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Sierra Nevada
Headwaters

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*Non-Native Trout in Natural
Lakes of the Sierra Nevada:
An Analysis of Their
Distribution and Impacts on
Native Aquatic Biota*

This report was funded in part by the Sierra Nevada Ecosystem Project (SNEP). Under the agreement with SNEP, I agreed to conduct a literature review of the distribution of non-native trout in the Sierra Nevada, and their impacts on native aquatic biota. Because existing literature did not allow an adequate analysis of the current trout distribution, I have included results based on a compilation of data from the California Department of Fish and Game and the National Park Service. The geographic information system (GIS) data compilation effort was funded by the U.S.D.A. Pacific Southwest Research Station.

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INTRODUCTION

The Sierra Nevada is largely federally-owned, with the majority of its 5 million hectares 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 designated wilderness (Palmer 1988). Because national parks and wilderness areas are supposedly managed primarily for natural ecosystems, a widely-held public perception is that the Sierra Nevada, particularly the higher elevation areas, are largely protected from anthropogenic impacts. Although recent research on forest ecosystems, fire ecology, and air quality illustrate that anthropogenic influences are impacting even the most remote portions of the Sierra Nevada (see SNEP chapters), until recently there has been little evidence to suggest that high elevation aquatic ecosystems are at risk. Recent research, however, suggests that these ecosystems are among the most disturbed in the range.

Prior to the mid-nineteenth century, nearly all lakes and streams in the Sierra Nevada above 1800 m (6000') were fishless. As a result of 150 years of fish stocking throughout the Sierra Nevada, however, all watersheds now contain as many as five non-native trout species (Jenkins et al. 1994). Although fish stocking was curtailed in Sequoia, Kings Canyon, and Yosemite National Parks in the 1970's and completely halted in 1991, stocking of non-native trout species continues in the national forests, including designated wilderness.

Although the stocking of trout into lakes and streams has long been viewed as an activity that benefits recreationists and has few negative consequences, results of recent research into the effects of non-native trout on naturally-fishless ecosystems is challenging this view. Studies of aquatic ecosystems in the Sierra Nevada show that introduced trout can have severe impacts on native trout (e.g., Gerstung 1988), amphibians (Bradford 1989; Bradford et al. 1993), zooplankton (Stoddard 1987), and benthic macroinvertebrates (Melack et al. 1989; Bradford et al. 1994a), and suggest that some aquatic species might be driven to extinction by the current nearly ubiquitous distribution of non-native trout (Bradford et al. 1993). Similar effects of non-native trout appear to be common in mountain ranges throughout western North America (e.g., Anderson 1971; Bahls 1992). Interest in the effects of non-native fishes on aquatic ecosystems is likely to increase rapidly during the next decade, as several amphibian species are listed under the federal Endangered Species Act.

The purpose of this report was to provide an overview of the historic (i.e., pre-1850) and current fish distribution in the Sierra Nevada, and to review the impacts of non-native trout on Sierran aquatic ecosystems. Specifically, the report is divided into four major sections to address the following topics:

- (1) The historic distribution of native fishes in the Sierra Nevada. An understanding of the historic distribution provides the basis for comparisons with the current trout distribution, and is critical in order to assess the magnitude of changes that have occurred as a result of trout stocking.
- (2) The history of trout stocking in the Sierra Nevada. This brief review will summarize the agencies and groups responsible for fish stocking from the mid-nineteenth century to the present, and will highlight recent changes in fish stocking practices in the Sierra Nevada.

(3) The current state of knowledge pertaining to present-day trout distributions in the Sierra Nevada. This review utilizes information obtained from published papers, agency documents, and a geographic information system (GIS), to provide an overview of the current distribution of non-native trout in portions of three national forests and three national parks in the Sierra Nevada. This review also serves to highlight gaps in the available information pertaining to the distribution of non-native trout in the Sierra Nevada.

(4) The impacts of non-native trout on aquatic ecosystems in the Sierra Nevada. An improved understanding of these impacts will assist in designing aquatic ecosystem management strategies for which the consequences (both beneficial and harmful) are as well understood as possible.

Based on the review of the distribution of non-native trout in the Sierra Nevada and their impacts on native aquatic species, I then (1) discuss the risks associated with current management of aquatic ecosystems in the Sierra Nevada, (2) outline several alternatives to the current management of aquatic ecosystems and briefly discuss the ecological and sociological consequences of each alternative, (3) recommend several immediate changes to the current trout stocking program, and (4) suggest directions for future research aimed at providing a better understanding of the ecological consequences of alternatives to the current trout stocking program in the Sierra Nevada.

METHODS

The general geographic boundaries of this study coincide with those adopted by the Sierra Nevada Ecosystem Project (figure 1). Information on the historic fish distribution, the history of trout stocking, and the impacts of non-native trout on aquatic ecosystems within the study area was acquired through literature surveys of published papers and unpublished reports. Literature searches were conducted using CD-ROM facilities at the University of California, Santa Barbara. These searches were supplemented with information obtained during visits to offices of the California Department of Fish and Game (DFG) and the National Park Service. Information on the current fish distribution in the Sierra Nevada was obtained through literature reviews and compilation of data from the DFG and the National Park Service. Stocking records for lakes within the study area and any available site-specific information was obtained from the DFG Regions 2, 4, and 5 (northern Sierra, western Sierra, and eastern Sierra, respectively). These records were compiled into a geographic information system (GIS) utilizing 1:100,000 and 1:24,000 USGS digital line graphs (DLG's) of hydrologic features, with additional coverages including elevation, watershed boundaries, and land ownership.

RESULTS: FISH DISTRIBUTIONS

The GIS revealed major information gaps pertaining to the current distribution of trout in the Sierra Nevada. First, current lake-specific information is lacking for large portions of the Sierra Nevada. For example, DFG Regions 2 and 4 had information primarily on lakes that are currently stocked with trout. Within these regions, there was little information on lakes that are not currently stocked but are still likely to contain non-native trout (e.g., as a result of past stocking). In contrast, DFG Region 5 had

information on approximately 95% of the lakes larger than 1 ha within their jurisdiction. Yosemite and Sequoia-Kings Canyon National Parks both had data on a large proportion of lakes within their jurisdiction, although records from Yosemite National Park were more extensive and more detailed.

The second data gap pertains to the current distribution of trout in streams within the study area. This distribution is very poorly described by existing data, and records are available only for Yosemite National Park. As a result, I was unable to provide a detailed analysis of fluvial trout distributions within the study area, and was forced to restrict the scope of this report primarily to trout distributions in lakes.

As a result of these data gaps, I obtained summary information for the entire study area, but all detailed analyses of the current distribution of trout in the Sierra Nevada are based on Sequoia, Kings Canyon, and Yosemite National Parks and that portion of the Sierra Nevada within DFG Region 5 (figure 1). The presented data serve to describe the current trout distribution in a portion of the Sierra Nevada, cover a large fraction of the historically fishless areas in the Sierra Nevada (figure 1 and 2) where the most dramatic changes in fish distribution have occurred, and illustrate the large differences in trout distributions between national forests and national parks.

Historic fish distribution

Nearly all lakes and streams in the Sierra Nevada above 1800 m (6000') were historically fishless, but several native fish species were found historically in streams, rivers, and a few lakes at lower elevations around the perimeter of the Sierra Nevada (figure 2). A description of these native fish distributions is given in Moyle et al. (1995).

Brief history of trout stocking

Although many fish species have been introduced to the Sierra Nevada (Moyle 1976), trout were by far the most commonly introduced group at elevations above the valley floors. Starting in the mid-1800's and continuing until the 1960's, trout have been introduced into formerly fishless streams and lakes to provide recreational fishing (Christenson 1977). Although some of these introductions were interbasin transfers of trout native to the Sierra Nevada (e.g., golden trout, rainbow trout, Lahontan cutthroat trout), 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 (Christenson 1977). Early trout planting efforts were aimed primarily at establishing trout in formerly fishless waters, and were carried out largely by sporting groups (e.g., Bishop Fish Planting Club, Sierra Club, Visalia Sportsmens Club). In addition, the U.S. military conducted extensive trout planting in Sequoia, Kings Canyon, and Yosemite National Parks (Christenson 1977). 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 (DFG). Today, the DFG 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 or maintain existing non-native trout populations.

Sequoia, Kings Canyon, and Yosemite National Parks began phasing out trout stocking in 1969 as a result of recommendations in the Leopold Report (Leopold 1963). In 1972, the National Park Service (NPS) released its policy that stated, "No artificial stocking of fish species exotic to a park will occur; artificial stocking of fish or eggs may only be employed to reestablish a native species. Naturally barren waters will not be stocked with either native or exotic fish species" (NPS 1975). Limited stocking was continued until 1991, when an agreement was negotiated with the DFG to terminate all fish stocking in these parks. Trout stocking is permitted on all other federal lands in the Sierra Nevada (67% of the Sierra Nevada; Palmer 1988), including national forest wilderness areas, except those waters within wilderness areas that were not stocked prior to federal wilderness designation (Bahls 1992).

Although concern over the impacts of non-native trout on aquatic biota in the Sierra Nevada is increasing (Bradford et al. 1994a; Knapp 1995a, Bahls (1992) concluded that trout stocking is generally conducted with only minimal concern for native fish species (including trout), amphibians, and other native aquatic biota. Paradoxically, this is true even in federally designated wilderness areas, where lands are supposed to be managed in such a way as to maintain their natural conditions (Kloepfer et al. 1994). Although some states in the western U.S. attempt to minimize impacts to aquatic ecosystems by stocking trout only into lakes that have been surveyed, this is not the case in California (Bahls 1992). In addition, there appears to be little emphasis on determining whether currently-stocked lakes are actually self-sustaining. In a recently surveyed portion of the Sierra Nevada, the majority of stocked lakes do not need to be stocked to maintain their fish populations (Matthews and Knapp 1995).

Current fish distribution

Despite over a century of effort being expended to stock trout in the Sierra Nevada, information on the current distribution of trout is rudimentary at best. While DFG and NPS records indicate that all major watersheds in the Sierra Nevada contain at least one species of introduced trout, lake-specific and stream-specific information on the presence or absence of fish is generally incomplete and outdated. Much of the DFG data is not computerized, and has never been summarized to provide an overview of the current distribution of trout in the Sierra Nevada. Although estimates of the number of trout-containing versus troutless waters have been published for portions of the Sierra Nevada, these estimates were based on interviews with fishery managers (Bahls 1992) or on the results of surveys from a very small number of waters scattered throughout the Sierra Nevada (Jenkins et al. 1994), and may not provide an accurate picture of the Sierra-wide distribution of trout.

