

RESISTANCE AND RESILIENCE OF ALPINE LAKE FAUNA TO FISH INTRODUCTIONS

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Abstract. This paper reports on the response by amphibians, benthic macroinvertebrates, and zooplankton in naturally fishless alpine lakes to fish introductions and subsequent fish disappearance. We assessed resistance (the degree to which a system is altered when the environment changes) by comparing faunal distribution and abundance in lakes that have never been stocked with fish vs. the distribution and abundance in lakes that have been stocked and still contain fish. We assessed resilience (the degree and rate of a system's return to its previous configuration once the perturbation is removed) by comparing faunal distribution and abundance in lakes that were stocked at one time but have since reverted to a fishless condition (stocked-now-fishless lakes) vs. the distribution and abundance in lakes that have never been stocked. We quantified recovery rates and trajectories by comparing faunal assemblages of stocked-now-fishless lakes that had been fishless for 5–10, 11–20, and >20 yr.

Faunal assemblages in the study lakes had low resistance to fish introductions, but in general showed high resilience. The mountain yellow-legged frog (*Rana muscosa*), conspicuous benthic macroinvertebrates, and large crustacean zooplankton (>1 mm) were dramatically reduced in distribution and abundance by fish introductions but generally recovered to predisturbance levels after fish disappearance. Inconspicuous benthic invertebrate taxa, small crustacean zooplankton (<1 mm), and rotiferan zooplankton (<0.2 mm) were either unaffected by fish or increased in the presence of fish. For both the benthic macroinvertebrate community and the zooplankton community as a whole, fish disappearance was followed by a steady change away from the configuration characteristic of fish-containing lakes and toward that of lakes that had never been stocked. Both communities remained markedly different from those in never-stocked lakes 5–10 yr after fish disappearance and converged on the configuration of never-stocked lakes only 11–20 yr after fish disappearance.

Recovery was likely facilitated by the winged adult stages of many benthic macroinvertebrates, resting eggs of zooplankton, and nearby source populations of frogs. However, many frog populations have disappeared since the time that lakes in this study reverted to a fishless condition, and the viability of zooplankton egg banks should decline in fish-containing lakes over time. As a result, faunal resilience may be lower in lakes that revert to a fishless condition today than is suggested by the results of our study. These findings have important implications for the restoration of alpine lake ecosystems.

Key words: alpine lakes; amphibians; exotic species; fish; invertebrates; predation; recovery; resilience; resistance; Sierra Nevada; stability; zooplankton.

INTRODUCTION

The question of how natural communities respond to biotic and abiotic perturbations is central to many of today's most pressing ecological problems, including the maintenance of biodiversity in the face of escalating habitat alteration and the invasion of ecosystems by exotic species. Although these problems are often best studied at large spatial and temporal scales, these scales are rarely amenable to experimentation, and as a result many of the advances in our understanding of how communities respond to perturbations

have come from small-scale, short-term field experiments (Connell and Sousa 1983). The scaling up of these results to more relevant spatial and temporal scales is, at best, problematic (Brown et al. 1986, Yodzis 1988, Pimm 1991). As a consequence, while we often have a good understanding of how communities respond to perturbations at small spatial and temporal scales, this perspective may provide few insights into the nature of responses to perturbations that increasingly are occurring at the scale of landscapes and entire ecosystems (Pimm 1991).

Freshwater communities are subject to a wide range of both natural and anthropogenic disturbances, and whole-lake experiments have been a particularly ef-

fective means by which to describe in detail the response to perturbation at the scale of the entire ecosystem (Carpenter and Kitchell 1993, Frost et al. 1998). Whole-lake experiments, however, generally have several shortcomings that limit their generality. First, these studies are typically short term, often lasting only two to three years (Mittelbach et al. 1995). Such short temporal scales may only capture the transient dynamics that characterize food webs following a perturbation (Yodzis 1988, Tilman 1989). Second, experimental perturbations of whole lakes have usually been conducted in only a single direction (e.g., a species is either added or removed). As suggested by Mittelbach et al. (1995), studies that examine the effect of a perturbation followed by removal of the perturbation would allow us to examine not only system resistance (the degree to which a system is altered when the environment changes), but also resilience (Carpenter and Kitchell 1993, Persson et al. 1993, Mittelbach et al. 1995, Frost et al. 1998), where resilience is the degree to and the rate at which a system returns to its previous configuration once the perturbation is removed (sensu Pimm 1991). Lastly, whole-lake experiments are generally conducted only at a single site or pair of sites, making it difficult to generalize from the observed response to how other similar sites might respond to the same perturbation.

Overcoming these limitations by conducting long-term experiments, examining both system resistance and resilience, and replicating these experiments at numerous sites will often be logistically impossible. However, many perturbations, such as invasions of exotic species (Huckins et al. 2000), have been occurring for decades over large landscapes. Some of these perturbations offer rare opportunities to understand system resistance and resilience over spatial and temporal scales not possible with traditional experiments. For example, the mountains of western North America contain thousands of glacially formed alpine lakes, nearly all of which were historically fishless (Bahls 1992, Knapp 1996). During the past century, many of these lakes have been stocked with nonnative fishes to create recreational fisheries. In some of these lakes, fish introductions failed to result in a self-sustaining population and the fish eventually disappeared (Donald 1987). Comparison of faunal assemblages among many lakes that either remain in a natural fishless condition, have been stocked and still contain fish, or were stocked in the past but have since reverted to a fishless condition, would provide a valuable perspective on the long-term community response to fish introductions and the capacity of these communities to recover after fish disappearance. While the effect of introduced trout on alpine lake faunal assemblages has been described using such a single-survey (snapshot) approach (Anderson 1980, Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998, Knapp and Matthews 2000), these studies have generally relied on relatively coarse presence/absence data (but see Carlisle and Hawkins

1998). In addition, we are not aware of any studies that have used the snapshot approach to evaluate faunal recovery after fish disappearance.

Here we present the results of a study of the response by alpine lake faunal assemblages to fish introductions, based on snapshot samples of hundreds of lakes with or without introduced fishes. In addition to evaluating the resistance of amphibian, zooplankton, and benthic macroinvertebrate communities, we also evaluate the resilience of these communities by quantifying faunal assemblages in lakes that were stocked in the past but have since reverted to a fishless condition. A key advantage of our data set is that we can reliably estimate the year of fish disappearance. Within the class of lakes that lost their fish populations, there was a wide range of durations since fish disappearance, which enabled us to indirectly examine recovery dynamics. Although the snapshot approach had several limitations, our study design allowed us to compare resistance and resilience of lake fauna at a much larger temporal and spatial scale than in any previous study. We show that the taxonomic composition and abundance of faunal assemblages in lakes with or without introduced fishes were dramatically different, as expected based on previous studies. Using data from previously stocked but now fishless lakes, taxonomic composition and abundance of amphibian, zooplankton, and benthic macroinvertebrate communities appeared generally to have recovered within 10–20 yr after fish disappearance. Therefore, while these alpine lake faunal assemblages show low resistance to fish introductions, they appear to be fairly resilient.

METHODS

Study area description

The study area was located in the Sierra Nevada of eastern California, and encompassed portions of the John Muir Wilderness (Inyo and Sierra National Forests) and Kings Canyon National Park (see Knapp and Matthews 2000 for a map of the study area). The 1400-km² study area contains hundreds of lakes (defined as water bodies with surface areas ≥ 0.5 ha), the majority of which are located in the subalpine and alpine zones (>2800 m). Lakes throughout the study area are generally small (<10 ha), oligotrophic, depauperate, and cold (maximum temperature $<17^{\circ}\text{C}$, ice-free for 4 mo/yr; Melack et al. 1985, Stoddard 1987, Bradford et al. 1998). Lakes are similar in physical and chemical characteristics due to their common glacial origin and their location in watersheds dominated by intrusive igneous bedrock (California Division of Mines and Geology 1958, Melack et al. 1985). The entire study area was naturally fishless as a result of numerous barriers to upstream movement by fishes (Knapp 1996). Between 1900 and 1960, $\sim 60\%$ of these fishless lakes were stocked with trout (golden trout, *Oncorhynchus mykiss aguabonita*; rainbow trout, *O. mykiss*; brook trout, *Sal-*

velinus fontinalis; and brown trout, *Salmo trutta*) to create recreational fisheries (Knapp and Matthews 2000; National Park Service and California Department of Fish and Game, unpublished stocking records).

Study design

As part of a larger study of the effects of introduced trout on alpine lake ecosystems, field surveys were conducted during 1995–1997 to describe the physical characteristics and fish and amphibian populations in all lakes and ponds in the study area ($n = 2258$; Matthews and Knapp 1999). In addition, zooplankton and benthic macroinvertebrate samples were collected from a subset of water bodies. The present study includes only those larger, deeper lakes located in the subalpine and alpine zones ($n = 533$; surface area ≥ 0.5 ha, maximum depth >3 m, elevation 2870–3600 m). We used this restriction to reduce habitat variation among lakes and to ensure that only those lakes capable of supporting trout were considered. Lakes were visited once during the survey, during 26 July–14 September 1995, 22 July–13 September 1996, or 29 June–14 September 1997. Most of the precipitation in the study area falls as snow, and snowfall in 1995, 1996, and 1997 was 168%, 108%, and 100% of the mean, respectively (California Department of Water Resources, online reports DLYSWEQ.19950331, DLYSWEQ.19960331, DLYSWEQ.19970331; accessed on 31 October 2000.)⁴

Prior to sampling, we used fish stocking records provided by the California Department of Fish and Game and National Park Service to divide the study lakes into three categories based on their fish stocking histories. These categories were (1) lakes that were never stocked (“never-stocked”; $n = 215$), (2) lakes that were stocked at least once and still contained a trout population due to continued stocking or natural reproduction (“stocked-fish-present”; $n = 289$), and (3) lakes that were stocked at least once, but no longer contained trout due to a halt to stocking and a lack of spawning habitat (“stocked-now-fishless”; $n = 29$). Stocked-now-fishless lakes included only those that had been fishless for ≥ 5 yr (range = 5–59 yr). Stocking records were also used to estimate the year in which each stocked-now-fishless lake reverted to a fishless condition. We assumed that trout disappeared from individual lakes 10 yr after the last stocking. This assumption was based on a mean maximum trout age in the study area of 8.3 yr (range = 2–16, $SD = 2.8$), which we determined by aging 1570 fish collected from 103 lakes (see *Methods: Fish surveys*). This assumption is further supported by the fact that all four lakes that were surveyed 10–15 yr after the last stocking date were found to be fishless.

We used these three lake categories (never-stocked, stocked-fish-present, stocked-now-fishless) to quantify (1) the impacts of fish introductions (resistance) by

comparing faunal assemblages of never-stocked vs. stocked-fish-present lakes, (2) the ability of communities to recover from the perturbation caused by trout introductions (resilience) by comparing faunal assemblages of never-stocked vs. stocked-now-fishless lakes, and (3) recovery rates and trajectories by comparing species composition of stocked-now-fishless lakes that had been fishless for 5–10, 11–20, and >20 yr.

Fish surveys

To verify the presence/absence of trout in each lake, we used visual encounter surveys and gillnets. In relatively small, shallow water bodies in which the entire bottom could be seen, trout presence/absence was determined visually while walking the entire shoreline and the first 100 m of each inlet and outlet stream ($n = 35$). In larger, deeper water bodies, we determined fish presence/absence and species composition using a single monofilament gill net set for 8–12 h combined with a visual survey ($n = 498$).

