Effects of Nonnative Fishes on Wilderness Lake Ecosystems in the Sierra Nevada and Recommendations for Reducing Impacts

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Abstract—Wilderness areas of the Sierra Nevada, California contain thousands of lakes and ponds, nearly all of which were historically fishless. After more than a century of fish stocking, introduced trout are now present in up to 80% of larger lakes. These nonnative fishes have had profound impacts on native fishes, amphibians, and invertebrates. Several of these native species are either already listed under the Endangered Species Act, or are likely to be petitioned for listing in the near future. Reducing impacts to aquatic ecosystems within wilderness areas should be a high priority, and will require that some lakes be restored to their historic fishless condition.

One of the primary purposes of the National Wilderness Preservation System is to protect natural ecosystems. As human-caused modification of lands outside of wilderness intensifies, the protection of wilderness ecosystems will be increasingly important and challenging. These protected areas already are being affected by anthropogenic impacts both internal and external to wilderness areas (Cole and Landres 1996). Attempts to minimize these impacts have typically focused on protection of terrestrial ecosystems, using tactics such as regulation of visitor use and allowing the return of natural fire regimes. In contrast, little attention has been focused on impacts to aquatic ecosystems in wilderness, habitats that have also been substantially altered.

In the western United States, where wilderness areas typically encompass high-elevation montane ecosystems, the most ubiquitous impact to aquatic ecosystems is the introduction of nonnative fish species (Bahls 1992). Many of the lakes in these areas were historically fishless, but have been stocked with several different trout species to create a recreational fishery. When the National Wilderness Preservation System was created in 1964, language was included in the governing legislation to ensure that fish stocking could continue in these areas (Kloepfer and others 1994). Today, fish stocking in the western U.S. continues in many national forest wilderness areas, as well as at least one national park.

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Despite the potential impacts caused by fish introductions into wilderness lakes, Bahls (1992) concluded, after interviews with state fishery managers, that the practice of stocking trout into mountain lakes was generally conducted with "little concern for protection of native fish species in lakes or downstream systems, no evident concern for maintaining representative pristine lakes, and no consideration of the effects of trout stocking on indigenous fauna, aquatic ecosystems, and lakeshore recreational impacts". In addition, Bahls (1992) found that although stocking effort is intensive, research is minimal. As a result, changes in the distribution of fish caused by fish stocking and the effects of fish introductions on aquatic ecosystems remain relatively poorly understood. This lack of information has generally precluded comprehensive efforts to reduce these impacts.

The effects of nonnative fish introductions on aquatic ecosystems in wilderness areas of the Sierra Nevada, California are relatively well-studied, compared with aquatic ecosystems in wilderness areas in other parts of the western U.S. Although the results of these studies have important implications for the management of wilderness fisheries throughout the western U.S., this body of research has only rarely been reviewed. The goals of this paper are to 1) review the changes in fish distribution resulting from over a century of fish stocking in wilderness lakes of the Sierra Nevada, 2) review the impacts of these fish introductions on lake ecosystems, and 3) provide recommendations aimed at reducing these impacts. By making this information more accessible to scientists, federal wilderness managers, and state fisheries managers, we hope that this paper will help to focus much needed attention on how to better balance the interest of providing recreational fisheries in wilderness with the need to maintain or restore natural ecosystems.

Study Area

The Sierra Nevada of California is largely federally owned, with the majority of its five million ha (12 million acres) lying within national parks, national monuments and national forests (Palmer 1988). Eighty-four percent of the national park acreage and 24% of the national forest acreage is officially designated as wilderness (Palmer 1988). The area above 1,800 m (6,000 ft) contains thousands of lakes and ponds, and most of these habitats are located within designated wilderness. More than 99% of these lakes and ponds were historically fishless (Moyle and others 1996). Instead of fish, these water bodies were inhabited by a unique assemblage of amphibians, zooplankton and benthic invertebrates.

