

## FAUNA OF YOSEMITE NATIONAL PARK LAKES HAS LOW RESISTANCE BUT HIGH RESILIENCE TO FISH INTRODUCTIONS

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**Abstract.** The ratio of the number of taxa observed at a site to that expected to occur in the absence of anthropogenic impacts (*O/E*) is an ecologically meaningful measure of the degree of faunal alteration. We used *O/E* ratios to describe the response by amphibian, reptile, benthic macroinvertebrate, and zooplankton taxa in originally fishless lakes in Yosemite National Park to the introduction and subsequent disappearance of nonnative fish. To quantify resistance (the degree to which a system is altered when the environment changes) and resilience (the degree to which a system returns to its previous configuration once the perturbation is removed), we compared *O/E* ratios between lakes that were never stocked, were previously stocked and still contained fish, or were previously stocked but had reverted to a fishless condition.

On average, stocked-fish-present sites had 16% fewer taxa than never-stocked sites (*O/E* = 0.84 vs. 1.00, respectively). This statistically significant difference in *O/E* ratios indicates that native fauna had relatively low resistance to fish introductions. Resistance was inversely related to fish density and elevation, and directly related to water depth. Vulnerability to impacts of trout predation differed markedly between faunal groups, being high for amphibians, reptiles, conspicuous benthic invertebrates, and zooplankton and low for inconspicuous benthic invertebrates. *O/E* ratios in stocked-now-fishless sites were significantly higher (1.00) than those in stocked-fish-present sites and were not significantly different from those in never-stocked sites, indicating that this fauna had high resilience. For stocked-now-fishless sites, the relationship between the *O/E* ratio and the number of years since fish disappearance indicated that taxonomic composition recovered to closely resemble that of never-stocked lakes in less than two years following fish disappearance. Collectively, these results indicate that despite strong effects of an introduced predatory fish on community structure, these systems recover quickly and predictably following fish removal.

**Key words:** amphibians; benthic macroinvertebrates; introduced fish; mountain lakes; predictive models; recovery; resilience; resistance; RIVPACS; Sierra Nevada; zooplankton.

### INTRODUCTION

The increasing anthropogenic alteration of ecosystems highlights the urgent need to understand both the degree to which systems are altered when the environment changes (resistance) and the degree to which systems return to their previous configuration once the perturbation is removed (resilience; sensu Pimm 1991). One of the most widespread human influences on ecosystems is the introduction or extirpation of species (Wilcove et al. 1998), and these perturbations are increasingly being used to test theory related to the factors influencing resistance and resilience. Although an early review argued that species invasions cause few

changes to recipient communities (Simberloff 1981), the scientific literature now available shows convincingly that communities often have low resistance to species additions (e.g., Herbold and Moyle 1986, Savidge 1987, Nichols et al. 1990, Mittelbach et al. 1995, Knapp et al. 2001). Characteristics of invaders or of recipient communities can influence the degree of community resistance (Rejmanek and Richardson 1996, Kolar and Lodge 2002, Stachowicz et al. 2002), but the scarcity of studies conducted across appropriately large spatial and temporal scales (e.g., Connell and Sousa 1983) continues to limit our understanding of the conditions that determine community resistance and resilience.

Freshwater communities have been subjected to a wide range of human impacts, and whole-lake experiments have been particularly useful for describing resistance and resilience at the scale of the entire ecosystem (Carpenter and Kitchell 1993, Mittelbach et al. 1995, Frost et al. 1998). Whole lake experiments have

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several important limitations, however, including their typically short duration and general lack of replication (Mittelbach et al. 1995). The spatial and temporal scale of whole lake experiments could be expanded by running experiments over many years and replicating the perturbation at many sites, but both options will often be logistically impossible.

An alternative approach to describing system resistance and resilience that overcomes some of the limitations of whole lake studies involves comparisons of fauna across many lakes that either were never exposed to the perturbation, were exposed to the perturbation, or were exposed in the past but no longer. For example, Donald et al. (2001) and Knapp et al. (2001) assessed resistance to fish introductions by comparing the fauna of lakes that were never stocked versus the fauna of lakes that contained an introduced fish population. Resilience was assessed by comparing the fauna of lakes that were never stocked versus of lakes that were stocked in the past but from which fish populations had subsequently disappeared. Comparisons of faunal composition in stocked-now-fishless lakes that varied in the number of years since fish disappearance provided estimates of recovery rates. Although this comparative approach has its own limitations (e.g., cannot unambiguously determine cause and effect, potential for confounded effects due to nonrandom assignment of treatments), it provided a broader spatial and temporal perspective of resistance and resilience than was possible in most previous studies of lake ecosystems.

In the Donald et al. (2001) and Knapp et al. (2001) studies, direct comparison of faunal composition between the three lake types was only possible because all water bodies were similar in elevation, habitat structure, temperature, and chemistry. As a consequence, all lakes likely contained a similar fauna prior to fish introductions. Although necessary to minimize confounding habitat effects, this environmental homogeneity provides few general insights into the biotic and abiotic factors that influence resistance and resilience to fish introductions. Including a wider variety of lake types could expand this perspective, but how can faunas be compared amongst sites when those sites differ in their original species composition (e.g., due to differences in habitat conditions)? One possibility is to use statistical models to predict faunal assemblages expected at sites in the absence of anthropogenic impacts, and then compare those expectations with observations. The ratio of the observed number of taxa to that expected to occur in the absence of anthropogenic impacts ( $O/E$ ) is an ecologically meaningful measure of the degree of faunal alteration, with values near one indicating no alteration and values substantially less than one indicating adverse effects of one or more environmental stressors (Wright 1995, Moss et al. 1999, Hawkins et al. 2000, Clarke et al. 2003). Importantly,  $O/E$  ratios allow direct comparison of the degree of faunal alteration between sites that differ in their orig-

inal fauna (i.e.,  $E$ ). For example, although two sites may differ markedly in  $E$ ,  $O/E$  ratios of 0.5 indicate that both sites have lost 50% of their original taxa. Because an  $O/E$  ratio provides a measure of the loss of those specific taxa that were expected to occur at a site, these ratios are a powerful means of quantifying changes in community structure. Although predictive models based on  $O/E$  are currently in wide use by scientists and government agencies in Great Britain, Australia, and the United States, their use has typically been restricted to assessing the degree of faunal alteration in streams and rivers based on data from a single assemblage, typically benthic macroinvertebrates (e.g., River Invertebrate Prediction and Classification System (RIVPACS); Wright 1995, Moss et al. 1999, Hawkins et al. 2000, Clarke et al. 2003).