Amphibian surveys

Mountain yellow-legged frogs (*Rana muscosa*) were the most common amphibian species in our study lakes. Other amphibian species (*Hyla regilla*, *Bufo canorus*) were found primarily in shallow ponds and were too rare in our lakes to be included in this study. Surveys for the mountain yellow-legged frog were conducted at all 533 study lakes. The number of frogs at each water body was determined using visual encounter surveys (Crump and Scott 1994) of the entire shoreline. During the summer, adults and larvae occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes by shoreline searches (Bradford 1989). In addition, larvae overwinter 2–3 times before metamorphosing into subadult frogs, and larvae are therefore present in lakes year-round. As a result, visual surveys produce counts of mountain yellow-legged frogs that are highly repeatable between years (Knapp and Matthews 2000). If frogs were present, we counted the number of adult (i.e., post-metamorphic) frogs and larvae. Frog density (number of individuals/m of shoreline) was calculated by dividing the total number of adults or larvae by the lake perimeter. Lake perimeters were obtained from a geographic information system (GIS).

Benthic macroinvertebrate sampling

Benthic macroinvertebrate samples were collected from a subset of the 533 study lakes. Samples were collected from 67 never-stocked lakes, 100 stocked-fish-present lakes, and 22 stocked-now-fishless lakes, selected at random. Benthic macroinvertebrates were sampled from the littoral zone of each lake by conducting 15 standard sweeps with a D-net (mesh size = 1 mm). A standard sweep consisted of a 1-m sweep in one direction followed immediately by a 1-m sweep across the same area in the opposite direction. D-net

⁴ URL: <http://cdec.water.ca.gov/cgi-progs/lisiodir>

sweeps followed bottom contours and sampled epibenthic, water column, and surficial sediment habitats in portions of each lake that were ≤ 1.2 m deep. All littoral habitats were sampled, and each common habitat was sampled approximately in proportion to its availability. Benthic macroinvertebrates were separated from detritus and sediment in the field and preserved in 70% ethanol. Macroinvertebrates were identified (Merritt and Cummins 1984) at 12–40 \times under a dissecting microscope. All taxa were identified to genus except mites and oligochaetes (identified to Order Acari and Oligochaeta, respectively). Following identification at the generic level, several genera of dytiscid beetles were grouped into the tribe Hydroporini. Similarly, two corixid genera were grouped into family Corixidae. A subsample of each taxon was measured for total length. Sample sizes for measurement of total length differed by taxon, but averaged 18 (range = 8–42).

Zooplankton sampling

Zooplankton samples were collected from all 533 study lakes. Zooplankton were sampled from a float tube (small raft used by anglers) by taking vertical tows from the bottom to the surface with a conical plankton net (29.5 cm diameter, 64- μ m mesh) in the deepest part of each lake. One to five replicate tows were made until substantial numbers of zooplankton were present in samples (Stoddard 1987, Bradford et al. 1998). Samples were preserved in 5% sugar formalin.

We analyzed a subset of the 533 zooplankton samples in the laboratory. Several samples were discarded due to improper preservation or presence of excessive amounts of silt. Samples were analyzed for all stocked-now-fishless lakes for which samples were available ($n = 26$), and for 62 never-stocked and 89 stocked-fish-present lakes selected at random. Lakes selected for zooplankton analysis were not necessarily selected for benthic macroinvertebrate sampling and vice versa; both zooplankton and benthic invertebrate samples were processed for 65% of selected lakes.

In the laboratory, zooplankton samples were rinsed through a 64- μ m sieve and then diluted with tap water to create a highly concentrated sample. A 1-mL subsample was withdrawn from this concentrated sample and scanned at 40 \times under a compound microscope to roughly estimate species composition and density. The scanned subsample was then returned to the sample, and based on the density of observed taxa, the sample was further diluted with a known volume of tap water to create a final concentration sufficient to ensure that all taxa present would be represented in 1-mL subsamples. In the cases where some taxa were much more abundant than others, the low density taxa were counted at one dilution and the high density taxa were counted at another dilution. After determining the correct dilution, three subsamples (1-mL) were removed from the diluted sample with a wide-bore pipette, and zoo-

plankton in each subsample were identified and counted in a Sedgwick-Rafter cell at 40 \times under a compound microscope. Depending on the abundance of zooplankton, from 1 to 30% of each sample was counted. Crustaceans were identified using Edmondson (1959) and Pennak (1989), and rotifers were identified using Stemberger (1979). Crustaceans and rotifers were identified to species except for cyclopoid copepods, which were identified to family (Cyclopoda), and the rotifers *Kellicottia*, *Keratella*, and *Polyarthra*, which were identified to genus. The density of each taxon (number of individuals/L) was calculated assuming a net efficiency of 50% (Walters and Vincent 1973). For each sample, up to 100 individuals of each taxon were measured using a computer-based image analysis system.

Habitat description

To allow comparison of the physical attributes of never-stocked, stocked-fish-present, and stocked-now-fishless lakes, we used information on lake elevation, surface area, maximum depth, littoral zone substrate composition, isolation from other waterbodies, and solar input. Lake surface area was obtained from a GIS and lake elevation was obtained from 1:24 000 U.S. Geological Survey topographic maps. Maximum lake depth was determined by sounding with a weighted line. Littoral zone substrate composition was quantified by visually estimating the dominant substrate along ~ 50 , 3-m long transects evenly spaced around the lake perimeter and placed perpendicular to shore. Substrates were categorized as silt (< 0.5 mm), sand (0.5–2 mm), gravel (> 2 –75 mm), cobble (> 75 –300 mm), boulder (> 300 mm), or bedrock. The frequencies of these substrate categories were highly intercorrelated (e.g., lakes with abundant silt had little boulder or bedrock substrates) so only the percentage of the littoral zone dominated by silt was used to describe littoral zone substrate characteristics. Two measures of water body isolation, the number of lakes (water bodies with surface area ≥ 0.5 ha) within 1 km of the shoreline of each study lake and the number of ponds (water bodies with surface area < 0.5 ha) within 250 m of the shoreline of each study lake, were calculated using a GIS. For these isolation measures, only water bodies within the same drainage as the target lake were considered because we assumed that the movement of frogs, benthic macroinvertebrates, and zooplankton among lakes was most likely to occur within, rather than between drainages.

Solar input, used as a surrogate for water temperature and the duration of the ice-free period, was calculated for each water body using the program SOLARFLUX (Dubayah and Rich 1995). SOLARFLUX calculates direct-beam radiation across a digital elevation model according to slope and aspect. We first divided the study area into 10×10 -m cells by inputting 50 m contour intervals from USGS digital line graphs into the TOPOGRID algorithm in Arc/Info version 7.1 (ESRI 1992). Next, we estimated the daily radiation

received by a particular lake by calculating radiation loads for each cell whose center lay within the water body. Radiation loads were calculated for all daylight hours using a 1-h time step and then averaged across time steps and across all cells associated with that water body. Daily radiation was calculated on the longest and shortest days of the year and on the days halfway between the longest and shortest days of the year. Radiation levels for these four dates were highly correlated and were averaged to produce a single relative measure of mean daily solar radiation.

Statistical analyses

Comparisons of faunal assemblages between the three lake categories were made only for common taxa (amphibians found in $\geq 10\%$ of all 533 study lakes, invertebrate taxa found in $\geq 10\%$ of the 189 analyzed benthic samples or the 177 analyzed zooplankton samples). Rare taxa (present in $< 10\%$ of all samples) were eliminated because sample sizes associated with these taxa were too small to allow meaningful comparisons between lake categories. Given that rare taxa occurred in only a small number of samples in each lake category and, when present, made up a small proportion of the total sample, the inclusion of only common taxa in this study should not have introduced any biases into our analyses. For benthic invertebrates, rare taxa occurred in 1–15 (1–8%) of the 189 samples that were collected (median = 2 samples), never occurred in $> 18\%$ of the samples from any one lake category, and were uncommon even in those lakes where they were present (median = 6% of the total individuals per sample). Two of the 189 samples (one from a never-stocked lake, one from a stocked-fish-present lake) were eliminated from the data set because they contained only rare taxa. Similarly, rare zooplankton taxa occurred in 1–17 (1–10%) of the 177 samples that were processed (median = 2 samples), never occurred in $> 16\%$ of the samples from any one lake category, and were uncommon even in those lakes where they were present (median = 3% of the total individuals per sample). None of the 177 zooplankton samples were eliminated from the data set as all contained at least one common taxon.

Benthic macroinvertebrate taxa were divided into three groups based on their likely vulnerability to predatory trout. “Clinger/swimmer” taxa were those that cling to substrate surfaces (e.g., mayfly larvae) or swim up in the water column (e.g., water beetles) and are therefore likely to be highly vulnerable to trout. “Case-dwelling” taxa were caddisfly larvae (Order Trichoptera), taxa that cling to substrate surfaces but reside in a self-constructed case or web that might afford some protection from predators. The third group included the burrowing taxa, *Sialis*, *Pisidium*, and *Oligochaeta*, and the distasteful taxon, Acari (mites; Smith and Cook 1991). “Burrowing/distasteful” taxa should be the least vulnerable to predatory trout due to their inconspicuousness or unpalatability.

We compared the frequency of occurrence (percentage of lakes) of frogs, benthic macroinvertebrates, and zooplankton between never-stocked lakes vs. stocked-fish-present lakes and never-stocked lakes vs. stocked-now-fishless lakes using Pearson’s chi-square tests when expected values were > 5 and Fisher’s exact tests when expected values were ≤ 5 . We did not test the significance of the overall 3×2 table (presence/absence of a particular taxon in the three lake categories) because we were not interested in the comparison of stocked-fish-present lakes vs. stocked-now-fishless lakes. To allow comparison between taxa of the magnitude of differences in percent occurrence in never-stocked and stocked-fish-present lakes, we calculated an “effect size” as percentage of occurrence in Category 1 divided by percentage of occurrence in Category 2 (where Category 1 was the lake category with the higher percentage of occurrence). We compared abundances of frogs, benthic macroinvertebrates, and zooplankton in never-stocked vs. stocked-fish-present lakes and in never-stocked vs. stocked-now-fishless lakes using Wilcoxon rank-sum tests. We used a non-parametric test because it often was not possible to normalize distributions or stabilize variances via transformation. Results for frog adults and larvae were similar, so only results based on larvae are presented.

We used nonmetric multidimensional scaling (NMMDS) to ask whether there were significant differences in overall community structure between the three lake categories. NMMDS is an ordination technique based on ranked distances, and is better suited to data that are not normally distributed (such as most animal abundance data) than more commonly used linear techniques (e.g., principal components analysis; Minchin 1987, Clarke 1993). Ordinations were based on abundances of all taxa found in $\geq 10\%$ of samples. Rare taxa generally have little influence on ordinations (Jongman et al. 1995), and preliminary analyses of our data indicated little difference between ordinations using all observed taxa and those using only common taxa. Absolute abundances were $\log_{10}(x + 1)$ transformed, and benthic macroinvertebrate and zooplankton data were analyzed separately. Ordinations were performed using the “autopilot” mode in PC-ORD v. 4.14 (McCune and Mefford 1999). The optimal dimensionality (i.e., the number of dimensions beyond which additional dimensions provide only small reductions in stress) was first determined using 40 “runs” performed on the real data followed by 50 runs using randomized data, with each run stepping down in dimensionality from six axes to one axis. The final ordination was then obtained using the optimal dimensionality (optimal dimensionality = 3 for both the benthic macroinvertebrate and zooplankton data) and the best starting configuration as determined from the previous runs. Differences in NMMDS scores between the three lake categories were analyzed using one-way ANOVAs and Tukey’s HSD tests. To provide information

on the rates and trajectories of recovery, we also divided the NMMDS scores for the stocked-now-fishless lakes into three categories based on the time since fish disappearance: 5–10 yr, 11–20 yr, and >20 yr. To simplify the graphical display of the ordination results, only two of the three NMMDS axes were used to define the ordination space. The two axes used in these figures were those that showed the strongest associations with fish stocking history.

