Trends data Sierra Nevada lakes

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Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes

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Abstract: In an alpine area of the Sierra Nevada of California, naturally acidic waters and introduced fishes both strongly affect the distributions of native amphibians, zooplankton, and macroinvertebrates. The study area in Kings Canyon National Park contains 104 lakes with pH values between 5.0 and 9.3, including 10 lakes with pH < 6.0 (defined here as acidic lakes) and 18 lakes with introduced trout. We surveyed 33 of these lakes (8 acidic, 7 non-acidic with trout, 18 non-acidic without trout) for water chemistry and faunal assemblages. Yellow-legged frog tadpoles (*Rana muscosa*), common microcrustaceans (*Daphnia, Hesperodiaptomus, Diaptomus*), and larvae of a caddisfly (*Hesperophylax*) were rare or absent in acidic lakes but common in non-acidic lakes, and microcrustacean and macroinvertebrate species richness decreased with decreasing pH. Large and (or) mobile, conspicuous taxa, including tadpoles, large-bodied microcrustaceans (*Hesperodiaptomus, Daphnia middendorffiana*), and many epibenthic or limnetic macroinvertebrates (baetid and siphlonurid mayfly nymphs, notonectids, corixids, limnephilid caddis larvae, and dytiscid beetles), were rare or absent in trout lakes but were relatively common in lakes lacking trout, and the taxon richness of macroinvertebrates was reduced by trout.

Résumé : Dans un secteur alpin de la chaîne de la Sierra Nevada, en Californie, les eaux acides naturelles et les poissons introduits exercent une profonde influence sur la répartition des espèces indigènes d'amphibiens, de zooplancton et de macroinvertébrés. La zone d'étude, située dans le parc national Kings Canyon, renferme 104 lacs dont le pH varie entre 5,0 et 9,3, y compris 10 lacs présentant un pH < 6,0 (définis ici comme des lacs acides) et 18 lacs contenant des truites introduites. Nous avons étudié la chimie de l'eau et la composition faunistique de 33 de ces lacs (8 lacs acides, 7 lacs non acides contenants des truites et 18 lacs non acides sans truites). Des têtards de la grenouille *Rana muscosa*, des microcrustacés communs (*Daphnia, Hesperodiaptomus, Diaptomus*) et des larves d'un éphéméroptère (*Hesperophylax*) étaient rares ou absents dans les lacs acides, mais communs dans les lacs non acides, et le nombre d'espèces de microcrustacés et de macroinvertébrés diminuait en fonction de l'acidité. Les taxons de plus grande taille et(ou) mobiles et plus visibles comme les têtards, les gros microcrustacés (*Hesperodiaptomus, Daphnia middendorffiana*) et de nombreux macroinvertébrés épibenthiques ou limnétiques [larves de baetides et de siphlonurides (éphéméroptères), notonectides, corixides, larves de limnéphilides (Trichoptères) et dystiscides] étaient rares ou absents dans les lacs contenant des truites, mais relativement communs dans les lacs sans truites. Le nombre de taxons de macroinvertébrés était moins élevé dans les lacs contenant des truites.

[Traduit par la Rédaction]

Introduction

It is well known that abiotic factors, such as water chemistry, and biological interactions, such as predation, can affect the diversity, biomass, and species composition of freshwater animal communities (Brett 1989; Magnuson et al. 1984; Locke 1992; Brezonik et al. 1993). For example, the effects of fish on freshwater zooplankton communities are strong and well documented (Brooks and Dodson 1965; Anderson 1980). Moreover, chemical characteristics of lakes, such as acidity, impose constraints on the distribution of freshwater organisms with repercussions for the structure of the community and the intensity of biological interactions (Freda 1990; Havens 1993; Locke 1992). There have been few studies, however, on the effects of acidity and trophic structure on lake communities in the western U.S.

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(Stoddard 1987; Barmuta et al. 1990; Bradford et al. 1993, 1994*b*).

Although almost all lakes at high elevations in the Sierra Nevada (i.e., >2600 m elevation, defined herein as "High Sierra") have a pH > 6, a small number of acidic lakes (pH < 6) were recently discovered in the Mt. Pinchot area of Kings Canyon National Park, California, U.S.A. (Whiting et al. 1989; Bradford et al. 1994*a*). The source of acidity in this area is sulfuric acid produced by the oxidation of pyrite found in metamorphic and granitic rocks (Mahood and Gansecki 1993; Bradford et al. 1994*a*). Unlike typical Ca^{2+}–Na^{+}–HCO_3^{-}-dominated Sierran lakes, SO_4^{-2} is the dominant anion in 19 of the lakes in this area, including all of the acidic lakes (Melack and Stoddard 1991; Bradford et al. 1994*a*). The mixture of acidic and non-acidic lakes found in this area allowed us to evaluate relationships between long-term, acidic conditions and the distribution of the aquatic biota. Because most of the lakes in the High Sierra are very dilute and weakly buffered, there is concern that future increases in acid loading from anthropogenic sources could result in acidification of these lakes with attendant decreases in aquatic biodiversity (Melack et al. 1989; Barmuta et al. 1990; Melack and Stoddard 1991; Bradford et al. 1994*b*). The characteristics of naturally acidic lakes, then, may provide an indication of the long-term effects of potential cultural acidification on the composition of lake communities in the High Sierra.

Furthermore, many of these lakes have not been stocked with fish because of their remote locations, allowing us to evaluate the effects of trophic structure (presence vs. absence of fish) on lake communities. Nearly all of the montane lakes and streams in western North America were originally devoid of fish (Bahls 1992). In the last century, however, many of these waters were stocked with fish, particularly trout, to provide recreational fisheries. It has been estimated that approximately 60% of the montane lakes in western North America now contain fish, including 95% of the larger (>2 ha) and deeper (>1.5 m) lakes (Bahls 1992). The effects of non-native fish introductions on the native biota have been little studied in High Sierra waters; however, limited observations suggest that introduced fish have caused declines in native aquatic invertebrates and amphibians (Melack et al. 1989; Stoddard 1987; Bradford et al. 1993). Because most High Sierra waters now contain introduced trout, the effects of these introductions on biodiversity may be substantial (Knapp 1996).

The goal of this study was to examine relationships among lake acidity (e.g., pH), other water chemical parameters (e.g., major ion concentrations), the presence of nonnative fish, and zooplankton, macroinvertebrate, and amphibian assemblages (e.g., taxon presence–absence, abundance, and (or) taxon richness). We hypothesized that large, conspicuous, exposed taxa would be reduced or eliminated where fish predators are present (Brooks and Dodson 1965; Northcote 1988) and that taxa shown to be especially sensitive to acidic conditions would be rare or absent in acidic lakes (Brett 1989; Melack et al. 1989). We surveyed chemical conditions and the presence–absence of vertebrate populations in 104 lakes in the Mt. Pinchot area and then chose a subset of 33 of these lakes for detailed analyses of water chemistry, fish, amphibians, zooplankton, and macroinvertebrates. We compared our survey results with the results of earlier short-term, small-scale field experiments and laboratory studies in which acidity was manipulated to examine congruence between these observational and experimental approaches.

