Non-Native Fish Introductions and the Reversibility of Amphibian Declines in the Sierra Nevada[1]

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Amphibians are declining worldwide for a variety of reasons, including habitat alteration, introduction of non-native species, disease, climate change, and environmental contaminants. Amphibians often play important roles in structuring ecosystems, and, as a result, amphibian population declines or extinctions are likely to affect other trophic levels (Matthews and others 2002). Avoiding declines or reversing the declines of amphibian populations that are already underway should be a major concern of land and wildlife managers.

The 1996 Sierra Nevada Ecosystem Project (SNEP) included two chapters that reviewed the state of knowledge regarding the status of amphibians in the Sierra Nevada. Jennings (1996) provided a detailed summary of the status and trends of all 32 amphibian species known from the Sierra Nevada and showed that the majority of taxa were declining. The most imperiled species were the true frogs (*Rana* sp.) and true toads (*Bufo* sp.), several of which are endemic to the Sierra Nevada. Knapp (1996) reviewed the effects of non-native trout introductions on naturally fishless lake ecosystems in the Sierra Nevada, and concluded that these introductions were a likely cause of the decline of the mountain yellow-legged frog, *Rana muscosa (R. muscosa.)* Due to a general lack of detailed information on the distribution of amphibians and causes of declines, however, both chapters provided little guidance on the extent to which amphibian declines in the Sierra Nevada are reversible and, if so, what management actions were necessary.

The objective of this paper is to review the results of selected studies conducted on amphibian declines in the Sierra Nevada since the completion of the Sierra Nevada Ecosystem Project. Although several Sierran amphibian species are in decline, *R. muscosa* has been the focus of the majority of recent research due to the severity of its decline, the recent petition to list this species under the Endangered Species Act, and the potential of such a listing to dramatically alter current trout stocking practices. As such, this review focuses exclusively on *R. muscosa* and concludes that (1) the introduction of non-native trout are a major cause of the decline of *R. muscosa*, (2) this decline can be reversed by removing non-native trout populations, and (3) the current science is sufficiently well developed to inform policy and management related to the species. Additional research, however, is needed to quantify the effects of other potential causes of amphibian declines in the Sierra Nevada, including disease and airborne agricultural contaminants.

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State of the Science

Background

Mountain yellow-legged frogs are endemic to the Sierra Nevada of California and Nevada, and to the Transverse Ranges of southern California. In the Sierra Nevada, *R. muscosa* was historically a common inhabitant of lakes and ponds at elevations of 1400 to 3600 meters (m). *R. muscosa* is highly aquatic, with adults overwintering underwater and rarely found more than a few meters from water during the summer active season. In addition, the aquatic larvae require two or more summers to develop through metamorphosis. The majority of *R. muscosa* habitat lies within designated national parks and National Forest wilderness areas. Despite this high level of protection, *R. muscosa* is now extirpated from at least 50 percent of its known historic localities (Jennings 1996).

The Sierra Nevada contains abundant streams and natural lakes, nearly all of which were historically fishless. Starting in the mid-1800s, Euro-American settlers began stocking these waters with several species of non-native trout. This practice was greatly expanded in the early 1950s when the California Department of Fish and Game began stocking trout in backcountry lakes using airplanes. Between 1977 and 1990, Sequoia, Kings Canyon, and Yosemite national parks phased out all fish stocking, but the practice continues to the present day on National Forest lands, including within designated wilderness areas. This stocking is conducted by the California Department of Fish and Game and is intended to augment or maintain existing non-native trout populations (see Knapp [1996] for additional details). As a result of this stocking program, non-native trout are now present in approximately 70 percent of naturally fishless lakes (greater than 0.5 hectares in surface area) on National Forest lands, and approximately 35 percent of such lakes in national parks (Knapp and Matthews 2000; Knapp, unpublished data).

