Chapter 6.4—Lakes: Recent Research and Restoration Strategies

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Summary

The Sierra Nevada and southern Cascade Range support thousands of montane lakes, from small, remote tarns to iconic destinations such as Lake Tahoe. Their beauty and recreational opportunities instill high social value, in particular by serving as destinations for hiking, camping, swimming, and fishing. Lakes also have high ecological value because they support a diverse aquatic fauna, including rare species such as the mountain yellow-legged frog (*Rana muscosa*/*R. sierrae*), and they provide food for terrestrial and aquatic predators. A number of stressors interact to affect lake ecosystems in the synthesis area. Climate change is expected to affect lakes by altering physical processes and reducing water levels. In shallow lakes and ponds, reduced hydroperiods could directly reduce the amount of available habitat for lentic amphibians and increase the instances of stranding mortality of eggs and tadpoles. Introductions of fish into lakes have altered food webs and particularly affected native amphibians. Chytridiomycosis, an amphibian-specific fungal disease caused by *Batrachochytrium dendrobatidis* (*Bd*), has caused significant declines and extirpations in populations of amphibians native to the Sierra Nevada and southern Cascade Range. Research is ongoing to determine ways to reduce impacts of *Bd* on native amphibian populations. Air pollution has potential to negatively affect lake-dwelling amphibians, especially owing to interactions with other stressors; however, recent studies from the synthesis area did not find associations between frog population status and measured pesticide concentrations. A metric using the ratio of the number of taxa observed at a site to that expected can be an effective tool for assessing resistance and resilience of expected native taxa to threats. Successful restorations will likely depend on the control of introduced fish, the presence and virulence of *Bd*, and habitat conditions that help frogs to withstand these and other stressors.

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Socioecological Significance of Lakes

The Sierra Nevada and southern Cascade Range contain thousands of natural lakes that provide both ecological and recreational values. In high-elevation environments characterized by low productivity, lakes provide food and energy to terrestrial consumers, such as birds (Epanchin et al. 2010) and snakes (Matthews et al. 2002, Pope et al. 2008). In addition, native endemic species, such as the Sierra Nevada yellow-legged frog (*Rana sierrae*) (fig. 1) and Yosemite toad (*Anaxyrus* [=*Bufo*] *canorus*), are found in California's mountain lakes. These species, in addition to the Sierra Nevada population of mountain yellow-legged frog (*R. muscosa*), were recently added to the federal list of threatened and endangered species.

Because of their great beauty, lakes also serve as important destinations for recreational activities, including hiking, camping, swimming, and fishing. Historically, nearly all lakes in the high Sierra Nevada (above 1800 m) were fishless, but the introduction of nonnative trout has been a common practice since the early 1900s (Knapp 1996). Currently, the majority of large, deep lakes support introduced populations of fish, including brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) (CDFG 2011, Knapp and Matthews 2000). This fishery supports a multimillion dollar recreational industry by bringing anglers to the region.

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Figure 1—Recent metamorph and adult forms of the Sierra Nevada yellow-legged frog.

Conservation Issues and Restoration Options

Climate Change

Lakes serve as sentinels of climate change because they provide easily detectable signals that may reflect the influence of the change on the broader catchment area (Williamson et al. 2009). Changes in lake temperatures and water levels are easy to measure. Available records can span extended periods; for example, Schneider et al. (2009) found that six large lakes in California (including Lake Tahoe) have been warming an average of 0.11 ± 0.02 °C per year since 1992. These rates of change are about twice as high as regional trends in air temperature (Schneider et al. 2009). As a consequence of climate change, increased surface water warming rates will likely affect lake ecosystems of the Sierra Nevada by potentially decreasing lake levels, but also by altering critical physical processes, such as stratification and deep mixing (Sahoo et al. 2012). In addition, predicted treeline advancement (Harsch et al. 2009) and increases in terrestrial vegetation surrounding alpine lakes (Luckman and Kavanagh 2000) may result in increased inputs of terrestrially derived dissolved organic matter into montane lakes (Sommaruga et al. 1999). These coupled changes in climate variability and physical and chemical processes have been found to dramatically alter the distribution and abundance of important lake zooplankton such as the grazer, *Daphnia* (Fischer et al. 2011). In addition, lake warming and increased nutrient inputs were found to enhance the exchange of energy and organisms between lakes and neighboring terrestrial ecosystems by increasing emergence of aquatic insects and increasing decomposition rates (Greig et al. 2012).

