

# Assessing the Consequences of Nonnative Trout in Headwater Ecosystems in Western North America 

Intentional introductions of nonnative trout into headwater lakes and streams can have numerous effects on the receiving ecosystems, potentially threatening native species and disrupting key ecological processes. In this perspective, we focus on seven key issues for assessing the biological and economic consequences of nonnative trout in headwater ecosystems: (1) effects of nonnative trout can span multiple biological domains, (2) effects of nonnative trout can extend beyond waters where they are introduced, (3) nonnative trout do not travel alone, (4) not all habitats are equal, (5) ecosystems vary in their resistance and resilience to nonnative trout, (6) prioritization can improve management of nonnative trout, and (7) economic costs of recreational fisheries in headwater ecosystems can be substantial. Assessments that address these issues could provide more effective guidance for determining where recreational fisheries for nonnative trout are justified in headwater ecosystems and where they might be terminated to support other ecosystem values.

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Nonnative trout have been successfully introduced into a variety of freshwaters and represent one of the most widespread invasions of nonnative species on the planet (Lever 1996; Lowe et al. 2000). Most introductions were intended to provide recreational fisheries, with a minority conducted for conservation of threatened species (e.g., Young and Harig 2001). In western North America, most headwater ecosystems were entirely devoid of trout or any species of fish prior to introductions by humans (Bahls 1992). Native trout and other native salmonids often occur naturally in downstream portions of watersheds, below upstream movement barriers. Sometimes native trout are introduced above these barriers in headwater lakes and streams outside their histori-
cal distributions within a watershed. Populations established from these introductions, however, do not represent "native" trout from the perspective of the receiving ecosystems. On a global scale, distinctions between "native" and "nonnative" status are often unambiguous because trout have been widely established hundreds to thousands of kilometers outside their native ranges (Lever 1996).

In the United States, management of nonnative trout in headwater ecosystems often centers on issues related to management of national parks or the Wilderness Act and its policy and regulatory implications for land use (Duff 1995; Landres et al. 2001; Pister 2001; Wiley 2003). However, nonnative trout are not confined to wilderness areas, and limiting the discussion to such areas diverts attention from the critical biological implications of maintaining nonnative species in headwater systems in general. A growing body of evidence suggests nonnative trout can substantially change aquatic ecosystems wherever they are present


Stocking trout in Sawtooth National Forest, circa 1926.


Harbor Lake, Bighorn Crags, ID.
(Simon and Townsend 2003). Despite concerns over these effects, the popularity of many fisheries and the difficulty of eradicating established populations will result in nonnative trout remaining ubiquitous in many aquatic ecosystems for the foreseeable future. The challenge for managers will be to identify critical problems and develop effective assessments of management alternatives for nonnative trout (Dunham et al. 2002).

In this essay, we attempt to transcend the muchdebated ethical, political, and social issues in managing specific lands and fisheries (see Duff 1995; Landres et al. 2001; Pister 2001; Wiley 2003 for perspectives), and instead focus on applied questions regarding the biological and economic consequences of introducing and maintaining nonnative trout in headwater ecosystems. Over the past decade, attention to the issue of nonnative trout in headwater ecosystems in western North America has substantially increased. In 1992, a broad survey of the status of fish populations in mountain lakes in 11 western U.S. states brought attention to the magnitude and potential consequences of nonnative trout in headwater ecosystems within the region (Bahls 1992; Table 1). Here, we draw on existing research to address seven key issues for assessing the consequences of nonnative trout in these ecosystems and discuss the challenges of evaluating and implementing changes in headwater fisheries.

## Seven Key Issues for Assessing the Consequences of Nonnative Trout in Headwater Ecosystems

Issue 1. Effects of nonnative trout can span multiple biological domains. The effects of nonnative trout can range across several biological domains from genetic and ecological influences on individual species to ecosystem processes (Simon and Townsend 2003). At the individual and population level, native amphibians have received much attention with regard to adverse influences of nonnative trout in headwater ecosystems. At least eight amphibian species have negative associations with nonnative trout in mountain lakes in western North

America (Table 2). The ecological effects of nonnative trout on native salmonids in North America have been extensively reviewed (Dunham et al. 2002; Peterson and Fausch 2003) and imply that a variety of negative interactions are common, but not inevitable. Genetic interactions through hybridization between nonnative and native salmonids also pose a substantial threat to native salmonids in the region (Allendorf et al. 2001).