In the current study, we used a multi-assemblage predictive model that included amphibians, reptiles, benthic macroinvertebrates, and zooplankton to quantify faunal resistance and resilience to fish introduction and disappearance in lakes in Yosemite National Park. Unlike the high elevation lakes in the southern Sierra Nevada used by Knapp et al. (2001), lakes and ponds in Yosemite National Park are distributed across a wide elevational gradient and consequently vary considerably in habitat structure and original faunal composition. Because these differences could confound direct comparisons of faunal composition amongst lake types, we quantified resistance and resilience using ratios of the observed-to-expected fauna ( $O/E$ ) at never-stocked, stocked-fish-present, and stocked-now-fishless sites. The specific objectives of the current study were to describe (1) faunal resistance to introduced fish by comparing  $O/E$  in never-stocked sites (reference sites) versus stocked-fish-present sites, (2) faunal resilience following fish disappearance by comparing  $O/E$  in stocked-now-fishless sites versus both never-stocked and stocked-fish-present sites, (3) effect of biotic and abiotic factors on site-specific faunal resistance, (4) response by different faunal groups to fish presence and disappearance, and (5) the rate of faunal recovery as measured by  $O/E$  ratios in stocked-now-fishless sites as a function of the number of years since fish disappearance.

## METHODS

### *Study design*

Yosemite National Park contains >2000 lakes and ponds. These lentic habitats range from those at low elevations (~2000 m) that are relatively warm, contain abundant aquatic vegetation, and are surrounded by forest, to those at high elevations (~3200 m) that are cold, oligotrophic, lack aquatic vegetation, and are surrounded by alpine meadows and rock (see Plate 1; also see Appendix A). All lentic water bodies in Yosemite were originally fishless, but, between the late 1800s and 1990, the majority of larger lakes (>2 ha) were



PLATE 1. (Left) A low-elevation site (Swamp Lake, 1529 m), and (right) a high-elevation site (Lower Edna Lake, 3005 m) in the Yosemite National Park study area. Photo credits: Swamp Lake, R. A. Knapp; Lower Edna Lake, Jay Pape.

stocked repeatedly with one or more trout species (primarily *Oncorhynchus mykiss* and *Salvelinus fontinalis*; Elliot and Loughlin 1992). Most trout stocking in Yosemite was halted by 1977, and all stocking was permanently halted in 1990. Following stocking termination, approximately 25% of previously stocked lakes reverted to their original fishless condition (Boiano 1999; R. A. Knapp, *unpublished data*).

Prior to any sampling, all water bodies in Yosemite were assigned to one of three fish stocking categories based on existing data sources (Botti 1977, Elliot and Loughlin 1992, Boiano 1999). These categories were defined as follows: (1) never-stocked—no record of any fish stocking and past fish surveys indicated that the water body was fishless; (2) stocked-fish-present—record of at least one stocking event and/or records indicated that the water body contained a self-sustaining population of one or more species of trout; and (3) stocked-now-fishless—record of at least one stocking event and records indicated that the water body had reverted to a fishless condition (as a result of a lack of suitable spawning habitat; Boiano 1999). A few water bodies (<2%) were reassigned to a different category based on the results of fish surveys conducted as part of the current study (e.g., site categorized as never-stocked was found to contain trout). Based on the fact that never-stocked water bodies in Yosemite National Park have been very minimally impacted by human activities, we assumed that the faunal composition of never-stocked sites would accurately represent the original faunal composition of stocked-fish-present and stocked-now-fishless sites prior to any fish introductions.

We used a stratified sampling design to provide a description of faunal composition in a wide range of never-stocked sites against which we could compare the fauna of stocked-fish-present and stocked-now-fishless sites. To select sites for sampling, we classified all lakes and ponds into six elevation categories (1500–1800 m, 1801–2100 m, 2101–2400 m, 2401–2700 m,

2701–3000 m, >3000 m) and five size categories (surface area <500 m<sup>2</sup>, 500–2000 m<sup>2</sup>, 2001–5000 m<sup>2</sup>, 5001–20 000 m<sup>2</sup>, >20 000 m<sup>2</sup>). All water bodies >20 000 m<sup>2</sup> (2 ha) in each of the six elevation categories were sampled, and included numerous sites categorized as never-stocked and nearly all stocked-fish-present and stocked-now-fishless sites. In addition, seven never-stocked water bodies were randomly selected for sampling from each of the remaining 24 elevation and size categories. If a category contained fewer than seven water bodies, all water bodies were sampled. Therefore, of the sites selected for sampling, only the never-stocked sites <2 ha ( $n = 116$ ) were chosen at random. These randomly selected water bodies represented 71% of the sampled never-stocked sites. Of the 294 sites selected for sampling, 277 were suitable when visited. The remaining 17 sites were either dry or too shallow (<20 cm) to be sampled. The sampled sites included 164 never-stocked sites, 72 stocked-fish-present sites, and 41 stocked-now-fishless sites.

Field surveys to describe fauna and habitat characteristics were conducted during single site visits made from 18 June to 27 September 2000 or 10 June to 28 August 2001. Eighty-five percent of sites were surveyed in 2000 and 15% in 2001. Precipitation during these years was 103% and 75% of the long-term average, respectively (California Department of Water Resources report for Tuolumne Meadows, Yosemite National Park, *available online*).<sup>6</sup> Environmental differences between the 2000 and 2001 summers are unlikely to have influenced the study results, as surveys conducted at ten sites in both years indicated nearly identical taxonomic composition (R. A. Knapp, *unpublished data*).

#### Faunal surveys

The presence or absence of each amphibian and reptile species was determined at each water body from

<sup>6</sup> <http://cdec.water.ca.gov/cgi-progs/snowQuery>

visual encounter surveys (Crump and Scott 1994) of the entire shoreline. Each species was determined to be present at a site if one or more life stages (eggs, larvae, juveniles, adults) were detected. The presence or absence of trout was determined at each water body from visual encounter surveys or gillnets (for additional details, see Knapp and Matthews 1998, 2000).