Climate change may interact with other stressors to alter lake community dynamics. Warmer air temperatures are predicted to result in less annual snowpack in the Sierra Nevada (Cayan et al. 2008, Young et al. 2009), which in turn will affect the hydroperiod of small lakes and ponds. Sierra Nevada yellow-legged frogs and mountain yellow-legged frogs (hereafter referred to as mountain yellow-legged frogs) have a 2- to 3-year larval stage and may experience an interactive effect of lower water levels and introduced fishes, with fish preventing breeding in the majority of deep lakes (Vredenburg 2004) and climate change increasing the likelihood of drying of shallow lakes and ponds that do not support fish (Lacan et al. 2008). Based on this expected interaction, mitigations for climate change effects on native lentic species include removing fish from some larger lakes to provide additional fish-free, permanent, cool water refuge habitat (see discussion below).

Threatened amphibians face threats from introduced fishes in deep lakes and drying out in shallow ponds that do not support fish.

Introduced Species

Invasive species are a major threat to freshwater ecosystems and can cause a range of impacts, including behavioral shifts of native species and restructuring of food webs (e.g., Cucherouset and Olden 2011, Simon and Townsend 2003). Climate change is expected to accelerate the spread of aquatic invasive species (Rahel and Olden 2008). Although many invasive species have not entered the high Sierra Nevada's natural mountain lakes, some, such as the American bullfrog (*Lithobates catesbeiana*) and signal crayfish (*Pacifastacus leniusculus*), do occur in many of the reservoirs and constructed ponds in the range. These impoundments are much more likely to harbor invasive species than are natural lakes (Johnson et al. 2008), and they can allow invasive species to establish self-sustaining populations that can then spread to the adjacent natural waters (e.g., Ding et al. 2008). Additional detrimental invaders, such as the New Zealand mudsnail (*Potamopyrgus antipodarum*) and Quagga mussel (*Dreissena rostiformis bugensis*), are spreading rapidly in California's freshwater habitats (Karatayev et al. 2012, Richards 2002). The Sierra Nevada's natural lakes are relatively discrete ecosystems separated by dry land that is inhospitable to most aquatic species. In addition, limited road access to many lakes, as well as inspection programs, may inhibit unintentional spread of aquatic invasive species via recreational boats (Johnson et al. 2001). As a result, dispersal of invasive species may be expected to be slow, and many suitable mountain lake ecosystems have remained uninvaded for long periods (Johnson et al. 2008).

Nonetheless, aquatic invasive species pose a serious threat to native biodiversity and associated ecological services (Johnson et al. 2008). Once established, invasive species such as crayfish, sunfish, bass, and aquatic weeds have been shown to affect native biodiversity, reduce water quality, and create food and other habitat conditions that benefit other nonnative species (Caires et al. 2013, McCarthy et al. 2006, Nilsson et al. 2012). Losses of ecosystem services associated with introductions of species such as crayfish appear to have outweighed gains in some areas. Aquatic invertebrates are major components not only of aquatic communities but also adjacent terrestrial habitats. Larval insects and zooplankton serve as prey for larger aquatic insects and amphibians, and the winged adult stages of insects feed terrestrial predators, such as birds, bats, and spiders (Nakano and Murakami 2001, Sanzone et al. 2003). In high-elevation lakes, introduced trout can produce strong top-down effects on aquatic invertebrates (Knapp et al. 2005, Pope et al. 2009, Vadeboncoeur et al. 2003). This is important because changes in invertebrate abundance and composition can have cascading consequences for nutrient cycling (Schindler et al. 2001) and terrestrial communities (Epanchin et al. 2010, Finlay and Vredenburg 2007, Knight et al. 2005). For example, Knight et al. (2005) found that fish reduce dragonfly emergence, with subsequent consequences on native pollinators and terrestrial plant reproduction. In the Sierra Nevada, Epanchin et al. (2010) linked introduced fish to dramatic decreases in mayfly emergence, with indirect consequences for feeding gray-crowned rosy-finches (*Leucosticte tephrocotis dawsoni*). These studies show that the effects of introduced trout permeate beyond the lake boundary and have ramifications for neighboring terrestrial ecosystems. These complex interactions are an important topic for further investigation to better understand potential implications of managing nonnative species.

Preventing establishment of aquatic invaders is recognized as a core management strategy because eradication and control are costly and difficult following establishment (Simberloff et al. 2005). When the basic biology of an invasive species is known, recent studies have been successful in identifying vulnerable sites so that prevention efforts can be targeted to where they are likely to produce the greatest ecological benefit (Olden et al. 2011, Vander Zanden and Olden 2008). Development and implementation of comprehensive invasive species plans for lake habitats of the synthesis area could help prevent or slow the secondary spread of California's freshwater invaders into the Sierra Nevada's backcountry lakes (e.g., Vander Zanden and Olden 2008).

