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The Introduction of Nonnative Fish into Wilderness Lakes: Good Intentions, Conflicting Mandates, and Unintended Consequences

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Because they have the potential to provide the best remaining standards of relatively unmodified landscapes, protected areas in North America (such as wilderness areas and national parks) have tremendous ecological and scientific value (Cole and Landres 1996). Although the montane ecosystems of western North America are particularly well represented in this complex of protected lands, aquatic habitats within these protected areas are often subject to management practices that are inconsistent with the goal of maintaining natural processes. The most prevalent of these practices is the introduction of salmonid fishes (such as trout) into historically fishless ecosystems to create recreational fisheries.

These montane landscapes are the result of repeated glaciation during the Pleistocene epoch. The recession of glaciers 10,000 years ago created thousands of lakes, most of which were separated from downstream fish populations by impassible barriers on rivers and streams. These extensive fishless habitats were subsequently colonized by a diversity of aquatic species, many of which required fishless habitats for their persistence. Starting in the mid-1800s, Euro-American settlers began introducing salmonid fishes into these lakes and streams. By the mid-1900s, these fish-stocking efforts had been largely subsumed by the various agencies responsible for the management of fish and wildlife. Trout stocking was halted in most national parks in western North America during the 1970s and 1980s (Knapp 1996; Parker and others 2001), but the practice continues in other protected areas, such as wilderness areas in the western United States managed by the US Forest Service (Landres and others 2001).

These stocking programs have dramatically transformed the formerly fishless aquatic ecosystems within protected areas of western North America. For example, of the estimated 16,000 naturally fishless mountain lakes in the western US, the majority of which are located within national parks and wilderness areas, 60% of all lakes and 95% of larger, deeper lakes now contain nonnative trout (*Oncorhynchus* spp., *Salmo* spp., *Salvelinus* spp.) (Bahls 1992). Many of these introduced fish populations persisted even after the termination of stocking (Donald 1987; Boiano 1999). In the western US, trout are still stocked into more than 7000 mountain lakes on a regular basis, usually with the use of aircraft (Bahls 1992). The purpose of this ongoing stocking is generally not to introduce trout into the remaining fishless lakes, but instead to supplement nonnative trout populations maintained by natural reproduction or to maintain nonnative trout popu-

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lations in lakes where trout are unable to reproduce successfully.

The management of nonnative trout populations in protected areas is highly controversial due in large part to increased awareness of the ecological effects of introduced fishes on naturally fishless ecosystems (Duff 1995; Fraley 1996). Although the state agencies charged with managing aquatic ecosystems within protected areas have historically focused on providing recreational fishing while placing little emphasis on ensuring the maintenance of natural processes, fisheries managers are increasingly being asked to justify their stocking programs in light of a growing body of literature that documents the effects of fish introductions into naturally fishless lakes. These studies have repeatedly demonstrated that fish introductions dramatically alter native vertebrate and invertebrate communities, often resulting in the extirpation of native fishes, amphibians, zooplankton, and benthic macroinvertebrates (Anderson 1972; Stoddard 1987; Bradford and others 1998; Carlisle and Hawkins 1998; Tyler and others 1998; Knapp and Matthews 2000). However, these studies have typically focused narrowly on the direct impact of fish introductions on the native fauna and ignored the possible disruption of ecosystem processes (but see Leavitt and others 1994) as well as indirect landscape-scale impacts transmitted beyond the boundaries of those habitats subject to fish introductions. Perhaps as a result, the efforts by managers attempting to lessen the impact of introduced fishes have also been narrowly focused. For example, in California's Sierra Nevada, where these fish introductions have been shown to have severe deleterious impacts on amphibians (Bradford 1989; Bradford and others 1993, 1998; Knapp and Matthews 2000), some managers have recently agreed to stop stocking lakes that serve as habitats for particular amphibian species. Although this policy change is an important step in reducing the ecological impact of fish introductions, it still represents the continuance of a narrowly focused lake-specific and species-specific approach that does not take potential larger-scale impacts into account.

The papers in this issue were motivated by a 3-day workshop on fish stocking in wilderness areas held in October 1998 at the Flathead Lake Biological Station, Polson, Montana (Corn and Knapp 2000). The purpose of the workshop was to promote a dialogue between managers and scientists by exposing the managers to current research while also making the scientists aware of the concerns and constraints of managers. In this special feature, we highlight (a) the history and political framework for fisheries management in protected areas, and (b) recent advances in our understanding of the ecosystem and the landscape-scale effects caused by the introductions of fish into naturally fishless mountain lakes.

