

trends data

Zooplankton recovery after fish removal: Limitations of the egg bank

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Abstract

The Allee effect, operating via mate limitation, theoretically reduces the probability of recovery from local extinction of dioecious zooplankton relative to species that can reproduce asexually. We removed fish from four alpine lakes in the Sierra Nevada in which both *Hesperodiaptomus shoshone* (a calanoid copepod) and *Daphnia middendorffiana* were historically present but had become locally extinct after fish stocking. After complete fish removal, *D. middendorffiana* returned to all four lakes, whereas *H. shoshone* failed to return in any of the lakes, despite diapausing eggs observed in the sediments of two lakes and a few individuals in the water column of one lake during the first summer after fish removal. We estimated the potential magnitude of the Allee effect, as it may have affected the recovery of *H. shoshone*, by comparing estimates of minimum founding population size of *H. shoshone* with estimates of actual founding population sizes of *D. middendorffiana*. It took 4 yr for *D. middendorffiana* to recover to detectable levels in one of the four lakes, which we suggest was the result of a very small founding population. The latter was three to four orders of magnitude smaller than the minimum founding population size we calculated for *H. shoshone*, indicating the potential for a large effect of mate limitation on the copepod's ability to recover. *H. shoshone* might never return to these lakes without human intervention because of the combined effects of mate limitation and low rates of overland dispersal.

The introduction of fish into historically fishless alpine lakes is known to lead to local extinctions of many invertebrate species (Anderson 1972; Parker et al. 1996; Bradford et al. 1998; Donald et al. 2001). What is less well known is whether, and at what rate, locally extinct species return to such lakes after the extirpation of exotic fish. Part of the reason for this dearth of knowledge is the rarity of complete exotic removal. In both the Rocky Mountains and the Sierra Nevada of North America, the cessation of fish stocking has, in a few cases, been sufficient to eliminate exotic fish populations, allowing opportunities to study the recovery of invertebrate assemblages (Donald et al. 2001; Knapp et al. 2001b). Recovery of zooplankton is facilitated by the presence of a bank of diapausing eggs in the sediments (Hairston and De Stasio 1988; Parker et al. 2001), whereas insect recovery is fostered by winged adult stages.

In a large-scale survey of alpine lakes in the Sierra Nevada, in which lakes that were once stocked but lost their fish populations and lakes that were never stocked were compared, Knapp et al. (2001b) reported that zooplankton communities tended to reassemble to their prefish state after fish disappearance. In this case, the structure of the prefish zooplankton assemblage was not known with certainty but was assumed to be equivalent to that in never-stocked lakes (see also Donald et al. 2001). In contrast, more detailed analyses of smaller numbers of lakes with known prefish zooplankton composition have revealed that large species of cal-

anoid copepods (*Hesperodiaptomus shoshone* in the Sierra Nevada, *H. arcticus* in the Rocky Mountains) do not always return after fish disappear from alpine lakes (Knapp et al. 2001b; Parker et al. 2001). Moreover, a recent analysis of 36 Sierra Nevada lakes with known fish and zooplankton histories found that the recovery rate of *H. shoshone* was considerably lower than that of *Daphnia middendorffiana* (58% vs. 84% recovery, respectively; Knapp and Sarnelle unpubl. data). One possible explanation for the difference in recovery rate between these two species is the difference in mode of reproduction between copepods and cladocerans. Copepods are obligately dioecious, whereas cladocerans are able to reproduce parthenogenetically. The requirement for mating in copepods can lead to an Allee effect (Courchamp et al. 1999), which in this case imposes a lower limit on the size of a founding population (Gerritsen 1980). This lower limit presents a potentially large obstacle to colonization and recovery in sexually reproducing zooplankton.

In this study, we used data on zooplankton recovery following removal of nonnative trout from four alpine lakes to address two objectives. Our first objective was to test the hypothesis that *H. shoshone* has a lower probability of recovering from local extinction after experimental fish removal than *D. middendorffiana*. Our second objective was to estimate the potential magnitude of the Allee effect as it might influence the recovery of *H. shoshone*, relative to *D. middendorffiana*. To accomplish the latter objective, we relate recovery data to a conceptual model of how the Allee effect, in this case via mate limitation, reduces the probability of recovery of an obligately dioecious species relative to a parthenogenetic species. Our data do not conclusively demonstrate that mate limitation is the mechanism leading to a lower probability of recovery for *H. shoshone*; rather, we suggest that the Allee effect might be at work and then

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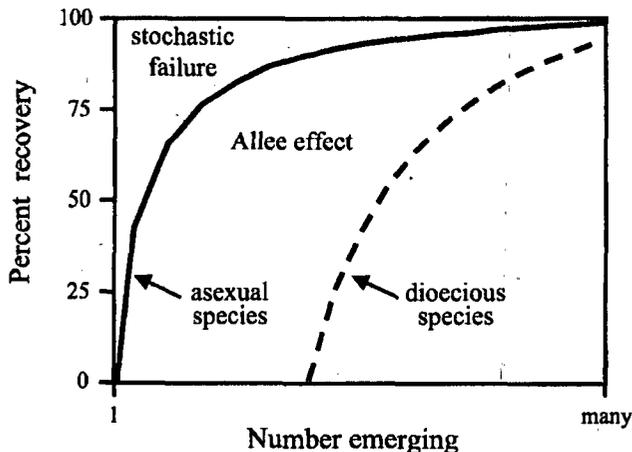


Fig. 1. Conceptual model of the effect of initial number of individuals emerging from an egg bank (or dispersing overland) on a population's probability of recovering from local extinction. In the absence of permanent changes in habitat suitability brought about by temporary perturbation (i.e., alternative equilibria), the probability of population recovery will attain the asymptote at 100% at high emergence rates. The solid curve represents a species that can reproduce asexually, for which it is theoretically possible for a population to recover via the emergence of a single diapausing egg. The dotted curve represents an otherwise similar species that is obligately dioecious. The requirement for mating in the latter species imposes a lower limit on the number that need to emerge to have any chance of population recovery (Allee effect). The distance between the two curves represents the magnitude of the Allee effect.

provide a quantitative evaluation of its potential importance. Given that mate limitation/Allee effects have not been considered in previous studies of zooplankton recovery, we hope that this evaluation will stimulate interest in this mechanism.