Some species are stocked and actively maintained because they have social and economic value, especially for recreational fishing, and are therefore not considered nuisances. However, some of these species, such as nonnative trout, may exert negative effects on native species that historically inhabited these ecosystems. For example, deep, permanent waters are critical as overwintering and breeding habitat for mountain yellow-legged frogs (Bradford 1989, Knapp and Matthews 2000). Introduced trout are significant predators of these frogs (Grinnell and Storer 1924, Vredenburg 2004), and many studies have found that breeding populations of mountain yellow-legged frogs rarely co-occur with nonnative trout (Knapp 2005, Knapp and Matthews 2000).

California is one of several states that initiated reviews of hatchery and stocking programs in response to concerns over effects on wild populations of species listed under the Endangered Species Act (Kostow 2009). Recent policy changes by the California Department of Fish and Wildlife (CDFW, the agency responsible for fish stocking) have reduced fish stocking in water bodies where sensitive native fish and amphibians may occur. Introduced fish are likely to remain ubiquitous in Sierra Nevada lakes even where they are no longer stocked. For example, Armstrong and Knapp (2004) found that lakes in the John Muir Wilderness with >2.1 m of spawning gravels that were <3520 m in elevation nearly always showed signs of supporting self-sustaining populations of rainbow and golden trout.

Nevertheless, the stocking of fish in aquatic water bodies represents a management action over which participating agencies have the ability to exert both direct and indirect controls. Because stocking has occurred throughout the Sierra Nevada and southern Cascade Range, actions taken on this issue have the potential to be far reaching. Further, the rapid recovery of native frog populations and other native species following fish removal in lentic systems (Knapp et al. 2001, Knapp et al. 2007, Pope 2008, Vredenburg 2004) indicates that fish removals have the potential to be effective restoration tools. Both CDFW and the National Park Service have integrated strategic fish removal projects into their resource management plans, and the Forest Service is implementing fish removal projects in the Sierra Nevada (e.g., Desolation Wilderness, El Dorado National Forest). These projects focus on headwater lake basins with high ecological value and they make up a small fraction of fish-containing lakes in the Sierra Nevada. Projects to remove fish from Sierra Nevada lakes have primarily used non-chemical methods, such as setting gill nets and electrofishing in inlets and outlets, to reduce impacts to nontarget organisms.

Determining lake basins to focus on native amphibian restoration involves science and management working together to maximize the positive outcomes of restoration actions while maintaining recreational fisheries.

Research to understand the mechanisms of recovery following fish removals can help managers determine characteristics of lakes and amphibian populations best suited for recovery. For example, Pope (2008) found that the high reproductive output of Cascades frogs (*Rana cascadae*) may allow rapid population growth, even with only a small number of breeding-aged frogs onsite. Knapp et al. (2007) found that following rapid population increases, mountain yellow-legged frogs disperse to neighboring suitable habitat if it is available. Determining lake basins to focus on native amphibian restoration involves science and management working together to maximize the positive outcomes of restoration actions while maintaining recreational fisheries. Important basin characteristics include the presence of target amphibians and additional nearby suitable habitat, the ability to successfully eliminate introduced fish, and the level of use by anglers. Because it is extremely difficult to remove fish from streams without the use of toxicants (e.g., rotenone), lakes with natural fish barriers near their inlets and outlets are better targets than lakes without natural fish barriers (e.g., Knapp et al. 2007, Pope 2008).

Amphibian Disease

Although amphibians are susceptible to a wide array of diseases, one disease has emerged as the greatest conservation concern for amphibians in the Sierra Nevada (and the world). Chytridiomycosis, an amphibian-specific fungal disease caused by *Batrachochytrium dendrobatidis* (*Bd*), has been implicated in declines and extinctions of amphibian populations worldwide (e.g., Bosch et al. 2001, Lips et al. 2004, Muths et al. 2003), and has contributed to widespread declines of mountain yellow-legged frogs throughout the Sierra Nevada (Briggs et al. 2010, Rachowicz et al. 2006, Vredenburg et al. 2010). Mass die-offs of frogs and population extirpations have been observed soon after the arrival of *Bd* in mountain yellow-legged frog populations (Vredenburg et al. 2010). Although many populations have been driven to extinction by *Bd*, some populations have survived the population crash and persist with the disease (Briggs et al. 2010, Knapp et al. 2011). Research is ongoing to determine factors that allow some populations to persist while others are extirpated (Knapp et al. 2011). One important finding is that large populations have a higher likelihood of persisting with the disease (Knapp et al. 2011). This finding suggests that although *Bd* can be devastating to populations even where fish have been removed, these "recovered" frog populations have a better chance of persisting in the long term than those facing the additional stressor of introduced fish.

