

RECOVERY AFTER LOCAL EXTINCTION: FACTORS AFFECTING RE-ESTABLISHMENT OF ALPINE LAKE ZOOPLANKTON

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Abstract. The introduction of fishes into naturally fishless mountain lakes often results in the extirpation of large-bodied zooplankton species. The ability to predict whether or not particular species will recover following fish removal is critically important for the design and implementation of lake restoration efforts but is currently not possible because of a lack of information on what factors affect recovery. The objective of this study was to identify the factors influencing recovery probability in two large-bodied zooplankton species following fish removal. We predicted that (1) *Daphnia melanica* would have a higher probability of recovery than *Hesperodiaptomus shoshone* due to differences in reproductive mode (*D. melanica* is parthenogenetic, *H. shoshone* is obligately sexual), (2) recovery probability would be a decreasing function of fish residence time due to the negative relationship between fish residence time and size of the egg bank, and (3) recovery probability would be an increasing function of lake depth as a consequence of a positive relationship between lake depth and egg bank size. To test these predictions, we sampled contemporary zooplankton populations and collected paleolimnological data from 44 naturally fishless lakes that were stocked with trout for varying lengths of time before reverting to a fishless condition. *D. melanica* had a significantly higher probability of recovery than did *H. shoshone* (0.82 vs. 0.54, respectively). The probability of recovery for *H. shoshone* was also significantly influenced by lake depth, fish residence time, and elevation, but only elevation influenced the probability of recovery in *D. melanica*. These results are consistent with between-species differences in reproductive mode combined with the much greater longevity of diapausing eggs in *D. melanica* than in *H. shoshone*. Our data also suggest that *H. shoshone* will often fail to recover in lakes with fish residence times exceeding 50 years.

Key words: alpine lakes; crustacean zooplankton; *Daphnia melanica*; diapausing eggs; *Hesperodiaptomus shoshone*; introduced fish; mate limitation; paleolimnology; recovery; Sierra Nevada, California.

INTRODUCTION

The introduction of fishes into naturally fishless mountain lakes is a common practice worldwide (Pister 2001, Schindler and Parker 2002), and causes dramatic changes in native aquatic communities. For example, conspicuous taxa such as amphibians, large zooplankton, and large benthic invertebrates are often driven locally extinct by fish predation (Anderson 1980, Bradford et al. 1998, Knapp and Matthews 2000, Knapp et al. 2001b). Recognition of the severity of these impacts has generated considerable interest in restoring these communities by removing nonnative fish populations. However, the success of such efforts will depend on the ability of the extirpated taxa to recover following fish removal, some of which are expected to have low resilience. Therefore, the ability to predict whether or not particular species will recover at sites being considered for fish removal is critically important for the design and implementation of effective lake restoration efforts. As a first step toward developing this

predictive framework, in this study we sought to identify the factors influencing recovery probability in two large-bodied zooplankton species following fish removal.

The resilience of zooplankton species is generally assumed to be high due to high dispersal rates (e.g., Louette and Meester 2005; but see Jenkins and Buikema 1998, Cáceres and Soluk 2002) and the presence of long-lived diapausing eggs in lake sediments (De Stasio 1989, Hairston 1996, Parker et al. 1996). Several studies have demonstrated relatively rapid recovery of zooplankton communities following removal of perturbations (Yan et al. 1996, Donald et al. 2001, Knapp et al. 2001b, 2005), supporting the assumption of high resilience. However, recovery failure has been documented in some zooplankton species, suggesting that high resilience may not be universal. For example, in mountain lakes large-bodied cladocerans generally recover following fish removal but large calanoid copepods often do not (McNaught et al. 1999, Sarnelle and Knapp 2004). Although lower resilience of copepods relative to cladocerans is not universal (Yan et al. 2004), recovery failure by copepods may be a consequence of relatively low dispersal capabilities (Jenkins and Buikema 1998, Cáceres and Soluk 2002), egg bank depletion during

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prolonged fish presence (Parker et al. 1996), or mate limitation (Sarnelle and Knapp 2004; Kramer et al. 2008).

In California's Sierra Nevada mountains, the widespread stocking of nonnative trout (primarily *Oncorhynchus* spp. and *Salvelinus fontinalis*) has eliminated the large-bodied zooplankton species, *Daphnia melanica* and *Hesperodiaptomus shoshone*, from hundreds of lakes (Bradford et al. 1998, Knapp et al. 2001b, 2005). (Genetic analyses indicate that the *Daphnia middendorffiana* referenced in earlier papers [Stoddard 1987, Bradford et al. 1998, Knapp et al. 2001b, 2005, Sarnelle and Knapp 2004, 2005] is actually *Daphnia melanica*; M. E. Pfrender, unpublished data.) In lakes that have never been stocked, these two co-occurring species are the dominant zooplankters (Stoddard 1987, Knapp et al. 2001b). Trout introduction nearly always results in the extirpation of *D. melanica* and *H. shoshone*; these species co-occur with trout in only 13% of lakes (based on sampling of 255 fish-containing lakes; R. A. Knapp, unpublished data). Strong interactions of *D. melanica* and *H. shoshone* with other ecosystem components suggest that their failure to recover would preclude the full recovery of lake ecosystem structure and function (Paul and Schindler 1994, McNaught et al. 1999, Parker et al. 2001, Sarnelle and Knapp 2005).

