

Distribution of introduced fishes and their effects on high elevation lake communities in Lassen Volcanic National Park, CA, USA

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Introduction

Stocking of nonnative fishes into historically fishless lakes represents one of the most widespread manipulations of high elevation aquatic ecosystems throughout mountainous regions of western North America (BAHLS 1992, DUNHAM et al. 2004, PISTER 2001). Ecological impacts of nonnative fish introductions have been well documented and include dramatic reductions and extirpations of large, mobile benthic invertebrate and zooplankton species (BRADFORD et al. 1998, CARLISLE & HAWKINS 1998, PARKER et al. 2001; but see WISSINGER et al. 2006 for contrasting results from New Zealand lakes) and amphibian populations (BRADFORD 1989, KNAPP 2005, PILLIOD & PETERSON 2001). These massive alterations of lake communities can lead to large-scale changes in ecological processes (SCHINDLER et al. 2001, WALTERS & VINCENT 1973) and may extend into the terrestrial environment (MATTHEWS et al. 2002).

Cessation of fish stocking in the 1970s and 80s within national parks and wilderness areas has resulted in many smaller lakes returning to a fishless condition, but self-sustaining fish populations continue to persist in most larger lakes (DONALD 1987, PARKER et al. 2001). Lack of systematic surveys in many areas limits knowledge of current fish distributions and ongoing impacts on native biota (BAHLS 1992). In this study we surveyed permanent lakes and ponds within Lassen Volcanic National Park (LVNP) to (1) describe current fish distributions 20–30 yr after stocking ceased, and (2) assess continuing effects of introduced fishes on the distribution and abundance of zooplankton and littoral benthos. Because most, if not all, natural lakes >2 m deep within LVNP were stocked in the past, current fishless lakes would have lost their fish populations after the cessation of stocking. Differences in invertebrate distribution and abundance between fish and fishless lakes should, therefore, reveal changes in response to fish loss and show whether communities within previously stocked lakes are resilient to major shifts in top predator abundance. This study was done in conjunction with a survey of amphibian distribution within LVNP reported elsewhere (J.E. STEAD et al., U.S. Forest Service, unpubl.) and is the first complete survey of lakes within LVNP.

Key words: Invertebrate assemblages, mountain lakes, non-native fishes.

Study site

LVNP is located in NE California in a region where the Cascade, Sierra Nevada, and Great Basin bioregions converge. This 43,065 ha national park was established in 1960 to showcase the volcanic landscape resulting from the 1915 eruption of Mt. Lassen (3187 m elev), the southernmost volcano in the Cascade Range. Within park boundaries are 151 permanent lakes and ponds that range 1760–2492 m in elevation, <0.1–240 ha in surface area, and <0.3–71.3 m in depth. All but perhaps 3 of these lakes were naturally fishless. Fish stocking in LVNP began as early as the late 1800s with the arrival of Euro-American settlers and became more extensive during the early to mid 1900s as the California Department of Fish and Game (CDFG) gained control of stocking programs statewide (e.g., PISTER 2001). Movement of fish among lakes by anglers was common as shown by the current distribution of non-game bait species. Stocking records from the 1960s and 70s show that at least 42 lakes were regularly stocked during this time (CDFG unpublished data). Past reports and current distributions of fish in lakes not reported in stocking records suggest that intentional stocking and anglers moving fish among lakes resulted in a broader distribution than records indicate. It is likely that most, if not all, larger ponds and lakes had fish introduced into them in the past. Rainbow trout (*Oncorhynchus mykiss*) was the species most widely stocked by CDFG (>90 % of lakes), followed by brook char (*Salvelinus fontinalis*; 20 % of lakes) and brown trout (*Salmo trutta*; <10 % of lakes).

Methods

From mid-June to mid-August 2004 we surveyed all permanent ponds and lakes (N = 151) within LVNP, including two small artificial impoundments on fish-bearing streams that are not included in this analysis. A combination of visual

encounter surveys and gillnetting was used to assess fish distribution and abundance. Gill net sets were typically 4 hr (range 4–7 hr), but at 14 pond sites sets were shorter (approximately 2–3.5 hr) because the entire bottom and water column were visible and visual surveys confirmed the absence of fish. Gill nets were made of sinking monofilament (36 m long by 1.8 m tall comprised of six 6 m long panels with mesh sizes ranging from 10–38 mm) and effectively captured fish ranging from small trout and cyprinids (> 60 mm FL) to large trout (up to 460 mm FL). All fish were identified to species, weighed to the nearest 1.0 g using a spring-loaded balance, and measured (TL and FL to the nearest mm).