Options to help ameliorate the impacts of *Bd* include developing protected populations and prophylactic or remedial disease treatment (Woodhams et al. 2011). Because sustainable conservation in the wild is dependent on long-term population persistence, successful disease mitigation would include managing already infected populations by decreasing pathogenicity and host susceptibility so that co-evolution with those potentially lethal pathogens can occur (Woodhams et al. 2011). Currently, researchers are working to identify mechanisms of disease suppression and develop adaptive management strategies to be tested in field trials with natural populations. Antimicrobial skin peptides and microbes that inhibit infection by *Bd* have been identified from the skin of mountain yellow-legged frogs and may be useful tools for increasing the frog's resistance to *Bd* (Harris et al. 2009, Woodhams et al. 2007).

Pollution

Exposure to pesticides transported to the Sierra Nevada by prevailing winds from California's Central Valley has been hypothesized as a cause of population declines of native amphibians, primarily along the west slope of the Sierra Nevada (Davidson 2004, Fellers et al. 2004). Pesticide residues from Central Valley agricultural areas have been found in samples of air, snow, surface water, lake sediments, amphibians, and fish across the Sierra Nevada (Cory et. al 1970, Fellers et al. 2004, Hageman et al. 2006, McConnell et al. 1998), and windborne contaminants have been linked to patterns of decline of mountain yellow-legged frogs (Davidson and Knapp 2007). However, a recent study that compared concentrations of historically and currently used pesticides with the population status of mountain yellow-legged frogs in the southern Sierra Nevada found no association between frog population status and measured pesticide concentrations (Bradford et al. 2011). In addition, in both the Sierra Nevada and southern Cascade Range, pesticide concentrations in water and amphibian tissue were consistently below concentrations found to be toxic to amphibians (Bradford et al. 2011, Davidson et al. 2012). Low concentrations of pesticides could, however, interact with other stressors and contribute to adverse effects on frogs. For example, the pesticide carbaryl was found to reduce production of amphibian skin peptides that inhibit the growth of *Bd,* the fungus that causes chytridiomycosis (Davidson et al. 2007). For practical reasons, most field studies continue to focus on single stressors; however, the few studies assessing interactive effects of low-level contaminants with other stressors highlight the need for additional multifactor studies.

Terrestrial Influences on Lakes

Mountain lakes receive organic material from two different sources: primary production that occurs within the system's boundaries (autochthonous sources) and primary production imported from the terrestrial watershed (allochthonous sources). It is important to understand the relative significance of those sources for particular lakes and how those relationships may change over time given disturbances and stressors. Determining the source and magnitude of inputs will help to predict the trajectories of variables important to management objectives (McIntire et al. 2007). New research using multiple techniques including stable isotopes has shown that terrestrial organic material provides major support for both benthic and pelagic organisms in small lakes (Bade et al. 2007, Cole et al. 2011). General disturbance ecology suggests that periodic human-induced watershed and riparian disturbances that emulate natural disturbance regimes may initiate renewal processes that are required for long-term sustainability of aquatic ecosystems (Kreutzweiser et al. 2012). Consequently, disturbance-based forest management approaches such as those described in PSW-GTR-220 (North et al. 2009) may result in long-term positive feedbacks in forested lake systems in the Sierra Nevada.

However, Spencer et al. (2003) cautioned that expanded fire activity and other treatments associated with fuel reductions could deliver nutrients to lakes and other surface waters that may already be threatened by eutrophication. Their study focused on the northern Rocky Mountains, where the reference fire regime ranged from decades to several hundred years. They suggested that there was potential to shift regimes from infrequent pulses of nutrients to an annual loading from the combination of wildfires, prescribed burns, pile burning, and agricultural burning. Another stressor to consider is the nutrient loading through long-distance aerial transport (see chapter 8.1, "Air Quality." They noted the need to evaluate impacts of large wildfires on aquatic ecosystems. Accordingly, an important avenue for scientific research is to better understand linkages between terrestrial and aquatic ecosystems, including lakes, especially in the context of large wildfires and various stressors (see chapter 1.5, "Research Gaps: Adaptive Management to Cross-Cutting Issues").