Materials and methods

Study area and design of study

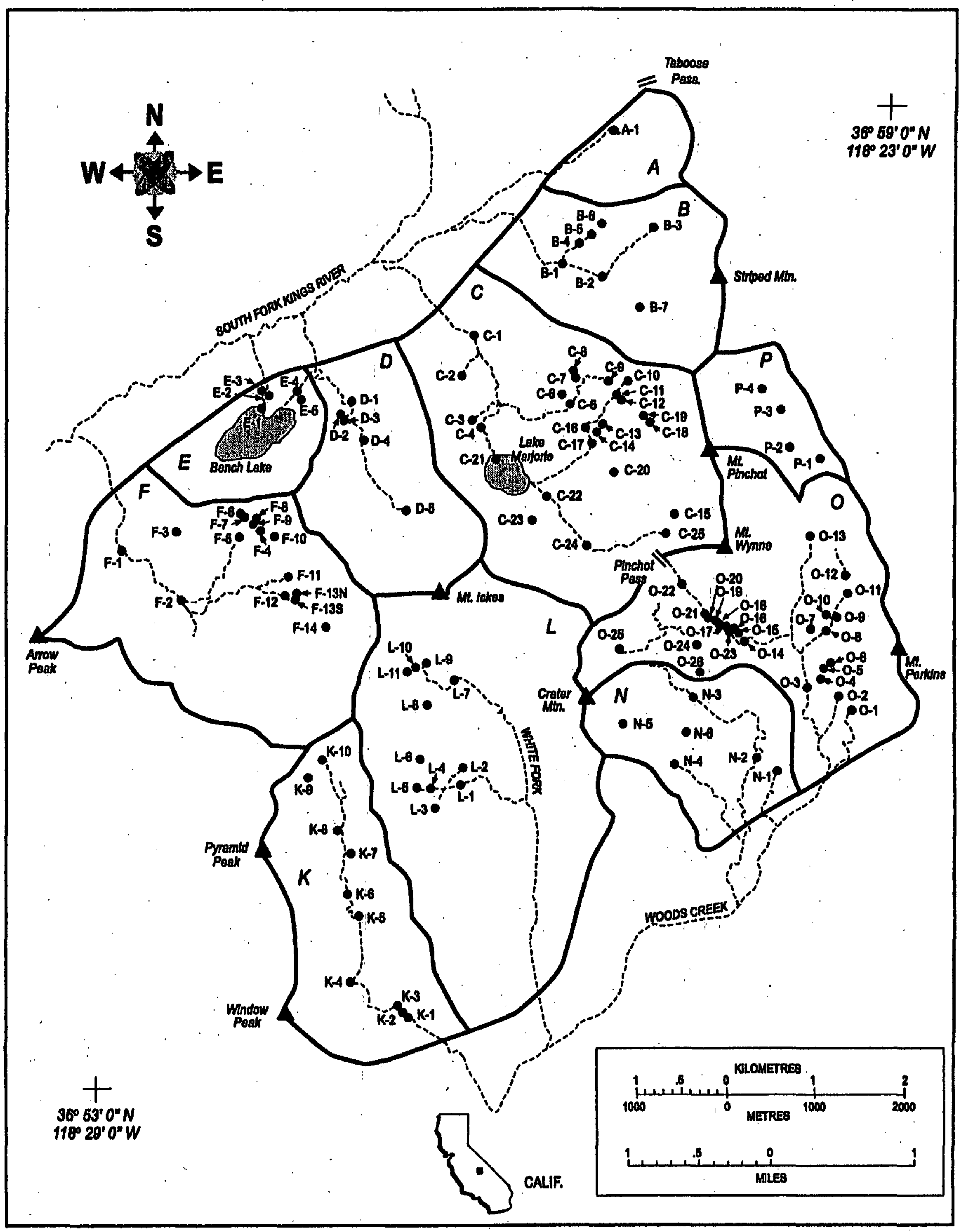
The study area was approximately 50 km^2 in area, located in Kings Canyon National Park in eastern California (Fig. 1). This area includes 11 catchments, six that drain into the South Fork of the Kings River and five that drain into Woods Creek (Fig. 1). The geological formations of the study area are a complex mixture of large granodiorite masses and metasedimentary roof pendants, including biotite schist, calc-hornfels, marble, and peltic hornfels and quartzite (Moore 1963). The study area encompassed four Sierra Nevada lakes recently found to have pH values of 4.6 to 5.2 (Whiting et al. 1989; Bradford et al. 1994*b*; Jenkins et al. 1994). These are lower than the lowest summer pH reported for other lakes in the Sierra Nevada (pH 5.6) and are also lower than pH values reported for all but one of the lakes surveyed in the western U.S. by the Environmental Protection Agency's Western Lake Survey (Melack et al. 1985; Landers et al. 1987; Melack et al. 1989; Whiting et al. 1989; Jenkins et al. 1994; Stoddard 1995).

The study consisted of a synoptic survey and a detailed survey. In the synoptic survey, we documented chemical conditions and the presence–absence of vertebrate populations in 104 high-elevation lakes (>3100 m elevation), representing all lakes in the study area (Fig. 1). For the detailed survey, 33 lakes were chosen from the above set for detailed analyses of their chemical and biological characteristics. We first chose all of the acidic lakes (pH < 6) in this area because of their rarity, except for two that were extremely shallow (<0.5 m depth) and near larger, deeper acidic lakes. Second, we chose two lakes (Bench and Marjorie), both containing fish, because chemical data had been collected from them in previous studies. We chose five additional fish lakes near acidic lakes, attempting to match the elevation, size, and depth of these lakes to the acidic lakes. These attempts to match the physical characteristics of fish and acidic lakes were only partially successful because fish tended to occupy the largest and deepest lakes in this area. Finally, we chose 18 non-acidic (pH > 6) fishless lakes near acidic and fish lakes so that their elevations, sizes, and depths matched those of acidic lakes (pH < 6.0) as closely as possible. We chose pH 6.0 as the cut-off for delineating acidic vs. non-acidic lakes because previous experimental studies indicated that sensitive taxa begin to decline between pH 5.5 and 6 (Melack et al. 1989; Barmuta et al. 1990). Because fish were absent in acidic lakes, these procedures provided 8 acidic lakes, 7 fish lakes, and 18 non-acidic, fishless lakes for comparisons.

Synoptic survey

The 104 lakes in the synoptic survey were surveyed between 29 June and 4 July, 1992, for the presence–absence of fish and amphibians by walking along the shoreline of most or all of each lake (Bradford et al. 1994*b*). Because these lakes were extremely clear and often small, large areas of these lakes could be viewed from shore. Later, gill net surveys (see Detailed survey section) showed that shoreline surveys accurately assessed the presence or absence of fish. Amphibians were captured by hand net if necessary to identify species. Amphibians were recorded as either tadpoles or "adults" (defined as metamorphosed individuals, regardless of size). pH and specific conductance were measured in the field on the same day as sampling using standard methods (described below). Elevation and lake area were determined from topographic maps. Maximum lake depth was estimated visually to 0.5 m up to

Fig. 1. Study area showing catchment boundaries, Kings Canyon National Park, California. Closed, labeled circles correspond to lakes shown on base map (U.S. Geological Survey, 7 1/2′ quadrangle, Mt. Pinchot, Calif., Provisional Edition, 1985). The 33 lakes in the detailed survey are as follows: acidic lakes (C-22, -24; F-1, -2, -13N, -14; L-7, -11), fish lakes (B-1; C-4, -5, -21; D-4; E-1; N-3), and non-acidic, fishless lakes (B-5; C-2, -10, -17, -23; D-5; E-4; F-4, -11, -12, -13S; L-1, -8, -9; O-7, -8, -21; P-3). Inset map shows location of this area in California.



a maximum of 5 m. Subsequent measurements of 32 lakes by plumb line in the detailed survey were highly correlated with these estimated values (Spearman rank correlation test, $p < 0.001$).

Detailed survey

For the 33 lakes chosen, we collected samples of fish, macroinvertebrates, zooplankton, and water and recorded observations of amphibians between 11 August and 1 September 1992. Fourteen of the 33 lakes were sufficiently shallow and clear that investigators could scan the whole water mass from the shoreline or a small raft to ascertain the presence or absence of fish. Fish populations were surveyed in the remaining 19 lakes by using a gill net, which was 43.5 m long, 1.5 m deep, and consisted of 6 equal-sized panels with mesh sizes of 2.5, 3.1, 3.7, 4.3, 4.9, 5.5, and 6.2 cm. The net was anchored on shore with the smallest mesh in the shallowest water and was deployed along the bottom perpendicular to the shoreline. This net was scanned continually and any fish captured were removed at 20-min intervals. If no fish were captured by nightfall, the net was left in place overnight and checked the following morning. Visual searches for amphibians were conducted from the raft and from shoreline areas.

Macroinvertebrates in the littoral zone of each lake were sampled by conducting multiple sweeps with a D-net (mesh size = 1 mm) over a 30-min period. Occasionally, sampling was done over shorter time periods when macroinvertebrates were extremely abundant. D-net sweeps followed bottom contours and sampled epibenthic, water column, and surficial sediment habitats that could be reached from shore. All habitat types were included, which consisted almost exclusively of silt-covered rocks with sand and silt between the rocks. Macroinvertebrates were sorted from debris and sediments in the field and then preserved in 70% ethanol. Macroinvertebrates were identified at 12–25× under a dissecting microscope using keys in Merritt and Cummins (1984) and Thorp and Covich (1991). Insects (other than chironomids), mollusks, and crustaceans were identified to genus. Chironomids were identified to tribe or subfamily, and mites were identified as the subclass Acari.

Zooplankton were sampled from a rubber raft by taking vertical tows with a plankton net (29.5 cm diameter, 40 µm mesh) from the deepest part of each lake at mid-day. The net was repeatedly lowered to the bottom and then retrieved until substantial numbers of zooplankton were present in samples. Filtered volumes for zooplankton samples were calculated assuming a net efficiency of 50% (Walters and Vincent 1973). Zooplankton samples were preserved in 5% formalin. In the laboratory, zooplankton samples were rinsed on a 45-µm sieve and then washed and diluted with water in a beaker. Subsamples (1 mL) were removed from the diluted sample with a wide-bore pipette, and subsamples of zooplankton were identified and counted in a Sedgewick–Rafter cell at 40× under a compound microscope. Depending on the abundance of zooplankton, from 1% to entire samples were counted. Microcrustaceans were identified using Edmondson (1959) and rotifers were identified using Stemberger (1979).

