., Emiliani F. & Peltzer P.M. (2001) Bacterias coliformes y otras bacterias de interés sanitario en larvas de *Bufo arenarum* Hensel, 1887 (Anura, Bufonidae) en Santa Fe (Argentina). *Alytes*, **18**, 197–208.
- Lips K.R. (1999) Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology*, **13**, 117–125.
- Lips K.R., Burrowes P.A., Mendelson J.R. & Parra-Olea G. (2005) Amphibian declines in Latin America: widespread population declines, extinctions, and impacts. *Biotropica*, **37**, 163–165.



- Lock M.A., Wallace R.R., Costerton J.W., Ventullo R.M. & Charlton S.E. (1984) River epilithon: toward a structural and functional model. *Oikos*, **42**, 10–22.
- Mendelson J.R., Lips K.R., Gagliardo R.W. *et al.* (2006) Biodiversity – confronting amphibian declines and extinctions. *Science*, **313**, 48.
- Methvin B.R. & Suberkropp K. (2003) Annual production of leaf-decaying fungi in 2 streams. *Journal of the North American Benthological Society*, **22**, 554–564.
- Muller-Navarra D.C., Brett M.T., Liston A.M. & Goldman C.R. (2000) A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature*, **403**, 74–77.
- Naitoh T., Miura A., Akiyoshi H. & Wassersug R.J. (1990) Movements of the large intestine in the anuran larvae, *Xenopus laevis*. *Comparative Biochemistry and Physiology*, **97C**, 201–207.
- Napolitano G.E. (1999) Fatty acids as trophic and chemical markers in freshwater ecosystems. In: *Lipids in Freshwater Ecosystems* (Eds M.T. Arts & B.C. Wainman), pp. 21–44. Springer, New York.
- Napolitano G.E., Pollero R.J., Gayoso A.M., MacDonald B.A. & Thompson R.J. (1997) Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca Estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). *Biochemical Systematics and Ecology*, **25**, 739–755.
- Neely R.K. & Wetzel R.G. (1997) Autumnal production by bacteria and autotrophs attached to *Typha latifolia* L detritus. *Journal of Freshwater Ecology*, **12**, 253–267.
- Parrish C.C., McKenzie C.H., MacDonald B.A. & Hatfield E.A. (1995) Seasonal studies of seston lipids in relation to microplankton species composition and scallop growth in South Broad Cove, Newfoundland. *Marine Ecology Progress Series*, **129**, 151–164.
- Pavignano I. (1989) Method employed to study the diet of anuran amphibians larvae. *Amphibia-Reptilia*, **10**, 453–456.
- Peterson B.J. (1999) Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. *Acta Oecologia*, **20**, 479–487.
- Peterson C.G. & Boulton A.J. (1999) Stream permanence influences microalgal food availability to grazing tadpoles in arid-zone springs. *Oecologia*, **118**, 340–352.
- Petranka J.W. & Kennedy C.A. (1999) Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? *Oecologia*, **120**, 621–631.
- Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.
- Pryor G.S. (2003) Growth rates and digestive abilities of bullfrog tadpoles (*Rana catesbeiana*) fed algal diets. *Journal of Herpetology*, **37**, 560–566.
- Pryor G.S. & Bjorndal K.A. (2005a) Effects of the nematode *Gyrodactylus batrachiensis* on development, gut morphology, and fermentation in bullfrog tadpoles (*Rana catesbeiana*): a novel mutualism. *Journal of Experimental Zoology*, **303A**, 704–712.
- Pryor G.S. & Bjorndal K.A. (2005b) Symbiotic fermentation, digesta passage, and gastrointestinal morphology in bullfrog tadpoles (*Rana catesbeiana*). *Physiological and Biochemical Zoology*, **78**, 201–215.
- Raikow D.F. & Hamilton S.K. (2001) Bivalve diets in a midwestern U.S. stream: a stable isotope enrichment study. *Limnology and Oceanography*, **46**, 514–522.
- Ranvestel A.W., Lips K.R., Pringle C.M., Whiles M.R. & Bixby R.J. (2004) Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biology*, **49**, 274–285.
- Rossi L. (1985) Interactions between invertebrates and microfungi in freshwater ecosystems. *Oikos*, **44**, 175–184.
- Schiesari L.C. (2004) *Performance Tradeoffs Across Resource Gradients in Anuran Larvae*. Ph D Dissertation, University of Michigan, Ann Arbor.
- Seale D.B. (1982) Obligate and facultative suspension feeding in anuran larvae: feeding regulation in *Xenopus* and *Rana*. *Biological Bulletin*, **162**, 214–231.
- Seale D.B. & Beckvar N. (1980) The comparative ability of anuran larvae (genera: *Hyla*, *Bufo*, and *Rana*) to ingest suspended blue-green algae. *Copeia*, **1980**, 495–503.
- Skelly D.K. & Golon J. (2003) Assimilation of natural benthic substrates by two species of tadpoles. *Herpetologica*, **59**, 37–42.
- Steinwascher K. & Travis J. (1983) Influence of food quality and quantity on early larval growth of two anurans. *Copeia*, **1983**, 238–242.
- Stock M.S. & Ward A.K. (1989) Establishment of a bedrock epilithic community in a small stream: microbial (algal and bacterial) metabolism and physical structure. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1874–1883.
- Stuart S.N., Chanson J.S., Cox N.A., Young B.E., Rodrigues A.S.L., Fischman D.L. & Waller R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.
- Stübing D., Hagen W. & Schmidt K. (2003) On the use of lipid biomarkers in marine food web analyses: an experimental case study on the Antarctic krill, *Euphausia superba*. *Limnology and Oceanography*, **48**, 1685–1700.

- Sushchik N.N., Gladyshev M.I., Moskvichova A.V., Makhutova O.N. & Kalachova G.S. (2003) Comparison of fatty acid composition in major lipid classes of the dominant benthic invertebrates of the Yenisei River. *Comparative Biochemistry and Physiology*, **134B**, 111–122.
- Test F.H. & McCann R.G. (1976) Foraging behaviour of *Bufo americanus* tadpoles in response to high densities of micro-organisms. *Copeia*, **1976**, 576–578.
- Tolozan E.M. & Diamond J.M. (1990) Ontogenetic development of nutrient transporters in bullfrog intestine. *American Journal of Physiology*, **258G**, 760–769.
- Wassersug R.J. & Hoff K. (1979) A comparative study of the buccal pumping mechanism of tadpoles. *Biological Journal of the Linnean Society*, **12**, 225–259.
- Whiles M.R., Lips K.R., Pringle C.M. *et al.* (2006) The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology and the Environment*, **4**, 27–34.
- Zhou W.L.M.-H., Zhang X.-Y. & He J.-F. (2005) Food comparison between tadpoles of *Rana catesbeiana* and *R. chaochiaoensis* collected from the same habitat. *Zoological Research*, **26**, 89–95.

(Manuscript accepted 7 November 2006)