

composition began to change dramatically in high elevation lakes and streams (Moyle *et al.* 1996). Some of the first practitioners of trout stocking in the Sierra Nevada were the Sierra Club, local sportsmen's clubs, private citizens, and the U.S. military (Knapp 1996; Pister 2001). As more hatcheries were built and distribution of non-native fish became better organized under State agency leadership, trout continued to be planted for the purpose of increased angler opportunities and success (Pister 2001). After World War II, the method of transporting trout to be stocked in high elevation areas changed from packstock to aircraft, which allowed stocking in more remote lakes and in greater numbers. It was at this point that CDFG began managing the bulk of the program, as it does today (Knapp 1996; Pister 2001).

Brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), and other trout species assemblages have been planted in most streams and lakes of the Sierra Nevada (Knapp 1996; Moyle 2002). National forests in the Sierra Nevada have a higher proportion of lakes with non-native fish occupancy than do national parks (Knapp 1996). This is primarily because the NPS adopted a policy that greatly reduced fish stocking within their jurisdictional boundaries in the late 1970s. Fish stocking was terminated altogether in Sierra Nevada national parks in 1991 (Bahls 1992; Knapp 1996).

Knapp's (1996) review of previous trout distribution estimates and other available data on trout distribution in the Sierra Nevada indicated that approximately 63 percent of lakes larger than 1 ha (2.5 ac) contain one or more non-native trout species, and as many as 85 percent of lakes larger than 1 ha (2.5 ac) within national forests currently contain fish. Lakes larger than 1 ha (2.5 ac) within Sierra Nevada national parks were estimated to have from 35 to 50 percent non-native fish occupancy, a 29 to 44 percent decrease since fish stocking was terminated (Knapp 1996). Though data on fish occupancy in streams is lacking throughout the Sierra Nevada, Knapp (1996) estimated 60 percent of the streams in Yosemite National Park were occupied by trout, despite the curtailment of stocking practices over 25 years ago. Grinnell and Storer (1924) observed that fish stocking in Yosemite National Park "nearly or quite eliminates the (mountain yellow-legged) frogs."

The most spatially comprehensive study of introduced fish and mountain yellow-legged frog distributions included an analysis of large landscapes

affected by different fish stocking regimes, watersheds with differing trout distributions, and individual water bodies with varying fauna assemblages (Knapp and Matthews 2000). The Knapp and Matthews (2000) study on the effects of introduced fishes on the mountain yellow-legged frog in the Sierra and Inyo National Forests' John Muir Wilderness indicated 65 percent of water bodies 1 ha (2.5 ac) or larger were stocked with fishes on a regular basis up through the time of the study. Over 90 percent of the total water body surface area in the John Muir Wilderness in the Sierra and Inyo National Forests is occupied by non-native trout (Knapp and Matthews 2000). All fish stocking was terminated in 1977 in the adjacent Kings Canyon National Park. Knapp and Matthews (2000) surveyed all lakes and ponds, more than 1,700 water bodies, for fishes and mountain yellow-legged frogs. They concluded that a strong negative correlation exists between introduced trout and mountain yellow-legged frogs across the landscape, the watersheds, the individual water bodies of the study area, and possibly throughout the Sierra Nevada (Knapp and Matthews 2000). Consistent with this finding are the results of an analysis of the distribution of mountain yellow-legged frog larvae that indicates that the presence and abundance of larvae are reduced dramatically in lakes that have fish as compared with lakes that were never stocked with fish (Knapp *et al.* 2001).

Several aspects of the mountain yellow-legged frog's life history may exacerbate its vulnerability to predation and extirpation by non-native trout (Bradford 1989; Bradford *et al.* 1993; Knapp 1996; Knapp and Matthews 2000). Mountain yellow-legged frogs are aquatic and are found mainly in lakes. This increases the probability that they will encounter non-native fishes whose distribution has been greatly expanded throughout the Sierra Nevada as a result of fish stocking. The multiple-year larval stage of the mountain yellow-legged frog necessitates their use of permanent water bodies that are deep enough so as not to freeze, and so that overwintering adults can avoid oxygen depletion when the water is covered by ice (Mullally and Cunningham 1956; Bradford 1983; Knapp and Matthews 2000). This further restricts larvae to water bodies suitable for and frequently inhabited by fishes (Knapp 1996) and isolates mountain yellow-legged frogs to fishless marginal habitats (Bradford *et al.* 1993; Knapp and Matthews 2000).

Mountain yellow-legged frog populations have also been extirpated at some fishless bodies of water (Bradford

1991; Drost and Fellers 1996). An explanation suggested for recent mountain yellow-legged frog population declines from fishless waters in the Sierra Nevada is the isolation and fragmentation of remaining populations by introduced fishes in the streams, which once provided the mountain yellow-legged frog with dispersal and recolonization routes (Bradford 1991; Bradford *et al.* 1993). Based on a survey of 95 basins within Sequoia and Kings Canyon National Parks, Bradford *et al.* (1993) calculated that the introduction of fishes into the study area resulted in approximately a ten-fold decrease in hydrologic connectivity between populations of mountain yellow-legged frogs. Knapp and Matthews (2000) believe that this has generally restricted mountain yellow-legged frogs to extremely isolated and marginal habitat. Trout influenced the isolation and fragmentation of mountain yellow-legged frog populations and metapopulations, making them more vulnerable to extirpation from random events (such as disease) than large, unfragmented metapopulations (Wilcox 1980; Hanski and Simberloff 1997; Bradford *et al.* 1993; Knapp and Matthews 2000). Given the metapopulation structure of the mountain yellow-legged frog, these isolated population locations may have higher extinction rates than colonization rates because trout prevent successful recolonization and dispersal to and from these sites (Bradford *et al.* 1993; Blaustein *et al.* 1994a; Knapp and Matthews 2000). In addition, amphibians may not recolonize unoccupied sites following local extinctions because of physiological constraints; the tendency for amphibians, including the mountain yellow-legged frog, to move only short distances; and high site fidelity (Blaustein *et al.* 1994a).

Knapp and Matthews (2000) suggest that the predation of mountain yellow-legged frogs by fishes as observed by Grinnell and Storer (1924), and the documented declines of the 1970s (Bradford 1991; Bradford *et al.* 1994a; Stebbins and Cohen 1995), are not the start of the mountain yellow-legged frog's decline, but rather the end of a long decline that started soon after fish introductions to the Sierra Nevada began in the mid-1800s. Knapp and Matthews (2000) note that metapopulation theory (Hanski 1997) predicts this type of time lag from habitat modification to population extinction.

Fish-induced declines of the mountain yellow-legged frog may be reversed in some locations with an