At the population and community level, nonnative trout markedly influence invertebrate taxa (Simon and Townsend 2003). In mountain lakes, large ( $>1 \mathrm{~mm}$ ) zooplankton species appear to be particularly sensitive to fish predation, most notably Hesperodiaptomus arcticus, H. shoshone, and Daphnia middendorffiana (Anderson 1980; Bradford et al. 1998; Knapp et al. 2001; Parker et al. 2001). Conspicuous benthic macroinvertebrates in lakes, such as clinger or swimmer taxa (e.g., mayfly nymphs, corixids, and dytiscid beetles) and some caddisfly taxa, can be suppressed or eliminated by nonnative trout (Luecke 1990; Bradford et al. 1998; Knapp et al. 2001). In streams, nonnative trout can reduce the abundance or alter behaviors of some invertebrates (Pecarsky et al. 2002; Simon and Townsend 2003).

Finally, nonnative trout have fundamental influences on ecosystem processes, leading to indirect effects on a variety of species. For example, effects of predation by nonnative trout in streams can lead to increases in primary productivity by reducing activity of grazing invertebrates (Simon and Townsend 2003). In lakes, introduced trout can alter nutrient cycles, productivity, and community structure, either by acting as nutrient sinks or by translocating benthic nutrients into pelagic food webs (Schindler et al. 2001).

Issue 2. Effects of nonnative trout can extend beyond waters where they are introduced. Often, effects of nonnative trout are considered in the context of a single system, such as an alpine lake or stream. But typically, lakes and streams are connected hydrologically and biotically by patterns of flow, topography, and proximity. Headwater lakes that drain into streams can serve as sources of nonnative trout that colonize downstream and potentially harm native species there (Adams et al.


Table 1. Summary of the number of lakes above 800 m and their fish status in 11 western U.S. states based on information supplied by 43 regional fishery managers and biologists working for state fish and wildlife agencies in 1988. Information reproduced from Bahls (1992).

| Fishery status <br> WA | AZ <br> WY | CA <br> Total | CO | ID | MT | NV | NM | OR | UT |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Total no. lakes ${ }^{1}$ | 60 | 4,131 | 1,446 | 1,791 | 1,650 | 36 | 50 | 877 | 1,080 | 2,700 | 2,000 | 15,891 |
| \% lakes with fish | 50 | 63 | 76 | 58 | 47 | 58 | 64 | 84 | 66 | 56 | 40 | 59 |
| \% lakes without fish | 50 | 37 | 24 | 42 | 53 | 42 | 36 | 16 | 34 | 44 | 60 | 41 |
| \% large, fishless lakes 24 | 0 | 3 | 3 | 3 | 8 | 0 | 0 | 0 | 0 | 4 | 10 | 4 |
| \% lakes currently stocked | 50 | 52 | 59 | 46 | 24 | 22 | 64 | 76 | 50 | 44 | 20 | 45 |
| \% lakes with brook trout ${ }^{3}$ | 0 | 21 | 20 | 12 | 17 | 42 | 6 | 70 | 38 | 22 | 21 | 23 |

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2001a). For example, Yellowstone cutthroat trout (Oncorhynchus clarki bouvieri) introduced into headwater lakes drifted downstream into the South Fork Flathead River main stem in Montana, where they threaten the genetic integrity of native westslope cutthroat trout (O. c. lewisi) (M. K. Young, unpublished data). In the case of headwater lakes, those with self-sustaining populations of nonnative trout are more likely to be connected to stream outlets, thus providing more opportunity for effects downstream. Even if not directly connected, the proximity of waters containing nonnative trout to other ecosystems facilitates illegal translocations. Lake trout (Salvelinus namaycush) illegally introduced to Yellowstone Lake in Yellowstone National

Park were recently linked to a source population established in nearby lakes (Munro et al. 2001).

Insertion of nonnative salmonids into a landscape may degrade key habitats and sever connections among networks of habitats that species require for different purposes (see examples in Dunning et al. 1992). Amphibians in particular may require a variety of discrete habitats to support different life stages or to survive seasonally stressful conditions (Knapp et al. 2001; Matthews et al. 2001; Pilliod et al. 2002). For example, Pilliod and Peterson (2001) found that Columbia spotted frogs (Rana luteiventris) bred successfully in fishless lakes, but had little recruitment because the recently transformed froglets had to migrate to nearby deepwater lakes to overwinter and these habitats

Table 2. Studies showing negative associations between nonnative fishes and occurrence or abundance of larval life stages of native amphibian species in headwater ecosystems in western North America. Fish Codes: BT = brook trout (Salvelinus fontinalis), BrT = brown trout (Salmo trutta), CT = westslope cutthroat trout (Oncorhynchus clarki lewisi), $\mathrm{GT}=$ golden trout (O. aguabonita), RT = rainbow trout (O. mykiss), YT = Yellowstone cutthroat trout (O. clarki bouvieri)

contained introduced populations of predatory trout. Thus, presence of nonnative trout in one water body may affect presence of species in other water bodies indirectly by eliminating complementary habitats or disrupting connectivity among habitats (Bradford et al. 1993; Pilliod et al. 2002).