The conceptual model first postulates that the probability of recovery for any species will be a positive, decelerating function of the number of individuals emerging from the egg bank, approaching a theoretical asymptote of 100% recovery at some large value of emergence (Fig. 1). Although we suspect that recolonization of zooplankton in alpine lakes is likely accomplished via emergence of diapausing eggs from the sediment, the model is also applicable to overland dispersal of propagules from other lakes. The probability of recovery for an asexual species (such as *Daphnia*) is only affected by what can be termed "stochastic failure," by which we mean a failure to recover resulting from unpredictable events such as climatic fluctuations (Grevstad 1999). As such, the model assumes that the temporary presence of fish does not permanently change the ecological suitability of the habitat with respect to recovering zooplankton species, for example, by allowing species to invade that prey on or compete with recovering species (i.e., there are no alternative equilibria). Pelagic predators, such as cyclopoid copepods and *Chaoborus* (Parker et al. 2001), that could conceivably prey on juvenile *H. shoshone* or *D. middendorffiana* are essentially absent from the class of lakes we consider in this paper, namely

lakes above 3,300 m in the Sierra Nevada (see Results). Indeed, *H. shoshone* is the only predatory zooplankton that is common in such lakes (Knapp et al. 2001b).

Mate limitation reduces the probability of recovery for a sexually reproducing species (such as *H. shoshone*) relative to an asexual species (the Allee effect, Fig. 1). The distance between the probability functions in Fig. 1 provides an estimate of the magnitude of the Allee effect, assuming the sexual and asexual species being compared are similar in terms of net population growth rate and length of growing season. Our conceptual model is analogous to Grevstad's (1999) simulation models of population establishment driven by stochastic processes with and without Allee effects.

Given the above logic, we calculate the potential magnitude of the Allee effect by comparing estimates of the minimum size of initial emergence required for re-establishment of *H. shoshone* (which has failed to recolonize any of our experimental lakes) with estimates of the actual size of initial emergence for *D. middendorffiana*. For *H. shoshone*, minimum emergence is estimated from Gerritsen's model (1980) of critical densities for population establishment in sexually reproducing zooplankton. For *D. middendorffiana*, actual initial emergence is back-calculated from data on recovery rates after fish removal in four experimental lakes.

Our observations of population recovery and community reassembly after fish removal are unique in that cessation of the perturbation was implemented experimentally and as a relatively discrete event (i.e., over a period of time that is very short—most fish were removed within a few weeks at the end of the growing season—relative to the life cycles of recovering populations). This means that the recovery rates we observed were not affected by gradual changes in environmental conditions, as might occur when fish gradually die out on their own after the elimination of stocking (Donald et al. 2001; Knapp et al. 2001b) or when other types of perturbations, such as acidification and eutrophication, are reversed (Edmondson and Lehman 1981; Keller et al. 2002). Discrete experimental reversal of the perturbation, combined with the low zooplankton diversity of high-elevation lakes, maximizes our ability to make inferences about species' intrinsic abilities to recover from perturbation.

Methods

Study sites—The four experimental lakes are located at or above tree line (elevation range: 3,300–3,600 m) in Humphreys Basin (37°16'N, 118°43'W), John Muir Wilderness, Sierra National Forest, California. The ice-free period in these lakes typically lasts from late June to late October. The lakes are small and shallow (Table 1), making it feasible to remove entire fish populations using gill nets (Knapp and Matthews 1998). Exceptional water clarity also enabled visual observations of large zooplankton via snorkeling in each lake (see below).

All lakes in Humphreys Basin were historically fishless, but most were stocked with nonnative trout in the early to mid-20th century. The experimental lakes contained nonnative trout for at least 50 yr prior to the initiation of our study in 1996. Knob Lake, Square Lake, and Marmot Lake were

Table 1. Characteristics of the experimental lakes. Temperature and total phosphorus (TP) data are means for the ice-free period. Phytoplankton productivity was measured twice per year in August–September. Data were averaged over the period 1997–2001.

Lake	Surface area (ha)	Mean maximum depth (m)	Fish residence time (yr)	Temperature (°C)	TP (mg m ⁻³)	Productivity (mg C m ⁻³ h ⁻¹)
Knob	3.4	1.8(5.5)	63	13.8	8.3	2.8
Square	1.7	1.9(3.5)	53	14.3	8.0	1.4
No Good	1.7	1.9(5.0)	56	12.9	6.7	1.6
Marmot	3.0	3.6(8.0)	53	11.8	5.7	No data

stocked with golden trout (*Oncorhynchus mykiss aguabonita*) every 2 yr between 1950 and 1995, despite the fact that trout populations in Knob Lake and Marmot Lake were self-sustaining. No Good Lake was stocked with brook trout (*Salvelinus fontinalis*) in the 1940s, and the population has been self-sustaining since then without further stocking.