Sierra-wide trout distribution. Bahls (1992) reported that of 4,131 mountain lakes in California (lakes higher than 800 m; these are primarily in the Sierra Nevada), 63% contained introduced fish and 52% were currently stocked. Of the estimated 37% of lakes that remain fishless, most are small (<2 ha), shallow (<3 m), and generally incapable of supporting trout populations (Bahls 1992). Only 3% of larger lakes (>2 ha, >3 m deep)

remain fishless. Based on a survey of 30 randomly selected high elevation lakes (>2400 m and >1 ha) throughout the Sierra Nevada, Jenkins et al. (1994) used the Environmental Monitoring and Assessment Program (EMAP) procedure (Paulsen et al. 1991) to extrapolate their results to all lakes above 2400 m in the study region. Jenkins et al. (1994) estimated that 1404 lakes in the Sierra Nevada met their selection criteria, and projected that one or more species of non-native trout would occur in 63%. Based on the relative frequency of occurrence, 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.

Trout distribution on three national forests. Christenson (1977) suggested that as many as 95% of California's naturally fishless mountain lakes outside of national parks currently contain fish. Although there are no published descriptions of the distribution of non-native trout on national forests, analysis of the data from DFG Region 5 suggests that this estimate may be quite accurate. The Sierra Nevada portion of the DFG Region 5 includes approximately 700 mountain lakes larger than 1 ha and 16 reservoirs. The DFG Region 5 database includes information on 649 lakes and all 16 reservoirs. The 649 lakes include 452 lakes on the Inyo National Forest, 116 lakes on the Sierra National Forest, and 81 lakes on the Toiyabe National Forest. Eighty-four percent of the lakes lie within four federally-designated wilderness areas (Ansel Adams, Golden Trout, Hoover, and John Muir), 2% lie within a Forest Service Research Natural Area (Harvey Monroe Hall), and the remaining 14% lie outside of wilderness areas. The majority of the lakes lie between 3000-3500 m (mean=3179 m, S.D.=285), and nearly all have surface areas of less than 10 ha (mean=6.0 ha, S.D.=13.4). Although all 649 were originally without trout, 85% now contain non-native trout, 7% are fishless, and the status of the remaining 8% is unknown. Fish-containing and fishless lakes do not differ in their elevations (Mann-Whitney U-test: $U=1.0$, $P>0.3$; figure 3), but fish-containing lakes are significantly larger than fishless lakes (Mann-Whitney U-test: $U=6.6$, $P<0.001$; figure 4). Brook trout are the most common species (51% of lakes), followed by rainbow trout, golden trout, brown trout, cutthroat trout, and kokanee salmon and hybrid trout populations. The frequency of occurrence of these fish species changes with elevation (figure 5), with the most common species being rainbow trout at the lowest elevations, brook trout at intermediate elevations, and golden trout at the highest elevations. Although fishless lakes are found at nearly all elevations (figure 3 and 5), they are relatively uncommon (figure 5) and nearly all are very small (<2 ha)(figure 4). Fishless lakes are most common at low and high elevations, and least common at intermediate elevations (figure 5). Many of these lakes may be fishless because they are too small and shallow to support fish populations.

The DFG regularly stocks trout into 46% of the 649 lakes. The remaining 54% either contain self-sustaining trout populations or are fishless. Thirty-five percent of the stocked lakes are stocked annually and 65% are stocked every two years. Stocked lakes are significantly lower in elevation than unstocked lakes (Mann-Whitney U-test: $U=2.6$, $P<0.01$; figure 6) and significantly larger than unstocked lakes (Mann-Whitney U-test: $U=8.8$, $P<0.0001$; figure 7). Of the 302 stocked lakes, nearly all are stocked with rainbow or golden trout fingerlings.

Although the mountain lakes within DFG Region 5 are subject to regular fish stocking, they are surveyed infrequently. During the past ten years (1985-94), only 32%

were surveyed for fish and 14% have never been surveyed. In addition, surveys have typically been restricted to fish populations, with no effort being made to determine the status of native aquatic species. The hundreds of small lakes and ponds not represented in the DFG Region 5 database also have not been surveyed.

Figures 8 and 9 illustrate the dramatic changes in fish distributions that have occurred within DFG Region 5 since approximately 1850. Prior to fish stocking, the upper portion of the French Creek and Piute Creek watersheds was entirely fishless (figure 8). Today, nearly all of the larger lakes (≥ 1 ha) and a substantial proportion of the smaller ponds (< 1 ha) contain fish (figure 9). Only two lakes are known to remain in a fishless condition. Within these watersheds, the DFG Region 5 has information on 56 of the lakes, and 70% of these are regularly stocked with trout. No information is available on the streams, but because trout readily move out of lakes to colonize inlet and outlet streams, nearly all stream sections shown in figure 9 are likely to contain non-native trout.

French +
Piute
Creeks

Trout distribution in national parks - Numerous gillnet and snorkeling surveys of non-native trout have been conducted in Sequoia, Kings Canyon, and Yosemite National Parks, but these surveys have generally been limited to a small subset of the total number of lakes in each park. Assuming that the sampled lakes are representative of park lakes, all three national parks contain a substantially greater proportion of fishless lakes than do national forests.

Extensive study of non-native trout distributions in Yosemite National Park lakes and streams was conducted during 1951-52 (Wallis 1952). This study involved the compilation of all available historical lake information (e.g., stocking records, angler surveys), and surveys of 78% of 343 park lakes larger than 1 ha and the majority of park streams. Based on his surveys, Wallis (1952) concluded that approximately 62% of the lakes and 78% of streams contained non-native trout populations.

Since the study by Wallis (1952), the number of lakes containing non-native trout has declined as a result of the termination of fish stocking. Botti (1977) surveyed 102 lakes in Yosemite National Park that had been stocked between 1963 and 1977, and found that non-native trout had disappeared from 22%. An additional 22% were likely to become fishless because of a lack of suitable spawning habitat. Therefore, 66% of the lakes surveyed by Botti (1977) should still contain non-native trout populations. Lakes that lost their trout populations after stocking was halted were at significantly lower elevations (Mann-Whitney U-test: $U=5.2$, $P<0.0001$; figure 10) and were smaller ($P<0.003$; figure 12) than lakes that retained trout. Of the lakes that lost their trout populations, nearly all were those formerly stocked with rainbow trout (figure 11). In contrast, brook trout were only lost from three lakes after the termination of trout stocking. As a result, the relative abundance of the four non-native trout found by Botti (1977) changed markedly after trout stocking was halted (figure 12). The combination of data from Wallis (1952) and Botti (1977) suggests that approximately 34% of Yosemite National Park lakes still contain fish (Elliot and Loughlin 1992). The stocking history and current trout status in Yosemite National Park lakes and streams is shown in figure 13.

Similar trout distributions are found in Sequoia and Kings Canyon National Parks. A recent survey of 312 of 2801 naturally fishless lake-sites (lakes and adjacent ponds, if present) scattered throughout Sequoia and Kings Canyon National Parks found introduced trout in 46% (Bradford et al. 1993). However, a considerable amount of inter-drainage

variation in the relative proportions of fish-containing versus fishless lakes is apparent from a second survey by Bradford et al. (1994a). This survey included 104 lakes in a particularly remote portion of Kings Canyon National Park, and trout were only found in 17%.

As in Yosemite National Park, the greater proportion of fishless lakes in Sequoia and Kings Canyon National Parks than on national forest lands is due at least in part to the termination of fish stocking. Zardus et al. (1977) sampled 137 lakes that had been stocked with trout between 1963 and 1977, and found that 13% of the lakes had returned to a fishless condition by 1977. An additional 16% were expected to eventually revert to a fishless condition because of poor spawning habitat.

RESULTS: IMPACTS OF TROUT ON NATIVE AQUATIC SPECIES

Trout are highly-effective predators and their impacts on prey species are well-documented (e.g., Northcote 1988). This impact may be particularly severe in oligotrophic lakes such as those found in the Sierra Nevada, since the relatively simple food webs of such lakes are believed to make them especially sensitive to impacts from introduced species (Li and Moyle 1981; McQueen, et al. 1986). In fact, based on an extensive survey of lakes in the Sierra Nevada, Bradford et al. (1994a) concluded that "the most profound human impacts on aquatic communities in the High Sierra appear to be related to historical and on-going stocking of exotic fish species into High Sierra waters". The following review documents the effect of introduced trout on native fishes, amphibians, zooplankton, lake benthic invertebrates, stream benthic invertebrates, and community structure in the Sierra Nevada.

Native fishes

The native fish fauna of the Sierra Nevada has been altered substantially by the introduction of non-native trout, with impacts of introductions being particularly severe for native trout. The range of the two golden trout subspecies was greatly reduced by the 1970's as a result of non-native trout introductions (USFS 1982). Extensive hybridization with introduced rainbow trout and displacement by introduced brook trout precipitated the listing of the Little Kern golden trout under the Endangered Species Act. Since its listing, non-native trout have been eradicated from the entire Little Kern River and pure populations of Little Kern golden trout are being re-established. During the 1950's and 1960's, introduced brown trout displaced the California golden trout from much of the South Fork Kern River. Recovery of this subspecies required the removal of brown trout from over 100 km of river and the construction of two fish barriers. The recent discovery of brown trout above the lower barrier, however, has increased the likelihood of brown trout reinvading the upper South Fork Kern River. Because of this threat, the U.S. Fish and Wildlife Service is currently considering listing the California golden trout under the Endangered Species Act.

The status of native rainbow trout on the west side of the Sierra Nevada is unclear. Although rainbow trout populations probably still occur in most streams and rivers where they occurred historically, extensive introgression with introduced hatchery rainbow trout is likely. Although no data are currently available to support this possibility in the Sierra

Nevada, introgression has been documented between hatchery rainbow trout and the native rainbow trout of the upper Sacramento Basin (Oncorhynchus mykiss stonei; (Behnke 1992).

The habitat of the Lahontan cutthroat trout has been reduced by over 90% throughout its native range by massive habitat alteration, water diversions, and overfishing. In the remaining highly isolated populations, however, cutthroat trout are subject to hybridization and competition with and predation by introduced trout (Gerstung 1988). Because of the severity of its decline, the Lahontan cutthroat trout was listed under the Endangered Species Act in 1970. The recently released Lahontan cutthroat trout recovery plan (Coffin and Cowan 1995) calls for the removal of non-native trout from portions of the native range of Lahontan cutthroat trout as a critical recovery strategy. Declines of non-trout fishes in the Sierra Nevada are widespread (Moyle and Nichols 1973; Moyle and Nichols 1974; La Rivers 1994), but the few studies detailing the causes of these declines suggest that they have been caused primarily by habitat alteration and not trout introductions (e.g., Moyle and Nichols 1974).

