Can Amphibians Help Conserve Native Fishes?

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Native fish populations have continued to decline worldwide despite advances in management practices. As such, new approaches are needed to complement the old. In many flowing and standing waters, larval amphibians are the dominant vertebrate taxa. This can be important to fisheries due to amphibians' ability to influence macroinvertebrate communities, alter benthic habitat, and supply nutrients in aquatic systems. These changes can, in turn, affect the ecology and fitness of other aquatic organisms such as fishes. Due to their large effects in some systems, it is suggested that fisheries managers carefully consider actions that may affect amphibian populations and actively conserve them in some cases. Preservation of riparian areas and amphibian-associated microhabitats may even be used as a tool to positively impact freshwater fisheries by conserving amphibians that help maintain aquatic systems. Therefore, knowledge of local amphibian life histories and behaviors may be important in conserving associated freshwater fisheries.

INTRODUCTION

Population management of fishes has historically employed a diverse array of techniques, including habitat management, hatchery-reared fish stocking, species conservation, and harvest regulation (Cowx and Gerdeaux 2004). Despite the many successes of these techniques, the overall abundance and distribution of native North American fishes steadily declined throughout the 20th century (Williams et al. 1989), and climate change is predicted to further impact freshwater fishes in the 21st century (Heino et al. 2009). As such, a complementary suite of techniques and approaches is needed if management is to prevent further losses. One such complementary approach is the preservation of organisms that maintain ecosystem processes and geomorphic functions (Mills et al. 1993). Indeed, freshwater organisms that are particularly dominant or have a high biomass can exert a significant influence on sympatric species (Vanni 2002). In many ponds, wetlands, and stream headwaters, larval amphibians of the orders Anura (frogs and toads) and Urodela (salamanders) are the dominant vertebrate taxa (Davic and Welsh 2004; Ranvestel et al. 2004; Gibbons et al. 2006). Fisheries management plans that incorporate amphibians will likely be beneficial to much of the aquatic community.

Due to their high biomass in some systems, amphibians can have measurable effects on lotic and lentic habitats (Seale 1980; Rantala et al. 2015) and food webs in aquatic systems (Burton and Likens 1975; Pough 1980; Unrine et al. 2007). These effects can be divided into three general categories: (1) trophic interactions, (2) direct habitat alteration, and (3) nutrient redistribution (Figure 1). Here, I describe the three primary roles of amphibians in freshwater ecosystems and provide direction for future conservation of native fish and amphibian populations, a common management objective. Additionally, I give some suggestions for incorporating amphibians into fisheries management plans following the precedent of Knapp et al. (2001).

TROPHIC INTERACTIONS

Trophic interactions in aquatic ecology are a well-established phenomenon in which changes in the abundance of one species may alter the structure of the entire food web (Vanni 2002). In freshwater habitats, larval salamanders and anurans typically occupy different trophic levels, because salamanders tend to be obligate carnivores (Davic and Welsh 2004), whereas tadpoles are generally herbivores (Altig et al. 2007). A number of studies have found that salamanders decrease the densities of their aquatic

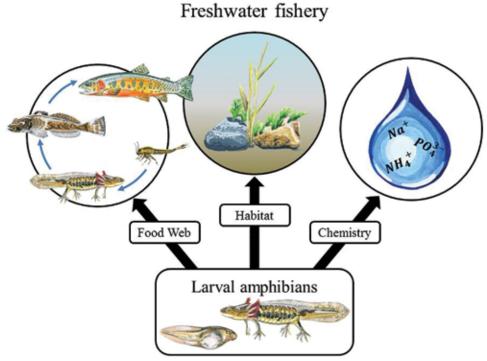


Figure 1. The three general effects of larval amphibians on freshwater fisheries: effects on other animals through trophic interactions, effects on aquatic habitat through grazing and bioturbation, and effects on water chemistry through nutrient redistribution. Figure by T. David Ritter.