Water samples were collected by hand from lake outlets for analyses of pH, acid-neutralizing capacity (ANC), specific conductance, major ions, and aluminum. Samples were collected by entirely filling high-density polyethylene bottles that had been rinsed with deionized water. Sample aliquots for field determinations of pH and specific conductance and for laboratory determinations of ANC were simply decanted into bottles, sealed, and kept in the dark and cool (<10°C) until analysis. An aliquot for Cl, NO_3, SO_4, Ca, Mg, Na, and K was filtered through a 0.45 µm pore polycarbonate filter membrane into a bottle, sealed, and kept cool. An aliquot for total Al was filtered through a 0.1 µm pore polycarbonate filter, acidified with purified nitric acid, and sealed in an acid-leached bottle.

pH and specific conductance were measured using a Fisher Accumet 1000 pH meter with Accuphast glass electrode and a portable digital conductivity meter calibrated with National Institute for Standards and Testing conductivity standards. ANC was determined by incremental titration with 0.1 N HCl (Gran titration; Talling 1973). The anions Cl, NO_3, and SO_4 were analyzed using ion chromatography (Dionex AS4A column, sodium bicarbonate eluent). The cations Al, Ca, Na, Mg, and K were analyzed by atomic absorption. For greater sensitivity, a graphite furnace was used to atomize Al for atomic absorption analysis. Maximum lake depth was measured by plumb line from a raft.

Statistical analyses

We tested for normality and homogeneity of variances of data using Shapiro–Wilk and F tests. Because these assumptions were sometimes not met, we present the results of nonparametric tests for most comparisons, including the Wilcoxon two-sample test for comparing two groups and the Kruskal–Wallis test or ANOVA on ranked values followed by Tukey's HSD test for multiple comparisons. Our analyses, however, showed that parametric and nonparametric tests produced nearly identical results. Fisher's exact test was used to examine associations between the presence–absence of macroinvertebrate, zooplankton, and amphibian taxa and lake acidity (acidic vs. non-acidic) or the presence–absence of fish. Principal components analysis was used on the relative (macroinvertebrates) or absolute (limnetic zooplankton) abundances of common taxa (present in >5 lakes), and principal component scores for the three lake categories (acidic, fish, and non-acidic, fishless) were compared using one-way ANOVAs and Tukey's HSD tests. Correlation or regression analyses were used to relate zooplankton abundance or species richness and macroinvertebrate species richness to lake pH. Data on the relative abundances of macroinvertebrate taxa were angularly (arcsine square root) transformed and data on the absolute abundances of zooplankton taxa were $\log(x + 1)$ transformed before analyses to meet assumptions of parametric tests. All statistical tests were two-tailed, $\alpha = 0.05$, unless otherwise stated.

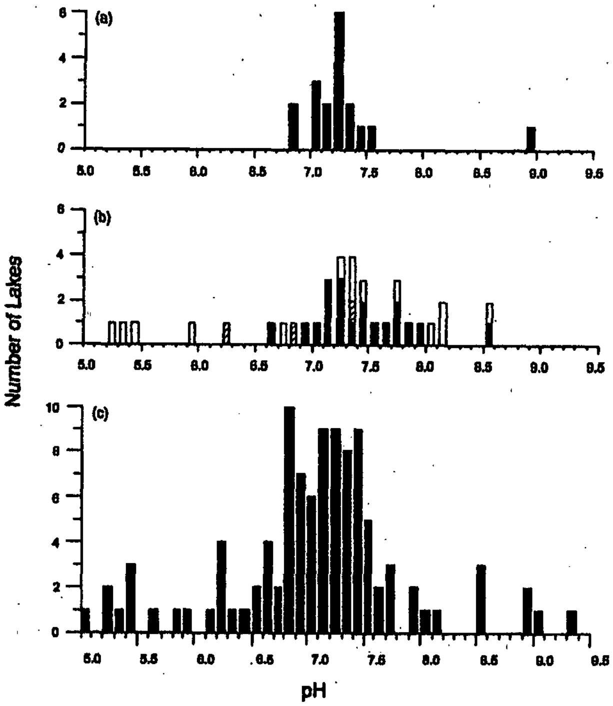
Results

Synoptic survey

The 104 surveyed lakes ranged in pH from 5.0 to 9.3 (median = 7.15) and included 10 lakes with pH < 6.0 (Fig. 2). Lakes ranged in conductivity from 2 to 102 µS/cm (median = 15 µS/cm), in elevation from 3130 to 3675 m (median = 3438 m), in estimated maximum depth from <0.5 to >5 m (median = 3.0 m), and in area from 0.03 to 30.5 ha (median = 0.31 ha). Acidic lakes had significantly higher conductivities than non-acidic lakes (medians = 35.5 and 14.8 µS/cm, respectively; Wilcoxon test, $p = 0.002$), whereas acidic lakes did not differ from non-acidic lakes in elevation, lake area, or maximum depth (Wilcoxon tests).

Golden trout (*Oncorhynchus mykiss aguabonita*), brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss irideus*), or brown trout (*Salmo trutta*) were found in 18 of the 104 lakes. Trout were absent from all 10 lakes with pH < 6 but were also absent from 76 of the 94 lakes with pH > 6 (Fisher's exact test on trout presence vs. absence in acidic vs. non-acidic lakes, $p = 0.20$; Fig. 2). Lakes containing trout were lower in elevation, larger in area, and deeper than lakes lacking trout. Median elevation was 3285 m in fish lakes and 3470 m in fishless lakes (Wilcoxon test, $p < 0.001$), and trout were not found in the 27 lakes above 3515 m elevation. Median lake area was 1.64 ha in fish

Fig. 2. Frequency distribution of pH in the synoptic survey. (*a*) Lakes where trout were observed ($n = 18$). (*b*) Lakes where yellow-legged frog (*Rana muscosa*) tadpoles and adults were observed ($n = 36$). Solid bars represent lakes containing both tadpoles and adults ($n = 19$); hatched bars represent lakes with tadpoles only ($n = 3$); and open bars represent lakes with adults only ($n = 14$). (*c*) All lakes surveyed ($n = 104$).



lakes and 0.26 ha in fishless lakes (Wilcoxon test, $p = 0.001$) and median estimated maximum depth was >5 m in fish lakes and 2.5 m in fishless lakes (Wilcoxon test, $p = 0.020$). Among non-acidic lakes, conductivity was higher in lakes containing fish (median = 23.1 μS/cm) than in lakes lacking fish (median = 12.9 μS/cm; Wilcoxon test, $p = 0.036$), but pH did not differ between fish and fishless lakes.

Amphibians observed in lakes were the tadpoles and adults of the mountain yellow-legged frog (*Rana muscosa*) and the tadpoles of the Pacific treefrog (*Hyla regilla*). Tadpoles of the yellow-legged frog were found in 22 lakes (19 with adults), and adults alone were found in 14 additional lakes (Fig. 2). In general, adults were found over a wider range of conditions (e.g., relative to presence of fish, pH, and depth) than tadpoles. Largely, tadpoles did not occur where fish were present. Tadpoles were found in only one of 18 trout lakes and 21 of 76 non-acidic (pH > 6) lakes lacking trout (Fisher's exact test, one-tailed, on presence–absence of tadpoles vs. presence–absence of trout, $p = 0.03$). In the single lake containing both fish and tadpoles (Lake N-3), tadpoles were found only in crevices in extensive shallow rocky areas. In contrast with tadpoles, the distribution of adults was not related to the presence of fish (present in 4 of 18 trout lakes and 25 of 76 non-acidic, fishless lakes (Fisher's exact test, $p = 0.57$)).

Yellow-legged frog tadpoles were not observed in any of the 10 acidic lakes (pH < 6; Fig. 2) but were seen in 21 of the 76 non-acidic lakes that lacked fish (Fisher's exact test, one-tailed, on frog presence–absence vs. acidic–non-acidic lakes, $p = 0.051$). When examining fishless lakes with estimated depths ≥ 1.5 m (approximate minimum depth required for overwintering tadpoles; Bradford 1989), tadpoles occurred in 0 of 8 acidic lakes but 20 of 57 non-acidic lakes (Fisher's exact test, one-tailed, $p = 0.043$). In contrast, yellow-legged frog adults were found in both acidic lakes (4 of 10) and non-acidic, fishless lakes (25 of 76) (Fisher's exact test, $p = 0.73$).

Among fishless, non-acidic lakes, the occurrence of yellow-legged frog tadpoles was significantly related to depth (Wilcoxon test, $p = 0.02$), whereas the occurrence of adults was not. Yellow-legged frog tadpoles were found only in lakes having maximum depths ≥ 1.5 m, whereas adult frogs were found in lakes as shallow as 0.5 m and less. Among fishless, non-acidic lakes, the occurrence of yellow-legged frog tadpoles and adults was not related to pH, conductivity, elevation, or lake area (Wilcoxon tests).