To determine whether the effect of lake category (never-stocked, stocked-fish-present, stocked-now-fishless) on benthic macroinvertebrate and zooplankton assemblages was confounded by differences among categories in habitat characteristics and sampling date, we used univariate and multivariate analyses of variance. We first used one-way ANOVAs and Tukey's HSD tests to determine whether habitat variables differed between the three lake categories, using the entire lake data set ($n = 533$). One-way ANOVAs based only on the subset of lakes for which we had zooplankton data or benthic macroinvertebrate data provided results that were identical to those based on the full data set and were therefore not reported separately. Independent variables analyzed were elevation, depth, surface area, percentage of the littoral zone dominated by silt, number of lakes within 1 km of the lake shoreline, number of ponds within 250 m of the lake shoreline, solar input, and sampling date (expressed as the number of days since January 1). Because significant differences in independent variables were observed between lake categories, we then used MANCOVAs to evaluate the influence of lake category on benthic macroinvertebrate and zooplankton assemblages after accounting for the effects of habitat and sampling date. Benthic macroinvertebrate and zooplankton data were analyzed separately. Response variables were the NMMDS scores on axes 1, 2, and 3 (optimal dimensionality = 3) for the benthic macroinvertebrate or zooplankton data, and independent variables included lake category and all eight variables related to habitat and sampling date. Prior to univariate and multivariate analyses, we normalized these data by applying \log_{10} transformations to depth and area, a $\log_{10}(x + 1)$ transformation to the number of ponds within 250 m, and an angular transformation to percentage of littoral zone composed of silt. We were unable to perform a similar analysis on the amphibian data because of a large number of zeros in the response variable, larval abundance.

MANCOVAs indicated that some habitat variables and sampling dates had significant effects on NMMDS scores (see *Results*). Therefore, to evaluate the effect of differences in habitat between lake categories on the outcome of the ordination analyses, we "corrected" the NMMDS scores using multiple linear regression with scores from each of the three NMMDS axes as the dependent variable and all eight habitat and sampling date measures as independent variables. Regression analyses were conducted in a stepwise manner,

using both forward and backward selection. Residuals obtained from the resulting regression equations represent the effect of fish, other unmeasured factors that influenced NMMDS scores, and error. These residuals were used instead of the raw NMMDS scores in one-way ANOVAs and Tukey HSD tests. While this procedure eliminated habitat effects on NMMDS scores, it could also have removed some effects that were actually associated with fish. Unintentional removal of fish effects would have resulted whenever fish presence/absence was associated with habitat differences. Because fish presence/absence was not included in the regression analysis, any effect due to fish but associated with habitat effects would have been attributed to the associated habitat effects and subsequently corrected for.

RESULTS

Adequacy of treatment contrasts

Never-stocked, stocked-fish-present, and stocked-now-fishless lakes were similar in physical characteristics and sampling date, although significant differences between lake categories were observed for most variables (Fig. 1). Overall differences between lake categories were statistically significant ($P \leq 0.05$) for six of the eight variables (elevation, depth, surface area, percentage of littoral zone composed of silt, number of lakes within 1 km, number of ponds within 250 m), marginally nonsignificant for sampling date ($P = 0.08$), and nonsignificant for solar input ($P = 0.24$). Pairwise differences between (1) never-stocked and stocked-fish-present lakes, (2) never-stocked and stocked-now-fishless lakes, and (3) stocked-fish-present and stocked-now-fishless lakes were statistically significant (Tukey's HSD, $P < 0.05$) for six of eight variables, two of eight variables, and one of eight variables, respectively (Fig. 1). Comparisons between never-stocked and stocked-fish-present lakes had high statistical power (>0.9) as a result of relatively large sample sizes ($n = 215$ and 289 , respectively); as a result, even small differences in habitat variables were often found to be statistically significant.

For both the benthic macroinvertebrate and zooplankton assemblages, MANCOVAs indicated that lake category had highly significant effects on NMMDS scores after the influence of habitat and sampling date was accounted for (Pillai-Bartlett trace: benthic macroinvertebrates, $n = 187$, $PB = 0.50$, $P < 0.0001$; zooplankton, $n = 177$, $PB = 0.30$, $P < 0.0001$). In addition to lake category, benthic macroinvertebrate NMMDS scores were influenced by sample date ($P = 0.03$), elevation ($P < 0.0001$), maximum lake depth ($P = 0.0002$), percentage of littoral zone composed of silt ($P = 0.0002$), and number of ponds within a 250 m radius ($P = 0.04$). Zooplankton NMMDS scores were influenced by elevation ($P = 0.001$) and lake area ($P < 0.0001$). Taken together, these results indicate that

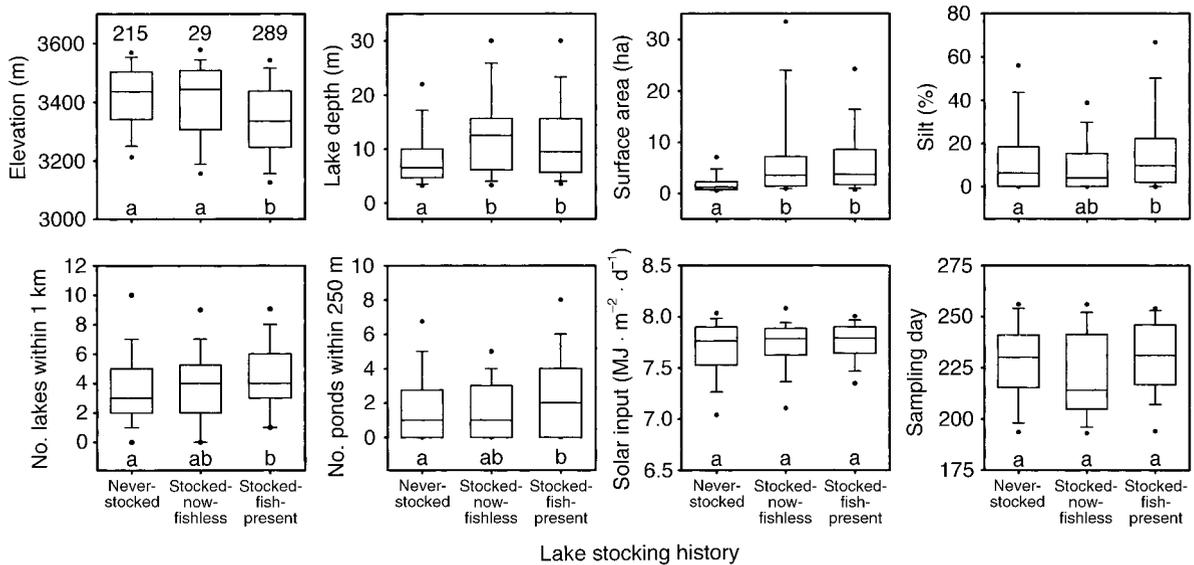


FIG. 1. Box plots showing elevation, lake depth, surface area, percentage of silt, number of lakes within 1 km, number of ponds within 250 m, solar input, and sampling day for never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes. The line within each box marks the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers below and above each box indicate the 10th and 90th percentiles, and the points above and below the whiskers indicate the 5th and 95th percentiles. Sample sizes are given in the first graph. Letters at the bottom of each graph indicate the statistical significance of differences between lake categories. Categories with different letters are significantly different at the $P < 0.05$ level (one-way ANOVA followed by Tukey's HSD).

while we were not completely successful in creating lake categories that eliminated all between-category differences in habitat characteristics, the strong effects of lake category on faunal assemblage structure were independent of the confounding influences of habitat variables.

Amphibians

Mountain yellow-legged frog larvae were much less likely to be found in stocked-fish-present lakes than in never-stocked lakes ($P < 0.001$; Fig. 2A). Densities of frog larvae were also much lower in stocked-fish-present lakes than in never-stocked lakes ($P < 0.001$; Fig. 2B). Frogs appeared to recover after fish disappearance, as percentage of occurrence and density were very similar between never-stocked and stocked-now-fishless lakes (Fig. 2A, B). Neither difference approached statistical significance ($P > 0.8$). For lakes that had been fishless for 5–10 yr, 11–20 yr, or >20 yr, mountain yellow-legged frog larvae were found in 0% ($n = 5$), 20% ($n = 10$), and 28% ($n = 14$), respectively. Abundance of frog larvae showed a similar pattern, and together with the frequency data suggest that recovery of frog populations may require >10 yr after fish disappearance.

Benthic macroinvertebrates

As predicted, five of the six “clinger/swimmer” taxa were found in a lower percentage of stocked-fish-present lakes than in never-stocked lakes (Fig. 3A). For

these five taxa, differences were most marked for the largest taxa (*Ameletus*, *Callibaetis*, *Agabus*, Corixidae; median effect size = 13.2) and least marked for the smallest taxon (Hydroporini; effect size = 1.4). In contrast to the reduced occurrence of these five taxa, *Culex* (mosquito larvae) were found in a much higher percentage of stocked-fish-present lakes than in never-stocked lakes ($P < 0.001$; Fig. 3A). Similar patterns were found for taxon-specific abundance data (Fig. 4A), with *Ameletus*, *Callibaetis*, *Agabus*, Corixidae, and Hydroporini all less abundant ($P < 0.001$) and *Culex* more abundant ($P < 0.001$) in stocked-fish-present lakes compared to never-stocked lakes. The frequency of occurrence and abundance for *Culex* increased despite its similar size to clinger/swimmer taxa whose frequencies of occurrence were reduced in the presence of trout (Fig. 3A).

At least four of the six clinger/swimmer taxa appeared to recover completely after fish disappearance, as indicated by the similar percent occurrence and abundance of *Ameletus*, *Callibaetis*, *Culex*, and Hydroporini in stocked-now-fishless and never-stocked lakes ($P_{\text{occur}} > 0.60$, $P_{\text{abund}} > 0.3$; Figs. 3A, 4A). The percent occurrence and abundance of *Agabus* was lower in stocked-now-fishless lakes than in never-stocked lakes (Figs. 3A, 4A), although these differences were not statistically significant ($P_{\text{occur}} = 0.26$, $P_{\text{abund}} = 0.13$). Percent occurrence and abundance of corixids was higher in stocked-now-fishless than never-stocked lakes (Figs. 3A, 4A), but only differences in abundance

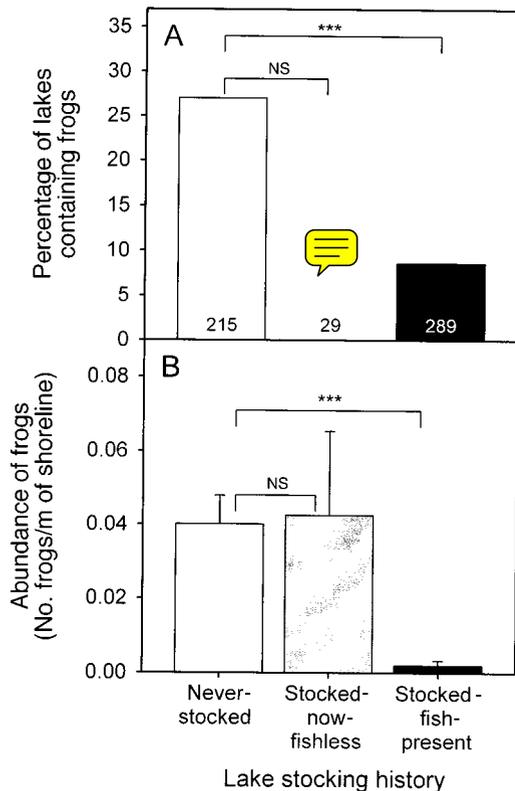


FIG. 2. (A) Percentage of never-stocked lakes (open bars), stocked-now-fishless lakes (gray bars), and stocked-fish-present lakes (black bars) containing mountain yellow-legged frog larvae. (B) The abundance of mountain yellow-legged frog larvae in never-stocked, stocked-now-fishless, and stocked-fish-present lakes. Abundance was measured as the number of larvae/m of shoreline and is expressed as $\log_{10}(\text{abundance} + 1)$. Bars indicate means + 1 SE. Sample sizes for each lake type are given inside the respective bar in (A). Lines and associated symbols connecting each bar provide the results of pairwise chi-square tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$).

approached statistical significance ($P_{\text{occur}} = 0.12$, $P_{\text{abund}} = 0.053$).