In two recent comparative studies of alpine lakes in the Sierra Nevada, the probability of occurrence by *D. melanica* and *H. shoshone* in lakes that had been stocked and are now fishless was statistically indistinguishable from lakes that had never been stocked, suggesting that both species fully recover following fish disappearance (Knapp et al. 2001b, 2005: Appendix B). In contrast, experimental removal of trout populations from five lakes, all of which contained both *D. melanica* and *H. shoshone* prior to fish introductions, resulted in *D. melanica* recovering in all five lakes but *H. shoshone* recovering in only one (Sarnelle and Knapp 2004; R. A. Knapp and O. Sarnelle, unpublished data). These contrasting results for *H. shoshone* could be a consequence of the relatively coarse-grained depiction of recovery obtained from synoptic surveys compared to experimental fish removals. Alternatively, these differences could be the result of the survey and experimental lakes differing with respect to a variable that is strongly associated with *H. shoshone* recovery.

The objective of this study was to provide a more thorough analysis of the factors that influence the probability of recovery by *D. melanica* and *H. shoshone*. We made three predictions. First, the probability of recovery should be lower for *H. shoshone* than for *D. melanica*. This prediction is based on differences between these species in their reproductive modes; reproduction in *H. shoshone* is obligately sexual, but *D. melanica* reproduces parthenogenetically. This requirement for mating in *H. shoshone* imposes a lower bound on the size of a founding population due to mate limitation (Gerritsen 1980, Courchamp et al. 1999,

Sarnelle and Knapp 2004; Kramer et al. 2008). Our second prediction was that the probability of recovery should be inversely related to fish residence time, because longer fish residence times would lead to greater depletion of egg banks. Egg longevity data for *H. shoshone* and for species closely related to *D. melanica* suggest that eggs of *D. melanica* may remain viable in sediments for more than 125 years (Cáceres 1998) while those of *H. shoshone* may remain viable for less than 50 years. This estimate of egg longevity in *H. shoshone* is based on results from sediment cores collected from eight lakes in our study area that showed that *H. shoshone* eggs were rare in sediments more than 50 years old (i.e., buried ≥ 25 mm below the sediment surface [Holmes et al. 1989, Knapp et al. 2001a; M. E. Pfrender, unpublished data]). Given that fish have generally been present in Sierra Nevada lakes for 50–80 years, fish residence time should have little effect on *D. melanica* recovery but could severely limit recovery by *H. shoshone*. Third, we predicted that the probability of recovery would be an increasing function of lake depth. This prediction is based on the assumption that the number of diapausing eggs in lake sediments is an increasing function of the number of *D. melanica* and *H. shoshone* in the overlying water column and therefore an increasing function of lake depth. Although it is intuitive that in clear-water lakes, deeper lakes should have larger zooplankton populations than shallower ones, our assumption that the number of diapausing eggs should increase with lake depth has to our knowledge, not been tested previously (within individual lakes, positive relationships between egg density and lake depth were reported by Carvalho and Wolf [1989] and Cáceres [1998]). Therefore, we evaluate this assumption using data from our study lakes before testing the prediction that the probability of recovery is an increasing function of lake depth. Given differences in reproductive mode and longevity of egg banks, any effect of lake depth should be much stronger for *H. shoshone* than for *D. melanica*. We evaluated all three predictions by sampling contemporary zooplankton populations and collecting paleolimnological data from lake sediments. Samples were collected from 44 stocked-now-fishless lakes that ranged widely in fish residence time and habitat characteristics.

METHODS

Lake selection and field sampling

Our study area was in the southern Sierra Nevada and encompassed Sequoia and Kings Canyon National Parks and the adjacent John Muir Wilderness, California, USA. All study lakes are located in the subalpine and alpine zones and were historically fishless (Knapp et al. 2001b). We used fish stocking records (Zardus et al. 1977; California Department of Fish and Game, unpublished data) and recent gill-net surveys of fish populations (Knapp et al. 2001b; R. A. Knapp, unpublished data) to identify all lakes in the study area

that (1) were stocked at least once in the past, and (2) had reverted to a fishless condition following a halt to stocking (usually due to a lack of suitable spawning habitat [Armstrong and Knapp 2004]). Forty-four lakes met both criteria. To get an initial assessment of whether *H. shoshone* and/or *D. melanica* had recovered following fish disappearance, we collected a single zooplankton sample from all 44 lakes (Fig. 1). Sampling occurred during the summer (late June to mid-September) and at least three weeks following ice-out. Zooplankton were sampled using a conical plankton net (29.5 cm diameter, 64- μ m mesh) towed vertically from just above the lake bottom to the surface in the deepest part of each lake. Replicate tows were made until substantial numbers of zooplankton were present in samples (two to five tows per lake). Samples were preserved in 5% sugar formalin (Knapp et al. 2001b). Presence/absence of *H. shoshone* and *D. melanica* in each sample was determined by scanning the entire sample using a dissecting microscope (40 \times magnification). Presence of these species in the zooplankton sample was interpreted as evidence that the species had recovered following fish disappearance (Fig. 1). Species absence could be the result of recovery failure or their absence prior to fish introductions.