Pacific treefrog tadpoles were collected from six non-acidic lakes and from one acidic lake (pH = 5.96). None of these lakes contained fish.

Detailed survey

Physical–chemical conditions and trout distribution

The 33 lakes ranged in pH from 4.78 to 8.61 (median = 6.98), in conductivity from 3 to 126 μS/cm (median = 31.2 μS/cm), in elevation from 3130 to 3672 m (median = 3470 m), in area from 0.12 to 30.5 ha (median = 1.4 ha), and in maximum depth from 0.3 to 10.0 m (median = 2.6 m). All four trout species were represented among the seven lakes with fish. Trout occurred only in non-acidic lakes over a relatively narrow range of lake pH (6.9 to 7.5) in comparison with a total range of 4.8 to 8.6.

Among the three lake types (i.e., acidic lakes, non-acidic lakes with fish, and non-acidic lakes without fish), differences were not observed for elevation and concentrations of Cl and Ca (Table 1). However, ANC was lower, and concentrations of NO_3, SO_4, NH_4, Mg, Na, K, and Al were higher, in acidic lakes than in at least one of the non-acidic lake types (i.e., fish or fishless). Lake area and depth were significantly greater in lakes with fish than in non-acidic lakes lacking fish. Chemical conditions did not differ between fish and fishless, non-acidic lakes.

Amphibians

Yellow-legged frog tadpoles were observed in 12 lakes (10 with adults), and adults alone were observed in an additional 8 lakes. Tadpoles occurred in a greater proportion of lakes in the detailed survey than in the synoptic survey simply because most of the shallowest (<1 m) lakes, which lacked tadpoles, were excluded from the detailed survey. As in the synoptic survey, tadpoles were generally absent where trout were present. However, this pattern was not significant (Fig. 3*a*; Fisher's exact test, $p = 0.09$) because the single lake containing both tadpoles and fish was included in the detailed survey. In contrast with tadpoles, the distribution of adults was not related to the presence of fish (Fig. 3*a*; Fisher's exact test, $p = 0.67$).

Tadpole distribution was significantly related to lake acidity (Fig. 3*c*). Tadpoles were not observed in any of the 8

Table 1. Physical–chemical characteristics of acidic lakes (Acidic) and non-acidic lakes containing fish (Fish) or lacking fish (Fishless) sampled in the detailed survey.

	Lake type			Significant differences
	Acidic	Fish	Fishless	
n	8	7	18	
Elevation (m)	3406	3390	3467	
	(53)	(42)	(22)	
Lake area (ha)	2.0	8.8	1.7	A=FL<F
	(0.7)	(4.1)	(0.7)	
Depth (m)	2.1	5.3	2.7	A=FL<F
	(0.5)	(1.0)	(0.5)	
pH	5.2	6.9	6.9	A<FL=F
	(0.2)	(0.1)	(0.1)	
ANC (μequiv./L)	−1.7	82.9	106.9	A<F=FL
	(2.6)	(11.0)	(24.0)	
Conductivity (μS/cm)	56.1	26.6	42.6	A>F
	(6.4)	(3.6)	(10.0)	
Cl (μequiv./L)	5.9	3.8	6.0	
	(0.8)	(0.4)	(1.1)	
NO_3 (μequiv./L)	14.2	3.2	5.1	A>F=FL
	(2.5)	(1.3)	(1.9)	
SO_4 (μequiv./L)	416.5	134.7	212.2	A>F=FL
	(61.0)	(30.0)	(61.8)	
NH_4 (μM)	0.6	0.2	0.6	A>F
	(0.1)	(0.1)	(0.2)	
Ca (μequiv./L)	218.4	174.3	278.5	
	(17.1)	(24.1)	(60.7)	
Mg (μequiv./L)	100.4	21.7	28.7	A>F=FL
	(16.8)	(4.4)	(5.9)	
Na (μequiv./L)	43.1	28.4	42.8	A>FL
	(4.8)	(5.4)	(17.1)	
K (μequiv./L)	17.8	6.9	10.7	A>F=FL
	(2.2)	(0.8)	(1.6)	
Al (μM)	13.04	0.81	1.19	A>F=FL
	(3.69)	(0.25)	(0.20)	

Note: *n* is the number of lakes in each category; numbers in the body of the table are mean values and numbers in parentheses are SEs for means. ANC refers to acid-neutralizing capacity. The right column summarizes statistically significant differences among lake types (A, acidic; F, non-acidic containing fish; FL, non-acidic without fish) based on ANOVAs on ranked values and Tukey's HSD test, α = 0.05. When only two lake types are listed in the right column, the third lake type is not significantly different from the two listed lake types.

acidic lakes (all lacked fish) but occurred in 11 of 18 non-acidic lakes lacking fish (Fisher's exact test, $p = 0.008$). Moreover, pH and ANC of fishless lakes lacking tadpoles was lower than in fishless lakes containing tadpoles (Table 2). Conductivity and concentrations of NO_3, Ca, Mg, and Al were higher in lakes lacking tadpoles. Among non-acidic, fishless lakes ($n = 18$), none of the chemical or physical parameters differed between lakes containing ($n = 11$) and lacking tadpoles ($n = 7$; Wilcoxon tests).

In contrast with tadpoles, the distribution of adults was not significantly related to any chemical or physical parameters (Table 2). Adults were seen in lakes with pH as low as 5.0, occurring in 5 of 8 acidic lakes and 10 of 18 non-acidic lakes lacking fish. This difference between the distributions of tadpoles and adults relative to pH was conspicuous in areas containing both acidic and non-acidic lakes in close proximity. For example, both acidic Lake F-14 and nearby acidic Lake F-13N contained only adult frogs, whereas non-acidic Lake F-11, which was located 0.1 km downstream from Lake F-13N, contained both adults and tadpoles. Similarly, non-acidic Lake F-13S was separated from acidic Lake F-13N by a narrow causeway (ca. 25 m wide); both contained adults, but only the non-acidic lake contained tadpoles.

No individuals of the Pacific treefrog were found in lakes in the detailed survey, although they occurred in some unmapped ponds near these lakes.