Starting in the mid-1800's, trout were introduced into formerly fishless lakes to provide recreational fishing (Moyle and others 1996). Although some of these introductions were interbasin transfers of trout native to the Sierra Nevada (Little Kern golden trout (*O. mykiss whitei*), California golden trout (*O. mykiss aguabonita*), Lahontan cutthroat trout (*O. clarki henshawi*), Paiute cutthroat trout (*O. clarki seleniris*) and coastal rainbow trout (*O. mykiss irideus*)), many were introductions of trout species not native to California. These included brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), and Atlantic salmon (*Salmo salar*) from eastern North America, kokanee salmon (*Oncorhynchus nerka*) from northwestern North America, and brown trout (*Salmo trutta*) from Europe (Moyle and others 1996). Early trout planting efforts were aimed primarily at establishing trout in formerly fishless waters, and were carried out largely by sporting groups and the U.S. military. In the early 1900's, the California Fish and Game Commission (the precursor to the current California Department of Fish and Game) began coordinating the fish planting effort, and by the 1940's fish stocking was conducted almost entirely by the California Department of Fish and Game (CDFG). Today, the CDFG is responsible for nearly all authorized trout stocking throughout the Sierra Nevada, although the emphasis has changed from introducing trout into fishless lakes and streams to stocking waters to augment existing nonnative trout populations.

Sequoia, Kings Canyon, and Yosemite National Parks began phasing out trout stocking in 1969 as a result of recommendations made in the Leopold Report (Leopold 1963). Limited stocking in these parks was continued until 1991, when all stocking was halted. Trout continue to be stocked into lakes within national forest wilderness areas, and stocking is accomplished using airplanes.

Distribution of Nonnative Fishes in Sierra Nevada Lakes

As a result of more than a century of fish stocking, the majority of historically fishless wilderness lakes in the Sierra Nevada now contain introduced trout. Bahls (1992) estimated that 63% of California's 4,000+ mountain lakes (natural lakes at elevations above 800 m, most of which are found in the Sierra Nevada) now contain nonnative fish populations and 52% are currently stocked. Of the estimated 37% of lakes that remain fishless, most are small (< 2 ha surface area), shallow (< 3 m), and generally incapable of supporting trout populations (Bahls 1992). Only 3% of larger lakes (> 2 ha surface area, > 3 m deep) remain fishless. Similar results were obtained by Jenkins et al. (1994), who projected that one or more species of nonnative trout would occur in 63% of high elevation lakes in the Sierra Nevada (lakes at elevations > 2400 m and > 1 ha surface area). Golden trout were projected to occur in 36% of lakes, rainbow trout in 33%, brook trout in 16%, brown trout in 8%, and cutthroat trout in 0.5% of lakes.

A greater proportion of lakes within national forest wilderness areas contain introduced trout populations than lakes within national parks. Based on a survey of fish populations in 2,000+ wilderness lakes in the Sierra Nevada, Matthews and Knapp (1999) reported that 80% of lakes larger than 1 ha within the John Muir Wilderness contained introduced trout versus 40% of lakes within the adjacent Kings Canyon National Park. Similar proportions of fish-containing lakes in national forest wilderness and national parks in the Sierra Nevada were reported by Botti (1977), Bradford and others (1993), Knapp (1996) and Wallis (1952). The lower percentage of trout-containing lakes in Sierra Nevada national parks than in national forests is likely the result of both a lower historical stocking intensity and the recent termination of all stocking in the national parks. The termination of fish stocking in Sequoia-Kings Canyon National Park and Yosemite National Park was expected to cause 30% and 40% of previously stocked lakes, respectively, to revert to a fishless condition (Botti 1977; Zardus 1977).