Amphibians

Numerous native species of amphibians are found in the Sierra Nevada (see Jennings 1995 for a detailed review). Several anuran species are reported to be declining in abundance (Yosemite toad: Bufo canorus; California red-legged frog: Rana aurora draytonii; foothill yellow-legged frog: R. boylei; and mountain yellow-legged frog: R. muscosa; Moyle 1973; Hayes and Jennings 1986; Bradford 1991; Sherman and Morton 1993; Bradford et al. 1994b; Drost and Fellers 1994). Declines of the three Rana species have been attributed in part to predation by introduced fishes, including trout (e.g., Hayes and Jennings 1986; Bradford 1989; Bradford et al. 1993). The California red-legged frog and the foothill yellow-legged frog are found in the western foothills of the Sierra Nevada below 1500 m, and inhabit ponds and streams, respectively (Zweifel 1955). The proposed negative effect of introduced fishes on the California red-legged frog and the foothill yellow-legged frog is based largely on observations of a lack of overlap between either of the species and introduced fishes (Hayes and Jennings 1986). These data, however, are confounded by the fact that habitats containing introduced fishes are also frequently inhabited by the bullfrog (Rana catesbeiana) (Hayes and Jennings 1986), another introduced species proposed as a cause for the decline (Moyle 1973; Hayes and Jennings 1986). In addition, former habitats of these species that now contain introduced fishes have often also been altered by land management practices. As a result, the importance of introduced fish relative to bullfrogs and habitat alterations as a factor leading to the declines of the California red-legged frog and the foothill yellow-legged frog remains unclear (Hayes and Jennings 1986).

The mountain yellow-legged frog is endemic to the Sierra Nevada and a few sites in southern California. Historically, the mountain yellow-legged frog was widespread throughout the Sierra Nevada at elevations above 1500 m (Zweifel 1955), having been present in all major watersheds on the west and east sides of the Sierra Nevada. However, based on a recent resurvey of historic localities in the central Sierra Nevada, Drost and Fellers (1994) reported that the mountain yellow-legged frog was present in fewer than 15% of the sites where it was found in 1915.

← trends

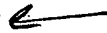
Several attributes of this species make it particularly vulnerable to predation and subsequent extirpation by non-native trout. First, adult mountain yellow-legged frogs are highly aquatic and are found primarily in lakes (most of which now contain trout). Second, in contrast to tadpoles of other Sierran anurans that complete metamorphosis to the terrestrial stage in a single summer, mountain yellow-legged frog tadpoles generally require at least two years before metamorphosis to the terrestrial stage. This overwintering requirement restricts breeding to bodies of water that are deep enough to avoid oxygen depletion when ice-covered (>1.5 m; Mullally and Cunningham 1956; Bradford 1983). The majority of these deeper lakes, however, now contain introduced trout.

There is substantial evidence that introduced trout have severely reduced the abundance of mountain yellow-legged frogs in the Sierra Nevada. As early as 1924, Grinnell and Storer (1924) reported that mountain yellow-legged frog tadpoles and introduced trout rarely co-occur in lakes and ponds in the Sierra Nevada. This observation has been quantified repeatedly in different parts of the Sierra Nevada (Bradford 1989; Bradford and Gordon 1992; Bradford et al. 1993; Drost and Fellers 1994). This lack of overlap is assumed to be the result of predation by trout on the mountain yellow-legged frog, an assertion supported by Needham and Vestal (1938), who observed trout preying on mountain yellow-legged frogs in a lake into which trout had recently been introduced. Given that the presence of fish generally makes a pond or lake unsuitable for mountain yellow-legged frogs, that lakes smaller than 1 ha are generally too shallow to support mountain yellow-legged frogs (Matthews and Knapp 1995), and that 34-85% of formerly fishless lakes larger than 1 ha now contain introduced trout (see Results: Current fish distribution), the amount of suitable habitat for mountain yellow-legged frogs has likely been reduced by a similar amount.

In addition to the direct impact that non-native trout have on mountain yellow-legged frogs via predation, Bradford et al. (1993) proposed that fish could also 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 sizes and a 10-fold reduction in connectivity between populations. Because amphibian populations often fluctuate widely under natural conditions (Pechmann et al. 1991; Gulve 1994), and small populations are more likely to go extinct under stochastic population fluctuations than are large populations (Wilcox 1980; Hanski 1989; Hanski and Gilpin 1991), Bradford et al. (1993) proposed that the reduction in mountain yellow-legged frog population size caused by trout introductions is likely to have increased the rate at which individual populations are extirpated. 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 reduction could result from the smaller size of potential source populations, increased distance from source populations, and predation by introduced trout on dispersing frogs (Bradford et al. 1993). Increased isolation of remaining populations could also result in increased inbreeding with a resulting decrease in genetic diversity within populations (Reh and Seitz 1990).

In a recent study, Blaustein et al. (1994) proposed that the transmission of pathogens by introduced fishes may be another means by which trout introductions

trends



indirectly impact amphibian species such as the mountain yellow-legged frog. Blaustein et al. (1994) reported that the extremely high mortality of western toad (Bufo boreas) egg masses in a lake in the Cascade Mountains in Oregon was caused by a Saprolegnia fungal infection. This fungus is frequently found on trout raised in hatcheries, including on those species commonly introduced into lakes in the Sierra Nevada (Seymour 1970; Richards and Pickering 1978; Pohl-Branschield and Holtz 1985; Willoughby 1986). The recent discovery of Saprolegnia fungus infecting eggs of the mountain yellow-legged frog in the Sierra Nevada (Knapp 1993a) suggests that this proposed impact should be investigated more fully in Sierran amphibians.

Several additional anuran and salamander species are found in the Sierra Nevada, but direct impacts to these species from introduced trout are either unlikely because of a lack of overlap in habitat use between the amphibian species and introduced trout, or are likely but undocumented. All of the non-Rana anuran species in the Sierra Nevada (western toad, Yosemite toad, Pacific chorus frog) are largely terrestrial and generally breed in shallow ponds. Because these ponds are subject to desiccation in summer and freezing in winter and are therefore unlikely to contain fish, direct effects of introduced trout on these amphibian species are probably minimal. Most salamanders found in the Sierra Nevada (Ensatina sp., Hydromantes sp., Batrachoseps sp.) live and breed in semi-aquatic sites such as springs and seeps, and are therefore also unlikely to be impacted by introduced trout. However, the long-toed salamander (Ambystoma macrodactylum), found in the central and northern Sierra Nevada, appears to be restricted largely to fishless lakes (Bradford and Gordon 1992). Similar distributions have been described for the long-toed salamander in other mountain ranges, and for other species of lake-dwelling salamanders whose habitat contains introduced trout. For example, in lakes in North Cascades National Park, densities of the long-toed salamander were reduced in the presence of introduced trout (Liss and Larson 1991). The closely-related Ambystoma gracile was also much less common in lakes containing introduced trout than in fishless lakes. Burger (1950) reported the extinction of neotenic Ambystoma tigrinum nebulosum in a mountain lake in Colorado after the introduction of trout. Therefore, ample evidence exists that trout can impact lake-dwelling ambystomatid salamanders, and suggests that the effect of introduced trout on long-toed salamander populations in the Sierra Nevada should be investigated more thoroughly.

Although existing data suggests that the introduction of trout into Sierran lakes has caused local extirpations of at least one amphibian species (mountain yellow-legged frog), there are no published studies that have investigated the likelihood of amphibians recolonizing habitats if fish are removed or disappear as a result of a termination in stocking. Some recent survey data, however, suggests that mountain yellow-legged frogs can readily recolonize lakes from nearby refugia. Zardus et al. (1977) presented biological data on 137 lakes in Sequoia and Kings Canyon National Parks, including the presence or absence of mountain yellow-legged frogs and introduced trout. They reported finding trout but no frogs in three lakes in the Palisade Basin ("Barrett Lakes 1, 2, and 3"). Stocking was apparently discontinued in these lakes in the late 1970's or early 1980's. When these lakes were revisited in 1993, Barrett Lake 3 still contained fish and no mountain yellow-legged frogs, but Barrett Lakes 1 and 2 had reverted to a fishless condition and contained large mountain yellow-legged frog populations (>100 adults;

Knapp 1993b). Several nearby ponds and lakes were probably never stocked with trout (Jenkins et al. 1994), and mountain yellow-legged frogs in Barrett Lakes 1 and 2 probably recolonized from these refugia. Second, in a study of the aquatic biota of several lakes in Kings Canyon National Park, Taylor and Erman (1980) reported that all lakes in their study contained trout, including "Lower Sixty" Lake. When this lake was revisited in 1990, it was fishless and contained a very large mountain yellow-legged frog population (>500 adults; Knapp 1990). Although it is possible that mountain yellow-legged frogs were present in "Lower Sixty" Lake during the Taylor and Erman (1980) study (since they apparently did not survey the lake for mountain yellow-legged frogs during their research), the scarcity of lakes in which trout and frogs coexist (Bradford 1989) makes it more likely that mountain yellow-legged frogs recolonized this lake after the disappearance of introduced trout. Several nearby lakes have never been stocked with trout, contain large mountain yellow-legged frog populations (Zardus, et al. 1977; Knapp 1993a), and could have served as sources for recolonization of "Lower Sixty" Lake. A third potential example of recolonization by mountain yellow-legged frogs is apparently occurring in Wolf Creek Lake, located north of Yosemite National Park. The California Department of Fish and Game poisoned this lake in 1991-92 to remove the resident brook trout population. No mountain yellow-legged frogs were seen in the vicinity of the lake before or during the treatment. In 1994, however, DFG biologists reported seeing mountain yellow-legged frog adults and tadpoles in a small pond immediately adjacent to the lake (Knapp 1995b).

Zooplankton

The ability by fishes to dramatically alter lake zooplankton assemblages is widely recognized (e.g., Carpenter et al. 1985, 1987). The introduction of fish to a lake 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 fish predation (Northcote 1988). Several studies have documented this effect of introduced trout on zooplankton communities in lakes in the Sierra Nevada. Stoddard (1987) found that the presence or absence of fish (primarily salmonids) was by far the most important predictor of the distribution of zooplankton species among 75 alpine and subalpine lakes in the central Sierra Nevada, with large-bodied species found in fishless lakes and small-bodied species found in lakes with trout. Other studies on Sierran lakes have produced very similar results (Richards et al. 1975; Morgan et al. 1978; Goldman et al. 1979; Melack et al. 1989; Bradford et al. 1994a). Effects of trout on zooplankton communities have also been reported for lakes in the Rocky Mountains and Europe (Anderson 1971, 1972; Northcote et al. 1978; Dawidowicz and Gliwicz 1983; Bahls 1990).

Fish introductions may result in the extirpation of vulnerable zooplankton species. In Sierran lakes, large bodied Daphnia and Diaptomus species are commonly found in fishless lakes but are rarely found in lakes with trout (Reimers 1958; Melack et al. 1989; Bradford et al. 1994a). These results are in agreement with the results of a model by Walters and Vincent (1973) that predicted that large-bodied zooplankton species would be eliminated by trout predation even at low trout densities. Although these Daphnia and Diaptomus species have apparently been extirpated from many lakes in the Sierra Nevada, they are still relatively common in the range (e.g., Melack et al. 1989; Bradford et al.