invertebrate prey through direct predation and nonconsumptive effects (Huang and Sih 1991). Members of the genera *Ambystoma, Amphiuma, Cryptobranchus, Desmognathus, Dicamptodon, Notophthalmus, Siren,* and *Taricha* have all been implicated in altering densities of freshwater invertebrates (Petranka 2010). In some cases, predation by larval salamanders may be so extensive that responses may cascade through multiple trophic levels and regulate algal production and detritus—litter food webs (Davic and Welsh 2004). Indeed, the large effect of some salamanders on invertebrate populations has led some authors to label them as "keystone species" (Paine 1969; Davic and Welsh 2004). Impacts on invertebrate populations are likely to affect insectivorous fishes that are sympatric with salamanders.

In contrast to larval salamanders, anuran tadpoles are largely herbivorous (see Altig et al. 2007) and therefore can change invertebrate communities by influencing the biomass or productivity of primary producers; for example, tadpole losses in a Panamanian stream led to decreases in macroinvertebrate biomass and diversity, most likely through the consumption of biofilm and changes in benthic algal communities (Rantala et al. 2015). An additional study in four Panamanian streams found no difference in macroinvertebrate biomass before and after the loss of its anuran populations, but it did report shifts in the functional feeding groups of the invertebrate community from shredder to scraper dominance (Colon-Gaud et al. 2008). However, tadpoles of some taxa, such as the American bullfrog Rana catesbeiana, can even directly prey upon fish eggs and juveniles, which can have critical management implications where such fish are endangered (Mueller et al. 2006).

Larval amphibians also constitute a food resource for other animals, both aquatic and terrestrial (Rundio and Olson 2003; Petranka 2010). A study in a New Hampshire forest found that metamorphosed salamanders were a more nutritious food source than birds, mice, and shrews and comprised a greater biomass than that of all breeding birds and was at least equal to that of all small mammals (Burton and Likens 1975). Additionally, deposited eggs and carcasses of larval anurans and salamanders can be a terrestrial-derived, seasonal food source for aquatic organisms (Seale 1980; Capps et al. 2015). Where fish are introduced into previously fishless lakes and ponds, amphibian populations often decline, and subsequent removal of these fish can lead to population recovery (Knapp et al. 2007). In addition, where fish and larval salamanders co-occur, salamanders can incur nonconsumptive effects such as size reduction and reduced likelihood of metamorphosis (Kenison et al. 2016). As such, management actions that prioritize presence of nonnative fishes or overabundance of native fishes over larval amphibian conservation may inadvertently impact an important part of a fisheries food web (Knapp et al. 2001). In short, larval amphibians of both orders can influence macroinvertebrate communities. Accordingly, fisheries professionals should consider how local amphibian populations influence the invertebrate food resources of a fishery and where amphibians act as a food resource themselves.

DIRECT HABITAT ALTERATION

Habitat management is one of the most widely appreciated and accepted tenets of fisheries conservation. The term "habitat" generally includes both physical and biological variables, such as water depth and quality, substrate type, amount of cover, and macrophyte abundance (Fisher et al. 2012). Tadpoles can alter their surrounding biotic and abiotic habitats, in streams and still waters, through two mechanisms: (1) grazing and (2) the mechanical disturbance of benthic sediment from swimming (Flecker et

al. 1999). These two mechanisms, though different, are inseparable. Several studies have found large decreases in benthic sediment and suspended particulate concentration with increasing tadpole abundance (Seale 1980; Flecker et al. 1999; Ranvestel et al. 2004). In addition to affecting primary producers, decreases in sediment can affect invertebrates and small fishes that are reliant on certain benthic conditions (Wood and Armitage 1997; Angradi 1999). Sediment can smother both primary and secondary producers (Power 1990); therefore, sediment removal may be one of the most important impacts of tadpoles in freshwater. Succinctly, tadpole foraging can change the benthic habitat of primary producers, invertebrates, and small fishes in both lotic and lentic habitats. In turn, this may affect fish species of management concern.