Benthic macroinvertebrates were collected from the littoral zone of each site by conducting 15 standard sweeps with a D-net (mesh size = 0.5 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 sweeps followed bottom contours and sampled epibenthic, water column, and surficial sediment habitats in portions of each lake that were  $\leq 1.2$  m deep. All common littoral habitats were sampled, each approximately in proportion to its availability. In 56 water bodies, the amount of material (e.g., leaves, aquatic vegetation, woody debris) collected in 15 sweeps would have been excessive. In these cases, the number of sweeps was reduced to six to 13 (with a median of six). Benthic macroinvertebrates were separated from detritus and sediment in the field. If the amount of collected material to be searched for invertebrates was too large to be processed in  $< 3$  h, the sample was split in half until the amount of material was manageable. For samples that were split ( $n = 162$ ), the percentage of the sample that was processed ranged from 12% to 75% (median = 50%). All collected benthic macroinvertebrates were preserved in 70% ethanol. We examined more than 82 000 individual benthic macroinvertebrates, and most were identified to genus (Appendix B; identifications based on Merritt and Cummins [1996], Eriksen and Belk [1999], and Belk and Rogers [2002]). These data were used to establish the site-specific presence or absence of each benthic macroinvertebrate taxon.

Crustacean zooplankton were sampled by taking vertical tows from the bottom to the surface with a conical plankton net (29.5 cm diameter, 64- $\mu$ m mesh) in the deepest part of each lake. In water bodies  $< 1$  m deep, tows were taken horizontally ( $n = 70$ ). One to five replicate tows were made until substantial numbers of zooplankton were present in samples (median, two tows; Stoddard 1987, Knapp et al. 2001). Samples were preserved in 5% sugar formalin. In the laboratory, zooplankton samples were rinsed through a 64- $\mu$ m sieve and then diluted with tap water. All crustacean zooplankton in two 1-mL subsamples were identified (Pennak 1989) and counted (for additional details, see Knapp et al. 2001). More than 101 000 individual zooplankton were examined, and most were identified to species (Appendix B). From 0.2% to 10% of each sample was processed (median = 3%). These data were used to establish the site-specific presence or absence of each zooplankton taxon. Up to 25 individuals of each taxon per subsample were measured for maximum length.

The subsampling procedures we used for benthic macroinvertebrates and zooplankton samples were similar or identical to those used in many previous ecological studies (Barbour et al. 1999, Harris et al. 2000), but we could not quantitatively assess the effectiveness of our subsampling procedures in producing subsamples whose taxonomic composition completely represented the fauna at each lake. Although subsampling of benthic macroinvertebrate samples remains a topic of discussion, the adequacy of our subsampling procedure is suggested by the fact that our subsamples generally contained numbers of individuals that were above the recommended minimum. For example, based on data from wetlands, King and Richardson (2002) concluded that subsample precision was relatively high and constant for subsamples with  $> 200$  individuals. Using data from streams, Ostermiller and Hawkins (2004) reported that the accuracy of RIVPACS models was quite robust to subsampling effort (ranging from 50 to 450 individuals per subsample), and that the effects of sampling error on model precision could be minimized by constructing models from subsamples of  $\geq 350$  individuals. Of the collections we made that were subsampled, the number of individual benthic macroinvertebrates per subsample ranged from nine to 5128 (median = 824). Eighty percent of subsamples contained at least 200 individuals and 61% contained at least 350 individuals.

#### *Habitat characterization*

Habitat attributes measured for each water body included elevation, surface area, maximum water depth, outlet width, and littoral zone (i.e., near shore) substrate composition (Table 1). Water body elevation and surface area were obtained from USGS 1:24 000 topographic maps. Maximum water depth was determined by sounding with a weighted line, and average outlet width in the first 100 m below each water body was visually estimated. Littoral zone substrate composition was characterized by visually estimating the dominant substrate along approximately 50 3-m transects evenly spaced around the water body perimeter and extending perpendicularly from shore into the water body. Substrates were categorized as silt ( $< 0.5$  mm), sand (0.5–2 mm), gravel ( $> 2$ –75 mm), cobble ( $> 75$ –300 mm), boulder ( $> 300$  mm), bedrock, or woody debris. Substrate composition for a site was expressed as the percentage of transects dominated by each substrate category. We calculated separately the percentage of transects occupied by aquatic vegetation. Sampling date was described as the number of days since 1 January.

#### *Development of predictive model and calculation of O/E*

Statistical procedures used in developing RIVPACS-type models have been described in detail elsewhere (Wright et al. 1984, Moss et al. 1987, Clarke et al.

TABLE 1. Characteristics (mean and range) of sites categorized by fish-stocking history.

Variable	Site type		
	Never-stocked	Stocked-fish-present	Stocked-now-fishless
Elevation (m)	2531 (1542–3432)	2608 (1746–3304)	2663 (1529–3463)
Surface area (ha)	1.6 (0.1–20.2)	11.4 (0.9–69.4)	7.2 (1.5–28.9)
Maximum depth (m)	5.0 (0.2–30.0)	12.0 (0.3–30.0)	13.7 (2.0–30.0)
Outlet width (cm)	43 (0–800)	151 (0–1000)	82 (0–350)
Days (1 January = 1)	220 (167–268)	220 (164–271)	209 (161–271)
Silt (%)	58 (0–100)	39 (0–100)	29 (0–92)
Sand (%)	7 (0–71)	18 (0–69)	17 (0–70)
Gravel (%)	4 (0–52)	11 (0–53)	7 (0–62)
Cobble (%)	9 (0–100)	11 (0–72)	13 (0–77)
Boulder (%)	5 (0–71)	7 (0–43)	12 (0–59)
Bedrock (%)	5 (0–43)	7 (0–32)	12 (0–39)
Woody debris (%)	11 (0–100)	7 (0–44)	11 (0–67)
Aquatic vegetation (%)	46 (0–100)	30 (0–100)	26 (0–92)
Number of taxa	20 (7–34)	17 (4–30)	20 (5–34)

1996, Marchant et al. 1997, Hawkins and Carlisle 2001), and we therefore provide only a brief summary of the procedures we used to develop and implement the predictive model. These procedures were as follows:

(1) Based on presence/absence data for all amphibian, reptile, benthic macroinvertebrate, and zooplankton taxa, never-stocked (reference) sites were classified into groups with similar faunal composition based on a cluster analysis (flexible beta unweighted pair-group arithmetic averaging (UPGMA) method with  $\beta = -0.1$ ; Belbin and McDonald 1993) following calculation of Sørensen similarities (Faith et al. 1987). Precision, accuracy, and sensitivity of RIVPACS models is typically improved by excluding rare taxa (Ostermiller and Hawkins 2004). Therefore, our classification step included only those taxa that occurred at  $\geq 5\%$  of sampled sites (Hawkins et al. 2000). However, following classification, rare taxa were included in subsequent predictions of biotic composition (see step 4 below).