To determine historical occupancy of the study lakes by *H. shoshone* and *D. melanica*, we analyzed lake sediment samples for the presence or absence of species-specific subfossil remains. This allowed us to eliminate from our data set all lakes in which *H. shoshone* and/or *D. melanica* were not present prior to fish introductions. Sediment samples were collected from the deepest portion of each lake using a weighted bucket. The bucket was lowered into the sediment, dragged across the bottom for \sim 5 m, and raised to the surface. Snorkeling observations indicated that the bucket generally sampled the top 10 cm of sediment. Given that sedimentation rates in Sierra Nevada lakes are typically <0.5 mm per year (Holmes et al. 1989; M. E. Pfrender, unpublished data) and that the 44 study lakes had harbored fish populations for 10–70 years (average = 34 years), this sampling depth ensured the collection of sediments deposited prior to fish introduction. The resulting samples were undoubtedly sufficient for determining the historical presence or absence of *H. shoshone* and *D. melanica*, but because the bucket did not sample sediments at different depths uniformly our sampling method could have produced biased estimates of diapausing egg density (used to evaluate the assumption that deeper lakes had a higher density of diapausing eggs; see *Methods: Statistical analysis*). Other sediment collection methods (e.g., sediment corer, Eckman sampler) would have allowed a more uniform sampling of sediment depths, but were not feasible because of the excessive weight of these samplers and the fact that our study lakes are remote (up 30 km from the nearest road) and could only be accessed on foot.

Following collection, sediment samples were allowed to settle for 10 minutes, after which surface water was

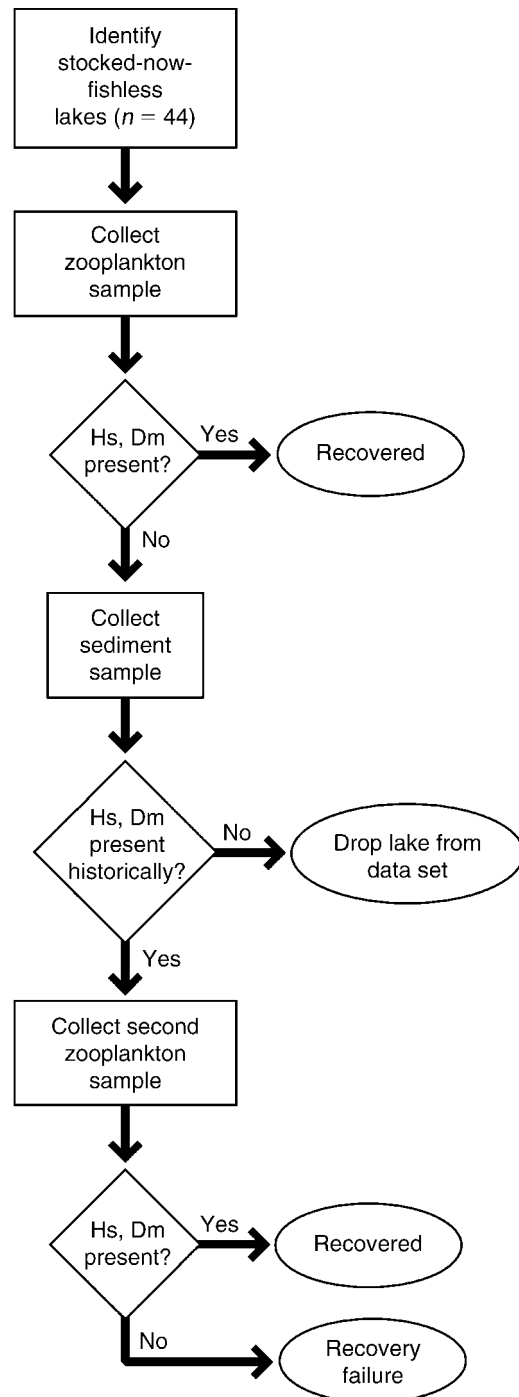


FIG. 1. Schematic of the study design, showing the sampling regime (in rectangles), results from samples (in diamonds), and conclusions reached (in ovals). The two large-bodied zooplankton species studied are *Hesperodiptomus shoshone* (Hs) and *Daphnia melanica* (Dm).

decanted. We then thoroughly mixed the sediment and collected a 60-mL subsample. In the laboratory, the subsample was sonicated for 30 seconds to break apart sediment clumps and then washed through a 150- μ m

mesh sieve to remove fine silt. We scanned everything on the sieve with a dissecting microscope and enumerated *H. shoshone* and *D. melanica* subfossil remains. Remains included *H. shoshone* eggs and egg shells (each egg produces two hemispherical shells upon hatching or decay; Knapp et al. 2001a) and *D. melanica* ephippia and carapace fragments (Frey 1991, Sarmaja-Korjonen et al. 2006). The term “ephippia” refers to the protective casings that surround the eggs of cladocerans. *Daphnia* post-abdominal claws are often used in paleolimnological studies (Frey 1986), but were never encountered in our samples. We assumed that the lack of *H. shoshone* and/or *D. melanica* remains in sediment samples indicated that the associated species was absent historically, and these lakes were eliminated from the data set (Fig. 1).