Before fish removal, the zooplankton communities in the experimental lakes were dominated (in terms of biomass) by *Leptodiatomus signicauda*, a small calanoid copepod, as is typical of many alpine lakes in the Sierra Nevada containing introduced trout (Stoddard 1987; Bradford et al. 1998; Knapp et al. 2001b). No *H. shoshone* or *D. middendorffiana* were detected in two summers of repeated sampling before fish removal. One of the experimental lakes (No Good Lake) was located downstream of a potential source of colonists of both *H. shoshone* and *D. middendorffiana* (Fig. 2). None of the other experimental lakes were downstream of a potential source of colonists of either species. Animals that could potentially serve as overland zooplankton dispersal vectors (Cáceres and Soluk 2002) were rare and included pied-billed grebes (*Podilymbus podiceps*), American dippers

(*Cinclus mexicanus*), and water shrews (*Sorex palustris*). Grebes are seen occasionally on the experimental lakes in the fall, whereas dippers and shrews are present throughout the summer but uncommon. Although ambystomid salamanders have been shown to be effective dispersal agents of zooplankton resting eggs in alpine ponds (Bohonak and Whiteman 1999), there are no aquatic salamanders in the southern Sierra Nevada, including Humphreys Basin.

All four experimental lakes were found to contain egg shells of *H. shoshone* and ephippia of *D. middendorffiana* in deep sediment layers (Knapp et al. 2001a), indicating that established populations of both species were present in all four lakes before fish stocking. In addition, we found ephippia of *D. middendorffiana* within 1 cm of the sediment surface in two of the lakes (Square Lake, Marmot Lake), but no *H. shoshone* diapausing eggs this close to the sediment surface in any of the lakes. However, two of the experimental lakes did contain *H. shoshone* eggs within 5 cm of the sediment surface (No Good Lake, 700 eggs m⁻²; Marmot Lake, 4,000 eggs m⁻²). Our detection limit for diapausing eggs of *H. shoshone* and ephippia of *D. middendorffiana* was ~350 m⁻², which is comparable to previous egg bank studies (Hairston and Van Brunt 1994; Parker et al. 1996).

Calculation of H. shoshone critical density and minimum initial hatch size—To estimate critical density (N_c , as adults only) for *H. shoshone*, we employed Gerritsen's (1980) equation for sexually reproducing zooplankton.

$$N_c = \frac{-3 \ln \left(\frac{R-1}{R} \right)}{2\pi t v d^2} \quad (1)$$

R is finite population growth rate calculated on a daily basis, t is the length of the breeding season (d), v is swimming speed (m d⁻¹), and d is encounter radius (m). On the basis of an adult length of 2.5 mm for *H. shoshone* (A. Kramer pers. comm.), we assumed that $v = 260$ m d⁻¹ and $d = 0.005$ m. The latter values are based on empirical observations in the literature (Gerritsen 1980) and the assumption that conspecific encounters are random. If copepods can detect each other from a distance via chemical cues, encounter radius (d) could be larger than our estimate, and consequently, critical density would be considerably lower, given that critical density is most sensitive to changes in encounter radius (Eq. 1). Although detection of pheromone trails by males has been demonstrated in marine calanoid copepods

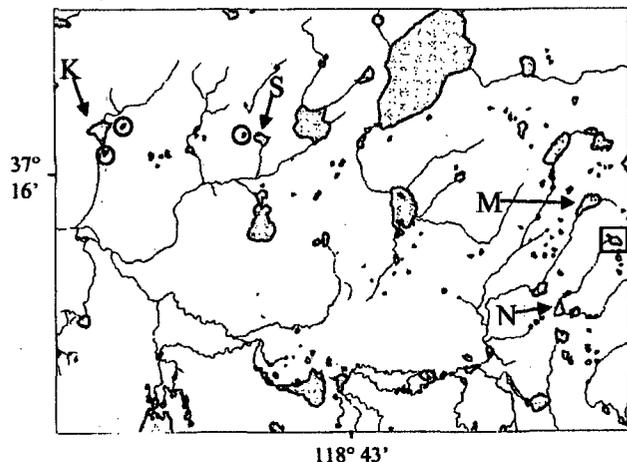


Fig. 2. Map of study area showing locations of experimental lakes and nearby lakes or ponds containing *H. shoshone* or *D. middendorffiana*. K, Knob Lake; S, Square Lake; M, Marmot Lake; N, No Good Lake. Circles are drawn around ponds from which *D. middendorffiana*, but not *H. shoshone*, have been collected. A square is drawn around a lake located upstream of No Good Lake from which both *D. middendorffiana* and *H. shoshone* have been collected.

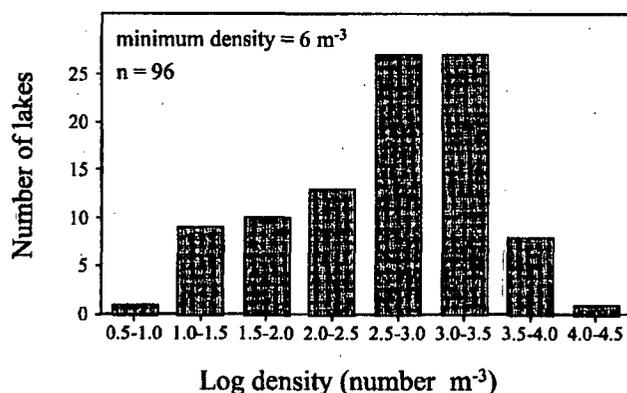


Fig. 3. Frequency distribution of natural densities of *H. shoshone* in high-elevation lakes in the Sierra Nevada. Note log scale of abscissa.

(Katona 1973; Doall et al. 1998), we know of no studies showing chemical detection of mates from a distance in freshwater copepods (Williamson and Reid 2001). Thus, we rely on Gerritsen's estimate of encounter radius in the absence of any information about chemical detection. We consider the potential effect of this assumption in the Discussion section. Using wide ranges for t (60–120 d, Kramer pers. comm.) and R (Allan 1976), we estimated that *H. shoshone*'s critical density lies between 0.5 and 5 m⁻³.