(2) We used stepwise multiple discriminant analysis of habitat data collected from never-stocked lakes to identify the measured habitat features that best discriminated among the groups defined in step 1, and then used this discriminant functions model to estimate the probabilities of group membership for stocked-fish-present and stocked-now-fishless sites. Collinearity of the 13 predictor variables was low (average correlation coefficient ( $|r|$ ) = 0.26, range = 0.01–0.65) and all variables were therefore included in the discriminant analysis. To determine how well the discriminant functions model predicted group membership, we used the jackknifing procedures within the SYSTAT (version 10) discriminant functions routine (SYSTAT 2000). Jackknife procedures iteratively drop individual observations from the larger dataset, build a model based on the reduced data, and then use the reduced model to predict the group memberships of dropped sites.

(3) Probabilities of group membership obtained from the discriminant functions model were used in

conjunction with group-specific frequencies of occurrence for all taxa ([number of sites within a group in which a taxon was observed]/[total number of sites within a group]) to estimate site-specific probabilities of capture ( $P_c$ ) for each taxon.

(4) Probabilities of capture were used to identify the specific taxa predicted to occur in samples from never-stocked lakes for both  $P_c \geq 0$  and  $P_c \geq 0.5$  and estimate the number of taxa expected to occur ( $E$ ) in the sample for both  $P_c$  thresholds ( $E = \sum P_c$ ). These data were then used to calculate  $O/E$  for both  $P_c$  thresholds (i.e.,  $O/E_0$  and  $O/E_{50}$ ), where  $O$  is the observed number of taxa with  $P_c$  greater than the threshold value.

(5) Model error was estimated by comparing the number of taxa observed at reference sites to that expected from the model and generating a distribution of  $O/E$  ratios for never-stocked lakes. This population of  $O/E$  ratios describes the distribution of errors in predicting species occurrence.

(6) We then calculated probabilities of capture and  $O/E$  ratios for stocked-fish-present and stocked-now-fishless sites following procedures described in steps 3 and 4. One stocked-fish-present site and two stocked-now-fishless sites were removed from the dataset because the percent littoral zone boulder (a predictor variable used by the model) for these sites was outside the range observed at never-stocked sites.

Two important points regarding the RIVPACS modeling approach should be emphasized. First, one might assume that the groups developed in the cluster analysis are meant to delineate distinct community types to which new sites are assigned. In fact, the RIVPACS approach is based on the view that changes in community structure across sites are best regarded as a continuum, and that sites may not naturally fall into completely distinct ecological types (Clarke et al. 2003). New sites are therefore not simply assigned to their most likely group based on their environmental attributes but are instead assigned to each of the classification groups probabilistically (Clarke et al. 2003).

As such, the groups developed in the cluster analysis may not represent real community types and should be viewed simply as a shortcut to estimating how probabilities of capture for individual taxa should vary along a continuum.

Second, RIVPACS model assessments are most sensitive to the loss of those taxa with high predicted probabilities of capture, i.e., common taxa. Moreover, a taxon not found in the reference sites, but that was common in the test sites (i.e., stocked-fish-present, stocked-now-fishless sites), would not be included in an assessment because it does not contribute to  $E$  and is not counted in  $O$  because it was not predicted to occur. However, this situation did not apply to our study. Of the 64 taxa that were found in at least 5% of the study lakes, all were present in one or more never-stocked and stocked sites. Therefore, all taxa that were relatively common in any of the three site types were included in our RIVPACS model assessments.

#### Statistical analyses

To describe faunal resistance and resilience, we compared  $O/E$  ratios between never-stocked, stocked-fish-present, and stocked-now-fishless sites using a one-way analysis of variance (ANOVA) followed by Tukey tests for unequal sample sizes (also called Tukey-Kramer tests). Only stocked-now-fishless sites that had been fishless for more than 10 years ( $n = 36$ ) were used in this comparison. We estimated the number of years that each stocked-now-fishless site had been trout-free by assuming that trout disappeared from individual sites 10 years after the last stocking event (Knapp et al. 2001). This assumption was based on the fact that trout in Sierra Nevada lakes rarely live longer than 10 years.

To determine what habitat and fish variables influenced  $O/E$  ratios for stocked-fish-present sites, we used tree regression (RPART routine in S-Plus Version 6; Therneau and Atkinson 1997) with  $O/E$  ratios as the response variable. Tree-based models are fit by binary recursive partitioning, in which a data set is successively split into increasingly homogeneous subsets that maximize the reduction in deviance produced by each partition (Clark and Pregibon 1992). We were unable to use a cross-validation procedure to determine the optimal size of the regression tree (De'ath and Fabricius 2000) due to the relatively small number of stocked-fish-present sites. Therefore, to minimize overfitting, the minimum number of observations in a node for which the routine would compute a split was set at 10. The final regression tree was represented graphically, with each node characterized by a mean value of the response variable, the number of observations, and the values of the predictor variables that defined it. Predictor variables included maximum water depth, elevation, littoral zone substrate composition, relative survey date, and a measure of trout density (catch per unit effort [CPUE] = number of trout captured per gill net per hour; Schindler et al. 2001). Col-

linearity of predictor variables was low (average correlation coefficient ( $|r|$ ) = 0.17, range = 0.01–0.64) and all variables were therefore included in the analysis. The dimensionality of the littoral zone substrate composition data was reduced to a single axis using principal component analysis. Principal component axis 1 scores accounted for 32% of the total variation in substrate composition. Seven of 71 stocked-fish-present sites were excluded from the analysis because fish populations at these sites were not gill netted and CPUE information was therefore lacking. We predicted that resistance (as measured by  $O/E$ ) would be inversely related to trout density and elevation. No similar regression analysis was possible for the stocked-now-fishless sites due to the prohibitively small sample size associated with this lake type.