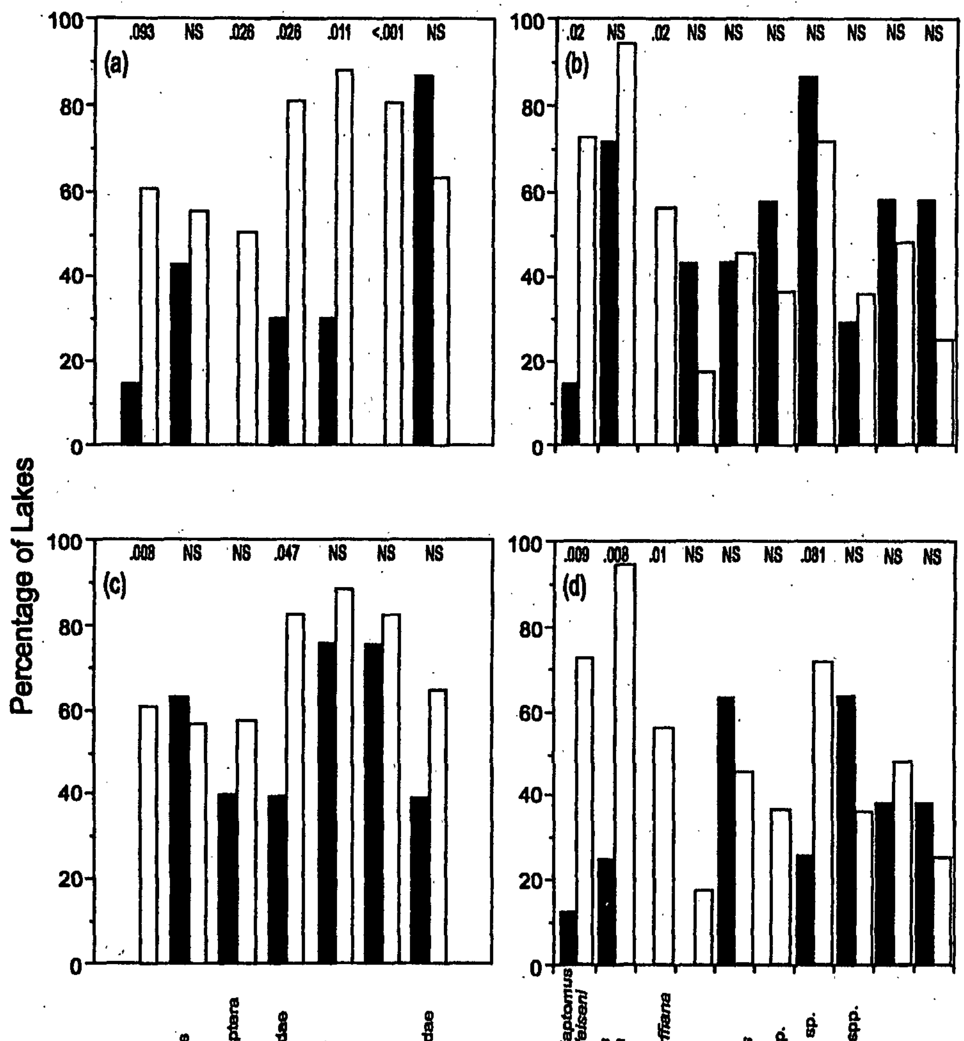
Macroinvertebrates

Most common macroinvertebrate taxa showed relationships with the presence or absence of fish. Limnephilid caddis larvae (Limnephilidae: primarily *Desmona mono* and *Hesperophylax*), mayfly nymphs (Baetidae: *Baetis*, *Callibaetis*; Siphlonuridae: *Ameletus*; Heptageniidae: *Cinygmula*), dytiscid beetles (Dytiscidae: *Agabus*, *Deronectes*, *Hydaticus modesto*, *Hydroporus*, *Hydrovatus*, *Rhantus*), and corixids (Corixidae: *Graptocorixa*, *Hesperocorixa*, *Sigara*) were rare or absent in fish lakes but were commonly collected in non-acidic lakes lacking fish (Fisher's exact tests for these four groups, $p = 0.001$ to 0.026; Fig. 3*a*). Chironomids, including Chironomini, Orthocladiinae, Tanypodinae, and Tanytarsini, were collected from lakes containing and lacking fish. Among rarer taxa (i.e., occurring in 3 to 6 lakes), backswimmers (*Notonecta*) were only collected in lakes lacking fish, the caddis larvae of *Polycentropus variegatus* were collected only in lakes containing fish, and alderfly larvae (*Sialis latreille*), acarids, and fingernail clams (*Pisidium*) were collected from both fish and fishless lakes. Amphipods (*Hyallela azteca*), adult whirligig beetles (*Gyrinus punctellus*), water striders (*Gerris*), and the larvae of a stonefly (*Isoperla*), the limnephilid caddisfly *Ecclisomyia*, a damselfly (*Enallagma*), a mosquito (*Culex*), and a dixid (*Dixa*) were each collected from only one or two lakes.

Of the common macroinvertebrate taxa, only limnephilid caddis larvae seemed to show any relationship with pH, being found in only 37% of the acidic lakes but 81% of the non-acidic lakes lacking fish (Fisher's exact test, $p = 0.047$; Fig. 3*c*). Within this family, *Hesperophylax* was not collected from acidic lakes but was collected from half of the non-acidic lakes without fish (Fisher's exact test, $p = 0.018$), whereas *Desmona mono* was present in both acidic and non-acidic lakes (Fisher's exact test, $p = 0.66$). Most other common taxa, including siphlonurid mayflies (*Ameletus*), Dytiscidae, Corixidae, and Chironomidae, were collected in similar frequencies in acidic and non-acidic lakes (Fig. 3*c*). Among rare taxa, baetid and heptageniid mayflies, *Sialis latreille*, *Notonecta*, sphaerid clams, and amphipods were not collected from acidic lakes but were collected from a small number of non-acidic lakes.

A principal components analysis (PCA) on the angularly transformed relative abundances of common macroinvertebrate taxa tended to confirm these patterns (Fig. 4*a*). Principal components axes 1 and 2 accounted for 26% and 22%, respectively, of the total variation in the macroinvertebrate data set. Scores for principal components axis 1, which were positively correlated with the transformed relative abun-

Fig. 3. Taxa in detailed survey. (*a*) Among non-acidic lakes (n = 23 to 25), the percentages of lakes containing fish (n = 7; solid bars) and lacking fish (n = 16 to 18; open bars) that were inhabited by mountain yellow-legged frog tadpoles and adults and macroinvertebrate taxa. (*b*) Among non-acidic lakes (n = 24 to 25), the percentages of lakes containing fish (n = 7; solid bars) and lacking fish (n = 17 to18; open bars) that were inhabited by designated zooplankton taxa. (*c*) Among fishless lakes (n = 24 to 26), the percentages of acidic lakes (pH < 6.0; n = 8; solid bars) and non-acidic lakes (pH > 6.0; n = 16 to 18; open bars) containing frogs and macroinvertebrate taxa. (*d*) Among fishless lakes (n = 25 to 26), the percentages of acidic lakes (pH < 6; n = 8; solid bars) and non-acidic lakes (pH > 6; n = 17 to 18; open bars) containing zooplankton taxa. Probability levels for Fisher's exact test are given at the top; NS, p values > 0.1.



dances of dytiscids, corixids, and ephemeropterans and negatively correlated with transformed chironomid relative abundance, were significantly different between lakes containing versus lacking fish (ANOVA, $F_{2,28}$ = 8.5, p = 0.001; acidic = non-acidic fishless > non-acidic fish, p < 0.05, Tukey's HSD). Principal components axis 2 was positively correlated with the transformed relative abundances of *Hesperophylax* and *Sialis* and negatively correlated with the transformed relative abundance of *Desmona*. Although the effect of lake type on the scores for this principal component was not statistically significant (ANOVA, $F_{2,28}$ = 2.0, p = 0.15), this axis tended to distinguish taxa that were absent from acidic lakes (*Hesperophylax*, *Sialis*) from a taxon for which relative abundance was higher in acidic than non-acidic lakes (*Desmona*).

Taxon richness was significantly higher in non-acidic fishless lakes than in acidic and fish lakes (non-acidic fishless: mean = 6.1, SE = 0.7, n = 16; acidic: mean = 3.8, SE = 0.4, n = 8; non-acidic fish: mean = 3.1, SE = 1.0, n = 7; Kruskal–Wallis tests, p = 0.024 and 0.037, respectively). For fishless lakes (n = 24), there was a significant direct relationship between taxon richness and pH (regression equation: richness = –2.21 + 1.19 pH; r^2 = 0.19; $F_{1,22}$ = 5.2, p < 0.032).

Zooplankton

The largest-bodied zooplankton taxa, i.e., *Hesperodiapto-*

Table 2. Water chemistry of fishless lakes containing and lacking yellow-legged frog tadpoles or adults.

	Tadpoles			Adults	
	Present		Absent	Present	Absent
n	11		15	11	15
pH	7.28	*	6.29	6.72	6.70
	(0.21)		(0.29)	(0.33)	(0.28)
ANC (μequiv./L)	103	*	43.5	58.1	78.1
	(31)		(20.1)	(24.8)	(27.1)
Conductivity (μS/cm)	38.0	*	46.2	42.3	43.0
	(12.8)		(4.2)	(6.1)	(9.3)
Cl (μequiv./L)	5.1		6.6	7.2	5.1
	(0.7)		(1.3)	(1.8)	(0.5)
NO_3 (μequiv./L)	1.9	**	12.7	11.1	5.9
	(0.9)		(2.3)	(3.0)	(2.0)
SO_4 (μequiv./L)	228		319	247	306
	(96)		(50)	(60)	(75)
NH_4 (μM)	0.89		0.53	0.70	0.65
	(0.27)		(0.10)	(0.16)	(0.19)
Ca (μequiv./L)	257	*	262	262	259
	(96)		(28)	(40)	(69)
Mg (μequiv./L)	26.6	**	68.3	47.1	53.3
	(8.7)		(13.0)	(12.7)	(13.3)
Na (μequiv./L)	55.6		33.6	27.6	54.2
	(27.5)		(4.5)	(5.4)	(19.9)
K (μequiv./L)	10.7		14.4	11.3	14.0
	(2.2)		(1.9)	(2.0)	(2.0)
Al (μM)	1.18	*	8.46	6.17	4.50
	(0.24)		(2.76)	(3.31)	(1.83)

Note: Values are means (SEs). Asterisks between the groups indicate significance levels for Wilcoxon two-sample tests (* $p < 0.05$, ** $p < 0.01$). Other definitions are as in Table 1.

mus eiseni and *H. shoshone*, and *Daphnia middendorffiana* (maximum size > 2 mm) were rare or absent in fish lakes (14 and 0% of lakes, respectively) but were commonly collected in non-acidic lakes lacking fish (72 and 55% of lakes) (Fisher's exact tests, $p = 0.02$; Fig. 3*b*). *Daphnia rosea* and *Keratella cochlearis* tended to be collected more frequently in fish lakes than in non-acidic fishless lakes; however, these patterns were not significant (Fig. 3*b*). *Diaptomus signicauda, Chydorus sphaericus, Trichotria tetractis, Lecane* spp., *Lepadella* spp., and *Polyarthra* sp. were collected with similar frequencies from fish and fishless lakes. Many rare (three to six lakes) or littoral taxa, including the cladoceran *Alona* sp., and the rotifers *Hexarthra mira, Trichocerca capucina, Collotheca mutabilis, Keratella taurocephala*, and *Conochilus unicornis* were collected in lakes both containing and lacking fish; however, the cladoceran *Macrothrix hirsuticornis* was only collected from fishless lakes (five lakes). The cladocerans *Polyphemus pediculus, Holopedium gibberum, Bosmina longirostris, Scapholebris kingii*, and *Eurycercus lamellatus*, and the rotifers *Monostyla lunaris, Notholca labis*, and *Cephalodella* sp. were each collected from only one or two lakes.