Association of subfossil remains with *H. shoshone* or *D. melanica* was straightforward. *H. shoshone* is the only large-bodied copepod inhabiting Sierran lakes (*Hesperodiaptomus eiseni* is found in shallow ponds [Stoddard 1987]) and produces eggs of a characteristic size (152–223 μm [Knapp et al. 2001a]). Similarly, *D. melanica* is the only large-bodied, darkly pigmented cladoceran in these lakes (Stoddard 1987, Knapp et al. 2001b). Comparisons of the size, shape, and pigmentation of ephippia and carapace fragments found in the sediments with specimens of all possible cladoceran species (*Alona* sp., *Alonella excisa*, *Ceriodaphnia laticaudata*, *Daphnia dentifera*, *D. melanica*, *Eurycerus lamellatus*, *Scapholeberis mucronata*, and *Simocephalus serrulatus* [Knapp et al. 2001b, 2005]) allowed us to unambiguously identify those originating from *D. melanica*.

If *H. shoshone* and/or *D. melanica* were not present in the zooplankton sample but evidence of their previous occurrence was found in the sediment sample, we collected a second zooplankton sample from the lake one to two years after collection of the initial zooplankton sample to ensure that the species had not been missed during the first sampling (Fig. 1). Sampling and enumeration methods were identical to those used initially except that every sample was made up of five replicate tows. Presence/absence results from the second set of samples were identical to those from the first set of samples. Therefore, failure to detect *H. shoshone* and/or *D. melanica* in the second sample was interpreted as indicating recovery failure by the species (Fig. 1).

Characterization of habitat and fish residence time

Study lakes were characterized by maximum depth (measured with a weighted sounding line), elevation (from U.S. Geological Survey 1:24 000 topographic maps), and fish residence time. Fish residence time in each lake was based on the year of fish introduction and the estimated year of fish disappearance (Zardus et al. 1977; California Department of Fish and Game, unpublished reports). We assumed that trout disappeared from lakes 10 years after the last stocking. This assumption is based on two lines of evidence (Knapp

et al. 2001b): (1) the average maximum trout age in the study area is 8.3 years, and (2) four lakes surveyed 10–15 years after the last stocking date were found to be fishless.

Statistical analysis

We compared the number of lakes showing recovery and recovery failure in *D. melanica* vs. *H. shoshone* (prediction 1) using Fisher’s exact test. We tested the assumption of a positive relationship between the size of the pre-fish egg bank and maximum lake depth for each species using linear regression. In *D. melanica*, we estimated the size of the pre-fish egg bank as the number of ephippia per sediment sample. For *H. shoshone*, intact eggs were rare in sediment samples (see also Knapp et al. 2001a) but egg shells were common, so the size of the pre-fish egg bank was estimated as $(\text{number of egg shells}) + 2(\text{number of intact eggs})$. The number of intact eggs was multiplied by two because at hatching or death, each egg produces two egg shells; as such, the formula estimates the size of the pre-fish egg bank using egg shells as the common unit of measurement. Using only the number of egg shells in the analysis produced very similar results. We restricted these analyses to lakes in which *D. melanica* and/or *H. shoshone* had not returned following fish disappearance to ensure that our estimates of egg bank density were not confounded by recent egg deposition from recovered populations of *D. melanica* and *H. shoshone*.

We tested our predictions that the probability of recovery would be a decreasing function of fish residence time (prediction 2) and an increasing function of lake depth (prediction 3) using univariate and multivariate analyses. We included lake elevation as an additional predictor variable to ensure that any effects due to elevation were accounted for and did not confound our analyses. Univariate analyses were conducted using nonparametric Wilcoxon rank-sum tests. In our multivariate analyses, we developed separate logistic regression models for *D. melanica* and *H. shoshone* to determine the relative importance of the predictor variables in influencing the probability of recovery. Following the logistic regression analyses, we used tree regression to describe in more detail the relationship between each predictor variable and the probability of recovery (RPART package; Therneau and Atkinson 1997). 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). Due to the relatively small sample sizes of the *D. melanica* and *H. shoshone* data sets, we were unable to use a cross-validation procedure to determine the optimal size of each classification tree (De’ath and Fabricius 2000). Therefore, to minimize overfitting, the minimum number of observations (lakes) in a node for which the routine would compute a split was set to 10.

RESULTS

Samples of contemporary zooplankton populations indicated that *D. melanica* was absent from 12, and *H. shoshone* absent from 22, of the 44 stocked-now-fishless lakes. For *D. melanica*, subfossil remains were absent in sediment samples from five of the 12 lakes in which it had not recovered. Sediment samples from the remaining seven lakes contained 1–88 carapace fragments (mean = 23) and 1–368 ephippia (mean = 119). For *H. shoshone*, subfossil remains were absent in sediment samples from three of the 22 lakes. The remaining 19 lakes contained 11–1122 egg shells (mean = 176) and 0–7 intact eggs (mean < 1). The historic presence of *D. melanica* and *H. shoshone* in seven and 19 lakes, respectively, but their contemporary absence was taken as evidence of recovery failure (Fig. 1). As predicted, the probability of recovery was significantly higher for *D. melanica* than for *H. shoshone* (32/39 = 82% vs. 22/41 = 54%, respectively; Fisher exact test: $P = 0.009$).