Contrary to expectation, the percentage occurrence and abundance of four of the five caddisfly taxa (Limnephilidae: *Hesperophylax*, *Desmona*, *Psychoglypha*; Polycentropidae: *Polycentropus*) were lower in stocked-fish-present lakes than in never-stocked lakes ($P < 0.003$; Figs. 3B, 4B). *Limnephilus* (Limnephilidae) was found in a similar percentage of stocked-fish-present and never-stocked lakes ($P = 0.71$; Fig. 3B) and at similar abundances ($P = 0.19$; Fig. 4B). The lack of a fish effect on *Limnephilus* did not appear to be related to its size, as its size was similar to that of taxa whose frequencies of occurrence and abundances were reduced by fish (Fig. 3B). However, across all five caddisfly taxa, body size was weakly correlated with effect size ($n = 5$, $r = 0.84$, $P = 0.08$).

Of the four caddisfly taxa whose distributions were influenced by the presence of fish, at least one (*Des-*

mona) completely recovered after fish disappearance. *Desmona* had a similar percentage of occurrence and abundance in stocked-now-fishless and never-stocked lakes ($P > 0.30$; Figs. 3B, 4B). *Hesperophylax*, *Polycentropus*, and *Psychoglypha* were found in fewer stocked-now-fishless lakes than in never-stocked lakes (Fig. 3B), but these differences approached statistical significance only for *Polycentropus* ($P_{\text{He}} = 0.31$, $P_{\text{Po}} = 0.08$, $P_{\text{Ps}} = 0.17$). Abundances of these three taxa were also lower in stocked-now-fishless lakes than in never-stocked lakes (Fig. 4B). These differences were marginally nonsignificant for *Polycentropus* and *Psychoglypha* ($P = 0.06$), but were not significant for *Hesperophylax* ($P = 0.20$). Therefore, *Polycentropus* and *Psychoglypha* may not have completely recovered after fish disappearance. The frequency of occurrence and abundance of *Limnephilus*, a taxon not affected by trout presence, was similar between stocked-now-fishless and never-stocked lakes ($P_{\text{occur}} = 0.30$, $P_{\text{abund}} = 0.20$; Figs. 3B, 4B).

As predicted, the distribution and abundance of two burrowing taxa, alderfly larvae (Sialidae: *Sialis*) and freshwater clams (Sphaeriidae: *Pisidium*), were similar between never-stocked and stocked-fish-present lakes ($P > 0.40$; Figs. 3C, 4C). In contrast, one burrowing taxon, oligochaetes (Oligochaeta), and one distasteful taxon, mites (Acari), occurred more frequently and were more abundant in stocked-fish-present lakes than in never-stocked lakes ($P < 0.007$; Figs. 3C, 4C). After fish disappearance, oligochaete frequency and abundance returned to levels similar to that in never-stocked lakes ($P_{\text{occur}} > 0.40$, $P_{\text{abund}} > 0.20$; Figs. 3C, 4C). The frequency of occurrence and abundance of mites also decreased after fish disappearance, but both were lower (marginally nonsignificant) in stocked-now-fishless lakes than in never-stocked lakes ($P = 0.06$; Figs. 3C, 4C). *Sialis* and *Pisidium*, taxa that were not affected by trout presence, had similar distributions and abundances in stocked-now-fishless vs. never-stocked lakes ($P > 0.50$; Figs. 3C, 4C).

The non-metric multidimensional scaling analysis of the benthic macroinvertebrate community generally supported the results of the taxon-specific analyses. NMMDS Axes 1, 2, and 3 accounted for 68% of the total variation in the ordination ($r^2 = 0.16$, 0.18, and 0.34, respectively; NMMDS axis numbers are arbitrary, so that percent of variance on a given axis does not necessarily decrease with increasing axis number; stress = 20.0). NMMDS scores on Axis 1 were not significantly different between lake categories ($F_{2,184} = 0.2$, $P > 0.8$), while differences in scores between lake categories on Axis 2 and 3 were highly significant (Fig. 5A; Axis 2: $F_{2,184} = 11.4$, $P < 0.0001$; Axis 3: $F_{2,184} = 51.2$, $P < 0.0001$). Taxa showing significant negative correlations with Axis 2 or positive correlations with Axis 3 were generally those associated with fishless lakes (Table 1). These included mayfly nymphs (*Ameletus*, *Callibaetis*), corixids (Corixidae), dytiscid

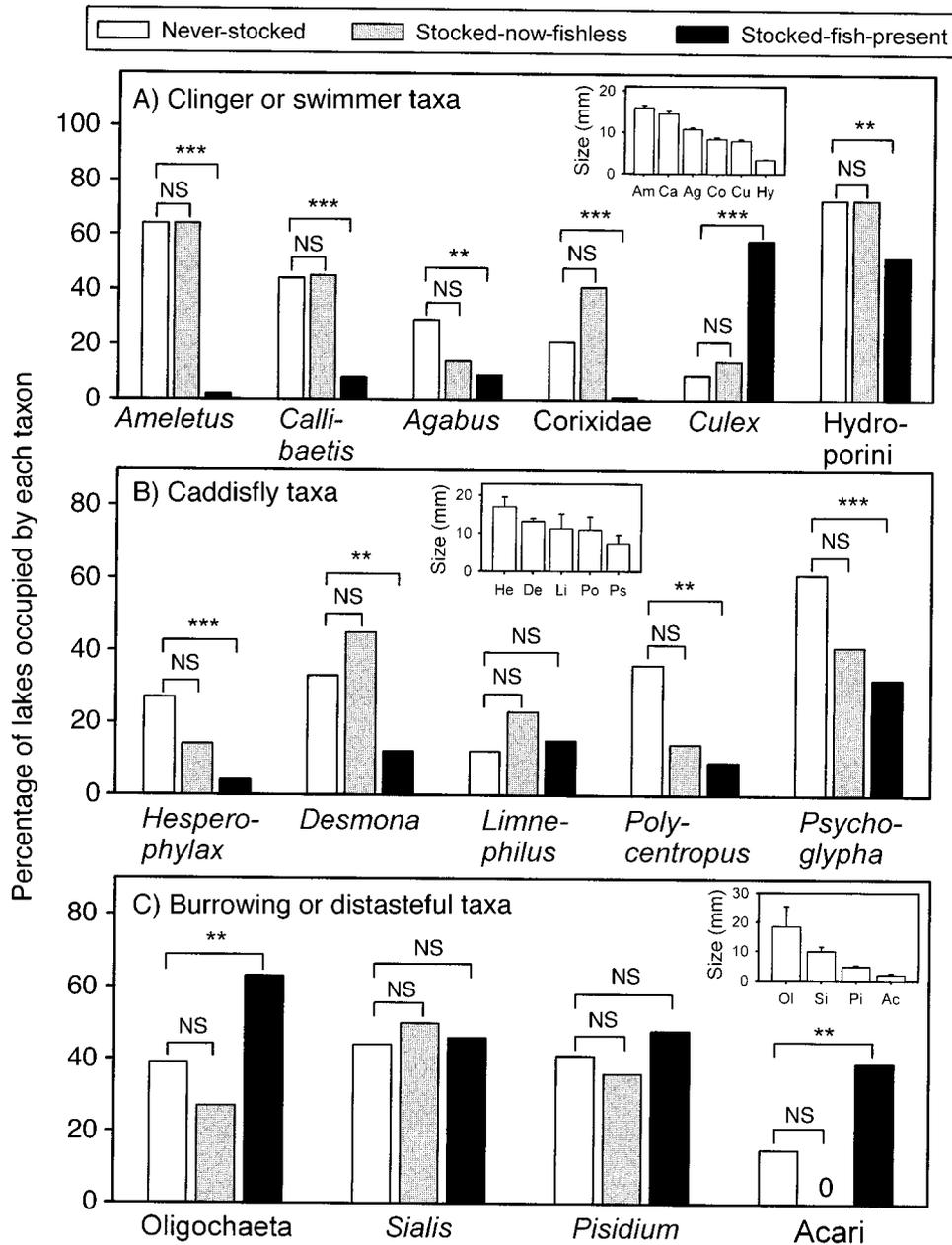


FIG. 3. For benthic macroinvertebrates, the percentage of never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes containing (A) clinger/swimmer taxa, (B) case-dwelling taxa, and (C) burrowing/distasteful taxa. Taxa are arranged from left to right in order of decreasing body size. Sample sizes for never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes are 66, 22, and 99, respectively. Lines and associated symbols connecting each bar provide the results of pairwise Pearson's chi-square tests or Fisher's exact tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$). Inset figures in (A), (B), and (C) show sizes ($\bar{X} + 1$ SD) of each of the taxa in the corresponding figure.

beetles (Hydroporini), and caddisfly larvae (*Desmona*, *Polycentropus*, *Psychoglypha*). Taxa showing significant positive correlations with Axis 2 or negative correlations with Axis 3 were generally those associated with fish-containing lakes (Table 1). These included mosquito larvae (*Culex*), oligochaetes (*Oligochaeta*), and clams (*Pisidium*). Taxa that showed significant cor-

relations with Axis 1 showed no obvious pattern related to fish effects (Table 1). The strong influence of fish on the benthic invertebrate community was shown by the significantly different scores of never-stocked and stocked-fish-present lakes on NMMDS Axis 2 and 3 (Fig. 5A; Tukey's HSD, $P < 0.05$). The significant difference between stocked-fish-present and stocked-

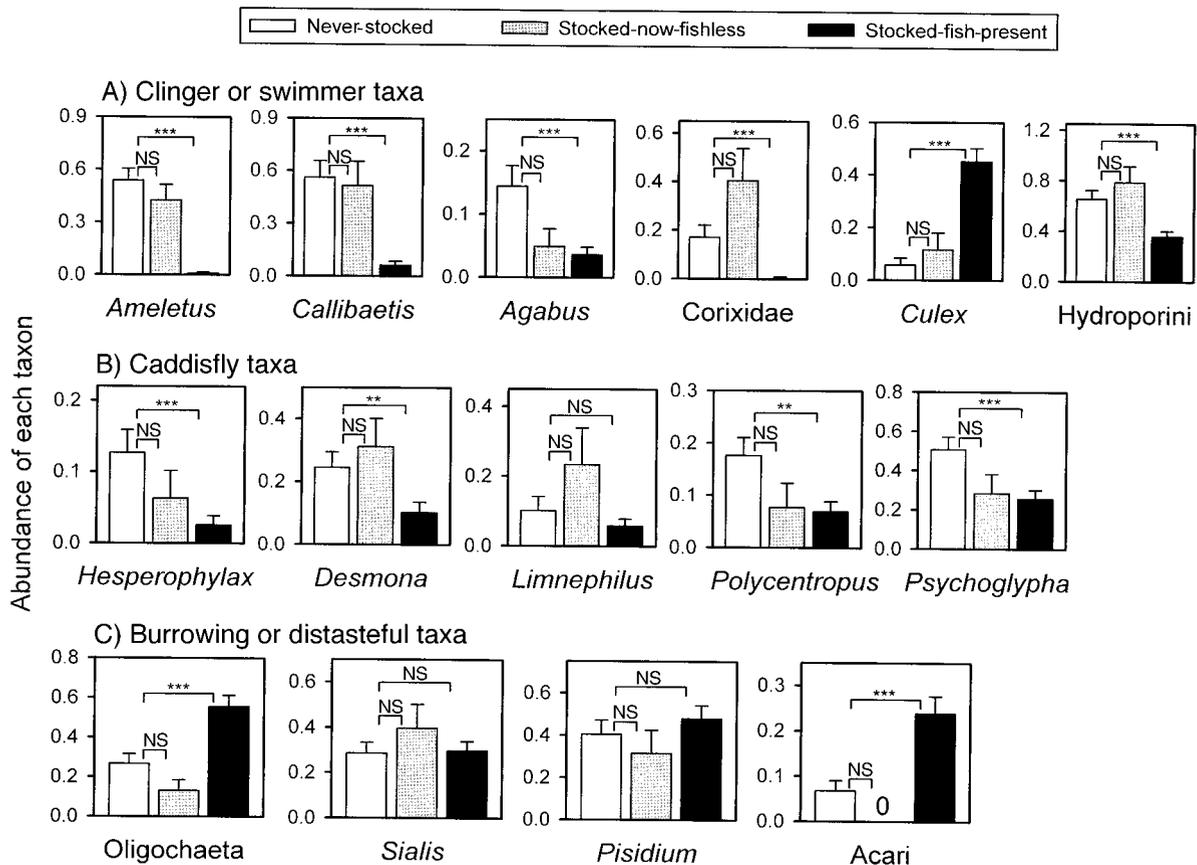


FIG. 4. For benthic macroinvertebrates, the abundance of (A) clinger/swimmer taxa, (B) case-dwelling taxa, and (C) burrowing/distasteful taxa in never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes. Abundance was measured as the number of individuals per 15 standard sweeps and is expressed as $\log_{10}(\text{abundance} + 1)$. Bars indicate means ± 1 SE. Lines and associated symbols connecting each bar provide the results of pairwise Wilcoxon rank-sum tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$). Sample sizes are as in FIG. 3.