If our estimates of critical density are reasonably accurate, we would not expect to find natural densities of *H. shoshone* adults commonly near or below 0.5–5 m⁻³. From a survey of mountain lakes in the Sierra Nevada (Knapp et al. 2001b), the minimum density of *H. shoshone* was 6 m⁻³, and 90% of the populations were at densities greater than 30 m⁻³ (Fig. 3), suggesting that these estimates of critical density are probably reasonable. Although survey densities include *H. shoshone* copepodids and adults, there is little mortality from the copepodid to adult stage within cohorts of univoltine copepods in fishless lakes (Comita 1956), which means that early-season copepodid densities are similar to late-season adult densities. On the basis of the range of critical densities we calculated and the area and volume of each lake, we estimated minimum hatch sizes for successful recolonization in the experimental lakes of 1–13 m⁻², which translates to minimum founding population sizes of 20,000–400,000 individuals per lake.

Fish removal—Trout populations in the experimental lakes were removed via intensive gill netting. Detailed methods are provided in Knapp and Matthews (1998) and are summarized here. Six to 10 gill nets with variable mesh-size panels were set in each lake and were initially cleaned of fish every 12 h and reset. Once fish populations were depleted (1–2 weeks), gill nets were cleaned and reset once per week. In Knob Lake, Square Lake, and Marmot Lake, gill netting began in mid-September 1997, and nearly all adult fish had been removed by mid-October. Nets were allowed to fish under the ice during the 1997–1998 winter and were fished throughout the summer in 1998 to ensure the capture of fish that were too small to catch during the pre-

vious year. Nets were also set in each lake on several occasions in 1999 to ensure that eradication was complete. In No Good Lake, gill netting began in July 2000 and continued through the 2000–2001 winter and the 2001 summer. Gill nets were deployed on several occasions in 2002 to ensure complete eradication. The number of years to initial detection of recovering zooplankton was calculated starting from the first summer after initiation of fish removal. Given that *D. middendorffiana* was detected in three out of the four experimental lakes after just 1 yr by this reckoning, we assume that this is a conservative method of counting years since fish eradication.

Three additional control lakes in Humphreys Basin (Mesa Lake, Lower Desolation Lake, and Summit Lake) were sampled for zooplankton in parallel to the experimental lakes. These lakes continue to be stocked with fingerling trout (last stocking in 2000), and no individuals of either *H. shoshone* or *D. middendorffiana* were found in the water column during the 7 yr of the study.

Each lake was sampled four times per summer (early July, late July, mid-August, and early September), except for 1996 and 1998, when only two and three sampling visits were made, respectively, because of unusually late ice-out of the study lakes. Two zooplankton samples were collected from the deepest part of each lake with a 30-cm-diameter, 64- μ m mesh net. Two vertical net hauls from just above the bottom to the surface were composited for each sample. One sample was preserved in 95% ethanol (for crustaceans), the other in 2% glutaraldehyde (for rotifers). Zooplankton were identified and counted in replicate 1-ml subsamples at $\times 40$ magnification with a Sedgwick-Rafter chamber. We also scanned the entire contents of all ethanol-preserved samples from the fish removal lakes for the presence of *H. shoshone*, which resulted in a detection limit for this species in a single sample of $\sim 1\text{--}3$ m⁻³ on the basis of the volume sampled by the net hauls (0.4–0.8 m³). Considering all zooplankton samples analyzed from the postmanipulation period (1999–2002, 8–16 samples per lake), our detection limit for *H. shoshone* falls to ≤ 0.1 m⁻³ in each lake. The latter is a reasonable way to estimate detection limit because *H. shoshone* is continuously present during the sampling season (early July to early September) in Sierra Nevada lakes with established populations (Kramer pers. comm.). In other words, in lakes that have never had fish, *H. shoshone* does not appear and disappear during the growth season, in contrast to what we have seen for "rare" species.

To further increase our ability to detect *H. shoshone*, we routinely snorkeled in each of the experimental lakes on two to four sampling visits every summer from 1997 to 2002. *H. shoshone* is large and highly pigmented, making adults visible underwater in these clear, shallow lakes. We also conducted more intensive snorkel surveys in 1998 and 2002 in Marmot Lake, one of the two experimental lakes in which *H. shoshone* eggs were found in the surficial sediments. We conservatively estimate that we visually searched about 1% of the volume of Marmot Lake (lake volume = 109,500 m³) during these surveys, which translates to a detection limit of ~ 0.001 m⁻³.

Water temperature was measured in Knob Lake, Square Lake, and Marmot Lake from 1996 to 2002 and in No Good

Lake from 2000 to 2002 with Onset Optic Stowaway probes. Probes were deployed in the center of each lake at a depth of 1 m from approximately 1 July to 15 September. To assess variation among the experimental lakes in nutrients and productivity, we routinely measured total phosphorus concentrations and phytoplankton productivity. Water samples for total phosphorus analysis were collected from a depth of 2.5 m with a kemmerer bottle and screened through 100- μ m mesh to remove macrozooplankton. Samples were kept cold until returned to the laboratory, where they were frozen until analysis. Total phosphorus was measured via persulfate digestion (Menzel and Corwin 1965) followed by ascorbic-molybdate colorimetry (Murphy and Riley 1962). Primary production was measured in the laboratory via 4-h incubations of lake water with 14 C.