To evaluate the response of individual taxa to fish presence and disappearance, we calculated a "sensitivity index" by dividing the total number of sites at which the taxon was observed by the total number of sites at which it was expected to occur (C. P. Hawkins, *unpublished manuscript*; see also Armitage et al. 1987). To ensure the robustness of index values, the sensitivity index was only calculated for taxa observed or expected to occur at  $\geq 10$  sites. Index values  $< 1$  indicate that a taxon was found less often than expected and values  $> 1$  indicate that a taxon was found more often than expected. To facilitate comparisons in sensitivity index values amongst different types of organisms, we grouped taxa into categories representing amphibians/reptiles, benthic macroinvertebrates, and zooplankton (Appendix B). Benthic macroinvertebrate and zooplankton taxa were further subdivided based on their presumed vulnerability to predation by nonnative trout (benthic macroinvertebrates: burrowing/distasteful  $<$  case-dwelling  $<$  clinger/swimmer; zooplankton: small bodied ( $< 1$  mm)  $<$  large-bodied ( $\geq 1$  mm); Knapp et al. 2001). The sensitivity of each faunal group was assessed by determining whether the 95% confidence interval associated with the average index value for each group included or did not include 1. For stocked-fish-present sites, an index value of 1 indicates complete insensitivity to fish presence. For stocked-now-fishless sites, an index value of 1 indicates complete recovery following fish disappearance.

To gain insight into the rate of community recovery, we examined the relationship between  $O/E$  ratios for stocked-now-fishless sites and the number of years since fish disappearance (range = 0–42 yr). The final stocking date for five of the sites was ambiguous and these sites were excluded from the analysis.

#### RESULTS

Based on faunal composition data from 164 never-stocked sites, the cluster analysis identified 15 relatively distinct groups, each containing 6–18 sites. The discriminant analysis identified seven of the 13 habitat variables as important in discriminating between the

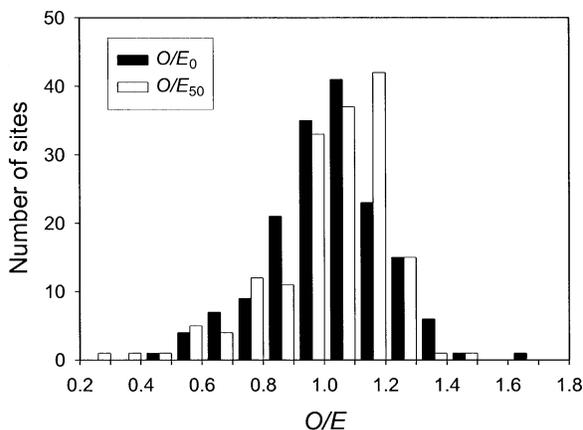


FIG. 1. Frequency histogram of observed-to-expected ratios calculated for never-stocked lakes based on probabilities of capture  $>0$  ( $O/E_0$ ) and  $>0.5$  ( $O/E_{50}$ ).

groups defined by the cluster analysis (Wilk's  $\lambda = 0.035$ ,  $F_{98, 913} = 6.49$ ,  $P < 0.0001$ ). Based on partial  $F$  values for removal of each variable from the final discriminant model, elevation was the most important predictor variable ( $F_{14, 143} = 11.01$ ), followed by relative survey date ( $F_{14, 143} = 4.57$ ),  $\log_{10}$ (maximum water depth) ( $F_{14, 143} = 3.65$ ), littoral zone silt ( $F_{14, 143} = 3.52$ ), littoral zone boulder ( $F_{14, 143} = 3.19$ ), littoral zone wood ( $F_{14, 143} = 2.33$ ), and  $\log_{10}$ (area) ( $F_{14, 143} = 2.25$ ). The jackknife test of the model indicated that it correctly reclassified 44% of the never-stocked sites. This error rate is similar to that reported for other RIVPACS analyses (e.g., Clarke et al. 2003).  $O/E_0$  ratios for the reference sites ranged from 0.42 to 1.66, whereas  $O/E_{50}$  ratios ranged from 0.27 to 1.43 (Fig. 1).  $O/E_0$  and  $O/E_{50}$  ratios both had a mean of 1.00 and a standard deviation of 0.19. Although assessments based on  $O/E_{50}$  are sometimes superior to those based on  $O/E_0$  (e.g., Hawkins et al. 2000, Ostermiller and Hawkins 2004), we used  $O/E_0$  values for the remainder of our analyses because the distribution of  $O/E_0$  ratios was closer to normal than was the distribution of  $O/E_{50}$  ratios (Fig. 1) and  $O/E_0$  used information from all taxa.

Mean  $O/E$  ratios for never-stocked, stocked-fish-present, and stocked-now-fishless sites were 1.00, 0.84, and 1.00, respectively (one-way ANOVA:  $F_{2, 268} = 16.69$ ,  $P < 0.0001$ ; Fig. 2).  $O/E$  ratios from stocked-fish-present sites were significantly lower than those from never-stocked sites and from stocked-now-fishless sites ( $P < 0.05$ ; Fig. 2). In contrast,  $O/E$  ratios from stocked-now-fishless sites were not significantly different from those from never-stocked sites (Fig. 2). Based on 95% confidence intervals, stocked-fish-present sites were missing 11–22% of their expected taxa, while few, if any, of the expected taxa were missing from stocked-now-fishless sites (95% confidence interval = 92–109%).

Tree regression results suggested that faunal resistance (as measured by  $O/E$  ratios from stocked-fish-

present sites) was influenced by trout density (i.e., CPUE), elevation, and maximum water depth (Fig. 3). Analysis of surrogate splits indicated that no alternative variables provided nearly as good a fit to the data as those included in the final model. Sites with CPUE  $\geq 2.2$  fish-net $^{-1}$ ·h $^{-1}$  had lower  $O/E$  ratios than those with CPUE  $< 2.2$ . Of those sites with CPUE  $\geq 2.2$ , shallower sites had lower  $O/E$  ratios than did deeper sites. Of the sites with CPUE  $< 2.2$ , those at higher elevations had lower  $O/E$  ratios than did sites at lower elevations. These lower elevation sites were further influenced by CPUE, with sites with CPUE  $\geq 0.96$  having lower  $O/E$  ratios than those with CPUE  $< 0.96$ .