Effects of nonnative trout introductions can even reverberate throughout the biotic community in an entire watershed. In California's Sierra Nevada, introduction of nonnative trout has not only led to the decline of amphibians (Knapp and Matthews 2000a; Matthews et al. 2001), but also of mountain garter snakes (Thamnophis elegans elegans), their primary native predator (Matthews et al. 2002). The loss of aquatic diversity could impact other predators, such as bears and eagles, in a trophic cascade (Ruzycki et al. 2003).

Issue 3. Nonnative trout do not travel alone. The introduction of trout into fishless ecosystems may also introduce associated nonnative species. For example, fish introductions inadvertently have introduced novel pathogens and parasites into many ecosystems. Recent studies have documented the transmission of a pathogenic water mold Saprolegnia ferax and iridoviruses between fish and amphibians (Mao et al. 1999; Kiesecker et al. 2001). The rapid spread of whirling disease caused by Myxobolus cerebralis in the western United States is partly attributable to introductions of diseased trout (Bartholomew and Wilson 2002). Nonnative fishes can facilitate the spread of other invasive species, such as bullfrogs (Rana catesbeiana) in western North America (Adams et al. 2003).

In most cases, nonnative trout were introduced to attract anglers. Whereas the positive benefits of a recreational fishery are often cited, the negative effects of anglers frequenting a specific water body can easily be overlooked. Anglers may be vectors for undesirable pathogens, parasites, and other nonnative species, such as New Zealand mud snails (Potamopyrgus antipodarum), which are rapidly spreading throughout waters in and adjacent to Yellowstone National Park (Richards et al. 2001). In addition, angler transfers of brook trout (Salvelinus fontinalis) over migration barriers have led to dramatic declines of some populations of federally listed greenback cutthroat trout (O. c. stomias; USFWS 1998). In lakes where fish are present, anglers often camp and create trails along shorelines, trample sensitive shoreline vegetation in prime casting areas, and leave fishing equipment (especially lures, plastic bobbers, and nylon monofilament) in lakes and surrounding bushes. Although individual anglers may be careful to minimize their impacts on headwater ecosystems, the cumulative effects of many anglers over the years are often very evident.

Issue 4. Not all habitats are equal. A basic tenet of ecosystem restoration is to provide conditions that represent a full range of natural variability
(Peters et al. 1996; Landres et al. 1999). Wiley (2003) presented a restoration strategy for headwater lakes in Wyoming that involved halting introductions of nonnative trout in lakes without self-sustaining populations and leaving lakes with self-sustaining populations to support recreational fisheries. One problem is that most (86\%) lakes within the areas considered contained self-sustaining nonnative trout populations (Wiley 2003). A similar example can be found in Sequoia-Kings Canyon National Park in the Sierra Nevada Mountains, where stocking of mountain lakes was terminated in the 1970s, yet nonnative trout remain in $70 \%-80 \%$ of the previously stocked lakes (K. Matthews, U.S. Forest Service, Pacific Southwest Research Station, pers. comm.).

Lakes that can support self-sustaining populations of nonnative trout are usually substantially different from those without fish (Bahls 1992; Knapp et al. 2001; Wiley 2003). For example, Bahls (1992) concluded that an average of $60 \%$ of nearly 16,000 water bodies above 800 m in the western U.S. contained nonnative fish, but fisheries man-

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Dragonfly nymph (Aeshna sp.) from Dempsy Creek Marsh, Thurston County, WA. Large, conspicuous invertebrates often disappear after fish are introduced into mountain lakes.
agers estimated that more than $95 \%$ of all large ( $>2$ ha), deep ( $>3 \mathrm{~m}$ ) lakes contained nonnative fish (Table 1). Although this trend varies among states, it seems a reasonable assumption that water bodies without trout are not representative of the full range of aquatic habitats. This condition also complicates restoration of complementary landscape patterns involving many aquatic habitats that may be essential for some key species, such as amphibians (Issue 2). Thus, restricting restoration efforts to only those lakes without self-sustaining fish populations may compromise representation of ecosystem diversity, both in terms of the kinds of individual habitats restored, and their spatial arrangement. A more detailed assessment of the range of conditions represented by waters with and without nonnative trout