Estimation of initial hatch size for recovering D. middendorffiana populations—Ideally, estimates of initial hatch size would be based on measurements of emergence rates in nature. Logistical constraints, however, rendered this approach infeasible in the experimental lakes. We set 1-m-diameter (0.8 m²) emergence traps in three of the lakes for 2-week periods during August–September 1997 but captured no emerging *D. middendorffiana*. Our failure was probably at least partly a function of low *D. middendorffiana* emergence rates (see Results), which made it unlikely that we would catch more than a few individuals at best, despite the large size of our traps. Emergence might also have been restricted to early in the growth season (Cáceres 1998), when it was impossible to set the traps because of ice cover on the lakes. Given these difficulties, we estimated initial hatch size (N_0) on the basis of observed dynamics of recovering *D. middendorffiana* populations and the following model of population growth in a seasonal environment.

$$N_0 = \frac{N_x}{(se^r)^x} \quad (2)$$

N_x is *D. middendorffiana* population size at first detection, x is the number of years between fish removal and first detection, r is the maximum per capita population growth rate during the growth season (we assume no density dependence in small, recovering populations), t is the length of the growing season, and s is the ratio of initial population size at the start of the growth season to final population size, at the end of the previous growth season. Estimates of N_x and x were based on *D. middendorffiana* dynamics in each lake, whereas estimates of r , s , and t were based on observed *D. middendorffiana* dynamics in Square Lake, where we had 4 yr of data. Thus, we assumed that the population growth parameters r , s , and t were equivalent across lakes. Large deviations from this assumption are unlikely and small deviations do not affect our overall conclusions (see Results). It is obvious from the structure of Eq. 2 that, given similar levels of natural variation in the values of each parameter, estimation of initial hatch size (N_0) is most sensitive to variation in r , t , and x and least sensitive to variation in N_x and s . We present an empirical sensitivity analysis in the Results section that is based on data from the study lakes.

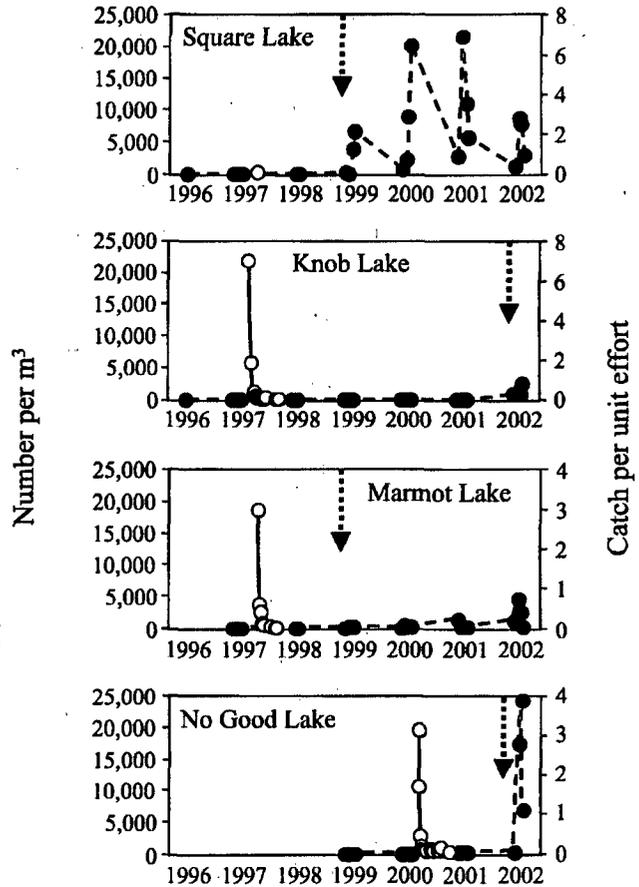


Fig. 4. Population dynamics (solid symbols) of recovering populations of *D. middendorffiana* in four experimental lakes after removal of exotic fish. Arrows indicate time of first detection of *Daphnia* in each lake. Open symbols illustrate the time course of decline in fish density during fish removal via intensive gill netting. The temporal scale of fish removal dynamics was magnified for illustrative purposes.

Results

Recovery of locally extinct zooplankton after fish removal—*H. shoshone* failed to recover in any of the four experimental lakes 1–4 yr after fish removal. However, one of us (R.A.K.) observed three *H. shoshone* individuals in Marmot Lake during an intensive snorkel survey in 1998, the first summer after fish removal was initiated. No *H. shoshone* were seen while snorkeling in Marmot Lake after 1998, nor in any of the other lakes, although we routinely observed *D. middendorffiana* while snorkeling.

In contrast to *H. shoshone*, *D. middendorffiana* recovered in all four experimental lakes, although the time between fish eradication and first detection varied from 1 to 4 yr across lakes (Fig. 4). Maximum population growth rates of *D. middendorffiana* varied only slightly among lakes, with the highest growth rate in Knob (0.11 d⁻¹) and the lowest in Marmot (0.07 d⁻¹), which indicates that there were not large differences among lakes in *D. middendorffiana* popu-

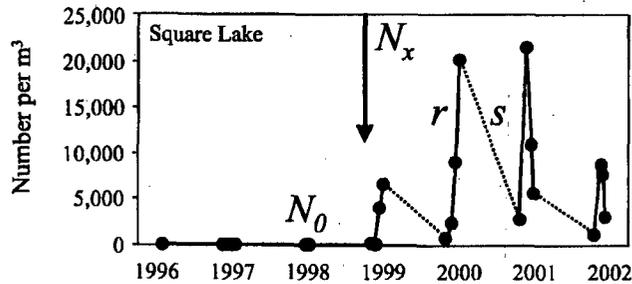


Fig. 5. Illustration of method of calculating initial number of *D. middendorffiana* emerging from lake sediments (N_0) on the basis of the observed dynamics of *D. middendorffiana* in Square Lake. N_x , *Daphnia* abundance at first detection; r , within-season *Daphnia* population growth rate; s , ratio of initial *Daphnia* population size at the start of the growth season to final population size at the end of the previous growth season (see text for details).

lation growth parameters, as assumed for the calculations that follow. In any case, our analysis critically depends on the assertion that initial hatch size was very small in Knob Lake, so the use of a *Daphnia* growth rate in our calculations that was slightly lower than what we observed in Knob Lake (see below) is a conservative source of error.