For stocked-fish-present sites, taxon-specific sensitivity index values ranged from 0.18 (amphibian: *Rana muscosa*) to 3.19 (small zooplankton: *Bosmina longirostris*) (Appendix B). Sensitivity index values for four of the six faunal groups had 95% confidence intervals that did not include 1, indicating that, on average, the presence/absence of taxa in these four groups was considerably influenced by the presence of trout. The average sensitivity index value for amphibians/reptiles was the lowest of the six faunal groups (Fig. 4A) and had a confidence interval that did not include 1. The sensitivity of the three groups of benthic macroinvertebrate taxa varied in accordance with their presumed vulnerability to trout predation (Fig. 4A). Average in-

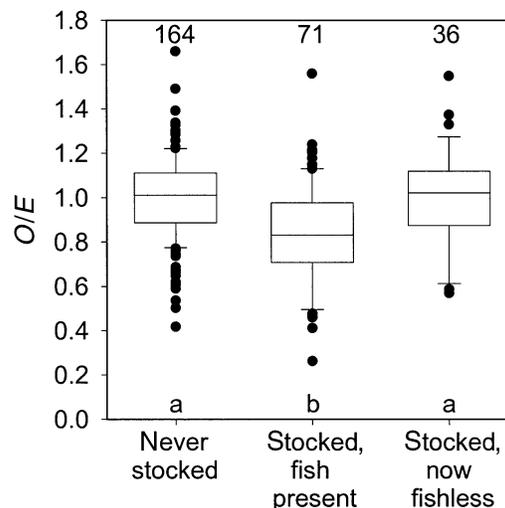


FIG. 2. Box plots showing the observed-to-expected ratios ( $O/E$ ) of never-stocked, stocked-fish-present, and stocked-now-fishless sites in Yosemite National Park. Stocked-now-fishless sites include only those sites that have been fishless for  $>10$  yr. The solid line within each box marks the median, 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 dots indicate points lying outside the 10th and 90th percentiles. Sample sizes are given above each box. Letters below each box indicate statistically significant differences in  $O/E$  ratios between site categories. Categories with different letters are significantly different at the  $P < 0.05$  level (one-way ANOVA followed by Tukey-Kramer tests).

FIG. 3. Regression tree of observed-to-expected ratios ( $O/E$ ) from stocked-fish-present sites as a function of habitat and fish variables. CPUE = catch per unit effort (number of fish captured in a single gill net per hour). Numbers given inside of each node are the mean  $O/E$  ratios for sites included in the node and the sample size. The inset figure shows the tree scaled to display the proportion of variance accounted for at each split.

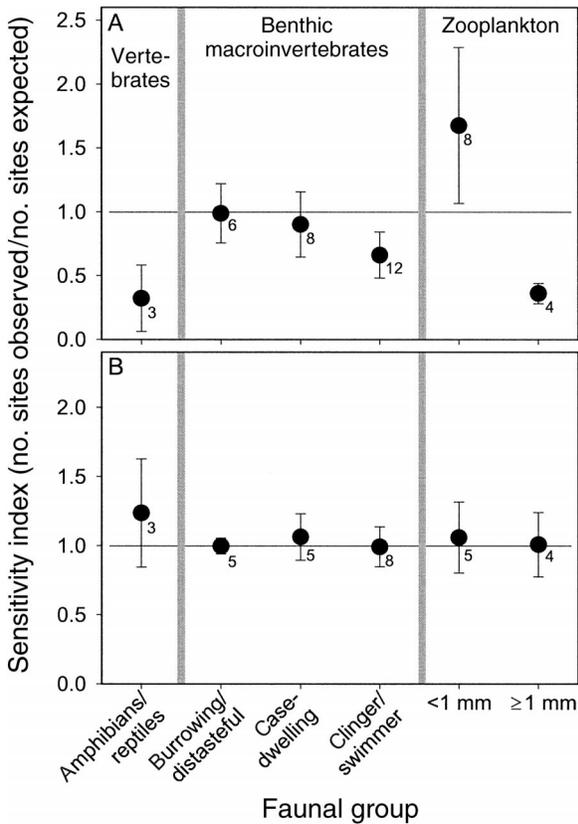
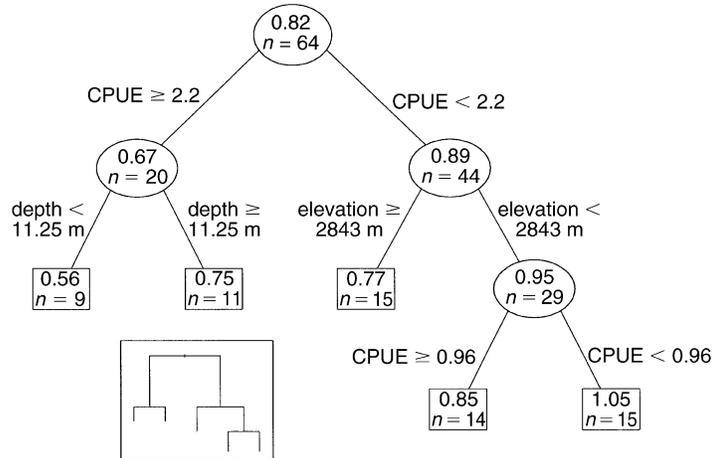


FIG. 4. Sensitivity indices ( $\bar{X} \pm 95\%$  confidence intervals) of vertebrate, benthic macroinvertebrate, and zooplankton taxa for (A) stocked-fish-present sites and (B) stocked-now-fishless sites. Values greater than 1 indicate that the faunal group was observed more often than expected, and values less than 1 indicate that a faunal group was observed less often than expected. Benthic macroinvertebrate and zooplankton taxa were grouped based on presumed vulnerability to predation by nonnative trout. Only those taxa observed or expected to occur at  $\geq 10$  sites were included. Sample sizes for each faunal group are provided adjacent to the point indicating the mean sensitivity index value.

index values for benthic macroinvertebrate taxa categorized as burrowing/distasteful or case-dwelling were near 1 and had confidence intervals that included 1, suggesting that the presence/absence of taxa in these groups was minimally influenced by the presence of fish. In contrast, the average index value for clinger/swimmer taxa was considerably less than 1 and had a confidence interval that did not include 1 (Fig. 4A). Therefore, the probability of occurrence by clinger/swimmer taxa was generally reduced by the presence of fish. The average index values for small and large zooplankton taxa both had confidence intervals that did not include 1, but small zooplankton had an average index value greater than one and large zooplankton had an average index value less than 1 (Fig. 4A). Therefore, the probability of occurrence for small zooplankton taxa increased while that for large zooplankton taxa decreased in the presence of fish.

For stocked-now-fishless sites, sensitivity index values ranged from 0.57 (Swimmer: *Hydroporus*) to 1.61 (*Rana muscosa*) (Appendix B). In contrast to the results from stocked-fish-present sites, average index values for the six faunal groups in stocked-now-fishless sites were all close to 1 and all had confidence intervals that included 1 (Fig. 4B). These results suggest that, on average, the taxa in each group recovered following fish disappearance.