now-fishless lakes on Axis 2 and 3 (Tukey's HSD, $P < 0.05$) and the lack of a significant difference between stocked-now-fishless and never-stocked lakes on Axis 2 and 3 (Fig. 5A; Tukey's HSD, $P > 0.05$) suggest that the benthic invertebrate community was able to recover to its previous configuration after fish disappearance. The strong similarity in mean NMMDS scores for stocked-now-fishless and never-stocked lakes on both Axis 2 and 3 (Fig. 5A) indicates that the lack of a statistically significant difference between these two lake categories was not simply the result of statistical power being too low to detect a difference.

Fish disappearance was followed by a steady and predictable change in the benthic macroinvertebrate community away from that characteristic of stocked-fish-present lakes and toward that characteristic of never-stocked lakes (Fig. 5B). The largest changes in community structure occurred in the first 5–20 yr after fish disappearance, followed by negligible changes after >20 yr when mean community structure was nearly identical to that of never-stocked lakes.

Correcting NMMDS scores for habitat differences

between lake categories had little effect on the ordination results. Stepwise multiple regression results used to correct the NMMDS scores are shown in Table 2. As with uncorrected scores, NMMDS scores on Axis 1 were not significantly different between lake categories ($F_{2,184} = 0.1$, $P > 0.9$), while differences in scores between lake categories on Axis 2 and 3 were highly significant (Axis 2: $F_{2,184} = 8.0$, $P < 0.0005$; Axis 3: $F_{2,184} = 17.2$, $P < 0.0001$). In addition, in comparisons between never-stocked and stocked-fish-present lakes on Axis 2 and 3, corrected NMMDS scores were significantly different (Tukey's HSD, $P < 0.05$) as were corrected NMMDS scores between stocked-fish-present and stocked-now-fishless lakes on Axis 2 and 3 (Tukey's HSD, $P < 0.05$). Differences between corrected NMMDS scores between stocked-now-fishless and never-stocked lakes on Axis 2 and 3 were not significant (Tukey's HSD, $P > 0.05$). Taken together, the lack of any significant changes in ordination results after accounting for habitat differences between lake categories suggests that lake stocking his-

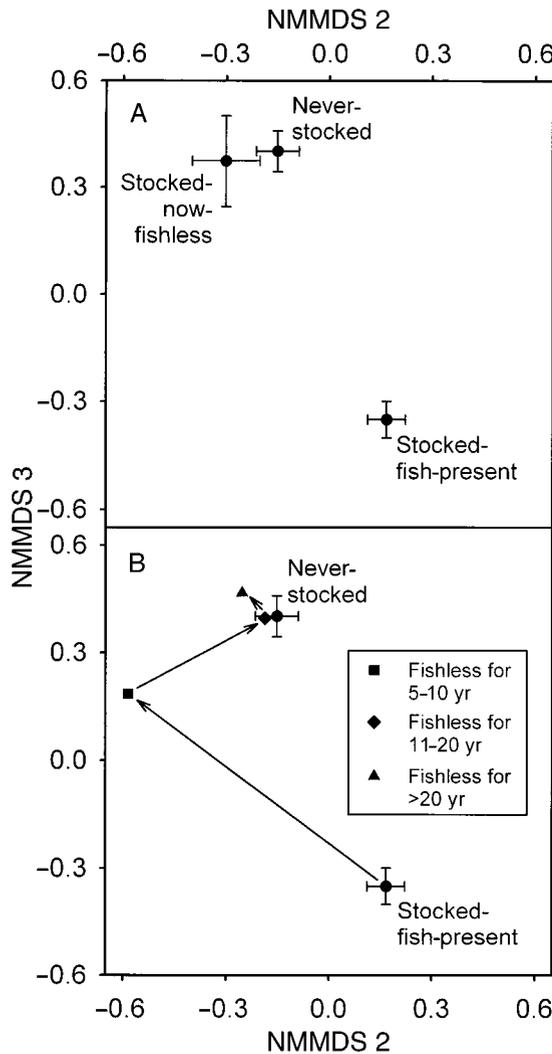


FIG. 5. (A) For common benthic macroinvertebrate taxa (present in $\geq 10\%$ of lakes), mean nonmetric multidimensional scaling (NMMDS) scores (± 1 SE) for never-stocked, stocked-now-fishless, and stocked-fish-present lakes on Axis 2 and Axis 3. Scores were derived from $\log_{10}(x + 1)$ -transformed abundances. Taxa showing significant associations with NMMDS axes are given in Table 1. (B) Same data as in (A) but with stocked-now-fishless lakes separated into three categories based on the number of years since fish disappearance. Error bars were removed from the stocked-now-fishless categories for clarity. Arrows indicate the trajectory of change following fish disappearance.

tories, not habitat effects, were largely responsible for the observed patterns.

Zooplankton

For the analyzed zooplankton samples, the mean volume filtered by the zooplankton net during sample collection (± 1 SD) was 1.47 ± 1.00 m³ with a range of 0.25–6.15 m³. The volume filtered per sample was not significantly different between lake categories (ANOVA; $n = 177$, $F_{2,174} = 0.95$, $P > 0.3$). The median

number of individuals counted per sample was 243, with a range of 2–7689.

Six crustacean taxa were commonly found in the study lakes, and the two largest (>1 mm; *Hesperodiaptomus shoshone*, *Daphnia middendorffiana*) were found much less often in stocked-fish-present lakes than in never-stocked lakes ($P < 0.001$; Fig. 6A). The remaining four taxa had mean sizes <1 mm, and three of these taxa (*Leptodiaptomus signicauda*, *Daphnia rosea*, *Chydorus sphaericus*) were found in a similar percentage of stocked-fish-present and never-stocked lakes ($P_{Le} = 0.22$, $P_{Dr} = 0.26$, $P_{Ch} = 0.88$; Fig. 6A). Cyclopoda were more likely to be found in stocked-fish-present than in never-stocked lakes, although this difference was marginally nonsignificant ($P = 0.06$; Fig. 6A). Zooplankton abundance data showed similar patterns, with *H. shoshone* and *D. middendorffiana* being less abundant in stocked-fish-present lakes than in never-stocked lakes ($P < 0.001$; Fig. 7A), and *L. signicauda*, *D. rosea*, and *C. sphaericus* having similar abundances in stocked-fish-present and never-stocked lakes ($P_{Le} = 0.13$, $P_{Dr} = 0.18$, $P_{Ch} = 0.97$; Fig. 7A). Cyclopoids were more abundant in stocked-fish-present lakes than in never-stocked lakes ($P = 0.03$; Fig. 7A). Due to a highly non-normal distribution, the mean abundance of cyclopoids in stocked-fish-present and never-stocked lakes shown in Fig. 7A does not reflect the relatively large differences in ranked data that were used in the statistical analysis.

Of the five common rotifer taxa, three were found in a similar percentage of stocked-fish-present and never-stocked lakes (*Kellicottia* sp., *Conochilus unicornis*, *Keratella* spp.; $P_{Ki} = 0.75$, $P_{Co} = 0.37$, $P_{Ks} = 0.25$; Fig. 6B) and two (*Keratella quadrata*, *Polyarthra* spp.) were found in a higher percentage of stocked-fish-present lakes than never-stocked lakes. These differences were significant for *K. quadrata* ($P = 0.012$; Fig. 6B) and marginally nonsignificant for *Polyarthra* spp. ($P = 0.07$; Fig. 6B). Rotifer abundances showed stronger

TABLE 1. Correlations of benthic macroinvertebrate taxa with nonmetric multidimensional scaling axes.

Taxon	Axis 1	Axis 2	Axis 3
<i>Ameletus</i>	-0.10	-0.09	0.45
<i>Callibaetis</i>	0.38	-0.35	0.08
<i>Agabus</i>	-0.11	-0.11	0.10
<i>Corixidae</i>	-0.03	-0.30	-0.04
<i>Culex</i>	0.32	0.18	-0.61
Hydroporini	0.12	-0.58	0.09
<i>Hesperophylax</i>	0.08	-0.03	0.15
<i>Desmona</i>	-0.39	-0.13	0.49
<i>Polycentropus</i>	-0.03	-0.21	-0.02
<i>Limnephilus</i>	0.20	-0.19	-0.13
<i>Psychoglypha</i>	0.22	0.26	0.37
Oligochaeta	-0.37	0.45	-0.39
<i>Sialis</i>	0.08	-0.25	-0.31
<i>Pisidium</i>	-0.34	-0.08	-0.38
Acari	-0.16	0.15	-0.14

Note: Correlations with $r \geq 0.16$ ($P < 0.05$) are shown in boldface type.

TABLE 2. Results of stepwise multiple regression analyses showing the relationship between nonmetric multidimensional scaling scores (NMMDS) obtained for the benthic macroinvertebrate community and habitat variables.

Dependent variable	Predictors in model†	Coefficients	Partial r^2	Model R^2	Model F	Model P
NMMDS Axis 1	(Intercept)	4.770		0.10	$F_{3,183} = 6.64$	0.0003
	Elevation	-0.001	0.034			
	Lake area	-0.233	0.030			
	Percentage of littoral silt	-0.008	0.032			
NMMDS Axis 2	(Intercept)	-1.933		0.04	$F_{2,184} = 4.10$	0.0182
	Sample date	0.004	0.010			
	Lake area	0.217	0.033			
NMMDS Axis 3	(Intercept)	-2.907		0.42	$F_{6,180} = 21.74$	0.0001
	Sample date	-0.009	0.025			
	Elevation	0.002	0.222			
	Maximum lake depth	0.494	0.032			
	Lake area	-0.271	0.031			
	Percentage of littoral silt	-0.013	0.070			
	No. ponds within 250 m	-0.421	0.040			

† Independent variables initially included in the model were sample date, elevation, maximum lake depth, lake area, percentage of littoral zone composed of silt, solar input, number of lakes within a 1-km radius, and number of ponds within a 250-m radius.

effects of trout than did presence/absence data, with abundances of *Keratella quadrata*, *Keratella* spp., and *Polyarthra* spp. all being significantly higher in stocked-fish-present lakes than in never-stocked lakes ($P < 0.006$; Fig. 7B). Abundances of *Kellicottia* spp. and *C. unicornis* were similar between stocked-fish-present and never-stocked lakes ($P_{Kl} = 0.78$, $P_{Co} = 0.24$; Fig. 7B).