1994a). In contrast, the phantom midge, Chaoborus americanus, may have been extirpated from the Sierra Nevada by introduced trout (Stoddard 1987). C. americanus, is common in high elevation lakes throughout western North America, but Stoddard (1987) did not find C. americanus in any of his samples from Sierran lakes. C. americanus was also absent from Sierran lakes sampled by Silverman and Erman (1979), Melack et al. (1989) and Bradford et al. (1994a). The possibility that trout introductions are responsible for the absence of Chaoborus in the Sierra Nevada is supported by studies showing the complete elimination of Chaoborus from lakes by introduced trout (Northcote et al. 1978).

Although trout introductions in the Sierra Nevada can apparently cause the extirpation of vulnerable zooplankton species from lakes, it is not clear whether these species reappear in lakes that revert to their original fishless condition. Some studies show that vulnerable zooplankton species do not reappear (Reimers 1958; Anderson 1972, 1974; Leavitt, et al. 1994), while others show that they do (Walters and Vincent 1973; Bahls 1990). Many zooplankton taxa have resting stages (e.g., Thorp and Covich 1991), including those of one species recently shown to remain viable for over 300 years (Hairston et al. 1995). If Sierran zooplankton also have long-lived resting stages, this "egg bank" could allow recovery of the original zooplankton community after fish disappearance. On the contrary, the introduction of fish may cause changes in lake food webs that reduce the ability of some zooplankton species to recolonize (Leavitt et al. 1994). Therefore, further research is necessary to determine the effects of trout introductions on Sierran lake food webs and zooplankton colonization dynamics.

Lake benthic macroinvertebrates

In addition to their effects on zooplankton communities, fish are also capable of altering the structure of lake benthic macroinvertebrate communities. In the Sierra Nevada, high elevation fishless lakes contain mayfly larvae (Ephemeroptera), caddisfly larvae (Trichoptera), aquatic beetles (Coleoptera), and true bugs (Corixidae) that are absent in lakes that contain introduced trout (Reimers 1958; Melack et al. 1989; Bradford et al. 1994a). Similar results have also been documented in other mountain ranges in the western United States (Walters and Vincent 1973; Bahls 1990). No data is currently available to determine the rate at which benthic macroinvertebrates recolonize lakes after trout disappearance.

Stream benthic macroinvertebrates

In contrast to the research effort that has been devoted to quantifying the impact of introduced trout on native lake biota, few studies have examined their effect on native stream biota. In the only study of trout impacts on Sierra Nevada stream benthic taxa that I am aware of, Melack et al. (1989) found significant differences in the macroinvertebrate assemblages of fish and fishless streams; these effects, however, were confined to a minority of the taxa present. Studies outside the Sierra Nevada are equivocal on the impacts of trout, with some studies showing no effect of trout on stream macroinvertebrates (e.g., Allan 1982; Culp 1986), and others showing strong effects (e.g., Hemphill and Cooper 1984; Cooper 1988; Flecker and Townsend 1994). Cooper et al.

(1990) suggest that vulnerability of particular taxa to trout predation is likely a function of a species exchange rate (i.e., immigration/emigration), with taxa with low exchange rates being more vulnerable than those with high exchange rates. If true, then stream communities may be more resistant than lake communities to changes caused by trout predation because of the much greater magnitude of prey exchange in streams.

In addition to direct predation effects on stream macroinvertebrates, trout can also have non-lethal effects. These effects include changes in diel behavior patterns (Douglas et al. 1994), diets, and growth rates (Wiseman et al. 1993).

Community-wide effects

Although the effect of introduced trout on native aquatic biota is often presented as an interaction between two trophic levels (e.g., trout preying on amphibians, trout preying on zooplankton), large changes in one trophic level (e.g., as a result of trout introductions) can have important cascading effects on all parts of the food web (Carpenter and Kitchell 1993). Although multiple trophic level consequences of fish introductions have not received much attention until recently, several potential community-wide effects of trout introductions have been suggested for aquatic ecosystems in the Sierra Nevada. Jennings et al. (1992) demonstrated that the garter snake, Thamnophis elegans, depends heavily on frog tadpoles 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 likely to be one of the causal factors leading to the decline of at least one Sierran amphibian (Bradford 1989; Bradford et al. 1993), trout may also indirectly cause the decline of T. elegans. The loss of tadpoles from aquatic communities may also have impacts on lower trophic levels, since tadpoles can significantly reduce algal biomass (Dickman 1968) and alter lake nutrient cycling (Seale 1980).

Changes in the zooplankton community in lakes as a result of fish predation may also have community-wide consequences. In subalpine Castle Lake (northern Sierra Nevada), a decrease in the density of rainbow trout following the cessation of trout stocking caused an increase in introduced zooplanktivorous fishes, a decrease in zooplankton, a decrease in water transparency, and an increase in primary productivity (Brett et al. 1994; Elser et al. 1995). In a study of alpine lakes in Canada, the loss of all non-native trout following the termination of trout stocking resulted in an increase in grazing zooplankton and a decrease in phytoplankton abundance (Leavitt et al. 1994). Similar results were found by Stenson et al. (1978) and Carpenter et al. (1985). Similar trophic cascades have also been documented in streams (Power 1990; Flecker and Townsend 1994).

INTERPRETATIONS AND MANAGEMENT IMPLICATIONS

My review shows that although trout were historically absent from large portions of the Sierra Nevada, they are now nearly ubiquitous throughout the range as a result of introductions. National parks have proportionally more fishless waters, due in part to the termination of trout stocking in the national parks and the continued stocking of trout in national forests. This change in national park stocking policies has allowed numerous lakes to revert to their original fishless condition. Introduced trout are having considerable deleterious effects on native fishes (including trout), amphibians, zooplankton, lake macroinvertebrates, and probably stream macroinvertebrates. Introduced trout are also likely causing community-wide effects as a result of direct impacts cascading to other trophic levels. These effects may reduce the chances of lakes reverting to their former community composition even after trout disappear or are removed.

The majority of natural lakes in the Sierra Nevada lie within designated national forest and national park wilderness areas. These areas are supposed to be managed to preserve their original condition (Kloepfer et al. 1994), in part to serve as refugia for species unable to tolerate the more anthropogenically-altered habitats, and to provide control areas against which the effects of anthropogenic influences can be measured. My report suggests that lakes and probably other aquatic habitats in the Sierra Nevada, including those in wilderness areas, may be so extensively modified by the introduction of non-native trout that they are unable to serve as refugia or as control areas. One species may already have disappeared (the phantom midge) and several others endemic to the Sierra Nevada have suffered dramatic population declines (e.g., golden trout, mountain yellow-legged frog). Continued decline of these species will likely result in listing under the Endangered Species Act, a step that could have far-reaching consequences for the management of aquatic ecosystems throughout the Sierra Nevada. The simplest and perhaps most effective way to reduce impacts of introduced trout is to modify current trout stocking programs to cause the die-out of some introduced trout populations. Such modification is perhaps most critical in wilderness areas to recreate their natural conditions. Below, I present three trout stocking alternatives for Sierra Nevada wilderness areas that differ in their consequences for the distribution of non-native trout and native aquatic species.

Alternative 1

Strategy: Continue the current policies of intensive trout stocking into national forest waters, and no stocking of trout into national park waters.

Consequences: The distribution of trout in the Sierra Nevada would remain much as it is today. In national parks, populations of some native aquatic species would expand as they recolonize habitats that have recently reverted to their naturally fishless condition. Populations of other less mobile species or species whose movement is restricted by the continued presence of trout in streams (e.g., the mountain yellow-legged frog) would persist in highly fragmented configurations, although fragmentation would decrease slowly as additional habitats were recolonized. These consequences to national park waters are common to all alternatives. On national forests, populations of most native aquatic

species would exist in highly fragmented configurations. Particularly sensitive taxa (e.g., mountain yellow-legged frogs) would continue to decline. On a Sierra-wide scale, national parks would become increasingly isolated refugia within a landscape of unsuitable national forest habitat. The increased isolation of populations of native aquatic species within national parks would likely result in the eventual extirpation of some species from the Sierra Nevada.

As a result of increasing evidence that introduced trout are having considerable impacts on native aquatic species, continued intensive fish stocking on national forests may meet with considerable resistance from members of the public. In addition, if native aquatic species decline to the point where they are listed under the Endangered Species Act, trout stocking would likely come under increased scrutiny from the U.S. Fish and Wildlife Service.

Alternative 2

Strategy: In national forest wilderness areas, continue trout stocking only in waters along heavily-traveled areas such as trail corridors. Within these areas, stock only waters that contain non self-sustaining trout populations. Continue the current policy of no trout stocking in national park waters.

Consequences: The distribution of trout would change in national forest drainages as some lakes in low-visitation areas reverted to a fishless condition. Populations of some native aquatic species would expand as they recolonized these recently fishless habitats. Populations of other less mobile species or species whose movement was restricted by the continued presence of trout in streams would persist in fragmented configurations. However, because fishless lakes would be recreated in all drainages, fragmentation of habitats for native aquatic species would be reduced compared with that resulting from Alternative 1. Across the Sierra Nevada, the trend toward increasing habitat fragmentation and population isolation would likely be halted, and may be reversed, as habitats in all drainages were slowly recolonized by native aquatic species. Populations of native aquatic species in national parks would be connected to populations on national forests by numerous drainages containing viable populations.

Resistance from angling groups and local communities to a termination of stocking in lakes within lightly-visited areas would be substantial given the public perception that fishing opportunities would disappear without stocking. Resistance would be less than under a "no stocking" alternative. Phasing out stocking over a several year period would further reduce resistance.

Alternative 3

Strategy: Terminate all trout stocking in national forest wilderness and continue the policy of no trout stocking in national park waters.

Consequences: The distribution of trout on national forests would change as 10-20% of the lakes reverted to their formerly fishless condition. After trout populations stabilized, populations of some native aquatic species would expand as they recolonized habitats that had recently reverted to their naturally fishless condition. Populations of other less mobile species or species whose movement is restricted by the continued presence of trout in

streams would persist in highly fragmented configurations, although fragmentation would decrease slowly as additional habitats were recolonized. In addition, because fishless lakes would be recreated in all drainages, fragmentation of habitats for native aquatic species would be reduced compared with that resulting from implementation of Alternative 2. Across the Sierra Nevada, the trend toward increasing habitat fragmentation would be reversed as habitats in all drainages were slowly recolonized by native aquatic species. Populations of native aquatic species in national parks would be connected by numerous drainages to populations on national forests.

Resistance from angling groups and local communities to halting trout stocking in all national forest wilderness areas would be considerable, and could lead to a backlash against protection of native aquatic species. As an example of the probable reaction to the complete cessation of trout stocking, when the Forest Service recently decided to terminate all trout stocking in the Desolation Wilderness and Mokelumne Wilderness, an outpouring of public reaction against the proposal forced the Forest Service to adopt a policy of evaluating stocking practices on a lake by lake basis. Resistance could be reduced by phasing out stocking over a several year period.