Hesperodiaptomus eiseni, H. shoshone, and *Diaptomus signicauda* were rarely collected in acidic lakes (13–25% of lakes), and *Daphnia* spp. were absent in acidic lakes, but these microcrustaceans were frequently collected from non-acidic lakes lacking fish (72–94% of lakes) (Fisher's exact tests, $p = 0.002$ to 0.009; Fig. 3*d*). Correlations between the abundances of these taxa and pH for fishless lakes were significant; however, there was a lot of scatter in the data at higher pH ($r = 0.46$ to 0.59; Fig. 3*d*). The rotifer *Lecane* was not collected from acidic lakes; however, its low frequency of occurrence in non-acidic fishless lakes (35% of lakes) precluded statistical significance (Fisher's exact test, $p = 0.13$). *Polyarthra* sp. also tended to be collected more frequently in non-acidic than acidic lakes (Fig. 3*d*). Other common zooplankton taxa, including the cladoceran *Chydorus sphaericus* and the rotifers *Keratella cochlearis, Lepadella* spp., and *Trichotria tetractis*, were collected at similar frequencies in acidic and non-acidic, fishless lakes (Fig. 3*d*), and their densities were not significantly related to pH (examples in Fig. 5). Among rare species, *Macrothrix, Alona, Trichocerca, Keratella taurocephala*, and *Conochilus* were absent from acidic lakes but were present in a small number of non-acidic lakes (three to six lakes depending on the species), whereas *Collotheca* was collected from both acidic and non-acidic lakes. An unidentified rotifer, tentatively assigned to *Pompholyx* sp., was collected predominantly in acidic lakes (5 of 8 acidic lakes, 1 of 17 non-acidic fishless lakes; Fisher's exact test, $p = 0.006$).

A principal components analysis on log-transformed absolute abundances of common limnetic taxa tended to confirm these results (Fig. 4*b*). Principal components axes 1 and 2 accounted for 26% and 20%, respectively, of the total variation in the zooplankton data set. Lake type had a borderline effect on principal components axis 1 (ANOVA, $F_{2,28} = 2.25$, $p = 0.10$) and a highly significant effect on principal components axis 2 (ANOVA, $F_{2,28} = 6.6$, $p = 0.003$), with generally higher scores for both axes in non-acidic lakes than in acidic lakes (Tukey's HSD, $p < 0.05$). Taxa positively correlated with each of these axes were taxa that were rare or absent in acidic lakes (*Daphnia middendorffiana, Daphnia rosea, Hesperodiaptomus* spp., *Diaptomus signicauda, Conochilus unicornis, Keratella* spp.). Although the data were highly variable, taxa positively associated with principal components axis 1 (*Keratella, Daphnia rosea, Diaptomus signicauda, Conochilus unicornis*) were equally abundant in non-acidic fish lakes and fishless lakes, whereas mean abundances of the taxa negatively associated with principal components axis 1 (*Lepadella, Trichotria*) were higher in non-acidic fishless lakes than in acidic or fish lakes. Two of the taxa positively associated with principal components axis 2 (*Daphnia middendorffiana, Hesperodiaptomus* spp.) were virtually absent from acidic lakes or lakes containing fish but were relatively common in non-acidic fishless lakes.

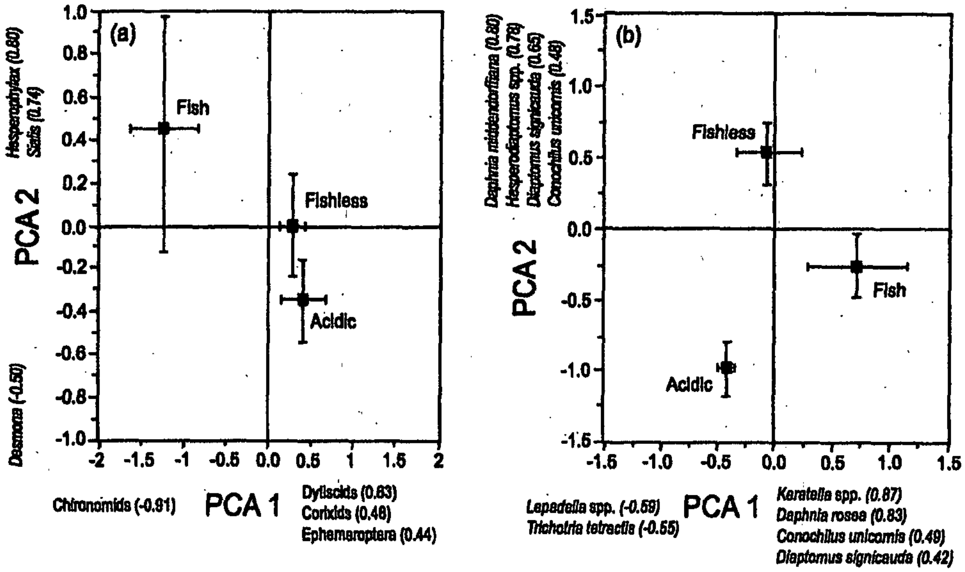
Microcrustacean species richness increased significantly with increasing pH in fishless lakes (Fig. 6), whereas rotifer species richness did not. Species richness of both microcrustaceans and rotifers was not significantly affected by the presence of fish.

Discussion

Effects of acidity

This study indicates that the distributions and abundances of some aquatic animals are affected by natural lake acidity. Tadpoles, large-bodied microcrustaceans (*Daphnia, Diapto-*

Fig. 4. Mean scores (± 1 SE) for principal components axes 1 and 2 for common taxa (i.e., present in >5 lakes) in the detailed survey. (*a*) Axes are derived for angularly transformed relative abundances of macroinvertebrate taxa for each of the three lake types (acidic and non-acidic with fish (Fish) and without fish (Fishless)). Taxa showing significant positive or negative association with each principal components axis are listed, and correlation coefficients (Pearson's *r*) are included in parentheses. (*b*) Axes are derived for log(x + 1)-transformed densities (no./m^3) of limnetic zooplankton taxa. Lake types and other designations are as in Fig. 4*a*.