Ecological Effects of Fish Introductions Into Sierra Nevada Lakes

Native Fishes

Although fish were absent historically from nearly all mid- to high-elevation lakes and ponds in the Sierra Nevada, native trout species were present in streams in several watersheds. These included the Little Kern golden trout, California golden trout, Lahontan cutthroat trout, Paiute cutthroat trout and coastal rainbow trout (Knapp 1996). Distributions of some of these native trout populations were altered when nonnative trout species were stocked into fishless headwater lakes, and subsequently moved downstream to hybridize with or displace the native populations. For example, the Little Kern golden trout (*O. mykiss whitei*) is native only to the Little Kern River in the southern Sierra Nevada. The introduction of nonnative brook trout into the headwater lakes of this drainage and their dispersal downstream caused the near-extinction of the Little Kern golden trout as a result of competitive displacement. Consequently, the Little Kern golden trout was listed as "threatened" under the Endangered Species Act (Stephens 1999).

Similarly, the California golden trout is native only to the South Fork Kern River and Golden Trout Creek in the southern Sierra Nevada. The stocking of hybridized golden trout into the headwater lakes of the Golden Trout Creek drainage resulted in extensive hybridization with the downstream native California golden trout population. Partly as a result of this threat, the U.S. Fish and Wildlife Service is currently considering listing the California golden trout under the Endangered Species Act (Stephens 1999). Similar impacts to native fishes resulting from the stocking of headwater lakes with nonnative trout species are apparently common in wilderness areas throughout the western U.S. (Adams 1999; Bahls 1992).

Amphibians

Populations of four of the nine anurans (frogs and toads) native to the Sierra Nevada are reported to be declining (Yosemite toad: *Bufo canorus*; California red-legged frog: *Rana aurora draytonii*; foothill yellow-legged frog: *R. boylii*;

and mountain yellow-legged frog: *R. muscosa*; Jennings 1996). Only one of these species, the mountain yellow-legged frog, was a common inhabitant of lakes historically and is therefore the species most likely to be affected by the introduction of trout into these habitats. Despite its former wide distribution throughout the Sierra Nevada (Zweifel 1955), a recent resurvey of historic localities in the central Sierra Nevada indicated that the mountain yellow-legged frog is now present at fewer than 15% of the sites where it was found in 1915 (Drost and Fellers 1996). Severe declines have also been noted elsewhere in the Sierra Nevada (Bradford and others 1994).

Increasing evidence from the Sierra Nevada indicates that introduced trout are a primary factor in the decline of the mountain yellow-legged frog. As early as 1915, Grinnell and Storer (1924) reported that predation by introduced trout on mountain yellow-legged frog larvae prevented the co-occurrence of these two taxa in lakes and ponds. This observation has now been quantified in several different areas in the Sierra Nevada (Bradford 1989; Bradford and others 1998). Although these studies have generally been done using a relatively small number of sites (< 100), recent research based on surveys at more than 1,700 sites in Kings Canyon National Park (KCNP) and John Muir Wilderness (JMW) provided similar results (Knapp and Matthews 2000). These results can be summarized as follows:

1) The KCNP study area had fewer trout-containing lakes than the adjacent JMW study area, and this difference in trout distribution was associated with a seven-fold higher percentage of lakes containing mountain yellow-legged frogs in the KCNP study area than the JMW study area.

2) Drainages with a higher percentage of total water body surface area containing trout had a lower percentage of total water body surface area containing frogs.

3) After accounting for habitat differences between lakes with and without trout, the probability of occurrence for mountain yellow-legged frog larvae in individual water bodies was three times higher and the abundance of larvae was six times higher in fishless than in fish-containing water bodies.

Together with the results of previous studies, there is now compelling evidence that the mountain yellow-legged frog has been extirpated from much of its historic habitat by the introduction of trout into historically fishless lakes. The results presented in Knapp and Matthews (2000) suggest that these impacts have been particularly severe in national forest wilderness areas, and that the severity of these impacts could eventually require the listing of the mountain yellow-legged frog under the Endangered Species Act.