Impacts of Non-native Trout

Grinnell and Storer (1924) were perhaps the first to describe the negative effect of introduced trout on *R. muscosa* populations. However, this possible impact received little attention until research by Bradford (1989) suggested that predation by non-native trout could be an important cause of the decline of *R. muscosa*. Knapp and Matthews (2000) and Knapp and others (2003) provided the first landscape scale study of the factors that influence the distribution of *R. muscosa* in which the effects of fish introductions were thoroughly analyzed. Based on surveys of 1,728 lakes and ponds in the Sierra Nevada *(fig. 1),* their analyses indicated that the probability of occurrence by *R. muscosa* at a site is positively influenced by lake depth and the proportion of the near-shore zone dominated by silt, and is negatively influenced by fish presence, lake elevation, and isolation from other *R. muscosa* populations. Therefore, the presence of non-native trout has a strong negative effect on the distribution of *R. muscosa*, even after accounting for effects of significant habitat variables. As an example of the landscape scale negative effects of non-native trout,

Knapp and Matthews (2000) reported that *R. muscosa* were present in only 5 percent of the water bodies in the John Muir Wilderness (Sierra National Forest) where non-native trout are common, but were present in 35 percent of the water bodies in immediately adjacent Kings Canyon National Park, where non-native trout are relatively uncommon.

Reversibility of Declines

To determine whether the decline of *R. muscosa* caused by fish introductions is reversible, researchers have recently studied whether *R. muscosa* is able to recolonize lakes after fish disappear. Knapp and others (2001) compared the probabilities of occurrence and density of