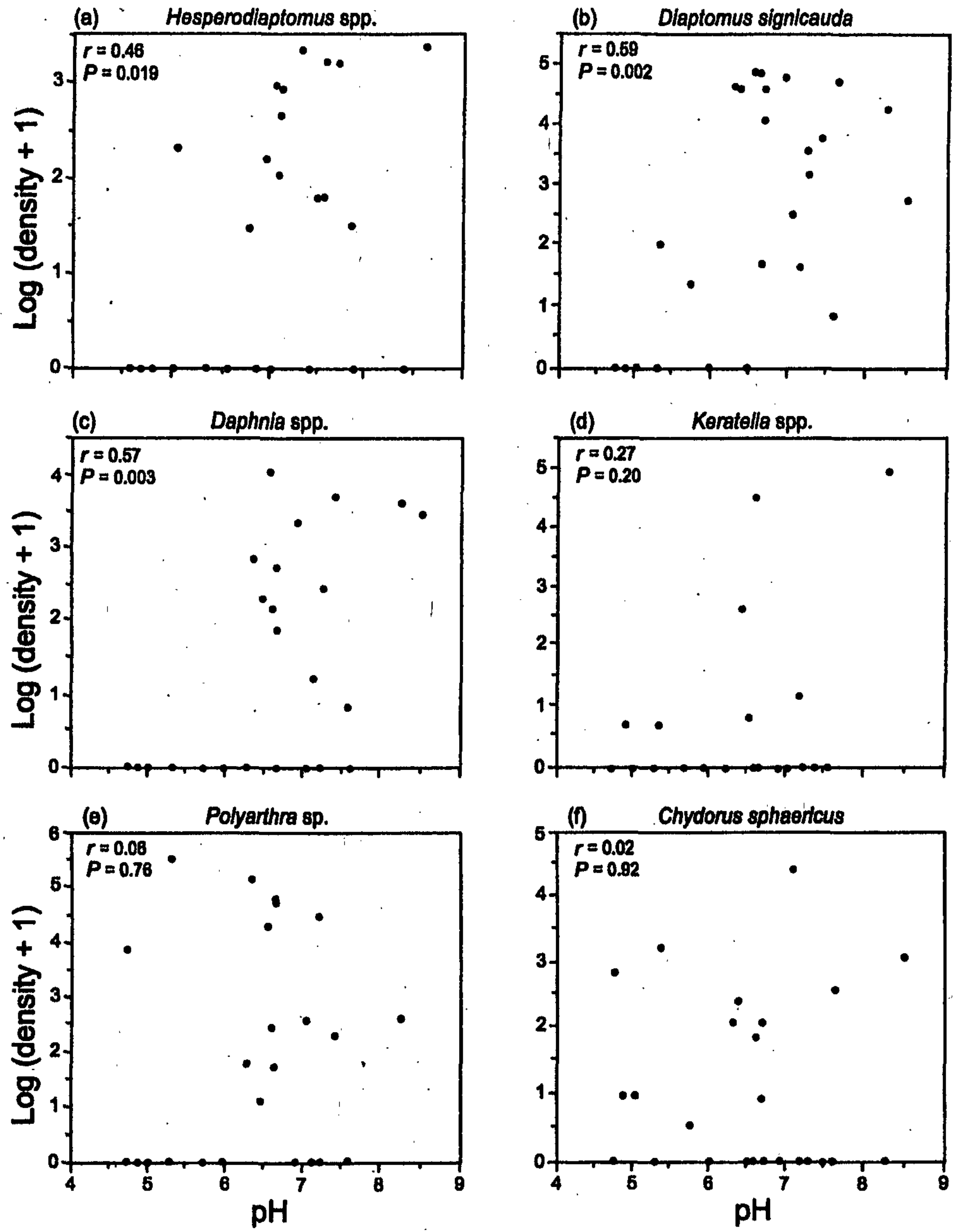


mus), and the larvae of a species of limnephilid caddisfly (*Hesperophylax*) were rare or absent in acidic lakes but relatively common in non-acidic lakes. Based on differences in the distributions of tadpoles versus adult frogs noted in this study, it appears that larval amphibians are more sensitive to acid conditions than adults, consistent with results reported from other survey and experimental studies (Freda 1990). The absence of tadpoles from acidic lakes where adults were present also could have been owing to disruption of frog mating activities, site selection for breeding, embryonic development, or metamorphosis. Embryonic stages of many amphibians, including the mountain yellow-legged frog, are more sensitive to increased acidity than larvae (Freda 1990; Bradford et al. 1992) and transitional processes, such as egg hatching or metamorphosis, appear to be easily disrupted by acid stress (Clark and LaZerte 1985).

With the exception of the limnephilid caddis larva, *Hesperophylax*, the distributions of common macroinvertebrate taxa were unrelated to lake acidity. Previous survey and experimental studies in the Sierra also have found little relationship between the distributions or abundances of macroinvertebrates and pH; however, previous surveys only examined a restricted range of pH values (>6.3) and experimental studies examined responses of the infauna at the bottom of lake enclosures (Melack et al. 1989; Barmuta et al. 1990). Our survey results extend this lack of a relationship between macroinvertebrate distributions and lake acidity to a wider range of pH values and to epibenthic and water column taxa. Macroinvertebrate taxa identified as sensitive to acidic conditions in previous studies, such as baetid mayflies, amphipods, and sphaerid clams (Mills and Schindler 1986; Okland and Okland 1986), were not found in acidic lakes in the present study; however, their infrequent collection in non-acidic lakes precluded rigorous statistical testing. *Sialis* larvae are generally thought to be tolerant of acidic conditions but were only collected from five non-acidic lakes, and mayflies, in general, are thought to be sensitive to acidic conditions (Sutcliffe and Carrick 1973). However, the dominant mayfly genus collected from our study lakes, *Ameletus*, was found in several acidic lakes. Other studies have reported that siphlonurid mayflies, including species of *Ameletus*, are insensitive to acidic conditions (Rosemond et al. 1992). In general, it appears that macroinvertebrate taxa sensitive to acidic conditions are rare in High Sierra lakes, even those with circumneutral or alkaline pH. Nevertheless, macroinvertebrate taxon richness was lower in acidic lakes than in fishless, non-acidic lakes, a finding consistent with the significant positive correlation reported between macroinvertebrate taxon richness and pH in Sierra Nevada lakes in a previous study (Jenkins et al. 1994).

In contrast with macroinvertebrates, zooplankton assemblages appeared to show a greater variety of responses to increased acidity. Common microcrustacean taxa, such as *Hesperodiaptomus eiseni, H. shoshone, Diaptomus signicauda, Daphnia middendorffiana*, and *Daphnia rosea*, were rare or absent in acidic lakes (pH < 6) but were collected commonly in non-acidic lakes. There also appeared to be differences in the responses of these sensitive taxa: *Hesperodiaptomus shoshone* was collected in low densities from a lake with pH 5.3, *Diaptomus signicauda* was collected from lakes with pH 5.3 and 5.7, but the lowest pH for waters from which *Daphnia* was collected was 6.3. The cladocerans *Macrothrix hirsuticornis* and *Alona* sp. and the rotifers *Conochilus unicornis* and *Lecane* spp. were also absent in acidic waters but were collected from 5, 6, 5, and 10 non-acidic lakes, respectively. In contrast, the common chydorid cladoceran *Chydorus sphaericus* and a number of rotifers, including *Keratella cochlearis, Polyarthra* sp., *Trichotria tetractis*, and *Lepadella* spp., were collected in both acidic and non-acidic lakes. Previous surveys of High Sierra zooplankton

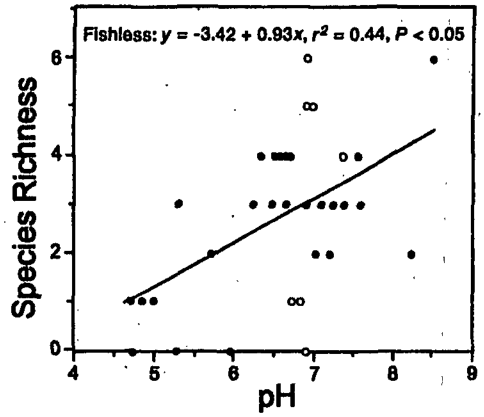
Fig. 5. Relationships between log-transformed abundances (no./m^3) of common zooplankton taxa and pH for fishless lakes sampled in the detailed survey (n = 25). r and P refer to Pearson's correlation coefficient and associated probability value, respectively.



assemblages (e.g., Stoddard 1987; Melack et al. 1989) found few relationships between the presence or abundances of zooplankton taxa and pH; however, these surveys did not include lakes with pH < 6.

Comparisons of our survey results with the results of previous small-scale experiments examining the effects of acid inputs on the survivorship and development of mountain yellow-legged frogs revealed some discrepancies. For example, although tadpoles were absent at pH < 6.0 in our survey, survivorship of embryos and tadpoles in the laboratory was not significantly affected by pH as low as 4.75 (Bradford et al. 1992). Developmental rates of embryos, however, were reduced at pH ≤ 5.25 in these experiments. The possibly greater sensitivity of early frog stages to acidic conditions in the field may stem from several factors. Many chemical species are negatively correlated with pH (Table 1), and concentrations of NO_3, Ca, Mg, and Al were significantly higher where tadpoles were absent. Possibly, these factors, rather than pH, may be directly affecting embryos or tadpoles in the field. For example, acidic lakes contained Al concentrations many times greater than levels used in the laboratory experiments, and aluminum can be toxic to amphibian embryos and larvae (Freda 1991). Acidic lakes contained a median of 13 μM aluminum (range: 2–25), whereas levels in laboratory experiments at similar pH were approximately 3 μM (Bradford et al. 1992). Other possible explanations include the following: *one-time sampling in the field* may have missed extreme pH depressions; only a restricted

Fig. 6. Relationship between microcrustacean species richness and pH for all lakes in the detailed survey (n = 33). Open circles represent lakes containing fish; solid circles represent lakes lacking fish. The regression line was fitted by the procedure of least squares to data from fishless lakes only (n = 26).