RECOMMENDATIONS FOR IMMEDIATE CHANGES IN STOCKING PROGRAMS

Although changes in fish stocking programs appear to be needed in order to maintain and restore populations of several native aquatic species, these changes will likely take years or decades to implement. Several immediate changes could reduce the impacts of trout stocking while changes to current policies are being decided upon and implemented.

(1) Trout stocking should occur only in lakes that have been surveyed for sensitive native aquatic species and for non-native trout. This would eliminate the stocking of lakes that contain sensitive species (e.g., mountain yellow-legged frogs) or that contain self-sustaining non-native trout populations.

(2) The aircraft used by the DFG to stock backcountry lakes should be outfitted with navigational systems to allow target lakes to be unmistakably identified before the trout are dropped. As of 1994, stocking planes did not have any navigational equipment, and target lakes were identified only by aerial photographs. Although the error rate associated with the current methodology is unknown, several incidences have occurred in recent years in which trout of the wrong species were stocked into a lake, and in one case, a fishless lake was stocked. The navigational system should also be configured to record the locations of all lakes into which trout were dropped. This would allow the determination of error rates associated with trout stocking, and would aid in determining what the sources of error are.

(3) The California Department of Fish and Game should be required to prepare environmental documentation under the California Environmental Quality Act (CEQA) to disclose the impacts of stocking trout into waters within wilderness areas. Currently, all fish stocking is classified as a "categorical exemption" under the California Code of Regulations (Title 14, Section 15301.j) because it is believed not to have a significant effect on the environment. Given the numerous published accounts of negative impacts of introduced trout on native aquatic biota in the Sierra Nevada, this exemption does not appear justified, particularly in wilderness areas.

RECOMMENDATIONS FOR FUTURE RESEARCH

A substantial research effort will be necessary in order to determine the full impacts of trout on aquatic ecosystems in the Sierra Nevada, and to better understand how these impacts can be reduced or eliminated. Several of the most critical research needs are discussed below.

(1) In order to determine the extent to which creation of additional fishless habitats will benefit native aquatic species, a better understanding of the rates at which extirpated species recolonize lakes is critical.

(2) Of the aquatic species native to the Sierra Nevada, the mountain yellow-legged frog appears to be the most strongly affected by the presence of non-native trout. It is therefore critical to conduct a metapopulation analysis for this species to determine the extinction probabilities for this species under different trout stocking management strategies. Critical information for such an analysis is still unavailable, including survivorship of all life stages, degree of natural population fluctuations, and dispersal capabilities of all life stages.

(3) Because mountain yellow-legged frogs utilize streams as movement corridors between lakes, and apparently do not utilize streams that contain fish (Bradford et al. 1993), it may be necessary to reintroduce this species to formerly occupied habitat after the habitat reverts to its naturally fishless condition. Although two reintroductions have recently been conducted in the Sierra Nevada, additional reintroductions are needed to evaluate the feasibility of this approach.

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FIGURES

Report Study Areas

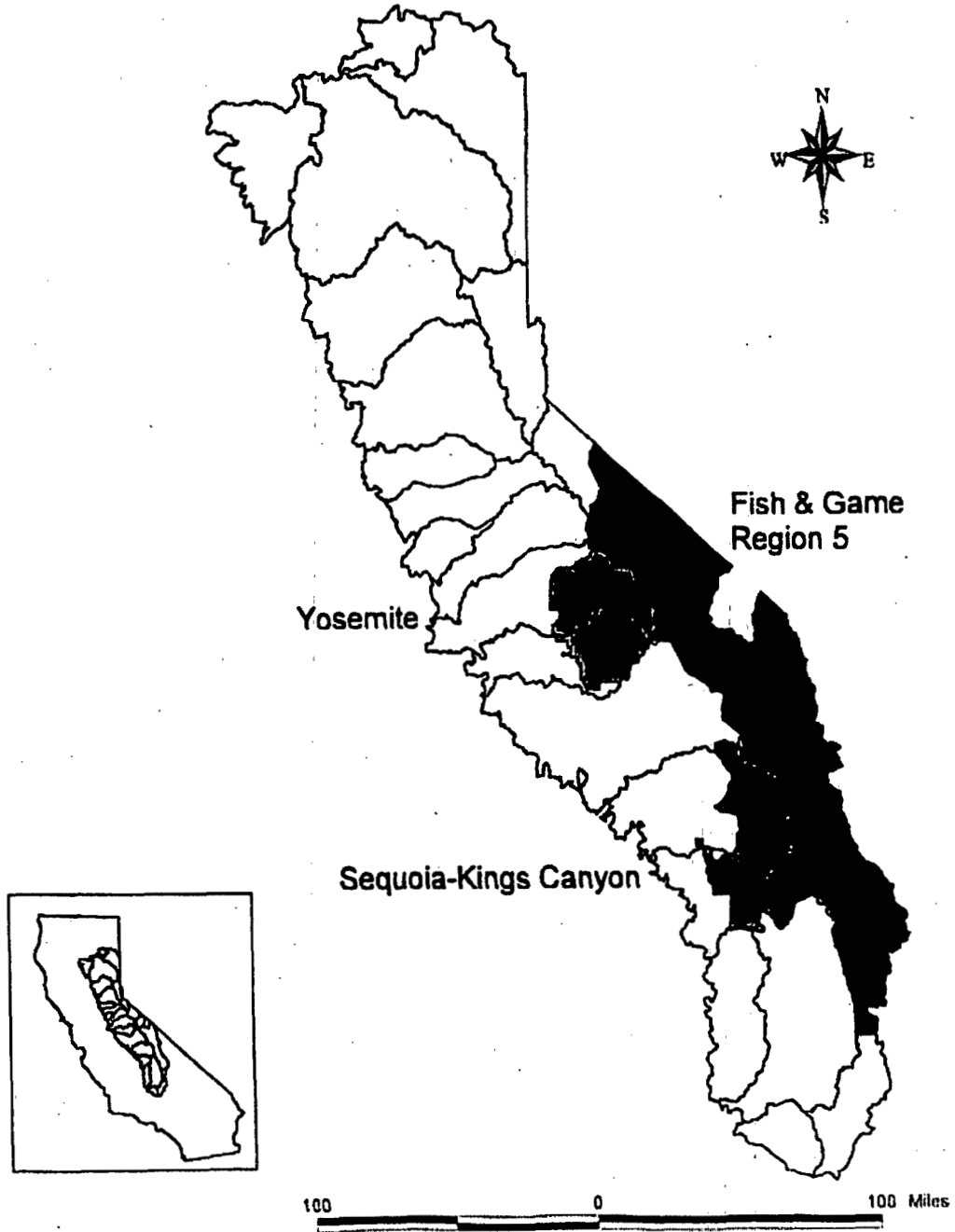
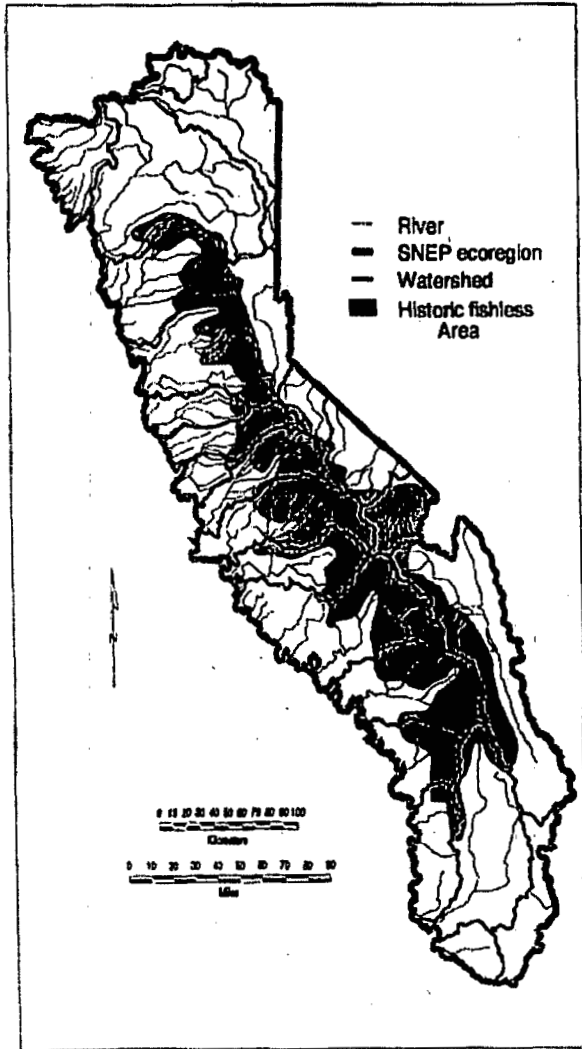


Figure 1. A map of the SNEP study area boundary, showing the portions of the Sierra Nevada covered in detail in this report.

Figure 2. A map showing the historical fishless area in the Sierra Nevada. The map was drawn by Paul Randall (UC Davis); the boundaries of the fishless area are based on the available literature on historical distributions of native fishes and on discussions with Eric Gerstung, California Department of Fish and Game.



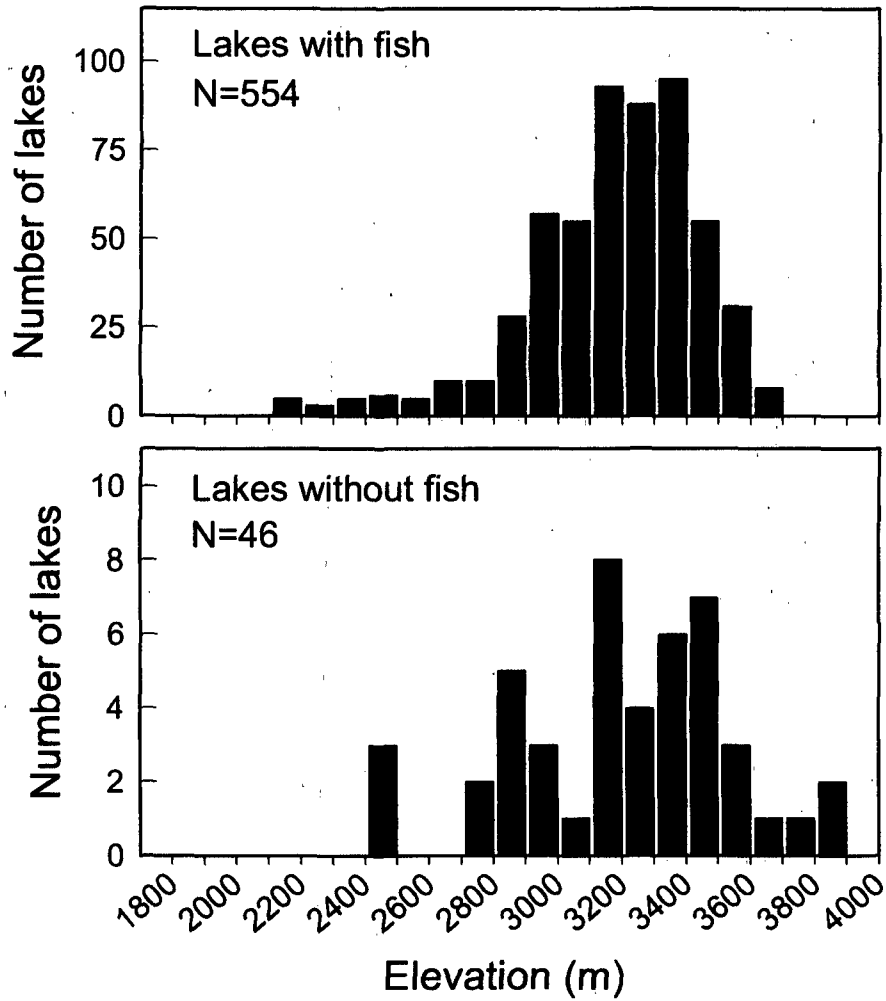


Figure 3. Frequency histograms showing the elevational distribution of lakes with and without fish within the jurisdiction of Region 5 of the California Department of Fish and Game. Lakes with fish are not different in their elevations than lakes without fish.