Estimation of initial hatch size for recovering *D. middendorffiana* populations—We back-calculated initial hatch size for *D. middendorffiana* by Eq. 2 and observed *D. middendorffiana* dynamics in Square Lake (Fig. 5). In Square Lake, the maximum estimate of r was 0.08 and s varied from 0.09 to 0.19 across years. On the basis of these data and the average length of the growth season (t), we assigned parameter values for the population growth model as $r = 0.1 \text{ d}^{-1}$, $s = 0.1\text{--}0.2$, and $t = 50 \text{ d}$. The model estimated similar initial hatch densities in Square Lake, No Good Lake, and Marmot Lake, reflecting a recovery rate for *D. middendorffiana* of 1 yr to detectable levels in all three lakes (Table 2). Initial hatch densities for *D. middendorffiana* in these lakes ($1\text{--}44 \text{ m}^{-2}$) were comparable to estimated minimum hatch densities for *H. shoshone* ($1\text{--}13 \text{ m}^{-2}$). In contrast, *D. middendorffiana*'s slow recovery in Knob Lake resulted in es-

timated hatch densities that were three to four orders of magnitude lower (Table 2) than minimum hatch density for *H. shoshone*.

Sensitivity analysis of the population growth model revealed that our estimates of r , t , and x are the most critical for accurate estimation of initial hatch density (Fig. 6). Of these, our estimates of x (years since first detection) have little uncertainty, leaving r and t as the most critical parameters. Given the importance of our assertion that *D. middendorffiana* initial density was much smaller in Knob Lake, we must consider whether we have grossly overestimated r and t (small deviations in these parameters are inconsequential relative to the magnitude of the effect of x on initial density, Fig. 6). Given that Knob Lake was about twice as productive and only slightly cooler than Square Lake (Table 1), it seems unlikely that we grossly overestimated r and t for Knob Lake by using values estimated from population growth in Square Lake. Even in the highly unlikely event that we grossly overestimated r and t in Knob Lake to the extent that their product (rt) was actually only half of the value we used from Square Lake (i.e., 2.5 instead of 5.0), this would still result in an initial *D. middendorffiana* density estimate for Knob Lake that was two orders of magnitude lower than in the other three fish removal lakes (initial density = $\sim 0.1 \text{ m}^{-2}$ for $x = 4$ and $rt = 0.25$; initial density = $\sim 10 \text{ m}^{-2}$ for $x = 1$ and $rt = 0.5$, Fig. 6). Given these considerations, we think it is reasonable to conclude that initial *D. middendorffiana* density in Knob Lake was, at the very least, one to two orders of magnitude smaller than initial *D. middendorffiana* densities in the other three fish removal lakes and than critical densities for *H. shoshone* ($1\text{--}13 \text{ m}^{-2}$).

Discussion

H. shoshone and *D. middendorffiana* were established (on the basis of sediment microfossils) in all seven experimental and control lakes before fish were stocked, and both species were locally extinct in all seven lakes when we initiated fish-removal manipulations. As evidence of the latter, we neither collected, nor observed via snorkeling, either species over 11 lake-yr of sampling in the experimental lakes (before re-

Table 2. Estimates of initial hatch size (as total number and hatch density) for recovering *Daphnia middendorffiana* populations and ephippial densities in the top 1 cm of sediment in four alpine lakes from which fish were completely removed. Estimates of initial hatch size were calculated on the basis of number of years between fish removal and first detection (x), *Daphnia* abundance at first detection (N_x), within-season *Daphnia* population growth rate (r), and the ratio of *Daphnia* population size at the start of the growth season to final population size at the end of the previous growth season (s). Estimates of r and s were based on observed *Daphnia* dynamics in Square Lake (Fig. 5; see text for details). The detection limit for ephippia in the sediment was $\sim 350 \text{ m}^{-2}$. ND, not detected.

Lake	x	N_x (No. in lake)	Initial hatch size (N_0) (No. in lake)	Initial hatch density (No. m^{-2})	Ephippial density (No. m^{-2})
Knob	4	5.5×10^7	1–2	0.0002–0.0003	ND
Square	1	1.5×10^6	18,000–35,000	1.1–2.2	175,000
No Good	1	3.4×10^6	117,000–234,000	7–14	ND
Marmot	1	2.0×10^7	656,000–1,372,000	22–44	69,000

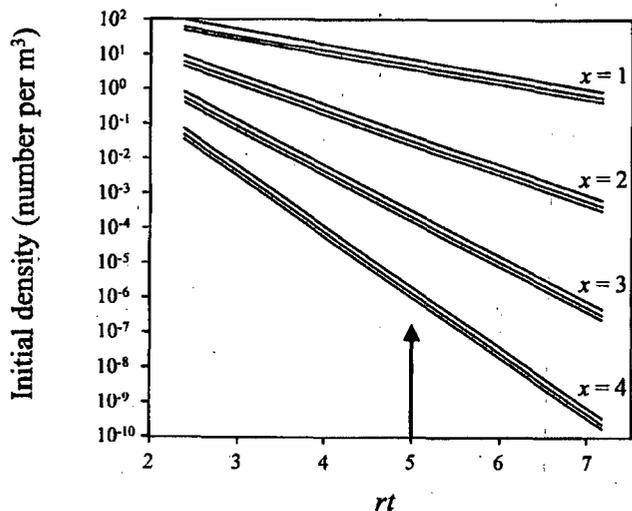


Fig. 6. Sensitivity analysis of the population growth model used to back-calculate initial *Daphnia* density from observations of population growth during recovery (Eq. 2). Initial density was calculated for a hypothetical population that was first detected (N_1) at a density of 100 m^{-3} . The abscissa represents observed variation in the product of maximum population growth rate (r [d^{-1}]; range, 0.06–0.12) and length of the growing season (t [d]; range, 40–60). The four sets of lines represent observed variation in the number of years between fish removal and first detection (x). The closely spaced lines at each value of x represent observed variation in the ratio of initial population size at the start of the growth season to final population size at the end of the previous growth season (s ; range, 0.1–0.2). The arrow indicates the value of rt used to calculate the initial densities listed in Table 2.

removal and the first summer after removal), nor over 20 lake-yr of sampling in the control lakes. Regular snorkeling in six of the seven lakes greatly reduced our detection limit for *H. shoshone* below what can be accomplished via conventional sampling alone. Thus, we are confident in asserting that recovery would have to be initiated from the hatching of diapausing eggs or propagules dispersed overland, rather than from the growth of reproducing populations that were below detectable levels.