The number of *D. melanica* ephippia and *H. shoshone* egg shells both increased with lake depth (Fig. 2). This relationship was highly significant for *H. shoshone* (Fig. 2B; $F_{1,17} = 9.12$, $P = 0.008$, $R^2 = 0.31$), but marginally nonsignificant for *D. melanica* (Fig. 2A; $F_{1,5} = 5.63$, $P = 0.064$, $R^2 = 0.53$). The *D. melanica* relationship was compromised by a small sample size and an absence of lakes with intermediate depths. Regardless, both results suggest the plausibility of our prediction that the probability of recovery should be an increasing function of lake depth.

Univariate analyses indicated that fish residence time and lake depth were not associated with *D. melanica* recovery (Fig. 3A, B), but recovery was significantly more likely in lakes at higher elevations (Fig. 3C). We were unable to fit a logistic regression model due to the small number of lakes in which *D. melanica* failed to recover ($n = 7$). Tree regression produced a single split: *D. melanica* had a much higher probability of recovery in lakes at elevations >3267 m (100%, 31 of 31 lakes) compared to lakes at elevations <3267 m (12%, one of eight lakes). For *H. shoshone*, univariate analyses indicated that lakes showing recovery had significantly shorter fish residence times (Fig. 3D), were significantly deeper (Fig. 3E), and were at significantly higher elevations (Fig. 3F). In the logistic regression analysis, the overall model was significant ($P = 0.013$), as were each of the three predictor variables. The probability of recovery was a decreasing function of fish residence time (coefficient = -0.102 , $P = 0.029$) and an increasing function of both lake depth (coefficient = 0.346 , $P = 0.042$) and elevation (coefficient = 0.010 , $P = 0.016$). Results from the tree regression were consistent with those from the logistic regression and provided additional details on the relationship between the predictor variables and *H. shoshone* recovery (Fig. 4). Of the 41 lakes in the data set, *H. shoshone* recovered in 30% of shallow lakes (<12.75 m) but in 100% of deep lakes. In

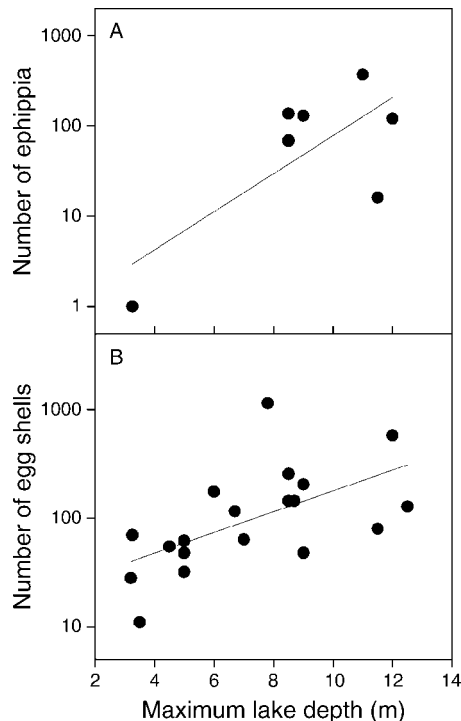


FIG. 2. Relationship between the number of subfossil remains in sediment samples and lake depth for (A) *Daphnia melanica* and (B) *Hesperodiaptomus shoshone*. In (A), the term “ephippia” refers to the protective casings that surround the eggs of cladocerans. Analyses included only those lakes characterized by recovery failure (sample sizes are 7 and 19 lakes, respectively, for *Daphnia* and *Hesperodiaptomus*). The y-axis is on a log scale.

shallow lakes, *H. shoshone* never recovered in lakes with long fish residence times (>47.5 years), but recovered in 47% of the lakes with short fish residence times. Finally, in shallow lakes with short fish residence times, *H. shoshone* recovered in 18% of low-elevation lakes (<3393 m) vs. in 100% of high-elevation lakes.

DISCUSSION

Probability of recovery

The probability of recovery was significantly higher for *D. melanica* than for *H. shoshone* (82% vs. 54%), as predicted. We suggest that the most likely cause of this difference is asexual reproduction in *D. melanica* vs. sexual reproduction in *H. shoshone* (Sarnelle and Knapp 2004, Kramer et al. 2008). Theoretically, *D. melanica* could recover from a single egg, and therefore only complete depletion of its egg bank (via hatching, death, or burial in lake sediments) would prevent recovery. In contrast, successful re-establishment by *H. shoshone* likely requires a founding population of thousands of individuals to overcome constraints imposed by mate limitation, and recovery failure could therefore occur even when the egg bank still contains viable eggs (Kramer et al. 2008). The importance of mate limitation