We collected littoral benthic and nektonic macroinvertebrates using a D-framed dip net (0.5 mm mesh) by making 3–5 “standard sweeps” along the lake bottom, 1–2 m from shore, within three distinct habitats: (1) aquatic vegetation, (2) fine organic or inorganic sediments, and (3) bare, rocky substrates. A standard sweep consisted of 2 one m passes following the contour of the lake bottom. An initial pass in one direction was immediately followed by a return pass over the same area in the opposite direction. Samples were preserved with 80% ethyl alcohol and returned to the laboratory for sorting, identification and enumeration.

We collected zooplankton from the deepest portion of each lake by making 3–5 vertical hauls from 0.5 m above the bottom to the surface with 11 cm diameter 64 µm mesh Wisconsin style plankton net. Samples were preserved with a 4% sugar formalin solution and returned to the laboratory for identification and enumeration. In addition to analyzing samples from all fish-bearing lakes, we selected for zooplankton analysis 11 fishless lakes representing the possible range of physical conditions.

From 15–26 August 2004, we visited all lakes with fish populations and 13 fishless lakes (including all lakes from which zooplankton samples were analyzed) to collect data on water clarity and Chl-*a*. Secchi depth was measured to the nearest 0.1 m from a small boat or float tube near the deepest portion of each lake. Integrated water samples were collected from the upper 2.5 m of the water column with a 3 m long by 2.54 cm diameter flexible tube and 1–2 L was filtered through a Gelman A/E glass fiber filter. Filters were placed in aluminum foil covered Petri dishes, stored frozen and returned to the laboratory where Chl-*a* was extracted with 90% buffered acetone (24 hr at 4 °C in the dark) and concentrations measured spectrophotometrically.

Results

Nine fish species were collected or observed from 10 natural lakes. These included 3 salmonids (rainbow trout [*Oncorhynchus mykiss*], brown trout [*Salmo trutta*], and brook char [*Salvelinus fontinalis*]), 5 cyprinids (tui chub [*Siphateles bicolor*], speckled dace [*Rhinichthys osculus*], Lahontan redbreast [*Richardsonius egregius*], golden shiner [*Notemigonus chrysoleucus*], and fathead

minnow [*Pimephales promelas*]), and 1 catostomid (*Catostomus tahoensis*). Three lakes were inhabited by a single trout species, 3 were inhabited by one or more cyprinid species but no trout, and 4 had mixed assemblages of trout and cyprinid species and in two cases the catostomid (Table 1). The 10 natural lakes represented 13.7% of lakes and ponds > 2 m deep (N = 73) but only 6.6% of all permanent lakes or ponds (Table 2).

Lakes inhabited by fish had significantly larger surface areas (P = 0.001, Mann-Whitney U), were deeper on average (though not statistically significant; P = 0.203), and were more productive, with significantly higher Chl-*a* concentrations (P = 0.0002) and shallower Secchi depths (P = 0.005) (Table 2). All of the fish-bearing lakes had one or more perennial inlets or outlets compared to only 6% of fishless lakes.

Table 1. Distribution of fish species among 10 natural lakes within Lassen Volcanic National Park. See text for common and complete scientific names.

Fish Species	Lakes
<i>O. mykiss</i>	Blue Lake Canyon
<i>S. fontinalis</i>	Ridge, Summit
<i>S. bicolor</i> ; <i>R. egregius</i>	Juniper
<i>S. bicolor</i> ; <i>R. osculus</i>	Widow
<i>N. chrysoleucus</i> ; <i>P. promelas</i>	Reflection
<i>O. mykiss</i> ; <i>S. bicolor</i> ; <i>R. osculus</i>	Snag
<i>C. tahoensis</i>	Snag
<i>O. mykiss</i> ; <i>S. bicolor</i> ; <i>R. osculus</i>	Butte
<i>R. egregius</i> ; <i>C. tahoensis</i>	Butte
<i>O. mykiss</i> ; <i>S. fontinalis</i> ; <i>S. trutta</i>	Manzanita
<i>N. chrysoleucus</i> ; <i>R. osculus</i>	Manzanita
<i>S. trutta</i> ; <i>S. bicolor</i>	Horseshoe

Table 2. Characteristics of fish and fishless lakes within Lassen Volcanic National Park. Mean surface area and depth values are based on lakes >2 m deep (N = 73), and values in parentheses are ranges.