In addition to the direct impact that nonnative trout have on mountain yellow-legged frogs via predation, Bradford and others (1993) suggested that fish could impact mountain yellow-legged frogs indirectly by isolating remaining populations. They reported that fish introductions into lakes in Sequoia and Kings Canyon National Parks have resulted in a four-fold reduction in effective mountain yellow-legged frog population size and a 10-fold reduction in connectivity between populations. Because amphibian populations often fluctuate widely under natural conditions (Hecnar and M'Closkey 1996; Pechmann and others 1991), and small populations are more likely to go extinct as a result of stochastic population fluctuations than large populations (Hanski 1994), Bradford and others (1993) proposed that the reduction in mountain yellow-legged frog population size caused by trout introductions probably increased the rate at which individual populations go extinct. In addition, they suggested that the increased isolation of mountain yellow-legged frog populations would reduce the probability of recolonization of formerly occupied sites. This lower probability of recolonization could result from the smaller size of potential source populations, increased distance from source populations and predation by introduced trout on dispersing frogs (Bradford and others 1993).

Several attributes of the mountain yellow-legged frog make it particularly vulnerable to predation and subsequent extirpation by nonnative trout. First, adult mountain yellow-legged frogs are highly aquatic and are found primarily in lakes (most of which now contain trout). Second, in contrast to the larvae of other Sierran anurans that complete metamorphosis to the terrestrial stage in a single summer, mountain yellow-legged frog larvae generally require at least two years to complete metamorphosis. This overwintering requirement restricts successful breeding to permanent water bodies (typically those deeper than 2 m; Bradford 1983; Knapp and Matthews 2000; Mullally and Cunningham 1956). The majority of these deeper lakes, however, now contain introduced trout.

Zooplankton

One of the best studied and most consistent effects of introduced fishes on lake ecosystems is the alteration of zooplankton communities (Brooks and Dodson 1965; Zaret 1980). The introduction of zooplanktivorous fishes into fishless lakes generally shifts the zooplankton community from one dominated by large-bodied species to one dominated by smaller-bodied species, as a result of size-selective predation. Several studies have documented this effect of introduced trout on zooplankton communities in wilderness lakes of the Sierra Nevada. Stoddard (1987) found that the occurrence of introduced trout was the most important predictor of zooplankton species composition in alpine and subalpine lakes, with large-bodied species found in fishless lakes and small-bodied species found in lakes with trout. A recent study by Bradford and others (1998) reported comparable results. Similar effects of trout on zooplankton communities have also been reported for mountain lakes throughout western North America (Anderson 1980; Bahls 1990; Carlisle and Hawkins 1998; Liss and others 1995).

Benthic Macroinvertebrates

The introduction of fish into fishless lakes also causes predictable effects on benthic macroinvertebrate communities in which large conspicuous species are eliminated, while burrowing or otherwise inconspicuous species are relatively unaffected (Zaret 1980). In the Sierra Nevada, the benthic invertebrate communities of high-elevation fishless lakes are typically dominated by several conspicuous taxa of mayfly larvae (Ephemeroptera), caddisfly larvae (Trichoptera), aquatic beetles (Coleoptera) and true bugs (Corixidae). These taxa are rare or absent in lakes with introduced trout.

Instead, the benthic macroinvertebrate community of trout-containing lakes is typically dominated by midge larvae (Chironomidae), alderfly larvae (*Sialis*), aquatic mites (Acari) and fingernail clams (*Pisidium*) (Bradford and others 1998; Reimers 1958), all taxa that either burrow into lake bottom sediments or are distasteful. Similar effects of trout on benthic macroinvertebrate communities have been reported from mountain lakes throughout the western United States (Bahls 1990; Carlisle and Hawkins 1998; Walters and Vincent 1973). As noted by Liss and others (1995), however, the effects of introduced trout may be less pronounced in areas where lakes contain naturally occurring vertebrate predators such as salamanders. In these situations, the long evolutionary history between predatory salamanders and their invertebrate prey may have resulted in adaptations by the prey to reduce predation risk, and these adaptations may also reduce their vulnerability to introduced trout. This possibility merits additional study.