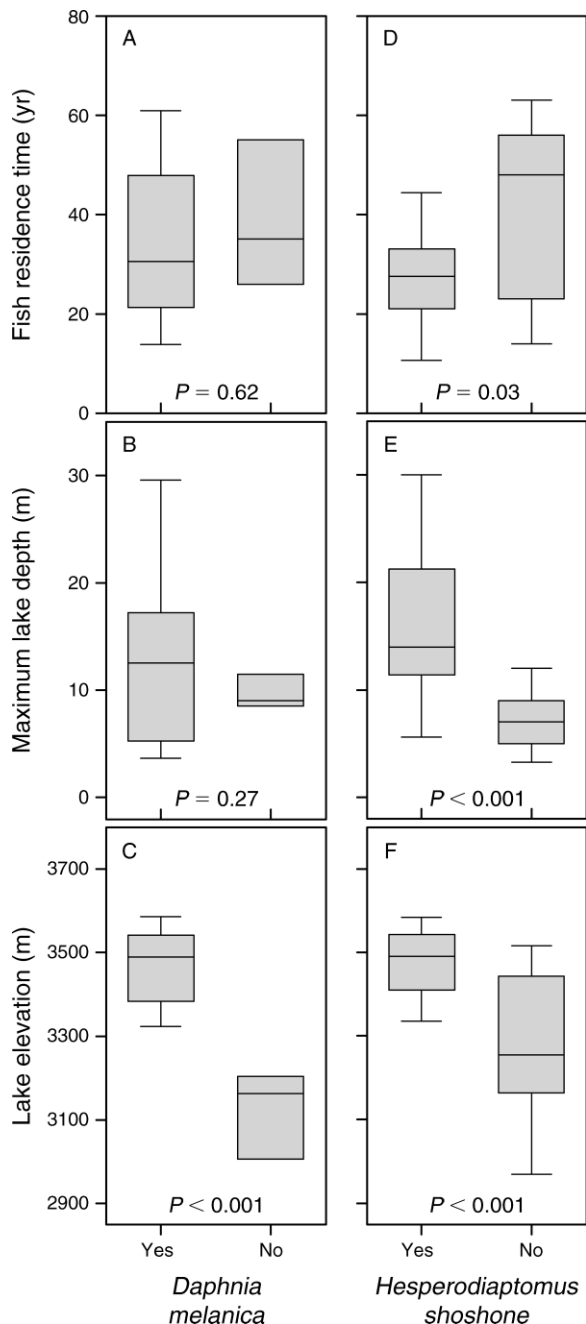


FIG. 3. Box plots showing fish residence time, maximum depth, and elevation for lakes in which (A–C) *Daphnia melanica* and (D–F) *Hesperodiptomus shoshone* recovered vs. did not recover following fish disappearance. The numbers of lakes showing recovery vs. non-recovery are 32 and 7 for *D. melanica*, and 22 and 19 for *H. shoshone*, respectively. The line within each box marks the median, the bottom and top of each box indicate the 25th and 75th percentiles, and the whiskers below and above each box indicate the 10th and 90th percentiles. *P* values from Wilcoxon rank-sum tests are given at the bottom of each panel.

as an obstacle to recovery is supported by our finding that sediment samples from four of the 19 lakes in which *H. shoshone* failed to recover contained two to seven, apparently viable, diapausing eggs (i.e., unhatched, intact, and brilliant red in color [Parker et al. 1996]). Furthermore, in 2003 we reintroduced *H. shoshone* into six stocked-now-fishless lakes at densities ranging from 0.01 individuals/m³ to 10 individuals/m³, and only the highest reintroduction density resulted in *H. shoshone* recovery (Kramer et al. 2008). The decline and eventual extinction of the lower density populations was associated with female mate limitation.

Several potentially confounding factors may have influenced our estimated recovery probabilities. First, if lakes sampled for *D. melanica* vs. *H. shoshone* were different with respect to an important environmental characteristic (e.g., depth), this could have biased our estimated recovery probabilities. However, the two data sets had 37 lakes in common, and restricting the analysis to these 37 lakes caused little change in the recovery probabilities (81% and 59% for *D. melanica* and *H. shoshone*, respectively). Second, our estimates could be biased if *D. melanica* exhibits a higher population growth rate than *H. shoshone* and the time since fish disappearance in our study lakes was long enough for *D. melanica* to increase to detectable densities but too short for *H. shoshone*. Population growth rates of both species are relatively rapid, but are likely higher in the multivoltine *D. melanica* than in the univoltine *H. shoshone* (Sarnelle and Knapp 2004; A. M. Kramer and O. Sarnelle, unpublished data). However, in our study lakes the average duration since fish disappearance was 22 years (range = 4–59 years) and in nearly all cases should have been long enough to allow both species to increase to detectable densities. This assertion is based on the rates of *D. melanica* and *H. shoshone* recovery in a replicated whole-lake fish-removal experiment. In that study, *D. melanica* recovered in five of five lakes following fish removal and increased to detectable densities (using the same sampling procedure as in the current study) within four years (Sarnelle and Knapp 2004, 2005; O. Sarnelle and R. A. Knapp, unpublished data). Similarly, although *H. shoshone* recovered in only one of the five lakes, this population increased to a detectable density in six years. Furthermore, restricting our analysis only to those lakes that had been fishless for at least 10 years had minimal effect on the estimated probability of recovery (81% and 62% for *D. melanica* and *H. shoshone*, respectively). Third, our estimates of recovery probabilities could be biased if *D. melanica* had a higher likelihood of being detected during zooplankton sampling than *H. shoshone*. However, our monitoring of zooplankton in Sierra Nevada lakes over the past 10 years indicates that both *D. melanica* and *H. shoshone* are nearly always detected in samples from lakes in which they are known to be present (*D. melanica*: 53 of 54 samples, *H. shoshone*: 60 of 60 samples; R. A. Knapp,