	With Fish	Without Fish
No. of Lakes > 2 m deep	10	63
All permanent lakes/ponds	10	137
Mean Surface Area (ha)	57.7	2.8
	(0.5–239.6)	(0.1–21.3)
Mean Depth (m)	14.7	7.3
	(2.8–71.3)	(2.0–25.9)
With perennial inlet/outlet (%)	100.0	6.5
Chlorophyll <i>a</i> (µg/l)	5.6	0.9
	(0.8–19.4)	(0.1–2.36)
Secchi Depth (m)	3.8	7.3
	(2.3–4.5)	(3.6–21.5)

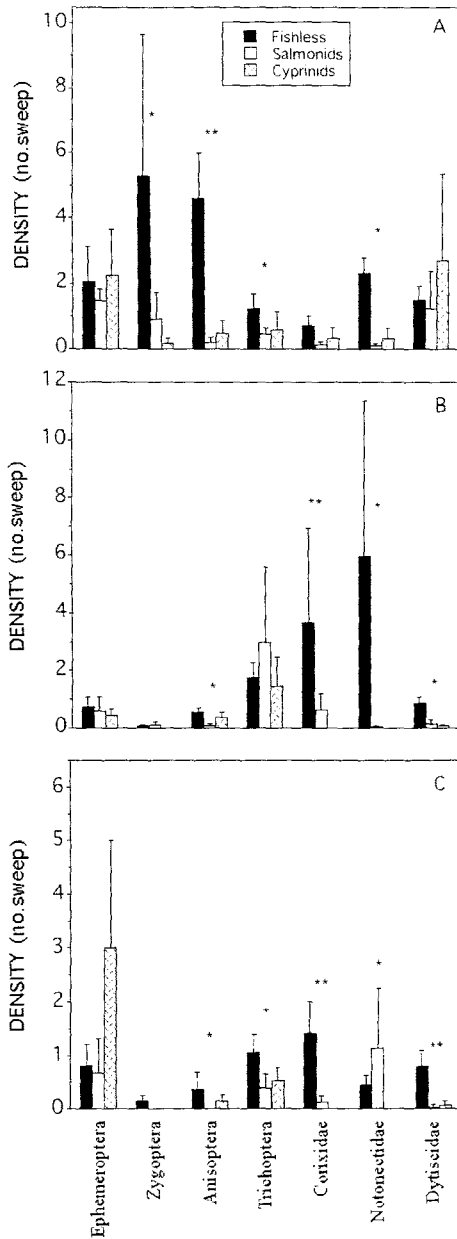


Fig. 1. Comparisons of the most abundant groups of littoral macroinvertebrates among (A) vegetated, (B) fine sediment, and (C) coarse rocky habitats and among lakes with or without fish. Lakes with trout alone and trout mixed with other species are combined. Asterisks indicate statistically significant differences among groups within habitats (Kruskall-Wallis tests; * $P < 0.05$, ** $p < 0.01$).

Many large-bodied, active macroinvertebrate taxa had significantly higher densities in the absence of fish in all three habitats sampled (Fig. 1), but small-bodied chironomid larvae were more abundant in the presence of fish in fine and coarse sediment habitats (Fig. 2). *Chaoborus americanus* was present in three of the fishless lakes, at

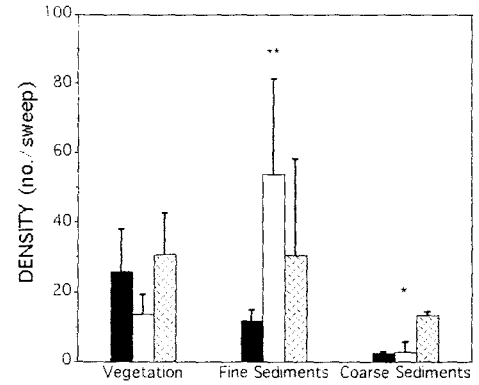


Fig. 2. Comparison of Chironomidae densities among vegetated, fine sediment, and coarse rocky habitats and among lakes with and without fish. Symbols the same as in Figure 1.

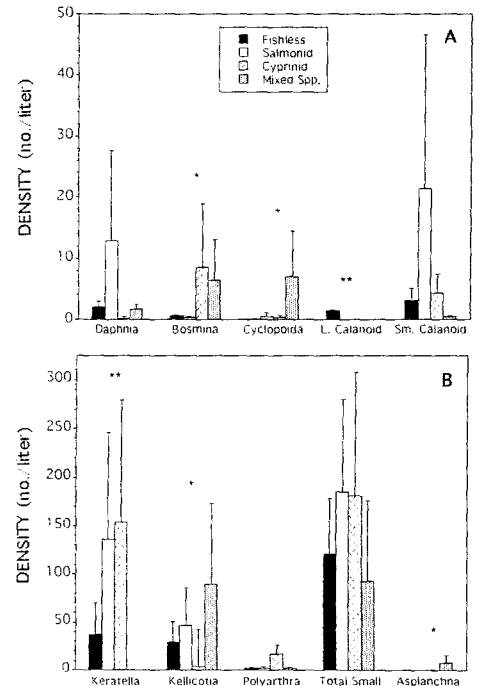


Fig. 3. Comparisons of (A) most abundant crustacean zooplankton and (B) rotifers among lakes with and without fishes. Asterisks same as in Figure 1.

very low densities ($< 0.1/L$) but was not observed in any lakes with fish.