PHOTOS: DAVID S. PILLIOD


Columbia spotted frogs in the Bighorn Crags use a variety of habitats during different life stages, some of which include deep lakes with introduced trout. Egg mass (above) and tadpoles, juvenile, and raw adult (below).

in the littoral zone to avoid predation and thus are able to coexist with introduced trout (Luecke 1990; see also Simon and Townsend 2003). While these behavioral or life history characteristics allow some species to persist, other species have less resistance and resilience. For example, in a whole-lake fish stocking experiment, Hesperodiaptomus arcticus was eliminated from lakes within 5 years, and did not reappear after nonnative brook trout were removed 30 years later (Parker et al. 2001). In contrast, Daphnia middendorffiana was absent within 1 year of stocking, but recovered after fish removal, apparently from viable eggs resting in lake sediments.

Issue 6. Prioritization can improve management of nonnative trout. The challenges to managing nonnative trout can be overwhelming, because invasions are widespread and their consequences often difficult to assess. Furthermore, management alternatives for nonnative trout are generally limited to two alternatives: no action or eradication (Dunham et al. 2002). Our understanding of environmental factors affecting nonnative trout invasions is presently insufficient to identify alternative measures, such as habitat protection or restoration, that could serve to limit invasions and their effects. Eradication is variably successful (see Issue 5), and the most effective methods of removing nonnative trout, such as the piscicides rotenone and antimycin, can pose serious risks to native species (Dunham et al. 2002). Nevertheless, in some circumstances, ecologically benign tactics can extirpate unwanted fish populations. In streams, systematic electrofishing eradicated rainbow trout from a stream once hosting native brook trout (Kulp and Moore 2000). In lakes up to at least 3 ha in surface area, gill netting can be an effective management tool for fish eradication (Knapp and Matthews 1998; Parker et al. 2001). In biological terms, strategic prioritization could be based on assessing the issues outlined herein. For example, what kinds of ecosystems are least represented in habitats that are currently fishless? Where are threats posed by nonnative trout the greatest? Where is information lacking for understanding potential threats? A complete and explicit consideration of the basic biological issues and their significance would form essential components of an effective prioritization strategy.

Issue 7. Economic costs of recreational fisheries in headwater ecosystems can be substantial. Many headwater ecosystems that support previously stocked populations of salmonids will lose them. Managers may be inclined to restock such waters, and continue stocking others that cannot support lasting fish populations, but is it worth it? Pister (2001) issued a challenge to fisheries managers to assess the costs and benefits of headwater fisheries in wilderness areas, arguing that it was unlikely that stocking was cost-effective. Wiley et al. (1993) stated, "Trout stocking programs can generate fur-
ther pernicious demand, resulting in increased and unnecessary dependence on hatchery trout, because people come to expect planted trout. Successful management programs address public interests as well as the biology of the fish so than angler expectations are at least partly met by foresighted management agencies."

Wiley (2003) reported that average costs for stocking subcatchable trout in headwater lakes in Wyoming were relatively low, about $\$ 260$ per lake. This estimate is for the short-run marginal cost of producing fish (i.e., limited to costs associated with operating hatcheries and distributing fish), which in Wyoming was $\$ 0.13$ per subcatchable and $\$ 0.68$ per catchable trout (1990 dollars; Wiley et al. 1993). Johnson et al. (1995) and Loomis and Fix (1999) derived similar estimates-\$0.57 (1988 dollars) and \$1.11 (1992 dollars) -to produce a catchable trout in Colorado state hatcheries. But these latter studies also assessed the long-run costs, which included administrative overhead, law enforcement, vehicles, eventual hatchery replacement, and the opportunity cost of the land used by

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Long-toed salamander larva (Ambystoma macrodactylum) from a high-elevation lake in the Cascade Range, Chelan County, WA.
hatchery facilities. These additions brought the total long-run costs to $\$ 1.47-1.85$ per catchable trout, and for fish actually returned to the creel, \$2.45-2.68.