For stocked-now-fishless sites, the relationship between the  $O/E$  ratio and the number of years since fish disappearance indicated that nearly all sites that had reverted to a fishless condition  $>2$  yr prior to our sampling had  $O/E$  ratios  $\cong 1$  (average = 1.03; Fig. 5). Only the site that lost its fish population in the year it was sampled (years since fish disappearance = 0) had an  $O/E$  ratio that was well below the range of variability of the remaining sites (Fig. 5). Therefore, the taxonomic composition of stocked-now-fishless lakes recovered to closely resemble that of never-stocked lakes in  $\leq 2$  yr following fish disappearance.

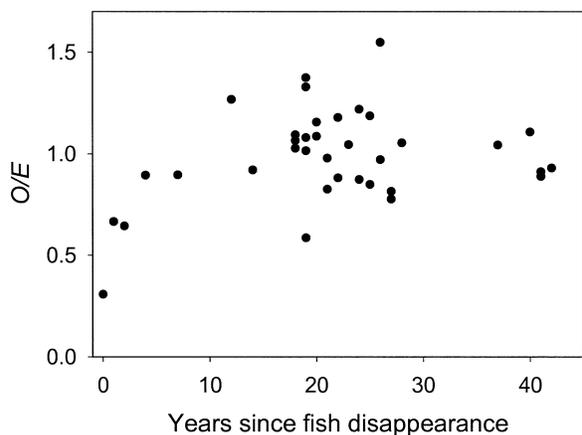


FIG. 5. For stocked-now-fishless sites, observed-to-expected ratios as a function of years since fish disappearance.

#### DISCUSSION

Our predictive modeling approach and the resulting *O/E* ratios provided a relatively straight-forward method of quantifying resistance and resilience of Yosemite's lentic fauna to fish introductions. The Yosemite study system was well-suited to the predictive modeling approach for at least two reasons. First, given that water bodies in Yosemite vary widely in elevation, associated habitat features, and original faunal composition, direct comparisons of faunal composition between the never-stocked, stocked-fish-present, and stocked-now-fishless sites (e.g., Knapp et al. 2001) would likely be highly confounded. In contrast, *O/E* ratios generated from our predictive model allowed direct comparisons of faunal alteration across sites that differed considerably in their original fauna (Wright 1995, Moss et al. 1999, Hawkins et al. 2000). Second, our study sites were located within a national park, where habitats are generally well-protected. As a consequence, our reference sites (never-stocked lakes) likely closely reflected undisturbed conditions. This contrasts with the typical situation, where disturbance is universal and minimally impacted sites must therefore suffice as reference sites (Reynoldson and Wright 2000).

#### Resistance

Stocked-fish-present sites had significantly lower *O/E* ratios than never-stocked sites, and were missing 16% of their expected taxa. This impact of trout predation on Yosemite's lentic fauna is consistent with the results of numerous previous studies that described effects of introduced fish on the amphibian, reptile, zooplankton, or benthic macroinvertebrate fauna of lakes throughout North America (Anderson 1980, Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998, Knapp et al. 2001, Pilliod and Peterson 2001, Matthews et al. 2002). The magnitude of the effect of fish predation on lake fauna in Yosemite is somewhat smaller

than that reported in the only other RIVPACS-type analysis of introduced fish effects on lake faunal assemblages that we are aware of (Hawkins and Carlisle 2001). In this study of alpine lakes in the Rocky Mountains of the United States, fish-containing lakes were missing 24% of their expected taxa.

Resistance (as measured by *O/E* ratios of stocked-fish-present sites) varied widely among sites, and this variation was partially explained by differences in trout density, elevation, and water depth. For the groups of sites developed by the tree regression analysis, *O/E* ratios ranged from 0.56 for shallow sites with high densities of trout, to 1.05 for low elevation sites with very low trout densities. Therefore, the impact of introduced trout ranged from quite severe (44% of expected taxa were missing) to nonexistent (none of the expected taxa were missing). This highly variable effect of introduced trout suggests that the consequences of trout introductions are considerably more complex than the uniformly strong effects that are suggested by the available literature describing changes in the faunal composition of mountain lakes following trout introductions. The view of uniformly strong effects is likely a consequence of this literature being made up almost exclusively of studies that focused on high elevation alpine lakes (Anderson 1980, Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998, Knapp et al. 2001, Pilliod and Peterson 2001), precisely those systems in which our results suggest that trout impacts should be the strongest.

*O/E* ratios were inversely related to trout density, presumably because predation pressure increases with fish density (Pierce and Hinrichs 1997, Leppa et al. 2003). *O/E* ratios and elevation were also inversely related, and this relationship could be the result of at least three factors. First, habitats in high elevation lakes are simpler than those in lakes at low elevations, and simple habitats may magnify the effects of fish predation because they provide little structural refuge (Savino and Stein 1982, Anderson 1984, Diehl 1992). Second, generation times of heterothermic animals are typically an increasing function of temperature (Birch 1948, Ward and Stanford 1982). As a result, warm temperatures in low elevation lakes may shorten generation times, decreasing the likelihood of prey extinction (Roy et al. 2003). Third, top-down control on at least large-bodied zooplankton may be strongest in lakes with low nutrient levels (high elevation lakes) and weaker in lakes with intermediate nutrient levels (low elevation lakes) (Jeppesen et al. 2003). This latter influence of elevation on resistance by Yosemite lake fauna remains speculative, as we currently lack water chemistry data for any of the study lakes. Unexpectedly, resistance increased with water depth. Similar effects of lake depth in mediating fish impacts on zooplankton were reported in past studies (Donald et al. 1994, Jeppesen et al. 2003). One possible mechanism for this effect is that in shallow lakes fish have simultaneous access to

both benthic and pelagic prey, thereby magnifying predation effects.

Based on sensitivity indices, faunal groups differed considerably in their vulnerability to fish predation. On average, amphibians, reptiles, clinger/swimmer benthic macroinvertebrates, and large zooplankton were negatively affected, small zooplankton were positively affected, and burrowing/distasteful and case-dwelling benthic macroinvertebrates were minimally affected by trout introductions. These results are largely consistent with those of other studies describing impacts of trout on the fauna of mountain lakes (Stoddard 1987, Bradford et al. 1998, Carlisle and Hawkins 1998, Knapp et al. 2001, Pilliod and Petersen 2001, Matthews et al. 2002). However, sensitivity indices identified at least one taxon whose response to trout predation in this study was markedly different from that described for alpine Sierra Nevada lakes by previous studies. In alpine lakes, the distribution of larval *Callibaetis* mayflies was significantly reduced by the presence of trout (Bradford et al. 1998, Knapp et al. 2001). In contrast, results from the current study indicate that in Yosemite lakes the distribution of this species was unaffected by trout (sensitivity index = 0.93; Appendix B). Future studies will be necessary to elucidate the roles of habitat complexity, water temperature, nutrient levels, and other factors in influencing whether or not *Callibaetis* can persist in the presence of trout.