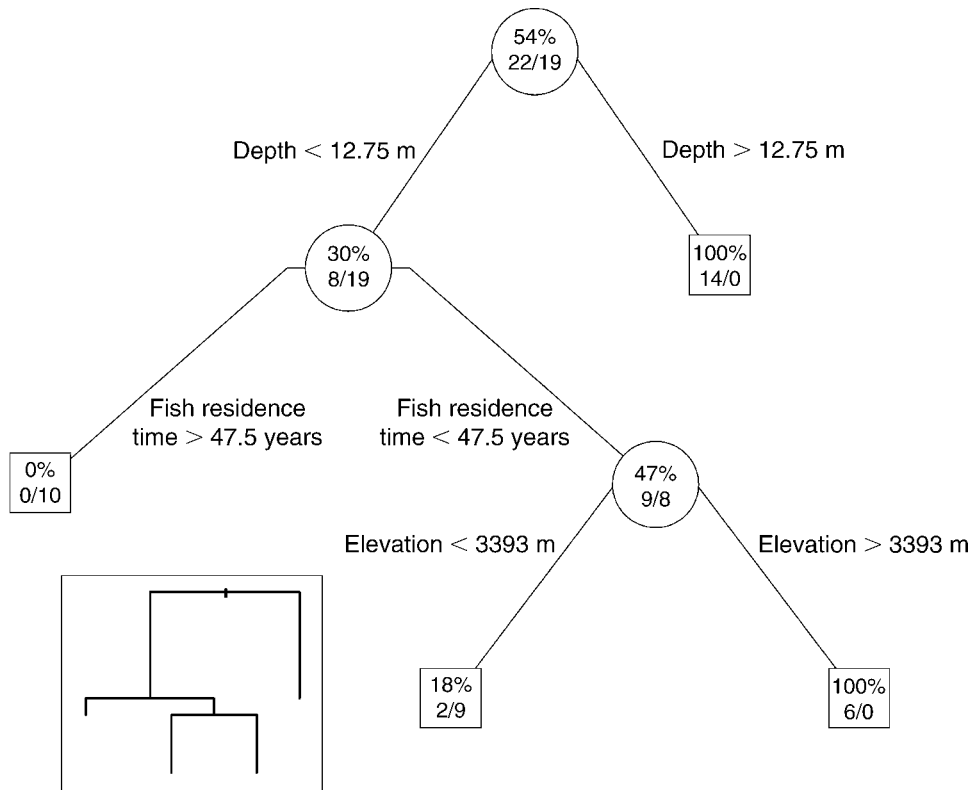


FIG. 4. Classification tree of the probability of *H. shoshone* recovery as a function of lake depth, fish residence time, and elevation. Numbers given inside each node are the percentage of lakes in which *H. shoshone* recovered and the actual number of lakes showing recovery vs. recovery failure. The inset figure shows the tree scaled to display the proportion of variance accounted for at each split.

O. Sarnelle, and A. M. Kramer, *unpublished data*). This high detectability is the result of high within-year and between-year stability in the species composition of planktonic crustacean zooplankton inhabiting these lakes (Sarnelle and Knapp 2005; R. A. Knapp and O. Sarnelle, *unpublished data*). Although high stability in zooplankton community composition is not universal (Arnott et al. 1999), it may be typical of lakes at high latitudes (Shurin et al. 2007) and high altitudes (J. B. Shurin, *personal communication*).

Effects of fish residence time, lake depth, and elevation

The effects of fish residence time and lake depth on the probability of recovery were also consistent with our predictions. Recovery by *D. melanica* was unrelated to either variable, despite at least weak support for egg bank size being an increasing function of lake depth. In *H. shoshone*, egg bank size increased with lake depth and the probability of recovery increased with lake depth and decreased with fish residence time. Results from the tree regression indicated that the importance of fish residence time to *H. shoshone* recovery was confined to shallower lakes (<12.75 m deep), perhaps because these lakes had smaller egg banks at the time of fish introduction and were therefore more sensitive to the

duration of fish presence. *H. shoshone* always recovered in deeper lakes (>12.75 m) despite fish residence times of up to 47 years, presumably because their larger egg banks were not depleted during the period of fish presence. An alternative explanation for the higher probability of *H. shoshone* presence in deep lakes could be that deep-water habitats provide *H. shoshone* a refuge from fish predation (Donald et al. 1994) and as a consequence *H. shoshone* were less likely to be driven to extinction in deep lakes following fish introduction. The importance of this alternative explanation are minimized for two reasons. First, Donald et al. (1994) reported that coexistence occurred primarily in lakes deeper than 16 m and only eight of 41 lakes in our *H. shoshone* data set were >16 m deep. Furthermore, based on extensive sampling of zooplankton and fish populations in lakes throughout the study area, *H. shoshone* were found to coexist with introduced fish in only 13% of sampled lakes (Knapp et al. 2001b). Therefore, in most if not all of our study lakes the presence of *H. shoshone* can be attributed to extinction followed by recovery instead of *H. shoshone* persistence during the period of fish presence.