When the costs of stocking are fully accounted for, some have argued they do not compare favorably in the context of benefits to anglers. For two highly popular river fisheries in Colorado, the marginal benefit to anglers of harvesting an additional trout was $\$ 0.70-1.40$ (Johnson et al. 1995), leading Loomis and Fix (1999) to question the costeffectiveness of the hatchery program for catchable trout when long-run costs were included. If subcatchable trout are used for stocking, as is common in many headwater ecosystems, costs could be even higher (Wiley et al. 1993). Most critical, perhaps, is the opportunity cost associated with stocking nonnative trout in headwater ecosystems (cf. Loomis and Fix 1999). As illustrated above, stocking such waters precludes other benefits, particularly ecosys-

tem conservation and services. And there may be far more significant economic consequences-such as those resulting from legal and management activities associated with avoiding or accommodating federal listing of species as threatened or endangered-that may result if nonnative pathogens or other introduced fauna or flora cause substantial declines of native aquatic species.

## Assessing the Consequences of Nonnative Trout: Challenges for Implementation

Our assessment of nonnative trout invasions admittedly leaves much to the details of implementation. We do not expect anyone to have all of the answers, but a broad consideration of the consequences of nonnative trout fisheries will lend more credibility and rigor to management decisions. A full consideration of all of the issues we highlighted in this essay would require an extensive effort. Given that managers are often confronted with limited resources, it is unrealistic to expect them to be accountable for collecting extensive information to address all of the potential issues. Accordingly, information likely will be incomplete or completely absent in many cases.

Even if we lack information or understanding of potential effects of nonnative trout, an explicit consideration of uncertainty is justified. What we do not know about the biological impacts of nonnative trout may be as critical as what we currently believe to be true. Selectively ignoring or minimizing issues or potential influences of nonnative trout due to uncertainty or lack of information can lead to poor management decisions. Assessments that explicitly acknowledge both the uncertainty about an issue and its management importance will be more effective (Peterson and Evans 2003). Presumably different issues could be weighted in their importance relative to what is known or not known, and policy relevance.

In any case, assessments of nonnative trout invasions will represent first approximations of potential


An October caddis (Dicosmoecus giluipes) case serves as a resting place for a foothill yellow-legged frog (Rana boylii) tadpole in the South Santiam River, OR. Stream amphibians are sensitive to fish predation.
threats and management opportunities. As such, they can be viewed as hypotheses to be tested through further research (Peterson and Fausch 2003) or management experiments (Dunham et al. 2002). Actions that follow from assessments represent important opportunities to learn more about nonnative trout invasions. We stand to learn very little from piecemeal research or management efforts that are poorly documented and rely on trial and error for inference. Improved coordination of research and management efforts would go a very long way to improve our understanding of nonnative trout invasions in the future (e.g., Knapp and Matthews 2000b; Pilliod and Peterson 2000; Dunham et al. 2002).

To finish on an optimistic note, we can cite two key advantages that headwater fisheries managers have relative to managing other systems. First, although seemingly complex as portrayed herein, threats posed by nonnative trout to headwater ecosystems may be simple in comparison to more complex ecosystems facing invasions by multiple species (e.g., Adams et al. 2003). Second, we do know a lot about both native and nonnative salmonids, even if the information is incomplete and sometimes of questionable management relevance (Dunham et al. 2002; Peterson and Fausch 2003; Simon and Townsend 2003). Thus, we have some basis for designing assessments based on a variety of known or suspected factors affecting different stages of the invasion process. In other words, if we cannot make progress in assessing nonnative trout invasions in headwater ecosystems, there seems little hope for attacking the problem of invasive species in other ecosystems.

## Conclusions

We see many opportunities to more comprehensively and effectively design and implement assessments of nonnative trout introductions and invasions. Increased public interest in assessments of nonnative species within the United States is evident in a variety of recent national and international initiatives (e.g., Lowe et al. 2000; National Invasive Species Council 2001). For the case of nonnative trout, questions about the practice of supporting recreational fisheries (or species-specific conservation actions) with potentially adverse effects on natural ecosystems are likely to continue. Accordingly, we anticipate increased support for more detailed assessments of the consequences of maintaining recreational fisheries for nonnative trout in headwater ecosystems

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[^0]:    1 Total number of lakes is approximate and biased towards lakes visible on 1:24,000 maps and aerial photographs. We suspect lakes <0.5 ha are greatly underrepresented.
    2 Large lakes were classified as 2 ha or greater in area and 3 m or greater in depth.
    3 In all 11 western states, brook trout are an introduced, nonnative fish.