The two crustacean species that were strongly affected by fish presence (*H. shoshone* and *D. middendorffiana*) were both able to recover after fish disappearance. The frequency of occurrence and abundance of these two taxa were similar between stocked-now-fishless and never-stocked lakes ($P_{occur} > 0.80$, $P_{abund} > 0.30$; Figs. 6A, 7A). The frequency of occurrence of *D. rosea* and Cyclopoda was higher in stocked-now-fishless lakes than in never-stocked lakes (Fig. 6A), but neither difference was statistically significant ($P_{Dr} = 0.13$, $P_{Cy} = 0.15$). The abundances of *D. rosea* and Cyclopoda were also higher in stocked-now-fishless lakes than in never-stocked lakes, but these differences approached statistical significance only for *D. rosea* ($P_{Dr} = 0.07$, $P_{Cy} = 0.12$; Fig. 7A). The large, but non-significant difference in mean abundance of cyclopoid copepods was the result of only two of 26 stocked-now-fishless lakes containing cyclopoids, but both lakes having high densities of this taxon. The percent occurrence and abundance of *L. signicauda* and *C. sphaericus* were similar between never-stocked and stocked-now-fishless lakes ($P_{occur} > 0.3$, $P_{abund} > 0.4$; Figs. 6A, 7A). Of the three rotifer taxa whose distributions or abundances increased in the presence of fish (*K. quadrata*, *Keratella* spp., *Polyarthra* spp.), all appeared to return to predisturbance levels after fish dis-

appearance. Frequencies of occurrence and abundances of *Keratella* spp. and *K. quadrata* were similar in stocked-now-fishless and never-stocked lakes ($P_{occur} > 0.50$, $P_{abund} > 0.20$; Figs. 6B, 7B). *Polyarthra* spp. was also found in a similar percentage of stocked-now-fishless and never-stocked lakes ($P = 0.75$; Fig. 6B), but its abundance was lower in stocked-now-fishless lakes than in never-stocked lakes. The latter difference was not statistically significant, however ($P = 0.71$; Fig. 7B). The percentage of occurrence and abundance of *Kellicottia* sp. and *C. unicornis* were similar between stocked-now-fishless and never-stocked lakes (occurrence, $P_{Ke} = 0.37$, $P_{Co} = 0.72$; abundance, $P_{Ke} = 0.27$, $P_{Co} = 0.53$).

A nonmetric multidimensional scaling analysis of the zooplankton community generally confirmed the results of the taxon-specific analyses. Axes 1, 2, and 3 accounted for 74% of the variation in the ordination ($r^2 = 0.23, 0.13, \text{ and } 0.37$, respectively; stress = 17.0). NMMDS scores on Axis 1 were not significantly different between lake categories ($F_{2,174} = 0.4$, $P > 0.6$), while differences in scores between lake categories were marginally significant on Axis 2 (Fig. 8A; $F_{2,174} = 2.9$, $P = 0.06$) and highly significant on Axis 3 (Fig. 8A; $F_{2,174} = 28.8$, $P < 0.0001$). Taxa showing positive correlations with Axis 3 were those associated with fishless lakes (*H. shoshone*, *D. middendorffiana*; Table 3) while those showing negative correlations with Axis 3 were those associated with fish-containing lakes (*L. signicauda*, *D. rosea*, Cyclopoda, *Kellicottia* sp., *K. quadrata*, *C. unicornis*, *Keratella* spp., and *Polyarthra* spp.; Table 3). Taxa significantly correlated with Axis 1 and 2 did not show any obvious association with fish, but taxa positively correlated with Axis 1 were gen-

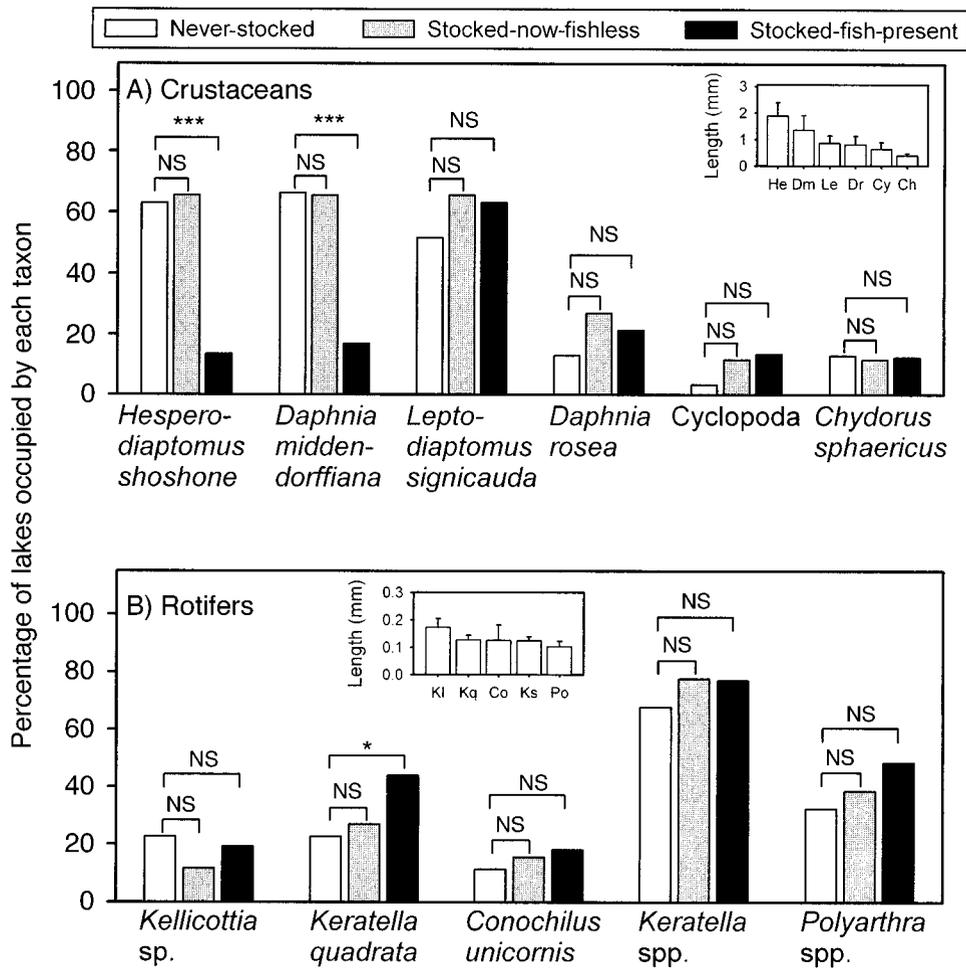


FIG. 6. For zooplankton, the percentage of never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes containing (A) crustaceans and (B) rotifers. Taxa are arranged from left to right in order of decreasing size. Sample sizes for never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes are 62, 26, and 89, respectively. Lines and associated symbols connecting each bar provide the results of pairwise Pearson's chi-square tests or Fisher's exact tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$). Inset figures in (A), (B), and (C) show sizes ($\bar{X} + 1$ SD) of each of the taxa in the corresponding figure.

erally those with high abundances (Table 3). The strong influence of fish on the zooplankton community was shown by the significantly different scores of never-stocked and stocked-fish-present lakes on Axis 3 (Fig. 8A; Tukey's HSD, $P < 0.05$). The significant difference between stocked-fish-present and stocked-now-fishless lakes on Axis 3 (Tukey's HSD, $P < 0.05$) and the lack of a significant difference between stocked-now-fishless lakes and never-stocked lakes on Axis 3 (Fig. 8A; Tukey's HSD, $P > 0.05$) suggest that the zooplankton community was able to recover to its previous configuration after fish disappearance. The similarity in mean NMMDS scores for stocked-now-fishless and never-stocked lakes on both Axis 2 and 3 (Fig. 8A) indicates that the lack of a statistically significant difference between these two lake categories was not simply the result of statistical power being too low to detect a difference.

As with the benthic macroinvertebrate community, fish disappearance was followed by a steady change in the zooplankton community away from that characteristic of stocked-fish-present lakes and toward that characteristic of never-stocked lakes (Fig. 8B). Eleven to twenty years were required before the configuration of the zooplankton community in stocked-now-fishless lakes approached that of never-stocked lakes. Changes in community configuration after 20 yr were negligible.

The correction of NMMDS scores for habitat differences between lake categories had little effect on the ordination results. Stepwise multiple regression results used to correct the NMMDS scores are shown in Table 4. As with uncorrected scores, corrected NMMDS scores on Axis 1 were not significantly different between lake categories ($F_{2,174} = 0.1, P > 0.6$) but were significantly different on Axis 3 (Axis 3, $F_{2,184} = 17.2, P < 0.0001$). The stepwise multiple regression of Axis

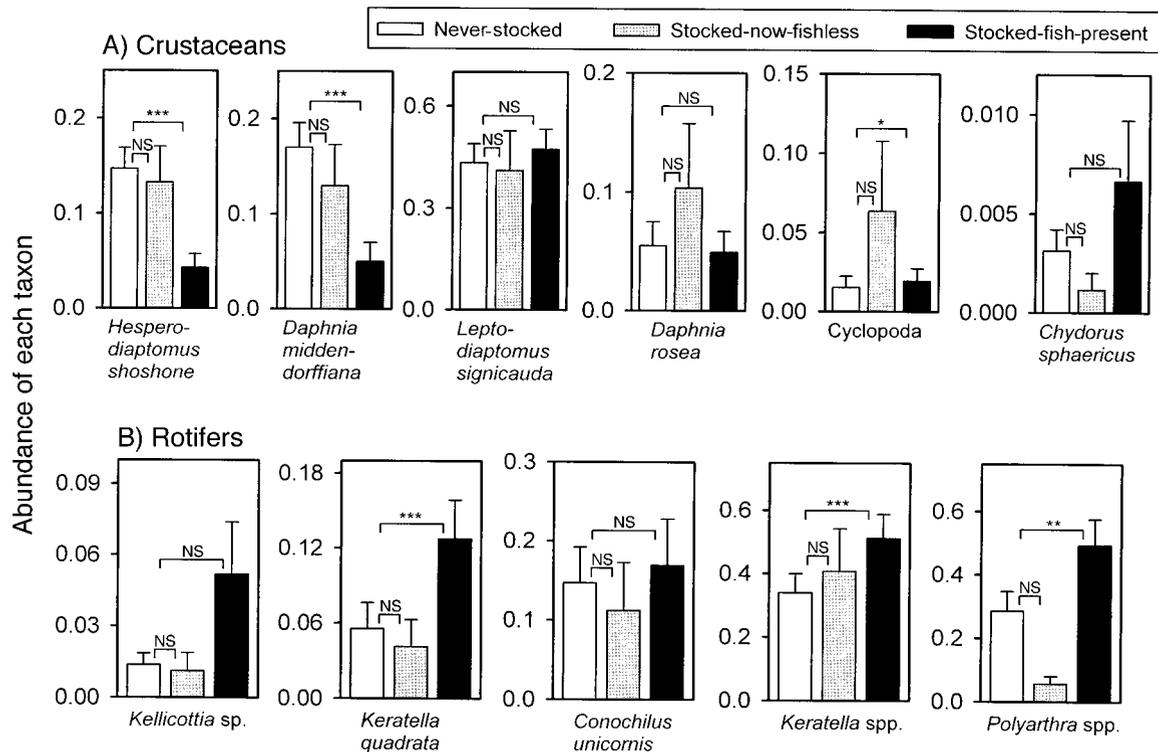


FIG. 7. For zooplankton, the abundance of (A) crustaceans and (B) rotifers in never-stocked lakes, stocked-now-fishless lakes, and stocked-fish-present lakes. Abundance was measured as the number of individuals per liter and is expressed as $\log_{10}(\text{abundance} + 1)$. Bars indicate means \pm 1 SE. Lines and associated symbols connecting each bar provide the results of pairwise Wilcoxon rank-sum tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$). Sample sizes are as in FIG. 6.