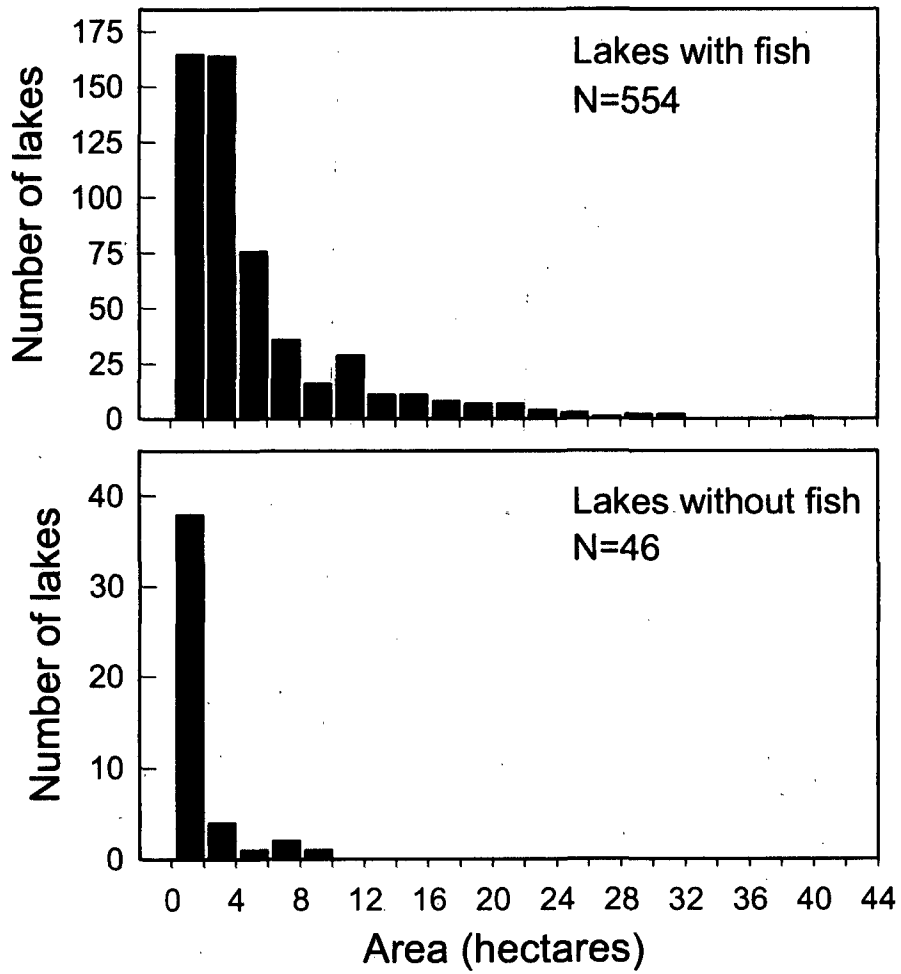


Figure 4. Frequency histograms showing the size distribution of lakes with and without fish within the jurisdiction of Region 5 of the California Department of Fish and Game. Lakes with fish are significantly larger than lakes without fish.

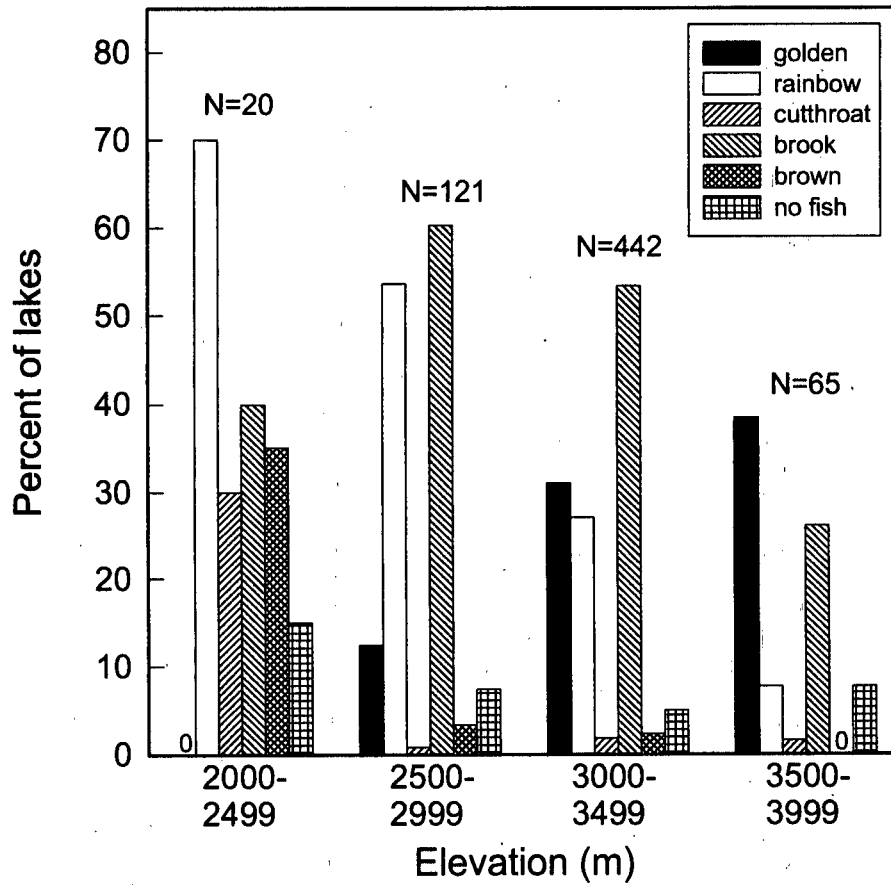


Figure 5. The relative frequency of five introduced trout species and fishless lakes at different elevations. The lakes are within the jurisdiction of Region 5 of the California Department of Fish and Game.

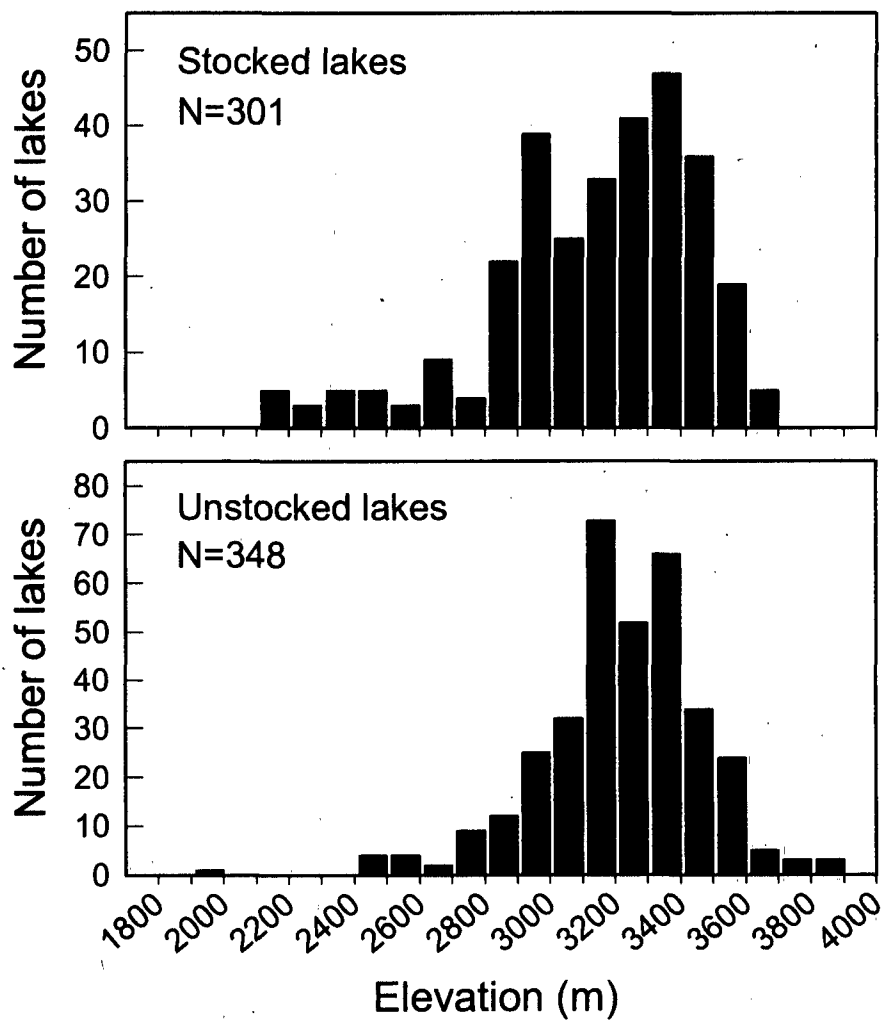


Figure 6. Frequency histogram showing the elevational distribution of stocked and unstocked lakes within the jurisdiction of Region 5 of the California Department of Fish and Game. Stocked lakes occur at significantly lower elevations than unstocked lakes.