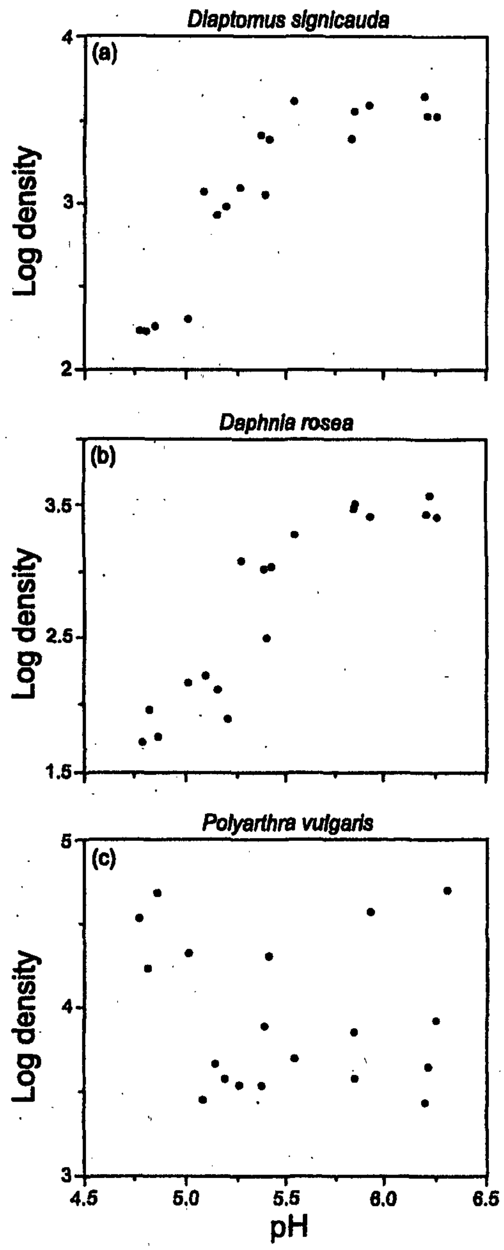


part of the mountain yellow-legged frog life cycle was examined in laboratory experiments (i.e., embryos and hatchling tadpoles); laboratory experiments were conducted at a "summertime" temperature of 15°C, whereas tadpoles overwinter under ice at 0 to 4°C for many months (Bradford 1989); and adults may choose not to breed in acidic waters.

In contrast with the discrepancies seen for amphibians, our survey results for zooplankton were nearly congruent with zooplankton responses to acid inputs in large experimental enclosures in a High Sierra lake (Emerald Lake, Barmuta et al. 1990; Melack et al. 1989). The survey suggested that *Daphnia* and *Diaptomus signicauda* were sensitive to pH < 6, whereas *Chydorus, Polyarthra,* and *Keratella* were relatively insensitive to acidity. Similarly, experimental manipulations of pH showed that *Diaptomus signicauda* and *Daphnia* declined in abundance when pH was reduced below 5.8–6.0, whereas *Chydorus sphaericus* and *Polyarthra* sp. were relatively unaffected by pH manipulations (Fig. 7). Furthermore, *Daphnia* seemed to be slightly more sensitive to acid inputs than *Diaptomus* in both our survey (Fig. 5) and in these experiments (Fig. 7). *Keratella* was unresponsive to pH in the survey but generally increased in abundance in enclosures as pH declined below 5.6 (Barmuta et al. 1990); however, it is difficult to specifically compare survey and experimental results because the dominant *Keratella* species was not the same in each case. *Keratella taurocephala* was the dominant species in the experiment, whereas *K. cochlearis* was the species typically collected in the survey; *K. taurocephala* is usually thought to be more tolerant of acidic conditions than *K. cochlearis* (Roff and Kwiatkowski 1977; Brezonik et al. 1993; Gonzalez and Frost 1994) but was only collected from three of the surveyed lakes (pH 6.53–6.91).

Our survey results corroborate an extensive literature documenting the high sensitivity of most species of *Daphnia* and many species of *Diaptomus* to acid inputs and the high tolerance of *Chydorus, Keratella,* and *Polyarthra* to acidic conditions (reviewed in Brett 1989). Our results are also consistent with literature showing positive relationships be-

Fig. 7. Relationships between log-transformed abundances (no./m^3) of three zooplankton taxa and pH in a field experiment (Barmuta et al. 1990) for comparison with data for the same or related taxa in the detailed survey (see Fig. 5). The field experiment was conducted for 35 days in 18 polyethylene enclosures (each 7.6 m^3) that extended from the bottom to the surface of a High Sierra lake. Nitric and sulphuric acid were added in varying amounts to enclosures to create six pH levels, with three replicate enclosures at each level. Data shown are mean abundances of designated zooplankton taxa in each enclosure versus mean pH of each enclosure after acidification over the duration of the experiment.



tween microcrustacean species richness and pH (see review in Brett 1989). In contrast with previous studies, however, we found no relationship between rotifer species richness and pH (Roff and Kwiatkowski 1977). As with yellow-legged frog tadpoles, it is possible that chemical parameters other than pH affected the distributions and abundances of macroinvertebrates and zooplankton. Because the concentrations of a number of chemical species are correlated strongly with pH, pH can be used as an index of the amalgam of chemical factors that are likely to change with increasing acidity and that may affect, alone or together, the distributions and abundances of aquatic animals. In addition, our survey results were congruent with the results of field experiments where primarily proton concentrations were manipulated, indicating that differences in hydrogen ion concentrations could explain differences in species composition and abundance among lake types.

Fish distributions within the study area appear to be related primarily to historical stocking patterns, rather than lake acidity. Trout were originally absent from most waters of the High Sierra, including all lakes in the study area (Knapp 1996). California Department of Fish and Game records show that stocking occurred between 1936 and 1979 in at least six lakes in the B, C, D, and E basins. We observed fish primarily in large deep lakes in these basins and in a few connecting lakes that lacked physical barriers to dispersal from these large lakes. There are no stocking records for fish in the F, L, O, and P drainages, where fish are currently absent. The only acidic lake that we know was stocked is Lake C-24, a lake currently devoid of fish. This lake was planted with rainbow trout at least five times between 1946 and 1979. Because this lake lacks inflowing and outflowing streams, which are necessary for spawning, and because rainbow trout are unlikely to live over 13 years, the absence of trout from this lake could be owing to lack of spawning habitat rather than acidic conditions (Moyle et al. 1996).

The results of this and other studies indicate that acidic conditions may restrict the distributions of larval amphibians, large microcrustaceans, and a few macroinvertebrates and reduce the species richness of microcrustaceans and macroinvertebrates. Currently, however, acidity has a very limited influence on aquatic animals in the High Sierra simply because acidic lakes are extremely rare. Of the approximately 4000 lakes in the Sierra Nevada, the 10 acidic lakes in this study are the only ones known to have been acidified either by natural or anthropogenic sources (Melack et al. 1985; Landers et al. 1987; Melack and Stoddard 1991; Bradford et al. 1994*b*). Moreover, the pH of lakes in the Sierra Nevada very rarely dips below 5.6 during snowmelt (Melack et al. 1989; Stoddard 1995). However, our survey results do provide an indication of how aquatic biodiversity in the Sierra will respond to long-term increases in anthropogenic acidification.

Effects of introduced fish

The results of the present study suggest that the introduction of fish has had profound effects on the structure and composition of faunal assemblages in High Sierra lakes. Large and (or) mobile, conspicuous taxa, including tadpoles, large-bodied microcrustacean zooplankton (*Hesperodiaptomus, Daphnia middendorffiana*), and many epibenthic or limnetic macroinvertebrates (baetid and siphlonurid mayflies, notonectids, corixids, limnephilid caddis larvae, and dytiscid beetles), were rare or absent in lakes containing fish but were commonly collected in lakes lacking fish. The disappearance of the mountain yellow-legged frog from many parts of the Sierra may be owing to the widespread introduction of trout to Sierran lakes (Bradford 1989; Bradford et al. 1993). Frog disappearances may have occurred both by direct fish predation on vulnerable life stages (e.g., tadpoles) and by isolation of remaining populations from one another (Bradford et al. 1993). An extensive literature documents that large-bodied zooplankton species are generally found only in fishless lakes, whereas small species dominate in lakes containing fish (Brooks and Dodson 1965; Walters and Vincent 1973; Zaret 1980; Stoddard 1987; Melack et al. 1989; Northcote 1988). Similarly, macroinvertebrate taxa that are conspicuous owing to their size, activity, and (or) exposure are often rare in lakes containing fish. Large, active, and epibenthic–limnetic macroinvertebrates (e.g., large mayflies, epibenthic odonates, hemipterans, limnephilid caddis larvae, dytiscid beetles) are often reduced or eliminated by fish predation, shifting dominance to smaller or more cryptic taxa (e.g., chironomids, oligochaetes) (Bendell and McNicol 1987; Northcote 1988; Evans 1989; Hoffman et al. 1996).

Trout have been introduced to the vast majority of lakes in the Sierra Nevada where fish formerly did not occur (Moyle et al. 1996; Knapp 1996). Data presented in Bahls (1992) indicate that 63% of high mountain lakes in California contain introduced fish, including 97% of the large lakes (>2 ha). About half of the Sierran lakes are regularly stocked with non-native fish. Our study and others indicate that introduced trout eliminate or greatly reduce the numbers of large, mobile, and epibenthic–limnetic taxa, including amphibians and invertebrates. At the current time, the widespread introduction of non-native fish appears to be affecting profoundly the native biodiversity of aquatic ecosystems in the High Sierra.

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