Food Web Effects

The effect of introduced trout on native aquatic taxa is often presented as an interaction between two trophic levels (trout preying on amphibians, trout preying on zooplankton). However, changes in one trophic level can have important indirect effects on all parts of the food web. Although multiple trophic-level consequences of fish introductions have not received much attention until recently, at least one such effect has been suggested for aquatic ecosystems in the Sierra Nevada. Jennings and others (1992) demonstrated that the garter snake, *Thamnophis elegans*, depends heavily on frog larvae as prey items, and they suggested that the decline of amphibians in the Sierra Nevada may also result in the decline of *T. elegans*. Because introduced trout are an important factor in the decline of at least one Sierran amphibian (Bradford 1989; Bradford and others 1993; Knapp and Matthews 2000), trout may also indirectly cause the decline of *T. elegans*.

Trout introductions may also cause trophic cascades, in which changes caused by the introduction of a new top predator (fish) propagate to cause substantial changes at the primary producer level (Carpenter and others 1985). Trophic cascades have now been reported from a diverse array of lake types (Carpenter and Kitchell 1993), but studies of trophic cascades from trout introductions into Sierra Nevada lakes are just beginning. In a study of alpine lakes in Canada, the introduction of nonnative trout resulted in a decrease in large-bodied herbivorous zooplankton and an increase in phytoplankton abundance (Leavitt and others 1994; McNaught and others 1999). The elimination of amphibian larvae following trout introductions may also influence lower trophic levels, since amphibian larvae can have important effects on algal biomass (Dickman 1968) and lake nutrient cycling (Seale 1980).

Conclusions and Management Recommendations

The management of nonnative fish populations in wilderness lakes of the western U.S. has been the focus of considerable controversy for at least two decades (Gottschalk 1976; Hall and May 1977), with debate generally focusing on the question of whether nonnative fishes impact wilderness ecosystems. The preponderance of evidence collected during the past two decades leaves little doubt that the introduction of nonnative trout into historically fishless lakes causes a series of predictable changes in the recipient ecosystems; therefore, discussions over the management of nonnative fishes in wilderness lakes should be shifted from whether there are impacts to determining what level of impact is acceptable and how to reduce current impacts to this level.

In the Sierra Nevada, introduced trout have caused dramatic changes in the distributions of several native trout species, one amphibian, and several invertebrate species. This current level of impact is clearly unacceptable if wilderness areas are to serve the purpose of maintaining natural processes. We suggest that an acceptable level of impact would be one that, at a minimum, allows for the long-term persistence of all native taxa across their historic distribution within wilderness lands. In the Sierra Nevada, reducing current impacts to this level will take significant resources from the state and federal agencies with jurisdiction over management of these ecosystems.

To reduce the impacts of introduced trout on wilderness lake ecosystems in the Sierra Nevada, it will be critical to (i) eliminate the stocking of lakes harboring self-sustaining trout populations, and (ii) restore fishless habitat for the native taxa most seriously effected by nonnative trout. The current California Department of Fish and Game stocking program for wilderness lakes is based on the untested assumption that stocking is required to maintain the target fisheries. Similar assumptions are commonly made by fisheries managers throughout the western U.S., and appear to result in the frequent stocking of self-sustaining trout populations (Bahls 1992). Available evidence for wilderness lakes in the Sierra Nevada indicates that the majority of stocked lakes have sufficient natural reproduction to maintain these fisheries in the absence of stocking (Botti 1977; Matthews and Knapp 1999; Zardus 1977). This unnecessary stocking brings with it considerable risks to native aquatic species, as a result of stocked fish hybridizing with or displacing native fishes and of fish being stocked into the wrong water bodies (fishless lakes).

Because most trout populations in Sierra Nevada wilderness lakes would be self-sustaining in the absence of stocking (Matthews and Knapp 1999), restoration of mountain yellow-legged frog populations to even a fraction of their historic habitat will require the active eradication of fish populations from some lakes. Remaining mountain yellow-legged frog populations within national forest wilderness areas are typically extremely isolated (Knapp and Matthews 2000), and are therefore unlikely to persist over the long term (Bradford and others 1993). To expand the few remaining mountain yellow-legged frog populations and enhance their likelihood of persistence, one of us (R. Knapp) is currently using gill nets (Knapp and Matthews 1998) to remove fish populations from lakes in the immediate vicinity of existing frog populations. The goal of this work is to create clusters of interconnected fishless lakes and ponds that would provide high quality habitat for mountain yellow-legged frogs and that could be naturally recolonized from nearby source populations. Preliminary results indicate that frogs are rapidly recolonizing these lakes after fish removal. The success of these pilot projects suggests that the creation of clusters of fishless habitat across the historic range of the mountain yellow-legged frog could reverse the decline of this species and reduce the need to list it under the Endangered Species Act. In addition to benefiting the mountain yellow-legged frog, these fishless habitat clusters would also benefit fish-sensitive invertebrate species.