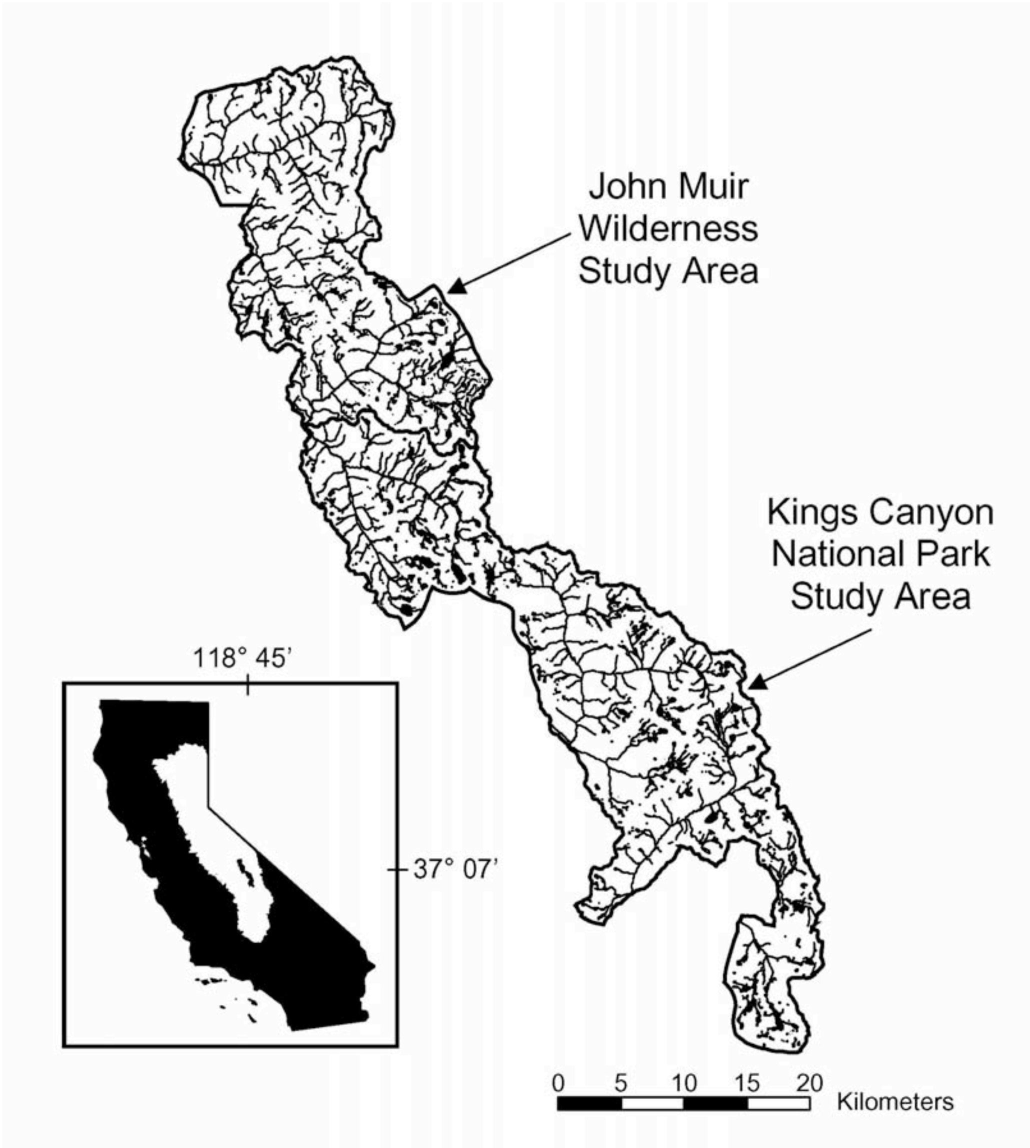

Figure 1— Map of the John Muir Wilderness and Kings Canyon National Park study areas described in Knapp and Matthews (2000) and Knapp and others (2003). Streams and lakes are shown in black. The inset map shows the state of California (black), the Sierra Nevada (white), and the study areas (black area in the Sierra Nevada).

R. muscosa at lakes that were never stocked and at lakes that were stocked historically but that have reverted to a fishless condition as a result of a halt to stocking and a lack of suitable trout spawning habitat. If *R. muscosa* was unable to recolonize lakes following fish introductions, the percentage of lakes containing frogs and the density of frogs should be significantly lower in "stocked-now-fishless" lakes than in "never-stocked" lakes. Instead, there was no significant difference in either the percentage of lakes containing frogs or the density of frogs between the two lake categories *(fig. 2),* indicating that *R. muscosa* was able to recolonize lakes following fish disappearance. Recent studies in which trout were eradicated from lakes using gill nets (Knapp and Matthews 1998) and the response of resident or nearby *R. muscosa* populations was monitored (Vredenburg 2002) provide additional evidence that declines of *R. muscosa* are reversible. In all cases in which *R. muscosa* were present either in the previously stocked but now fishless lake or nearby (N =

6), fish eradication resulted in rapid and dramatic increases in the number of *R. muscosa*. For example, before the eradication of trout from a lake in the John Muir Wilderness, counts indicated an *R. muscosa* population size of approximately 40 adults and 20 larvae. All fish were removed in 1997-1998, and by 2002 the *R. muscosa* population had increased to approximately 700 adults and 3,000 larvae. As a cautionary note, however, lakes that are separated from *R. muscosa* populations by fish-bearing lakes or by excessive distances will likely not be naturally recolonized following fish eradication. For example, Knapp eradicated trout populations from two lakes in the John Muir Wilderness that lacked any *R. muscosa* within 4 kilometers (km). Five years following the fish eradication, neither lake has been recolonized by *R. muscosa*. Recolonization failure in such situations appears to be a consequence of *R. muscosa* typically dispersing only relatively short distances (Matthews and Pope 1999, Pope and Matthews 2001, Vredenburg 2002) and increased dispersal mortality caused by trout predation.