The negative effect of elevation on the probability of recovery was unexpected and was remarkably consistent

for both *D. melanica* and *H. shoshone* (tree regression results: reduced recovery probability below 3267 m in *D. melanica* and below 3393 m in *H. shoshone*). The mechanism underlying this reduced recovery probability in lower elevation lakes is unknown, but several possibilities deserve mention. First, recovery failure at lower elevation may be a consequence of being at the edge of the habitat niche of these two species, both of which are restricted to high elevations (Anderson 1971, Stoddard 1987). In the Sierra Nevada, *D. melanica* and *H. shoshone* occur above 2800 m and 2200 m, respectively, with probabilities of occurrence for both species being highest above 2900 m (based on samples collected from 352 never-stocked lakes [Knapp et al. 2001b, 2005]). However, elevations of lakes in which *D. melanica* and *H. shoshone* failed to recover (*D. melanica*, 2957–3261 m; *H. shoshone*, 2957–3376 m) were well within the elevational ranges in which both species are common. Therefore, there is no evidence that lakes characterized by recovery failure were close to the lower elevational limit of either species. A second possible mechanism involves effects of elevation on the longevity of egg banks. These effects could result from positive correlations between water temperature and egg hatching rate or between water temperature, lake productivity, and sedimentation rate (i.e., egg burial rate). Unfortunately, data to evaluate these possibilities is lacking. Finally, the lower probability of recovery at low elevations may result from the effects of elevation on the distribution and abundance of invertebrate predators or competitors. Available evidence suggests that in the Sierra Nevada, several invertebrate predators have upper elevational limits near the elevation cut-offs identified in the tree regressions as associated with low vs. high recovery probability. *Chaoborus trivittatus* and *Notonecta* sp. (*N. undulata*, *N. kirbyi*) are common in low to mid-elevation lakes but are rare above 3100 m. Predation by these taxa can have strong effects on zooplankton species composition (Anderson 1980, Takayuki and Masayuki 1989, Shurin 2001) and could potentially preclude successful recolonization of *D. melanica* and *H. shoshone*.

As mentioned previously, two recent comparative studies (Knapp et al. 2001b, 2005) suggested high resilience by *H. shoshone* following fish disappearance but a whole-lake fish-removal study (Sarnelle and Knapp 2004) showed repeated recovery failure. Data from the current study suggest that differences in depths and fish residence times between lakes used in the comparative vs. experimental studies may well explain these different outcomes. In the two comparative studies, 46% and 52% of stocked-now-fishless lakes had maximum depths greater than the 12.75 m cut-off (R. Knapp, unpublished data) suggested by the current study as distinguishing between lakes with low vs. high recovery probability for *H. shoshone*. In contrast, all of the lakes in the experimental study were shallower than

12.75 m (average = 5.5 m, range = 3.5–8.0 m) and are therefore predicted to have low recovery probabilities. Furthermore, lakes in the comparative studies had average fish residence times of 27 years and 38 years (R. Knapp, unpublished data), compared to an average fish residence time of 56 years for lakes in the experimental study. Therefore, the majority of lakes in the two comparative studies had fish residence times that were considerably shorter than the 47.5 year cut-off that distinguishes between lakes with high vs. low recovery probability, but all lakes in the experimental study had fish residence times that exceeded this cut-off.

Implications for lake restoration

Recognition that introduced trout have dramatically altered mountain lake ecosystems has generated considerable interest in restoring lakes to their original fishless condition (Parker et al. 2001, Vredenburg 2004, Knapp et al. 2007). In California, Sequoia-Kings Canyon and Yosemite National Parks and the California Department of Fish and Game are all conducting fish removal projects and significant future expansion of these efforts is anticipated. The results of the current study suggest that recovery of *H. shoshone* following these fish removals is likely to be rare due to long fish residence times. The majority of trout-containing lakes in the Sierra Nevada were first stocked prior to 1950 (Knapp 1996) and therefore have fish residence times of at least 57 years. Consequently, although *D. melanica* will likely recover in Sierra Nevada lakes following trout eradication, *H. shoshone* will often fail to recover, especially in shallower lakes. Complete restoration of zooplankton communities to their historical condition will therefore likely require the active reintroduction of *H. shoshone*. The feasibility of such reintroductions is suggested by the recent successful reintroduction of *H. shoshone* to a lake in the Sierra Nevada (Kramer et al. 2008) and of the closely related *H. arcticus* to a lake in the Rocky Mountains (McNaught et al. 1999). To maximize the chances of successful *H. shoshone* re-establishment, *H. shoshone* will need to be reintroduced at densities that are high enough to minimize the effects of mate limitation (Kramer et al. 2008).

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