Implementation of these recommendations would represent a significant step toward reducing impacts to Sierra Nevada wilderness lakes from nonnative fishes. However, outside of the study area surveyed by Matthews and Knapp (1999), information on self-sustainability of fish populations and locations of fish-sensitive native species in the Sierra Nevada remain rudimentary at best. Resolving the ongoing controversy over the management of nonnative fisheries in these wilderness lakes will take a considerable and sustained effort to survey aquatic habitats for nonnative fish and native aquatic taxa, evaluate the self-sustainability of fish populations, and design and implement restoration measures for these sensitive species.

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References

Adams, S. B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Dissertation, University of Montana. 215 p.

Anderson, R. S. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. In: Evolution and Ecology of Zooplankton Communities. Edited by W.C. Kerfoot. Hanover: NH: University Press of New England: 635-641.

Bahls, P. 1990. Ecological implications of trout introductions to lakes of the Selway Bitterroot Wilderness, Idaho. Master's Thesis, Oregon State University. 85 p.

Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science. 66: 183-193.

Botti, S. 1977. Status of fish populations in 102 planted lakes. Unpublished file report, U.S. Department of the Interior, National Park Service, Yosemite National Park, California.

Bradford, D. F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. Ecology. 64: 1171-1183.

Bradford, D. F. 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: 775-778.

Bradford, D. F., F. Tabatabai, and D. M. Graber. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conservation Biology. 7: 882-888.

Bradford, D. F., D. M. Graber, and F. Tabatabai. 1994. Population declines of the native frog, *Rana muscosa,* in Sequoia and Kings Canyon National Parks, California. Southwestern Naturalist. 39: 323-327.

Bradford, D. F., S. D. Cooper, T. M. Jenkins, K. Kratz, O. Sarnelle, and A. D. Brown. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Canadian Journal of Fisheries and Aquatic Sciences. 55: 2478-2491.

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science. 150: 28-35.

Carlisle, D. M., and C. P. Hawkins. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. Journal of the North American Benthological Society. 17: 286-300.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience. 35: 634-639.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. New York, NY: Cambridge University Press. 385 p.

Cole, D. N., and P. B. Landres. 1996. Threats to wilderness ecosystems: impacts and research needs. Ecological Applications. 6: 168-184.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology. 49: 1188-1190.

Drost, C. A., and G. M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology. 10: 414-425.

Gottshalk, J. S. 1976. A symposium on the management of wilderness area waters: proceedings; 1976; Washington D.C., Washington, D.C.: American Fisheries Society: 23 p.

Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite. University of California Press. Berkeley, California. 752 p.

Hall, A. and R. May. 1977. A symposium on the management of high mountain lakes in California's national parks: proceedings; 1976 January 29; Fresno, CA. San Francisco, CA: California Trout: 69 p.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution. 9: 131-135.

Hecnar, S. J., and R. T. M'Closkey. 1996. Regional dynamics and the status of amphibians. Ecology. 77: 2091-2097.

Jenkins, T. M. Jr., R. A. Knapp, K. W. Kratz, S. D. Cooper, J. M. Melack, A. D. Brown, and J. Stoddard. 1994. Aquatic biota in the Sierra Nevada: current status and potential effects of acid deposition on populations. Final Report, Contract A932-138. California Air Resources Board, Sacramento.

Jennings, M. R. 1996. Status of amphibians. In: Sierra Nevada Ecosystem Project: final report to Congress. Volume II. Davis, CA: Centers for Water and Wildland Resources, University of California: 921-944.