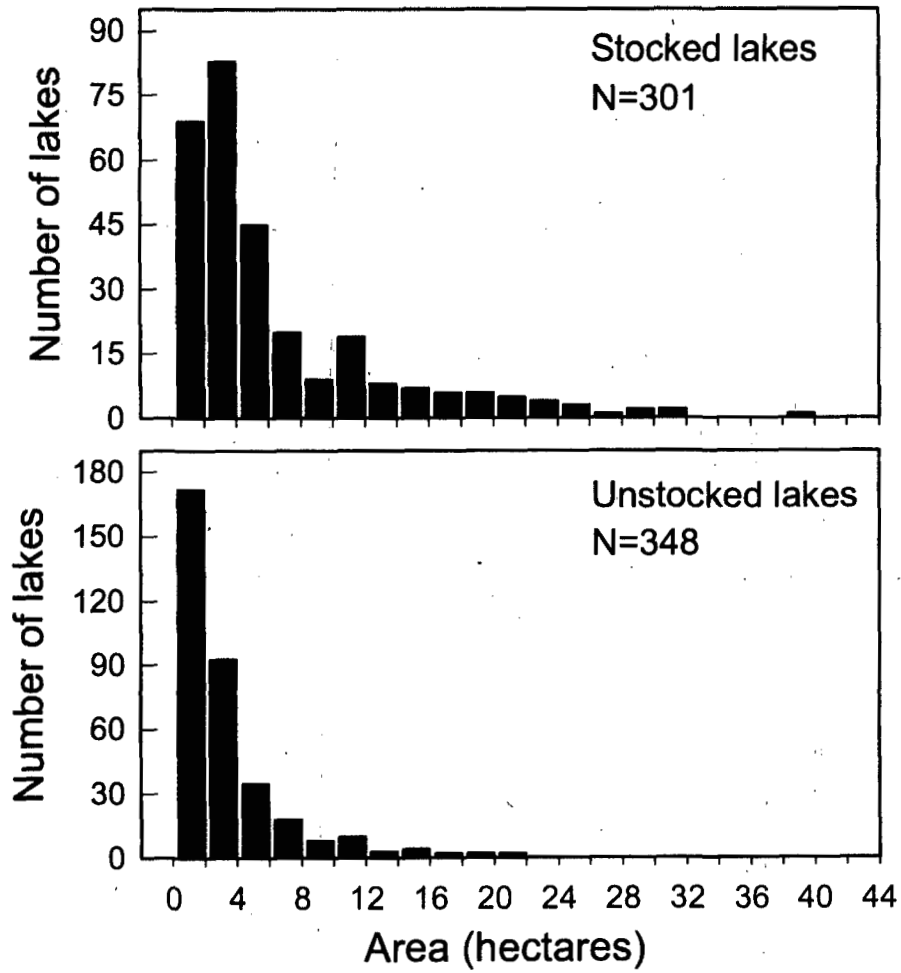


Figure 7. Frequency histograms showing the size distribution of stocked and unstocked lakes within the jurisdiction of Region 5 of the California Department of Fish and Game. Stocked lakes are significantly larger than unstocked lakes.

Upper Piute Cr. / French Cr. Watersheds Historic Fish Distribution

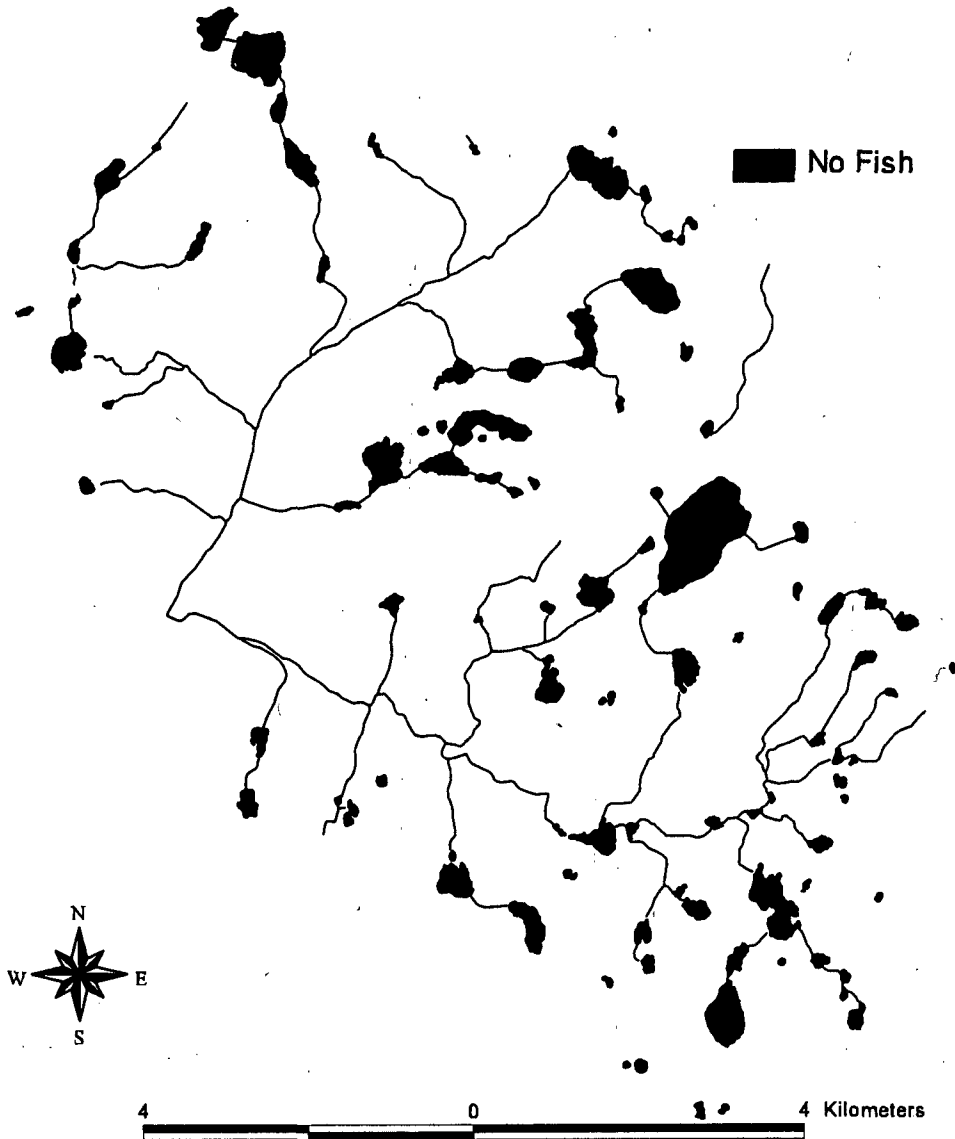


Figure 8. A map showing the historic fish distribution in the upper Piute Creek and French Creek watersheds, Sierra National Forest. The distribution is based on historical evidence (see text).

Upper Piute Cr. / French Cr. Watersheds Current Fish Distribution

S.F. SJR Basin

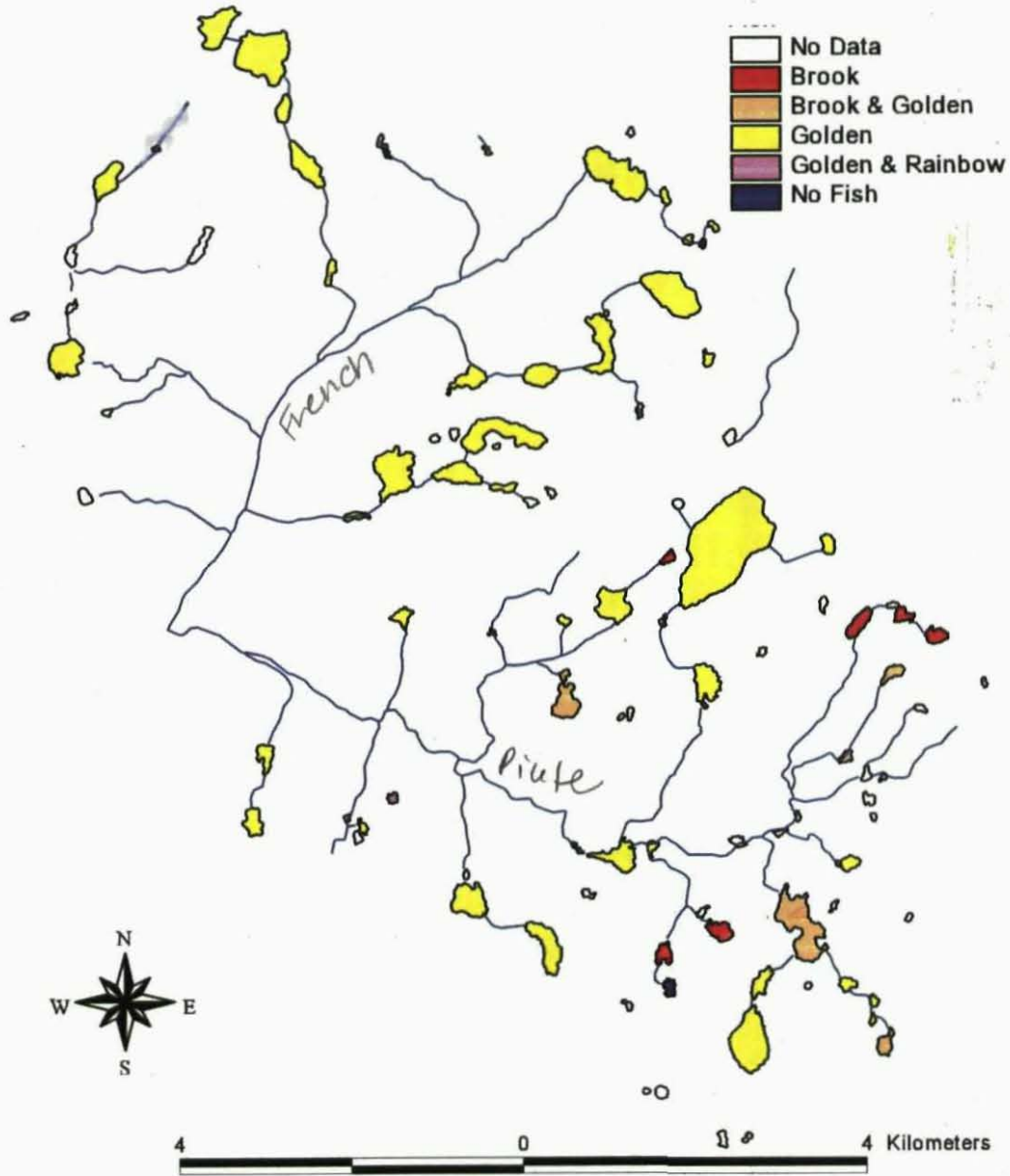


Figure 9. A map showing the current fish distribution in the upper Piute Creek and French Creek watersheds, Sierra National Forest. The distribution is based on records provided by Region 5 of the California Department of Fish and Game.