We begin with a historical overview by Pister that provides a perspective gained during his several decades experience of managing a wilderness fish-stocking program for the California Department of Fish and Game. First, he describes the history of fish stocking and the changing priorities that have driven the practice in California and outlines current policies and practices in the western United States. He also discusses the jurisdictional conflicts between state and federal agencies, noting that state wildlife managers often support continued fish stocking whereas federal wilderness managers contend that stocking compromises the ecological and social values of wilderness. He concludes that in the face of increasing public support for protecting natural processes, the continued stocking of fish into wilderness ecosystems is no longer justified.

Landres, Meyer, and Matthews examine the controversy over fish stocking from the perspective of the 1964 Wilderness Act, focusing on the judicial interpretation of the act, the policies of the US federal agencies charged with implementing the act, and formal agreements between federal and state agencies. They conclude that although US federal policy currently grants the authority for fish stocking to the states, case law allows the federal agencies to be directly involved in decisions regarding fish stocking in wilderness areas. This type of cooperation could improve the often adversarial relationship between state and federal agencies and create an environment in which both state and federal agencies share the responsibility for managing aquatic resources within wilderness.

Following these two overview/policy papers are 4 papers that describe the ecosystem and landscape-scale effects of fish introductions into naturally fishless mountain lakes. Adams, Frissell, and Rieman present a landscape analysis of the spread of introduced trout through stream networks. This work shows that the introduction of salmonid fishes into headwater lakes can result in disproportionately larger effects on native fishes than introductions lower in drainages. In many river basins, remaining populations of native fishes are concentrated in headwater refugia where they are protected by natural barriers from introduced fishes that are already established at lower elevations. However, introductions of nonnative fishes into headwater lakes provide point sources capable of invading all downstream habitats, as the fish surmount barriers that normally hinder upstream-directed invasions. The extent of such a potential invasion from headwater lakes depends on the geography of the stream network, and particularly on the density and distribution of headwater lakes and their locations relative to barriers inhibiting upstream dispersal.

Schindler, Knapp, and Leavitt use a fish bioenergetics model to evaluate the effect of trout introductions on nutrient cycles in naturally fishless oligotrophic lakes. Model results suggest that trout introductions routinely increase phosphorus (P) regeneration from previously inaccessible benthic and terrestrial sources. Because P derived from benthic and terrestrial sources represents a new source of nutrients for plankton, even small increases in nutrient availability can result in increased algal biomass and production. To support the importance of this increased nutrient subsidy to pelagic algae, they present paleolimnological evidence that algal production increased approximately 10-fold following trout introductions and show that this increased production was maintained for the duration of fish presence. These results suggest that widespread fish stocking has caused substantial changes to nutrient cycles in hundreds of lakes throughout montane-protected areas of western North America, with impacts being greatest in lakes stocked with high densities of trout.

Pilliod and Peterson use data on the distributions of native amphibians and nonnative trout in several drainages in the northern Rocky Mountains to evaluate the local and landscape effects of trout introductions. They report that at a local scale, after accounting for habitat differences between fish-containing and fishless water bodies, the abundance of all life stages of long-toed salamanders and spotted frogs was lower in water bodies containing nonnative trout than in water bodies remaining in a fishless condition. At the landscape scale, the presence of fish in some water bodies had important influences on the abundance of amphibians in the remaining fishless water bodies. These landscape-scale effects may be the result of a loss of source populations and overwintering sites when fish are introduced into the larger, deeper lakes and amphibians are therefore restricted to shallower, more ephemeral habitats.

Parker, Schindler, Donald, and Anderson describe changes in ecosystem structure in a lake in the Canadian Rocky Mountains following the removal of the entire trout population with gill nets. Of the two large zooplankton species believed to have been present in the lake prior to fish introductions, one reappeared while another failed to do so, apparently because the egg bank of this latter species had been depleted during the 30 years of fish presence. Overall zooplankton biomass remained unchanged following removal of the fish population. Contrary to predictions based on trophic cascade theory, no changes in phytoplankton biomass or chlorophyll-*a* concentration were observed. Nutrient concentrations also remained unchanged. These results add to the growing body of studies that evaluate the recovery of mountain lake ecosystems following the removal of nonnative trout (Parker and others 1996; McNaught and others 1999; Funk and Dunlap 1999; Drake and Naiman 2000; Knapp and others 2001).