2 against all habitat variables resulted in no habitat variables being included in the model (Table 4), so no correction was possible. In comparisons between never-stocked and stocked-fish-present lakes, corrected Axis 3 NMMDS scores were significantly different (Tukey's HSD, $P < 0.05$) as were corrected Axis 3 NMMDS scores between stocked-fish-present and stocked-now-fishless lakes (Tukey's HSD, $P < 0.05$). Differences between corrected NMMDS scores for stocked-now-fishless and never-stocked lakes on Axis 3 were not significant (Tukey's HSD, $P > 0.05$). Taken together, the lack of any significant changes in ordination results after correcting for habitat differences between lake categories suggests that lake stocking histories, not habitat effects, were largely responsible for the observed patterns.

DISCUSSION

Comparisons of the faunal assemblages between never-stocked, stocked-fish-present, and stocked-now-fishless lakes indicate that the introduction of trout into fishless alpine lakes in the Sierra Nevada caused dramatic changes in the configuration of these communities, and that most common taxa recovered after trout disappeared. The changes associated with trout introductions into our study lakes are consistent with those

reported in other studies of fish effects on mountain lake faunal assemblages (United States: Bahls 1990, Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998, Tyler et al. 1998, Knapp and Matthews 2000; Canada: Anderson 1980, McNaught et al. 1999; Spain: Braña et al. 1996), and suggest that effects of introduced trout on high elevation lakes are remarkably consistent across geographically disparate areas. The community-level response to fish disappearance has rarely been studied, but our results showing recovery by most taxa are similar to those reported by the few studies that have evaluated the resilience of faunal assemblages (Keller and Yan 1991, Locke and Sprules 1994, Mittelbach et al. 1995, Yan et al. 1996, Harig and Bain 1998; but see Parker et al. 1996, Frost et al. 1998).

Resistance of amphibian populations

Comparisons between never-stocked and stocked-fish-present lakes indicated that the distribution and abundance of mountain yellow-legged frog larvae was dramatically reduced by introduced trout. These results are consistent with those of Bradford (1989), Bradford et al. (1998), and Knapp and Matthews (2000), all of which suggested that predation by introduced trout has contributed to the decline of the mountain yellow-leg-

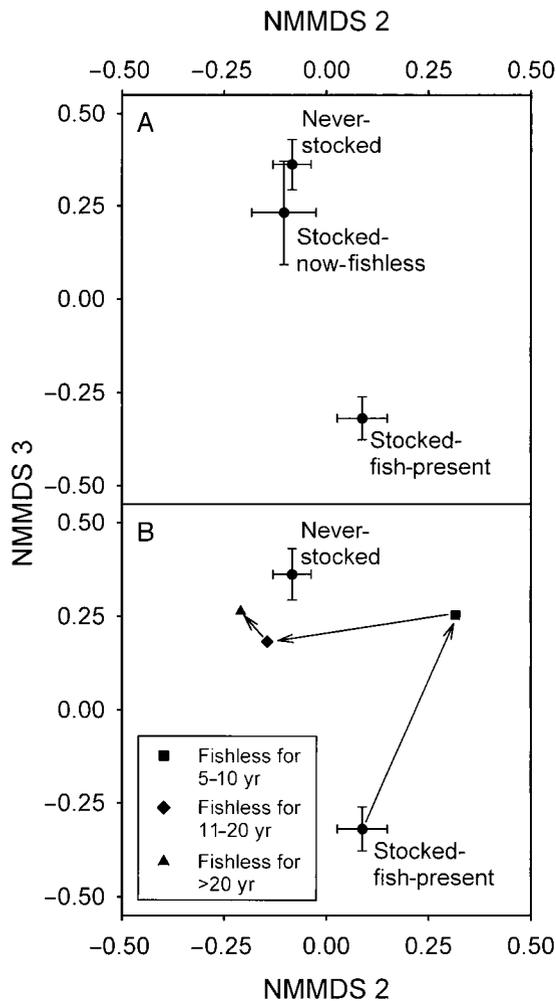


FIG. 8. (A) For common zooplankton taxa (present in $\geq 10\%$ of lakes), mean nonmetric multidimensional scaling (NMMDS) scores (± 1 SE) for never-stocked, stocked-now-fishless, and stocked-fish-present lakes on Axis 2 and Axis 3. Scores were derived from $\log_{10}(x + 1)$ -transformed abundances. Taxa showing significant associations with NMMDS axes are given in Table 3. (B) Same data as in (A) but with stocked-now-fishless lakes separated into three categories based on the number of years since fish disappearance. Error bars were removed from the stocked-now-fishless categories for clarity. Arrows indicate the trajectory of change following fish disappearance.

ged frog in the Sierra Nevada. Similar negative effects of fishes on other amphibians have also been reported (Macan 1966, Brönmark and Edenhamn 1994, Braña et al. 1996, Gamradt and Kats 1996, Hecnar and M'Closkey 1997, Tyler et al. 1998, Goodsell and Kats 1999). Negative effects of fish may be particularly strong for amphibians such as the mountain yellow-legged frog that require permanent water bodies for successful reproduction and overwintering (Knapp and Matthews 2000). Amphibians that are able to breed in temporary (and therefore fishless) habitats and have adult stages that overwinter in areas free of fish (e.g.,

terrestrial habitats) should be much less affected by fish introductions. Given that fish have been widely introduced into naturally fishless habitats worldwide (Nilsson 1972, Donald 1987, Bahls 1992, Braña et al. 1996, Townsend 1996), exotic fishes may play a more important role in global amphibian declines (Blaustein and Wake 1990, 1995) than is generally recognized.

Resistance of the benthic macroinvertebrate community

Introduced trout also had strong effects on the benthic macroinvertebrate community, and these effects were similar in direction and magnitude to those reported for alpine lakes by Bradford et al. (1998) and Carlisle and Hawkins (1998). Our results are also consistent with the results of several previous studies of fish effects on benthic macroinvertebrates conducted in a wide variety of lentic habitats (e.g., Macan 1966, Hall et al. 1970, Gilinsky 1984, Luecke 1990). In our study, the frequency and abundance of most of the taxa that swim up in the water column or cling to substrates, including case dwellers, was reduced in stocked-fish-present lakes relative to never-stocked lakes. There were two exceptions to this pattern; the distribution and abundance of *Limnephilus* caddisfly larvae was unchanged by the presence of fish, and more strikingly, the distribution and abundance of mosquito larvae (*Culex*) increased in the presence of fish. Although the reason for the lack of a fish effect on *Limnephilus* is unclear, one possibility is that its case, which is constructed from organic materials, affords more effective camouflage against the predominantly organic substrates of the study lakes than do the sand-grain cases of *Psychoglypha*, *Desmona*, and *Hesperophylax*, or the web retreat of *Polycentropus* (Otto and Svensson 1980). The unexpected increase in *Culex* in stocked-fish-present lakes may be the result of the elimination of invertebrate predators by fish. In our study lakes, *Culex* larvae are typically found in dense littoral zone aquatic vegetation. This habitat may provide a relatively high degree of protection from trout but relatively little protection from smaller invertebrate pred-

TABLE 3. Correlations of zooplankton taxa with nonmetric multidimensional scaling axes.

Taxon	Axis 1	Axis 2	Axis 3
<i>Hesperodiptomus shoshone</i>	0.17	-0.29	0.68
<i>Daphnia middendorffiana</i>	0.32	0.19	0.35
<i>Leptodiptomus signicauda</i>	0.67	0.09	-0.52
<i>Daphnia rosea</i>	0.20	-0.09	-0.29
Cyclopoda	-0.01	0.04	-0.22
<i>Chydorus sphaericus</i>	0.03	-0.10	-0.10
<i>Kellicottia</i> sp.	0.03	-0.10	-0.18
<i>Keratella quadrata</i>	-0.08	0.25	-0.23
<i>Conochilus unicornis</i>	0.24	-0.09	-0.19
<i>Keratella</i> spp.	0.28	-0.19	-0.56
<i>Polyarthra</i> spp.	0.11	0.36	-0.51

Notes: Correlations with $r \geq 0.16$ ($P < 0.05$) are shown in boldface type.

TABLE 4. Results of stepwise multiple regression analyses showing the relationship between nonmetric multidimensional scaling scores (NMMDS) obtained for the zooplankton community and habitat variables.

Dependent variable	Predictors in model†	Coefficients	Partial r^2	Model R^2	Model F	Model P
NMMDS Axis 1	(Intercept)	-1.605		0.05	$F_{2, 174} = 4.76$	0.0097
	Sample date	0.005	0.012			
	Maximum lake depth	0.418	0.040			
NMMDS Axis 2	none					
NMMDS Axis 3	(Intercept)	-6.444		0.22	$F_{3, 173} = 15.95$	0.0001
	Elevation	0.002	0.134			
	Maximum lake depth	0.557	0.063			
	No. ponds within 250 m	-0.267	0.020			

† Independent variables initially included in the model were sample date, elevation, maximum lake depth, lake area, percentage of littoral zone composed of silt, solar input, number of lakes within a 1 km radius, and number of ponds within a 250 m radius.

ators such as dytiscid beetles (Nilsson and Svensson 1995), taxa whose abundances were significantly reduced in our study by the presence of trout.

Our results indicated that burrowing or distasteful taxa either were unaffected by trout presence, or, as in the case of oligochaetes and mites, increased in the presence of trout. Carlisle and Hawkins (1998) also provided evidence that oligochaetes (*Lumbriculus*) were more abundant in trout-containing lakes and suggested that this could be the result of either decreased interspecific competition or of trout enhancing food availability to deposit feeding taxa such as oligochaetes by increasing the flow of nutrients to lake bottoms (e.g., Leavitt et al. 1994). Given the relatively high abundances of oligochaetes in alpine lakes, understanding the causes and consequences of changes in the abundance of this taxon may provide important insights into the food web structure and energy flow in these systems (Carlisle and Hawkins 1998).

Resistance of the zooplankton community

Comparisons between never-stocked and stocked-fish-present lakes showed that trout reduced the distribution and abundance of large zooplankton. Similar results have been reported in many others studies of fish effects on zooplankton communities in alpine lakes (Anderson 1980, Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998) and lentic systems in general (Brooks and Dodson 1965, Northcote et al. 1978, Vanni 1987, Mittelbach et al. 1995). Small crustacean zooplankton taxa were relatively unaffected by the presence of fish, with the exception of cyclopoid copepods which increased in abundance. The abundance of rotifer taxa also increased markedly in the presence of fish, although changes in rotifer distribution were small. Bradford et al. (1998), using presence/absence data, reported no effects of trout on rotifers in Sierra Nevada lakes. The similarity of our results based on rotifer presence/absence data to those of Bradford et al. (1998) but the much stronger effects we observed

based on abundance data highlights the importance of using abundance data to better characterize the subtler effects of fish on invertebrate communities. The positive response of cyclopoids and rotifers to fish presence is common in alpine lakes (Anderson 1972, Stoddard 1987, Carlisle and Hawkins 1998) and in other lentic habitats (Vanni 1987, Gilbert 1988, Christofferson et al. 1993). In alpine lakes, the increase in rotifer abundance may result from the elimination of planktonic predators (*Hesperodiaptomus*) and competitors (*Daphnia*) by fish (Anderson 1980, Gilbert 1988, Paul and Schindler 1994, Paul et al. 1995, Sarnelle 1997).