Jennings, W. B., D. F. Bradford, and D. F. Johnson. 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. Journal of Herpetology. 26: 503-505.

Kloepfer, D., J. Watson, and P. Byrnes. 1994. The Wilderness Act handbook. Washington, D.C.: The Wilderness Society. 68 p.

Knapp, R. A. 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: 363-407.

Knapp, R. A., and K. R. Matthews. 1998. Eradication of nonnative fish by gill-netting from a small mountain lake in California. Restoration Ecology. 6: 207-213.

Knapp, R. A., and K. R. Matthews. 2000. Nonnative fish introductions and the decline of the mountain yellow-legged frog (*Rana muscosa*) from within protected areas. Conservation Biology. 14: 1-12.

Leavitt, P. R., D. E. Schindler, A. J. Paul, A. K. Hardie, and D. W. Schindler. 1994. Fossil pigment records of phytoplankton in trout-stocked alpine lakes. Canadian Journal of Fisheries and Aquatic Sciences. 51: 2411-2423.

Leopold, A. S. 1963. Wildlife management in the National Parks. Report to the Secretary of the Interior (available online at www.halcyon.com/rdpayne/nps-leopold.html).

Liss, W. J., G. L. Larson, E. Deimling, L. Ganio, R. Gresswell, R. Hoffman, M. Kiss, G. Lomnicky, C. D. McIntire, R. Truitt, and T. Tyler. 1995. Ecological effects of stocked trout in naturally fishless lakes, North Cascades National Park Service Complex, WA, USA. Technical Report NPS/PNROSU/NRTR-95-03.

Matthews, K. R., and R. A. Knapp. 1999. A study of high mountain lake fish stocking effects in the U.S. Sierra Nevada wilderness. International Journal of Wilderness. 5: 24-26.

McNaught, A. S., D. W. Schindler, B. R. Parker, A. J. Paul, R. S. Anderson, D. B. Donald, and M. Agbeti. 1999. Restoration of the food web of an alpine lake following fish stocking. Limnology and Oceanography. 44: 127-136.

Moyle, P. B., R. M. Yoshiyama, and R. A. Knapp. 1996. Status of fish and fisheries. In: Sierra Nevada Ecosystem Project: final Report to Congress. Volume II. Davis, CA: Centers for Water and Wildland Resources, University of California: 953-973.

Mullally, D. P., and J. D. Cunningham. 1956. Ecological relations of *Rana muscosa* at high elevations in the Sierra Nevada. Herpetologica. 12: 189-198.

Palmer, T. 1988. The Sierra Nevada: a mountain journey. Washington D.C.: Island Press. 339 p.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science. 253: 892-895.

Reimers, N. 1958. Conditions of existence, growth, and longevity of brook trout in a small, high altitude lake of the eastern Sierra Nevada. California Fish and Game.44: 319-333.

Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology. 61: 1531-1550.

Stevens, S. 1999. Conversation between S. Stevens (California Department of Fish and Game, Region 4, Visalia, California) and R. Knapp, August 10.

Stoddard, J. L. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. Journal of Plankton Research. 9: 631-650.

Wallis, E. O. 1952. Comprehensive review of trout fishery problems of Yosemite National Park: A report of the Yosemite Trout Investigations, 1951-1953. U.S. Department of the Interior, National Park Service, Yosemite National Park.

Walters, C. J., and R. E. Vincent. 1973. Potential productivity of an alpine lake as indicated by removal and reintroduction of fish. Transactions of the American Fisheries Society. 102: 675-697.

Zardus, M., T. Blank, and D. Schultz. 1977. Status of fishes in 137 lakes in Sequoia and Kings Canyon National Parks, California. Unpublished file report, U.S. Department of the Interior, National Park Service, Sequoia-King Canyon National Parks.

Zaret, T. M. 1980. Predation and freshwater communities. New Haven, NJ: Yale University Press: 187 p.

Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. University of California Publications in Zoology. 54: 207-292.