Among the crustacean zooplankton, the large (1.8–2.1 mm) calanoid copepod *Hesperodiaptomus kenai* was absent from all fish bearing lakes but common among fishless lakes (Fig. 3a), occurring in 8 of 11 lakes sampled. The small cladoceran *Bosmina* had significantly higher densities in lakes inhabited by cyprinids (with or without trout) than in fishless lakes or lakes with trout alone and small cyclopoid copepods were most abundant

in mixed fish species lakes. There were very large differences in taxonomic composition and densities of crustaceans among the three lakes with either rainbow trout or brook char alone suggesting that factors other than trout predation were more important in determining zooplankton species composition and abundance in these lakes. The rainbow trout lake had high densities (40/L) of *Daphnia rosea*, one brook char lake had high densities (63/L) of a small *Diaptomus* species, while the other brook char lake had very low densities of all crustaceans (< 3/L).

Overall densities of small rotifers did not differ significantly between fish and fishless lakes, although densities of two small genera and the large, predatory *Asplanchna* did (Fig. 3b). *Asplanchna* was only collected from lakes with cyprinids (with or without trout) and had its greatest density in lakes with mixed fish assemblages. Of the two small species, *Kellicotia* also had its highest densities in lakes with mixed fish assemblages, whereas *Keratella* had its lowest densities in these lakes.

Discussion

Perhaps the most striking result of this study was the limited distribution of fish among LVNP lakes. Only 13.7% of deeper lakes were inhabited by fish, and only 9.5% had trout, suggesting that nearly 90% of historically stocked lakes have reverted to a fishless condition. In contrast, in Sierra Nevada national parks where fish stocking ceased at about the same time as LVNP, ARMSTRONG & KNAPP (2004) estimated that over half the lakes originally stocked may continue to support self-sustaining trout populations. Stead et al. (2005, unpubl.) found that proportions of lakes inhabited by fish in LVNP were much lower than two wilderness areas bordering the park in which 42–73% of lakes had fish. Among factors likely contributing to such disparities is the small proportion of LVNP lakes with perennial inlets and outlets that, therefore, lack spawning habitat. There is a distinct precipitation gradient within the park, with the more mountainous western side of the park typically receiving a greater snow pack and more overall precipitation than the drier eastern side. The density of lake basins is greater on the eastern side of the park, so surface water supply to them during dry summers may be limited. Porous volcanic soils and bedrock may also permit precipitation and snowmelt to rapidly penetrate the groundwater, supplying springs throughout the park but possibly limiting surface flows into and out of most lakes restricting both connectivity among water bodies and spawning.

Although the vast majority of lakes within LVNP currently lack fish, direct and indirect effects of fish predation

on food webs are obvious in the few lakes in which fish persist. These include the 4 largest, and 6 of the 10 largest, lakes within the park. Our results suggest that most lakes will probably remain fishless and return to conditions more similar to historic, pre-stocking conditions. For example, large mobile invertebrates, such as odonates, dytiscids and notonectids, will likely take on the role of top predator in most fishless lakes and large zooplankton, such as *Hesperodiaptomus kenai*, and perhaps *Chaoborus* may again be common within the zooplankton. PARKER et al. (2001) showed, however, that *Hesperodiaptomus arcticus* did not return to a Canadian lake 2 yr after fish removal indicating that recovery may depend on the duration of fish presence and the nature of the resting egg bank within the sediments.

That invertebrate assemblages appear to be relatively resilient in responding to the loss of fish predators, as also shown by KNAPP et al. (2001) for southern Sierra Nevada lakes, suggests that the policy to stop stocking nonnative fishes into LVNP lakes is allowing some components of the community to recover to pre-fish stocking conditions. Persistent and largely unexplained declines of amphibian populations at LVNP (e.g., FELLERS & DROST 1993, FELLERS et al. 2008), however, suggest that factors in addition to nonnative fish introductions will continue to plague efforts to sustain the entirety of native biodiversity within this and other protected areas.

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