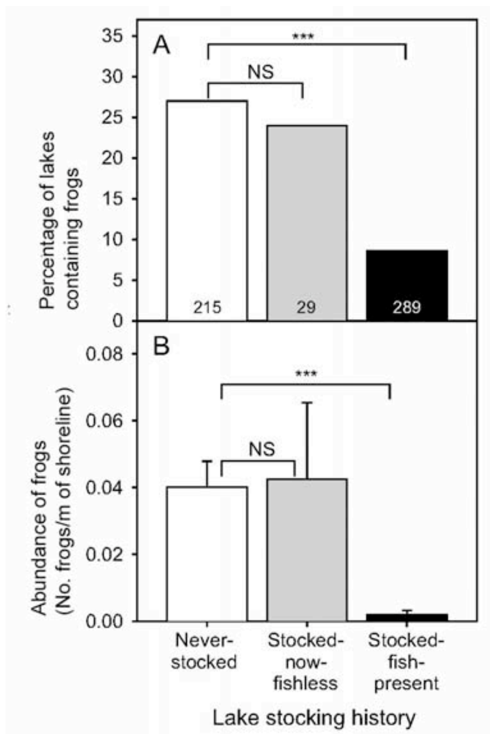

Figure 2— (A) Percentage of never-stocked lakes (open bars), stocked-now-fishless lakes (gray bars), and stocked-fish-present lakes (black bars) containing mountain yellow-legged frog larvae. (B) The abundance of mountain yellow-legged frog larvae in never-stocked, stocked-now-fishless, and stocked-fish-present lakes. Abundance was measured as the number of larvae/m of shoreline and is expressed as $\log_{10}$(abundance + 1). Bars indicate means + 1 SE. Sample sizes for each lake type are given inside the respective bar in (A). Lines and associated symbols connecting each bar provide the results of pairwise chi-square tests: ***P < 0.001; NS, not significant (P > 0.05).

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Interface of Science with Management and Policy

Since publication of the SNEP report (1996), the body of scientific information describing the role of non-native trout in causing the decline of *R. muscosa* has expanded dramatically and is now sufficiently well-developed to inform management and policy related to the protection and restoration of aquatic ecosystems in the Sierra Nevada. Indeed, notable changes in management and policy are already being made on the basis of recent research results. For example, given the critical need for information on the distribution of *R. muscosa* and non-native trout in developing restoration plans, the National Park Service (NPS) and California Department of Fish and Game (CDFG) have recently embarked on an ambitious program to conduct biotic inventories of all lakes and ponds on Federal lands in the Sierra Nevada that have not yet been surveyed. Inventories in Sequoia, Kings Canyon, and Yosemite national parks were completed in 2002, and CDFG surveys are expected to be completed by 2004. In addition, the USDA Forest Service is implementing a comprehensive monitoring program of *R. muscosa* populations on National Forest lands throughout the Sierra Nevada. Backcountry fish stocking by the CDFG is also being curtailed, pending completion of CDFG surveys and basin-specific management plans. In an effort to expand the few remaining *R. muscosa* populations, the CDFG and NPS recently initiated fish eradication projects in Kings Canyon National Park and the John Muir Wilderness. Both agencies are using techniques developed by researchers in previous frog restoration studies (Knapp and Matthews 1998; Vredenburg 2002). Critically needed management actions and policy changes that have not yet been implemented include (1) permanent termination of backcountry fish stocking from the range of *R. muscosa,* except where needed to maintain unique angling opportunities, (2) implementation of an amphibian monitoring program for Sequoia, Kings Canyon, and Yosemite national parks, and (3) a greatly expanded effort to restore *R. muscosa* populations throughout their historic range.

Future Research

Despite the considerable progress made in understanding the causes of amphibian declines in the Sierra Nevada during the past decade, additional research is urgently needed in two areas. First, it remains unclear what level of restoration will be necessary to ensure the long-term viability of *R. muscosa* populations. A formal population viability analysis would be of great utility in describing the conditions under which long-term population persistence could be expected. Such a modeling effort is currently under way. Second, although this review focuses solely on the impact of non-native trout introductions in causing the decline of *R. muscosa*, other stressors may also be playing important roles. These include disease and airborne agricultural contaminants. The disease caused by the fungus *Batrachochytrium dendrobatidis* has caused the decline of many amphibian species worldwide, and this organism is also infecting *R. muscosa* and other amphibians in the Sierra Nevada (Fellers and others 2001). A considerable research effort is currently under way to clarify the role of this chytrid fungus in causing amphibian declines in the Sierra Nevada. In addition, for several species of amphibians in the Sierra Nevada, including *R. muscosa*, Davidson and others (2002) showed that the probability of population extirpation was increasing as a function of the amount of upwind agriculture. Assuming that the amount of upwind agriculture is an accurate proxy of the intensity of pesticide application, these results suggest that agricultural contaminants may be negatively affecting a number of amphibian species in the Sierra Nevada.

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