Most impacts of nonnative trout on Yosemite's lentic fauna appear to result from direct trout predation, but some effects may be indirect. For example, the garter snake, *Thamnophis elegans*, was five times less likely to be detected at trout-containing vs. trout-free sites. This species is generally too large to be preyed upon by trout, and the negative effect of trout appears to be a consequence of competition between trout and snakes for shared amphibian prey (Jennings et al. 1992, Matthews et al. 2002). Other likely indirect effects are the increased probability of occurrence by small zooplankton and oligochaetes in the presence of trout (Appendix B). The increase by small zooplankton is likely due to reduced competition or predation from large zooplankton (Anderson 1980, Stoddard 1987). A similar mechanism may explain the increased oligochaete occurrence (see also Carlisle and Hawkins 1998, Knapp et al. 2001). Alternatively, oligochaetes may be more common in the presence of trout as a result of trout-induced changes in food webs that increase the flow of nutrients to the benthos (Leavitt et al. 1994, Schindler et al. 2001).

#### Resilience

Despite the relatively low resistance of Yosemite's native lentic fauna, the similar *O/E* ratios of stocked-now-fishless sites relative to never-stocked sites suggests high resilience. Similarly high resilience of lentic fauna to fish impacts is known for systems as different as a hypereutrophic lake in the midwestern United

States (Mittelbach et al. 1995) and oligotrophic alpine lakes in the Rocky Mountains (Donald et al. 2001) and Sierra Nevada (Knapp et al. 2001). In the current study, sensitivity indices suggested that, on average, all faunal groups were similarly capable of recovering following fish disappearance. Knapp et al. (2001) also reported the complete recovery of most native taxa following fish disappearance, and suggested that this high resilience was due in part to the fact that many benthic macroinvertebrates have winged adult stages with considerable dispersal abilities, and many zooplankton taxa have long-lived resting eggs that allow immediate reappearance following fish extinction (Hairston et al. 1995). However, they cautioned that two species that showed full recovery in their study (*Hesperodiaptomus shoshone*, *Rana muscosa*) may be increasingly unlikely to recover in the future. Both species also showed full recovery in the current study, but new evidence gathered since Knapp et al. (2001) underscores the concerns regarding future recovery of these species.

*H. shoshone* is a large-bodied copepod that is typically eliminated by trout predation (Stoddard 1987, Bradford et al. 1998, Knapp et al. 2001). However, in lakes with relatively short fish residence times (<30 yr), this species typically recovers following fish disappearance (Knapp et al. 2001). In contrast, *H. shoshone* failed to recover following experimental fish removal from four Sierra Nevada lakes that had fish residence times >60 yr (Sarnelle and Knapp 2004). A similar recovery failure following fish removal is also known for a related species, *Hesperodiaptomus arcticus* (McNaught et al. 1999). A likely reason for these recovery failures is depletion of the egg bank during the period of fish residence (McNaught et al. 1999) to a point where mate limitation precludes successful sexual reproduction (Sarnelle and Knapp 2004). Today, trout-containing lakes in Yosemite typically have fish residence times exceeding 60 yr and, as a consequence, *H. shoshone* may often fail to recover even if trout are removed from these lakes in the near future.

*Rana muscosa* (mountain yellow-legged frog) has declined dramatically during the past century, and is now absent from at least 80% of its historic localities (Bradford et al. 1994, Drost and Fellers 1996). Introduced trout are one of the causes of this decline (Bradford 1989, Knapp and Matthews 2000, Knapp et al. 2003), and trout removal can allow this species to recover (Vredenburg 2004; R. A. Knapp, unpublished data). Because *R. muscosa* rarely co-occurs with trout, recovery is generally initiated by emigration from source populations. However, the ongoing decline of *R. muscosa* is resulting in fewer source populations, and because the species typically moves only short distances (<1 km; Matthews and Pope 1999), its ability to recolonize appears on the wane. For example, six years after the removal of trout populations from a series of Sierra Nevada lakes, *R. muscosa* has recolonized only the two treated lakes located within 1 km

of a source population (R. A. Knapp, *unpublished data*). Two other lakes that are >4 km from a source population have not been recolonized, despite the fact that both sites contain high-quality *R. muscosa* habitat.

Our results suggest relatively low resistance but high resilience of the fauna in Yosemite lakes, but it could be argued that our exclusion of rare taxa from the classification step during model development may have caused us to over- or underestimate these measures of system stability. We acknowledge that our conclusions of low resistance and high resilience might be most directly applicable to the more common taxa found in our study lakes, and that our RIVPACS model provided few insights into how rare taxa responded to fish introductions and subsequent disappearance. However, for at least two reasons, we suggest that our conclusion of low resistance and high resilience is unlikely to be strongly influenced by the responses of rare taxa to introduced fish. First, many rare taxa are likely to be "accidentals," taxa that dispersed into a site prior to our sampling but that would not maintain viable populations (Hawkins et al. 2000). The distributions of these taxa are therefore transient, making it appropriate to give them little weight when quantifying faunal resistance and resilience. Second, although rare taxa might be more sensitive to disturbance than are common taxa, Hawkins et al. (2000) found that rare stream macroinvertebrates were no more sensitive as a group to perturbations than were common species.

#### *Implications for lake restoration*

The results of this study indicate that the native fauna of lakes in Yosemite National Park has relatively low resistance to trout introductions. These trout impacts conflict with the governing legislation of the National Park Service (Organic Act of 1916) that states that a fundamental purpose of national parks is "to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment for the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." Our results show that these lakes are excellent candidates for restoration because the effects of past fish introductions are largely reversible over reasonably short periods. Their potential for recovery may not last indefinitely, however, and we suggest that lakes with the lowest expected resistance to trout impacts (i.e., lakes at high elevations and/or with high trout densities) would be particularly important targets for immediate restoration.

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#### APPENDIX A

Color photographs of the study sites shown in Plate 1 are available in ESA's Electronic Data Archive: *Ecological Archives* A015-022-A1.

#### APPENDIX B

A table showing lentic taxa included in the predictive model and associated habit/category information and sensitivity index values are available in ESA's Electronic Data Archive: *Ecological Archives* A015-022-A2.