We are also confident that we have allowed enough time for *H. shoshone* to recover, except in No Good Lake (Fig. 4). Our calculations suggest that the density of a successful founding population would need to be $\geq 0.5 \text{ m}^{-3}$. At this density, it is highly likely that *H. shoshone* would be collected in our nets (detection limit for 1 yr of net sampling in one lake $\approx 0.1 \text{ m}^{-3}$), or observed during routine snorkeling surveys. Furthermore, no *H. shoshone* were observed in Marmot Lake during an extensive snorkeling survey conducted in 2002, despite our detection of live individuals of this species in this lake in 1998, as well as because our detection limit for the snorkeling survey ($\sim 0.001 \text{ m}^{-3}$) was orders of magnitude below estimates of critical density (0.5 m^{-3}).

As further support for the assertion that 4 yr is sufficient to assess recovery failure in *H. shoshone*, we note that *H. arcticus*, a closely related and ecologically similar species,

increased ~ 10 -fold per year after being reintroduced into Snowflake Lake, an alpine lake that is similar in temperature regime and productivity to the lakes we study (McNaught et al. 1999). At this rate of population growth, and using a conservative value for the detection limit of our net sampling regime (1 m^{-3}), founding population size would have to be $< 0.0001 \text{ m}^{-3}$ in order for a recovering population to be below detection in 2002, 4 yr after fish removal. For such a small founding population to grow (i.e., for critical density to be $< 0.0001 \text{ m}^{-3}$), the encounter radius of an individual *H. shoshone* would have to be $\sim 1 \text{ m}$ (Eq. 1), which equates to ~ 400 body lengths. Even if *H. shoshone* can detect mates from a distance via chemical cues, which has yet to be demonstrated for any freshwater copepod, the largest measured encounter distance in marine copepods that can use chemical cues to detect conspecifics is < 150 body lengths (0.5 m for *Calanus marshallae*; Tsuda and Miller 1998). Interestingly, *H. arcticus*'s 10-fold annual rate of increase after stocking translates to values for rt of 2.4–4.6, assuming that s varies between 0.9 and 0.1 (Eq. 2), suggesting that the maximal rate of population increase for *H. arcticus* in Snowflake Lake was not grossly different from what we estimated for *D. middendorffiana* in Square Lake (Fig. 6).

Our data show that *H. shoshone* had a lower probability of recovery from local extinction (0%) than *D. middendorffiana* (100%) in the four lakes from which fish were removed and that there was substantial variation in the rate of recovery of *D. middendorffiana* across the four lakes (Fig. 4). Taken together, these two observations suggest that the Allee effect (via mate limitation) might have a large influence on the probability of recovery of *H. shoshone*. The role of mate limitation is most strongly suggested by the differential responses of *H. shoshone* in Marmot Lake versus *D. middendorffiana* in Knob Lake. *H. shoshone* failed to re-establish in Marmot Lake despite the presence of diapausing eggs in the sediments and recently hatched individuals in the water column during 1998. We estimate that the hatching of 50,000 *H. shoshone* diapausing eggs per year in Marmot Lake would be insufficient to enable the population to re-establish (*H. shoshone* is univoltine in high-elevation Sierra Nevada lakes; Kramer pers. comm.). In contrast, the slow recovery of *D. middendorffiana* in Knob Lake suggests an extremely small founding population in that lake (Table 2). *D. middendorffiana* was able to re-establish in Knob Lake from an initial hatch density that we estimate was potentially three to four orders of magnitude smaller than the minimum founding density of *H. shoshone* (0.0002 – 0.0003 m^{-2} vs. 1 – 13 m^{-2}). This provides a rough estimate of the potential magnitude of the Allee effect as it might affect the probability of population recovery in *H. shoshone* (Fig. 1).

In general, the number of hatching diapausing eggs was likely larger for *D. middendorffiana* than for *H. shoshone* in the experimental lakes, and this can explain some of the difference between species in overall recovery probability in these lakes. We found ephippia of *D. middendorffiana*, but not diapausing eggs of *H. shoshone*, in the top 1 cm of sediment cores from two of the four experimental lakes. However, we do not know what proportion of these ephippia are viable, so it is perhaps not surprising that sediment den-

Table 3. Mean biomass (mg m⁻³ dry mass) of common planktonic crustaceans and rotifers in each of the experimental lakes, 1996–2002. Common taxa were defined as those that were detected in at least 20% of samples or contributed to >1% of mean total zooplankton biomass in at least one lake. ND, not detected.