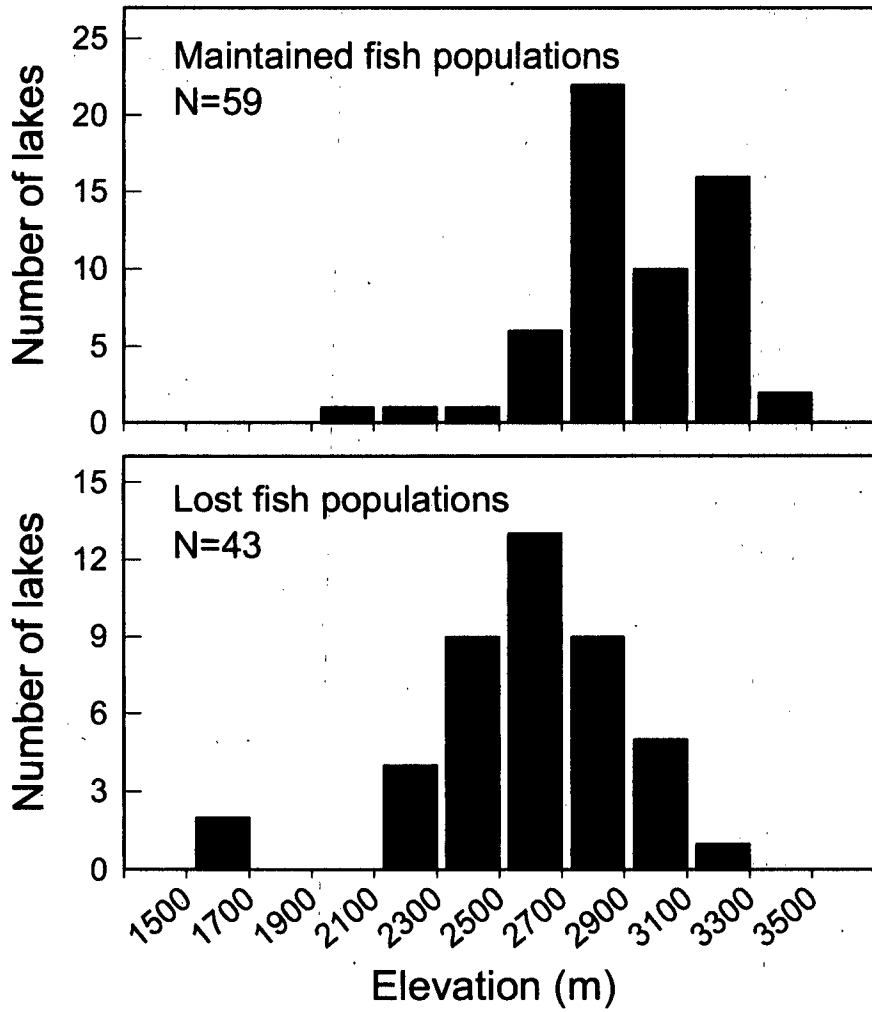


Figure 10. Frequency histograms showing the elevational distribution of lakes that maintained and lost fish populations in Yosemite National Park. Lake that maintained fish populations are found at higher elevations than lakes without fish. Data are from Botti (1977).

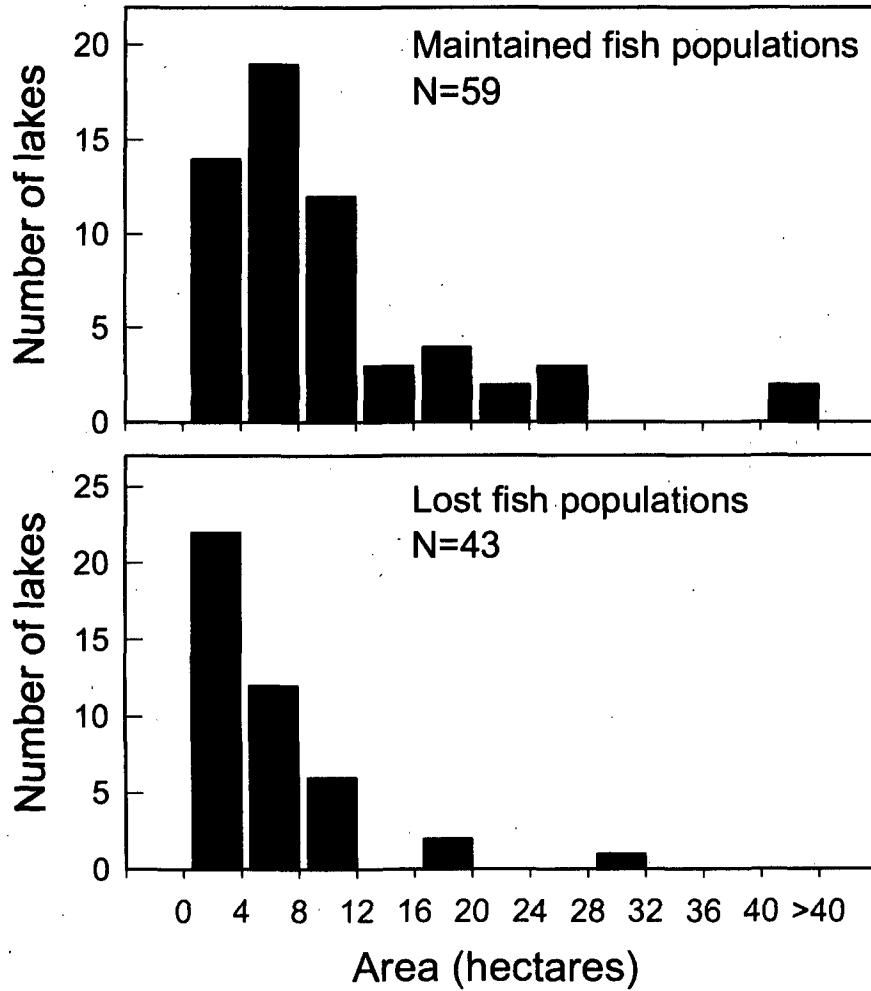


Figure 11. Frequency histograms showing the size distribution of lakes that maintained and lost fish populations in Yosemite National Park. Lakes that maintained fish populations are significantly larger than lakes without fish. Data are from Botti (1977).

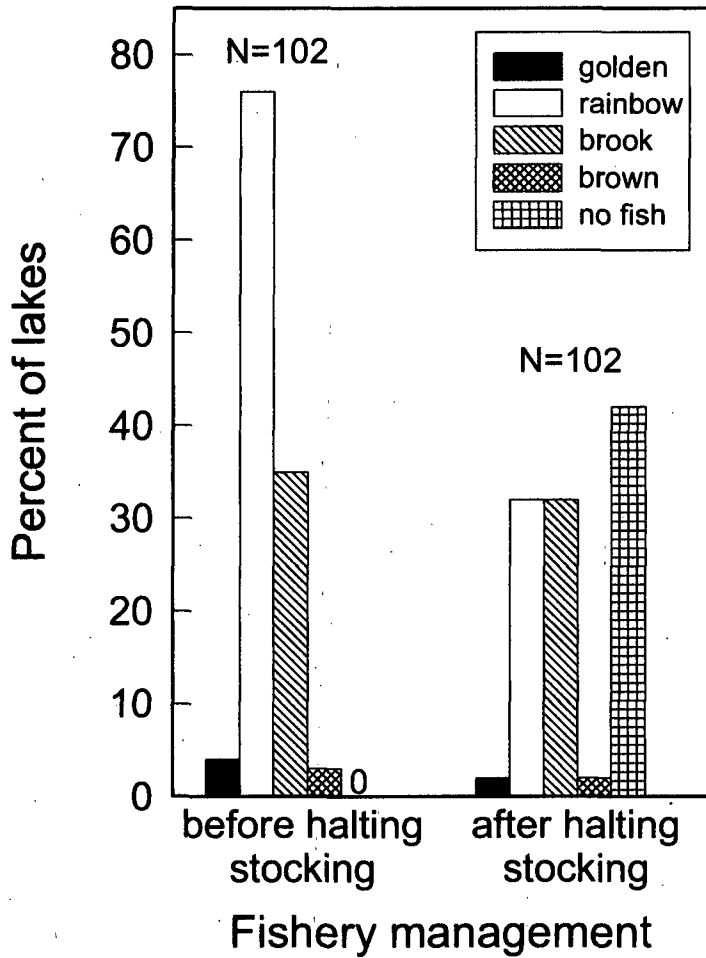


Figure 12. The relative frequency of four introduced trout species and fishless lakes in Yosemite National Park before and after trout stocking was halted. Data are from Botti (1977).

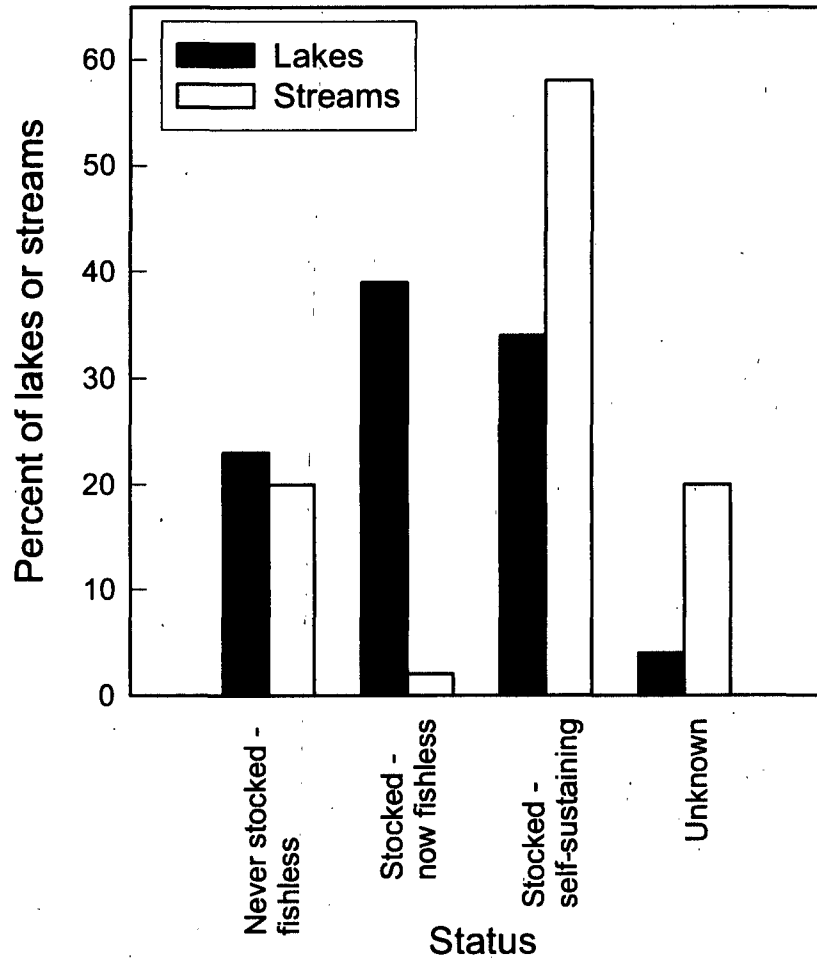


Figure 13. Frequency histograms showing the status of Yosemite National Park lakes and streams with respect to stocking history and the presence or absence of trout. Data are from Elliot and Loughlin (1992) and Wallis (1952).