Resilience of amphibian populations

One of the most striking results of our study was that mountain yellow-legged frog larvae recovered after fish disappearance to levels typical of those in never-stocked lakes. In light of the increasing alarm about worldwide amphibian disappearances (Blaustein and Wake 1990, 1995) and the likely role of introduced fishes in a number of these declines, our results suggest that some of these declines could be reversed simply by removing trout from some of the lakes where they have been introduced (Funk and Dunlap 1999). However, because the mountain yellow-legged frog is closely tied to water and apparently moves only relatively short distances (Matthews and Pope 1999), recolonization of lakes that have been returned to a fishless condition may be strongly influenced by the proximity of nearby source populations. This possibility is supported by the fact that in our study, stocked-now-fishless lakes that contained frogs were much more likely to have one or more reproducing mountain yellow-legged frog populations within 1 km than were stocked-now-fishless lakes that lacked frogs (77% vs. 5%; Fisher's exact test, $n = 29$, $P < 0.001$).

The apparent importance of nearby source populations for successful recolonization by the mountain yellow-legged frog has important implications for the resilience of this species. The majority of stocked-now-

fishless lakes in our study lost their fish populations >20 yr ago. Given that mountain yellow-legged frogs have declined by >80% during the past century (Drost and Fellers 1996) and remaining populations continue to disappear (R. Knapp, *unpublished data*—apparently as a result of habitat fragmentation and isolation by introduced trout; Bradford et al. 1993), lakes that revert to a fishless condition in the future will be increasingly unlikely to be recolonized as the number of potential frog source populations continues to diminish (Bradford et al. 1993).

Resilience of the benthic invertebrate community

Although the benthic macroinvertebrate community was profoundly altered by fish introductions, most taxa appeared to recover after fish disappearance to levels characteristic of never-stocked lakes, as did the configuration of the benthic community as a whole. These results support the conclusions of Niemi et al. (1990) that lake benthic macroinvertebrate communities are generally resilient to most disturbances that leave habitats unimpaired. In our study, none of 15 taxa had frequencies of occurrence that were significantly different between stocked-now-fishless and never-stocked lakes. All taxa in the clinger/swimmer category recovered to levels at or above that of never-stocked lakes, and this resilience may have been facilitated by the strong flying abilities of their adult stages. Adult mayflies are known to disperse tens of kilometers (Gibbs et al. 1998), a distance sufficient to allow recolonization of most stocked-now-fishless lakes by animals dispersing from never-stocked lakes. Oligochaetes and mites (burrowing/distasteful category) increased in the presence of fish, but also returned to predisturbance levels (or nearly so) after fish disappearance. Mites were not found in any of the 22 stocked-now-fishless lakes, but based on the occurrence of mites in only 15% of never-stocked lakes, they would only have been expected to occur in three stocked-now-fishless lakes. Therefore, our failure to detect mites in any of the stocked-fishless lakes is likely the result of sampling error and not recovery failure.

In contrast to the relatively high resilience of clinger/swimmer and burrower/distasteful taxa, case-dwelling caddisflies appeared to have relatively limited abilities to recover after fish disappearance. While *Desmona* did recover to predisturbance levels, *Polycentropus* and *Psychoglypha* may have failed to do so. The reasons for the low resilience of these taxa are unclear as little natural history information is available. However, dispersal by caddisflies is often relatively restricted (Kovats et al. 1996, Bunn and Hughes 1997, Collier and Smith 1997) and Sode and Wiberg-Larsen (1993) concluded that because of this limited dispersal, recovery of caddisflies after disturbance may often require decades.

Resilience of the zooplankton community

Despite the substantial alteration of the zooplankton community by fish introductions, after fish disappearance the distribution and abundance of most zooplankton taxa returned to levels characteristic of never-stocked lakes. This capacity to recovery after a disturbance has also been reported for zooplankton communities in other lentic ecosystems (Keller and Yan 1991, Locke and Sprules 1994, Mittelbach et al. 1995, Yan et al. 1996, Harig and Bain 1998; but see Parker et al. 1996, Frost et al. 1998). In our study, all of the 11 common taxa showed similar percent occurrences in stocked-now-fishless and never-stocked lakes. Abundances in stocked-now-fishless lakes and never-stocked lakes were similar for all taxa except *Daphnia rosea*, a species that was unaffected by fish introductions but may have increased slightly after fish disappearance. The reduction in rotifer abundances following fish disappearance was probably a consequence of an increase in the abundance of *Hesperodiptomus shoshone* and *Daphnia middendorffiana* to predisturbance levels. Reintroduction of *Hesperodiptomus arcticus* into an alpine lake in the Canadian Rocky Mountains also resulted in the rapid suppression of the rotifer community (McNaught et al. 1999).

The recovery of *H. shoshone* and *D. middendorffiana* after fish disappearance was likely facilitated by the relatively long-lived resting eggs characteristic of these two genera. Parker et al. (1996) presented evidence that the resting egg bank of *Hesperodiptomus arcticus* in alpine lakes of the Canadian Rocky Mountains could remain viable for at least 15–20 yr, and >100 yr-old eggs of a related copepod, *Diaptomus sanguineus*, have been hatched (Hairton et al. 1995). Similarly, resting eggs of *Daphnia* can remain viable for >125 yr (Cáceres 1998). However, if resting eggs of *H. shoshone* remain viable only for several decades (like those of *H. arcticus*), recovery of *H. shoshone* may be much less likely in lakes that return to a fishless condition in the future than in the lakes used in this study. On average, fish were first introduced to our stocked-now-fishless lakes in the mid-1940s. By the time stocking was halted and fish populations disappeared, these lakes had harbored fish populations for a mean of only 29 yr. By contrast, lakes that were first stocked at the same time but that still contain fish populations today (either because of continued stocking or because of natural reproduction) have had fish populations for >50 yr and may no longer contain a viable *H. shoshone* egg bank (e.g., Parker et al. 1996). The possibility that the resilience of *H. shoshone* populations is a function of fish-occupancy time is supported by recent research in which we used paleoecological analyses to establish the historical occurrence of *H. shoshone* in 25 stocked-now-fishless lakes. *H. shoshone* reappeared in 86% of those lakes that had contained an introduced trout population for <50 yr, while it failed to reappear in any

of the lakes that had contained a trout population for >50 yr (R. Knapp and O. Sarnelle, *unpublished data*). With depletion of the egg bank, the only means by which *H. shoshone* could recolonize stocked-now-fishless lakes is via over-land transfers from nearby *H. shoshone* populations. The likelihood of such transfers resulting in the successful reestablishment of a population is likely to be very low (Boileau and Hebert 1988).

Conclusions

Our snapshot sampling of never-stocked, stocked-fish-present, and stocked-now-fishless lakes was successful in providing a broad, albeit relatively coarse-grained view of the resistance and resilience of amphibian, benthic macroinvertebrate, and zooplankton communities to fish introductions. In doing so, we believe we have satisfied many of the criteria set forth by Connell and Sousa (1983) as necessary to demonstrate system stability. Our study was based on data collected at least 30 yr after fish introductions took place and given the short generation times of zooplankton and benthic macroinvertebrates (generally one year or less) this time frame would have allowed many complete turnovers of these communities. We evaluated recovery of these faunal assemblages over a similarly long time frame. In addition, our study utilized dozens of replicate lakes and demonstrated that, with some minor exceptions, the response of these systems to a perturbation and to the removal of the perturbation was highly predictable.

Our snapshot approach provided a greater spatial and temporal perspective of the resistance and resilience of lake fauna than any previous study, but our approach also had several limitations. First, our study was observational in nature and therefore did not allow us to unambiguously determine cause and effect. Such a determination would only be possible with a replicated whole-lake design, such as the one we are currently using to assess recovery of lake ecosystems after the experimental removal of exotic trout (R. Knapp and O. Sarnelle, *unpublished data*). Second, because our "treatments" were constructed from lakes with different fish stocking histories (never-stocked, stocked-fish-present, and stocked-now-fishless) instead of from lakes that had treatments randomly assigned to them, our study design confounded effects due to fish and those due to habitat differences between lake categories. The fact that correcting for habitat influences had little effect on the ordination results suggests that the observed differences in faunal assemblages between lake categories were largely the result of fish stocking history and not habitat effects. A third shortcoming of our approach is that one-time sampling may only poorly characterize benthic macroinvertebrate and zooplankton presence/absence and abundance due to the high seasonal and interannual variability of many taxa (Arnott et al. 1998, 1999). In the alpine lakes that were

the focus of our study, the summer growing season is short, allowing only a single generation for many taxa. Perhaps as a result, invertebrate species composition and richness changes little over the course of the summer (Stoddard 1987, Engle and Melack 1995; R. Knapp and O. Sarnelle, *unpublished data*). Our sampling undoubtedly failed to document the presence of some rare taxa, but inclusion of these rare taxa as a result of a more intensive sampling regime would likely have had little effect on the results due to their relative unimportance in describing community structure. Abundances of some species characteristic of our study lakes do fluctuate markedly over the course of a single summer (e.g., rotifers; R. Knapp and O. Sarnelle, *unpublished data*). Although these fluctuations make it impossible to precisely quantify species abundance from a single sample, these inaccuracies are a source of noise, not bias, and should therefore not have unduly influenced our results. The fact that correction of NMMDS scores for sampling date (and habitat variables) did not alter the ordination results further suggests that snapshot sampling was sufficient to describe resistance and resilience of the invertebrate communities. A final weakness of our study is that we were only able to estimate resilience by comparison of the frequency and abundance of taxa between stocked-now-fishless and never-stocked lakes. While this comparison should provide a reasonable approximation given our relatively large sample sizes, the strength of our inferences as to whether a taxon had recovered or not was considerably lower than what could be achieved by following faunal changes after fish disappearance in multiple lakes whose past community structure was known. To increase the strength of our inferences, we are currently combining our snapshot approach with paleoecological analyses (Knapp et al. 2001) to determine more accurately how often the large zooplankton species, *H. shoshone* and *D. middendorffiana*, fail to recolonize and what the consequences of such failures are for zooplankton community structure. Indeed, preliminary results from these finer scale analyses indicate that *H. shoshone* fails to reestablish in ~10% of lakes following fish disappearance.

Our finding that the fauna included in this study generally have high resilience after fish disappearance has important implications for restoration of these alpine lake ecosystems. The majority of high mountain lakes in the Sierra Nevada are located within national parks and national forest wilderness areas, areas set aside in part to protect natural processes. However, the introduction of trout into these naturally fishless habitats has dramatically altered these systems, and there is increasing interest in returning some lakes to a fishless condition (Knapp and Matthews 1998). The National Park Service has already initiated such a program by ending fish stocking on many of the lands under its jurisdiction. In the Kings Canyon National Park portion of our study area, all fish stocking was halted in 1977,

and many of our stocked-now-fishless lakes are the result of this policy change. The results of our study indicate that this policy change has accomplished its goal of allowing the fauna of these lakes to recover their predisturbance configurations, and argue for more intensive fish removal efforts not only in the national parks, but also in national forest wilderness areas, where upwards of 80% of larger lakes still contain introduced trout populations (Bahls 1992, Knapp and Matthews 2000). Given the declining status of the mountain yellow-legged frog and the likely decline in zooplankton egg bank viability with increasing duration of trout occupation, we suggest that any delay in undertaking these restoration activities may further reduce the chances that the target aquatic communities will fully recover.

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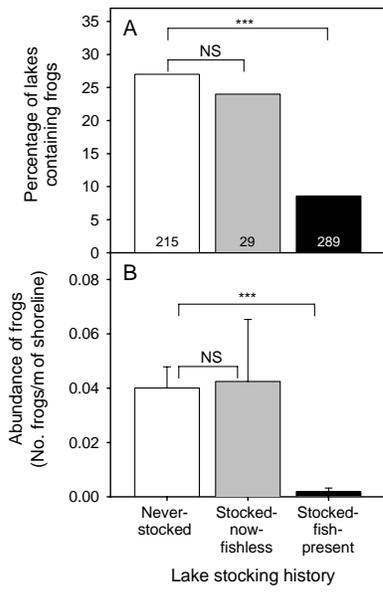


Figure 2A was misprinted in the Ecological Monographs paper. The corrected Figure 2 is provided here.