NUTRIENT REDISTRIBUTION

Nutrients such as nitrogen and phosphorus are extremely important to the growth and survival of all aquatic organisms (Sterner and Elser 2002). Freshwater animals can increase the concentration of nutrients through release of urea and solid waste. Larger animals, such as fish, can have similar or even greater total excretion rates than small, abundant animals, such as zooplankton (Vanni 2002). In habitats with and without fish, many amphibians also can substantially affect ecosystems due to nutrient redistribution (Connelly et al. 2011).

In some systems, both anuran and urodelan larvae can supply significant amounts of nutrients in streams, which often are important to primary producers and eventually other animals via nutrient flow through food webs (Vanni 2002; Connelly et al. 2011). However, nutrient inputs that contribute substantially on a localized scale may contribute more modestly over larger scales, and because amphibians leave freshwater following metamorphosis, aquatic nutrient subsidies are seasonal and depend on their specific life stage (Keitzer and Goforth 2013). Additionally, where temperature-related declines of fish cause a subsequent loss of nutrients supplied to a stream, the effect may be partially buffered where large populations of larval salamanders (Munshaw et al. 2013) and tadpoles are found. However, more research is needed to fully understand the effects of amphibian nutrient redistribution on freshwater systems.

MANAGEMENT IMPLICATIONS

As freshwater animal populations experience large global declines (World Wildlife Fund 2016), fisheries management must embrace new approaches and techniques to conserve native species. Larval frogs, toads, and salamanders can be important in maintaining the structure and function of freshwater ecosystems through trophic interactions, direct habitat alteration, and nutrient redistribution (Figure 1). Because of the abundance and subsequent effects of these vertebrates on the structure and function of some aquatic ecosystems, managers should incorporate amphibians into native fish conservation plans. Despite many management plans incorporating fish effects on amphibian populations, to the author's knowledge, few if any management plans have incorporated the reverse. Approaches for doing this can be broken into organismal and land management-based approaches.

Organismal approaches are often what fisheries managers are responsible for directly. Such approaches for incorporating amphibians include removal of invasive fishes where native amphibians are abundant, ceasing hatchery stocking of naturally fishless lakes (Knapp et al. 2001), and recording the types and numbers of amphibians observed during fieldwork. Recording amphibian sightings takes minimal effort and can be helpful to those attempting to compile information on anuran and urodelan popula-

tions and may aid in conservation efforts. Invasive amphibians, such as the American toad *Bufo americanus*, should also be carefully monitored and controlled if necessary. Additionally, population modeling efforts should determine whether incorporation of amphibian abundances can increase model accuracy.

In contrast to the manipulation of organisms, fisheries managers may not be directly responsible for management of riparian and aquatic habitats but may fill more of an advisory role. Therefore, land management approaches for conserving amphibians and fish must be tailored to specific land managers' needs. In areas of high amphibian abundance, these approaches should include limiting human impacts in headwater, pond, and wetland habitats; maintaining a riparian buffer zone (Petranka and Smith 2005); reducing pesticide application near waterways (Davidson and Knapp 2007); and maintaining or improving important amphibian microhabitats in both aquatic areas and the surrounding riparian areas during restoration activities. Some microhabitats that are especially important to amphibians include dense tree stands, rotting logs, leaf litter, backwaters, and wetlands (Semlitsch and Bodie 2003). In some cases, it may be useful to consider published thermal niches and habitat preferences for amphibian species of interest (Welsh 2011).

Overall, conservation of native amphibian populations and control of invasive populations may be an effective tool for managing freshwater fisheries. These actions will be most effective where larval amphibian populations are large. It should be noted that some actions may possibly have unforeseen consequences for fish populations of interest due to the inherent complexity of aquatic systems. As such, the aforementioned approaches should be applied in an adaptive management framework. Where amphibians and fishes coexist, the stream corridor can be thought of as a mosaic of amphibian and fish habitats. Maintenance of this mosaic is likely important for all organisms within, and it is possible that ignoring amphibian species may lead to unintended degradation of aquatic ecosystems.

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