Collectively, these papers indicate that the effects of widespread trout introductions into wilderness landscapes are not limited simply to direct effects on prey taxa, but instead can be transmitted throughout lake food webs and even beyond the shorelines of fish-containing lakes to fishless lakes. In addition, following fish removal, full recovery of ecosystem structure and function may not occur. These results pose a difficult challenge for fisheries and wilderness managers interested in better balancing the conflicting goals of maintaining nonnative fisheries in wilderness areas while also minimizing the effects of these fisheries on natural processes. If managers are to truly balance these often opposing goals, it is imperative that current fisheries management practices be evaluated in the context of their effects on ecosystem and landscape processes. It is our hope that this special feature will provide the impetus for such an evaluation and for the adoption of new management strategies to reduce the ecological impacts of nonnative fisheries in protected areas.

REFERENCES

Anderson RS. 1972. Zooplankton composition and change in an alpine lake. Verhandlung Internationale Vereinigung für Theoretische und Angewandte Limnologie 18:264–8.

Bahls PF. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Sci. 66:183–93.

Boiano DM. 1999. Predicting the presence of self-sustaining trout populations in high elevation lakes of Yosemite National Park, California [thesis]. Arcata (CA): Humboldt State University.

Bradford DF. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. Copeia 1989:775–78.

Bradford DF, Cooper SD, Jenkins TM Jr., Kratz K, Sarnelle O, Brown AD. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Can J Fish Aquat Sci 55:2478–91.

Bradford DF, Tabatabai F, Graber DM. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conserv Biol 7:882–88.

Carlisle DM, Hawkins CP. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. J North Am Benthol Soc 17:286–300.

Cole DN, Landres PB. 1996. Threats to wilderness ecosystems: impacts and research needs. Ecol Appl 6:168–84.

Corn, PS, and Knapp RA. 2000. Fish stocking in protected areas: summary of a workshop. In: Proceedings: Wilderness Science in a Time of Change. RMRS-P-O-VOL-5. Ogden (UT): US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p 301–3.

Donald DB. 1987. Assessment of the outcome of eight decades of trout stocking of the mountain national parks, Canada. North Am J Fish Manage 7:545–53.

Drake DC, Naiman RJ. 2000. An evaluation of restoration efforts in fishless lakes stocked with exotic trout. Conserv Biol 14: 1807–20.

Duff DA. 1995. Fish stocking in U.S. federal wilderness areas—challenges and opportunities. Int J Wilderness 1:17–19.

Fraley J. 1996. Cooperation and controversy in wilderness fisheries management. Fisheries 21:16–21

Funk WC, Dunlap WW. 1999. Colonization of high-elevation lakes by long-toed salamanders (*Ambystoma macrodactylum*) after the extinction of introduced trout populations. Can J Zool 77:1759–67.

Knapp RA. 1996. Nonnative trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. In: Sierra Nevada Ecosystem Project: final report to Congress. Volume III. Davis (CA): Centers for Water and Wildland Resources, University of California, Davis. p 363–407. Also available online at ceres.ca.gov/snep/pubs.

Knapp RA, Matthews KR. 2000. Nonnative fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv Biol. 14:428–438.

Knapp RA, Matthews KR, Sarnelle O. 2001. Resistance and resilience of alpine lake faunal assemblages to fish introductions. Ecological Monographs. Forthcoming.

Landres P, Meyers S, Matthews S. 2001. The Wilderness Act and fish stocking: an overview of legislation, judicial interpretation, and agency implementation. Ecosystems. 4:287–295.

Leavitt PR, Schindler DE, Paul AJ, Hardie AK, Schindler DW. 1994. Fossil pigment records of phytoplankton in trout-stocked alpine lakes. Can J Fish Aquat Sci 51:2411–23.

McNaught AS, Schindler DW, Parker BR, Paul AJ, Anderson RS, Donald D, Agbeti M. 1999. Restoration of the food web of an alpine lake following fish stocking. Limnol Oceanogr 44:127–36.

Parker BR, Schindler DW, Donald DB, Anderson RS. 2001. The effects of stocking and removal of a non-native salmonid on the plankton of an alpine lake. Ecosystems. 4:334–345.

Parker BR, Wilhelm FM, Schindler DW. 1996. Recovery of *Hesperodiaptomus arcticus* populations from diapausing eggs following elimination by stocked salmonids. Can J Zool 74:1292–7.

Stoddard JL. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. J Plankton Res 9:631–650.

Tyler T, Liss WJ, Ganio LM, Larson GL, Hoffman R, Deimling E, Lomnicky G. 1998. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. Conserv Biol 12:94–105.