Metrics for Lake Assessments

With multiple serious threats facing lake ecosystems in the Sierra Nevada (fig. 2), it is valuable to understand the degree to which these systems are altered. A metric using the ratio of the number of taxa observed (O) at a site to that expected (E) to occur at the site in the absence of anthropogenic impacts (abbreviated as O/E) has been applied to lakes with fish in the Sierra Nevada (Knapp et al. 2005). The authors found that amphibians, reptiles, benthic invertebrates, and zooplankton have relatively low resistance to fish introductions, but all taxa recover when lakes revert to a fishless condition. This metric proved effective at assessing resistance and resilience of expected native taxa in Sierra Nevada lakes to one threat (introduced fish), and it may be effective at assessing other threats. Since then, Van Sickle (2008) has suggested an alternative statistical approach that could be more sensitive

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Figure 2—Dusy Basin, Kings Canyon National Park.

to anthropogenic stressors; this approach uses BC, an adaptation of Bray-Curtis distance, instead of O/E to assess compositional dissimilarity between an observed and expected assemblage.

Although comparisons to reference systems are important, assessment of long-term trends in lake dynamics is another important component for understanding the patterns of change associated with both natural and human-caused stressors (e.g., Kowalewski et al. 2013, McIntire et al. 2007). Use of both paleolimnological evidence and long-term monitoring provide insight into mechanisms for observed changes and provide more accurate baselines for potential restoration efforts (Kowelewski et al. 2013). For example, a 16-year study at Crater Lake, Oregon, revealed that changes in lake productivity (and thus water clarity) were likely driven by long-term climatic changes that regulate the supply of allochthonous nutrients into the lake (McIntire et al. 2007).

Recent research has shown that successful restorations will likely depend on the elimination of introduced fish, regardless of whether *Bd* is present and how virulent it is if it is present, and habitat conditions that help frogs to withstand the effects of climate change and disease.

Although metrics based upon species composition may be useful in assessing the overall condition of the aquatic biota, priority will likely be given to restoration of lakes in the Sierra Nevada and southern Cascade Range to support populations of amphibian species, such as the Sierra Nevada and southern mountain yellow-legged frogs and the Cascades frog. Recent research has shown that successful restorations will likely depend on the elimination of introduced fish, regardless of whether *Bd* is present and how virulent it is if it is present, and habitat conditions that help frogs to withstand the effects of climate change and disease.

Box 6.4-1

Recent and Pending Studies on Frogs and Chytrid Disease

Pending research may suggest additional considerations to help frogs withstand the novel threat posed by the fungal disease chytridiomycosis, which is caused by *Batrachochytrium dendrobatidis* (*Bd*). For example, a recent lab study comparing the effects of *Bd* isolated from two localities in northern California found dramatic differences in the virulence of the isolates on Cascades frogs (*Rana cascadae*), with one isolate causing nearly complete mortality in test animals within 6 weeks and the other causing a mortality rate only slightly higher than that of unexposed animals.[3] This result suggests that in addition to environmental conditions and local host population size, the local strain of *Bd* may also play an important role in determining host population dynamics.

[3] Piovia-Scott et al., 2013. Unpublished data. On file with: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Redwood Sciences Lab, 1700 Bayview Drive, Arcata, CA 95521.

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Furthermore, preliminary field testing of supplementing microbes on the skin of mountain yellow-legged frogs have shown promising results in boosting survival with the disease.[4]

A recent study by the Pacific Southwest Research Station and University of California–Davis collaborators found that all the remnant populations of Cascades frogs in the southern Cascades survive with *Bd* and occur in habitats where adult frogs commonly move among different water bodies for breeding, summer feeding, and overwintering. When the frogs are in the breeding sites, they tend to have high prevalence and loads of *Bd*, but when they move to streams and channels, loads of *Bd* are dramatically reduced or eliminated.[5] One hypothesis is that the movement away from breeding sites where the disease may thrive allows the frogs to behaviorally eliminate the disease, and thus, the population is able to persist. If this is true, restoration of lake basins with additional stream and meadow habitats nearby may be most effective where *Bd* is a concern.

[4] Vredenburg, V.T.; Briggs, C.J.; Harris, R. 2011. Host-pathogen dynamics of amphibian chytridiomycosis: the role of the skin microbe in health and disease. In: Olsen, L., ed. Fungal diseases: an emerging threat to human, animal and plant health: workshop summary. Washington, DC: National Academies Press: 342–354.

[5] Pope et al. 2013. Unpublished data in final report to the Lassen National Forest (ISA #12-05-06-02) on the status of the Cascades frog (*Rana cascadae*) in the southern Cascade Mountains of California. On file with: U.S. Department of Agriculture, Forest Service, Lassen National Forest, 2550 Riverside Drive, Susanville, CA 96130.

Management Implications

- Removal of introduced fish is an important strategy to help priority amphibians species withstand combined stressors including climate change and disease.
- Chytridiomycosis continues to be a major conservation concern for frogs in mountain lake ecosystems. Researchers are working to develop treatment options to help infected populations.

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