Taxon	Knob Lake	Square Lake	No Good Lake	Marmot Lake
Copepoda				
<i>Leptodiaptomus signicauda</i>	126.0	132.4	48.5	49.0
Cladocera				
<i>Daphnia middendorffiana</i>	12.7	53.1	118.0	8.7
<i>Ceriodaphnia laticaudata</i>	18.3	0.3	0.2	0.1
<i>Bosmina longirostris</i>	5.0	ND	ND	ND
<i>Daphnia rosea</i>	ND	ND	ND	0.7
Rotifera				
<i>Polyarthra dolichoptera</i>	1.9	0.6	3.9	0.6
<i>Keratella</i> spp.*	1.5	1.5	0.1	<0.1
<i>Conochilus unicornis</i>	3.1	ND	ND	<0.1
<i>Ascomorpha</i> sp.	<0.1	ND	ND	ND
<i>Lepadella</i> sp.	<0.1	ND	ND	<0.1
<i>Ploesoma</i> sp.	0.3	ND	ND	ND
<i>Synchaeta</i> sp.	<0.1	ND	<0.1	<0.1

* *K. cochlearis* and *K. taurocephala*.

sities of diapausing eggs do not correlate well with *Daphnia* recovery times (Table 2). We note only that *D. middendorffiana* could have recolonized No Good Lake from upstream (Fig. 2), which makes the minimal egg bank in this lake less critical. Consequently, the minimal egg bank in Knob Lake could be taken as further evidence of minimal initial density. Our calculations of initial hatch density (Table 2) suggest that *D. middendorffiana* recovered in Knob Lake from an initial egg bank emergence that was far below what could be detected by any conceivable methodology. In addition, quantitative sampling of the sediment with conventional coring devices (maximum diameter, 8 cm; area sampled, 0.005 m²; detection limit, 200 m⁻²) could easily fail to detect egg bank densities that are large enough to allow rapid recovery of *Daphnia* (Table 2). Thus, the likelihood of a larger egg bank for *D. middendorffiana* than *H. shoshone* does not diminish the potential for a large Allee effect in the recovery of sexually reproducing zooplankton. The magnitude of the Allee effect, as suggested by our data, implies that merely finding viable eggs in surficial sediments or emerged individuals in the water column (as we did) does not guarantee that a sexually reproducing zooplankton population will re-establish. This conclusion contrasts with a previous study, in which success/failure of *Hesperodiaptomus* recovery was attributed to presence/absence of an egg bank (Parker et al. 1996). At a minimum, the above considerations highlight the methodological limitations associated with sampling the egg bank and monitoring neonate emergence in the study of zooplankton recovery.

Our suggestion about the potential magnitude of the Allee effect is based largely on the combined observations of *H. shoshone*'s failure to recover, particularly in Marmot Lake, where newly hatched individuals were seen initially, and *D. middendorffiana*'s delayed recovery in Knob Lake. Given that we can only provide indirect evidence for an Allee effect, we must consider alternative hypotheses for each of these observations.

We have presented evidence in support of the idea that the recovery failure by *H. shoshone* in part could be a consequence of mate limitation. An alternative explanation for *H. shoshone*'s general failure to recover is that these lakes are no longer suitable habitat for *H. shoshone* because of previous fish presence (i.e., that the zooplankton communities of fishless alpine lakes exist as alternate stable states; Scheffer et al. 2001). For this explanation to be correct, the temporary presence of fish must create a permanent shift in species composition that prevents reinvasion by *H. shoshone*. This explanation cannot be absolutely ruled out without field experimentation because we cannot fully define the niche requirements of *H. shoshone*. However, we can comment on the plausibility of alternative community states in our experimental lakes by considering the most likely mechanisms by which it would occur, namely via the rapid re-establishment of *D. middendorffiana* (Fig. 4) or via the establishment of invertebrate predators that prey on juvenile stages of *H. shoshone* (Parker et al. 2001). We think that strong suppression of *H. shoshone* population growth via competition (or other indirect pathways) from *D. middendorffiana* (Paul et al. 1995) is unlikely because of the positive association between these species across Sierra Nevada lakes (Stoddard 1987; Knapp et al. 2001b). The widespread co-occurrence of these species suggests that *D. middendorffiana* does not strongly inhibit *H. shoshone* invasion. We think that suppression of *H. shoshone* population growth via invertebrate predation is even less likely simply because planktonic predators are rarely encountered in our experimental and control lakes (always <1% of total zooplankton biomass). Besides *D. middendorffiana*, the dominant species in these lakes is the small herbivorous copepod, *Leptodiaptomus signicauda* (Table 3). None of the common zooplankters in these lakes can eat nauplii.

We have argued that the delayed recovery of *D. middendorffiana* in Knob Lake was a consequence of a very small founding population. An alternative explanation is that, rath-

er than recovering slowly (starting in 1998–1999, following fish removal) from a small number of eggs as we have postulated, the population recovered rapidly (i.e., in 1–2 yr) as a result of a sudden (but delayed) influx and hatching of large numbers of diapausing eggs from other lakes/ponds. However, this would require the input and hatching of >10,000 eggs in 2000 or >1,000,000 eggs in 2001 to result in the observed pattern of recovery. If the Knob Lake population was initiated in 1998–1999 by a small influx of diapausing eggs from other lakes/ponds, our conclusions would be unaffected because it would still mean that *D. middendorffiana* can recover from a founding population size that is orders of magnitude smaller than for *H. shoshone*. There are no data on hatching rates of diapausing eggs transported overland for these or any other lakes with which to directly evaluate this alternative hypothesis. However, a recent study of natural colonization in 150-liter mesocosms found large species of *Daphnia* to be relatively slow colonizers (took >1 Illinois growth season to reach detectable levels), despite the presence of source populations <10 m away (Cáceres and Soluk 2002). Assuming an exponential growth rate (r) = 0.15 d⁻¹ in the relatively warm mesocosms used by Cáceres and Soluk (2002), it would take only ~40 days for a single *Daphnia* colonist to increase to a detectable population density. This suggests a low rate of arrival, hatching, or both of dispersing ephippia. In Humphreys Basin, the paucity of animal dispersal vectors and the relative isolation of the experimental lakes from large source populations lead us to conclude that overland transport of large numbers of diapausing eggs is highly unlikely. Small source populations of *D. middendorffiana* were within 100, 150, and 400 m of Square Lake, Knob Lake, and Marmot Lake, respectively, so proximity to a potential source does not correlate with recovery rate in these three lakes (Table 2). For these three lakes, it seems much more likely that variation in *D. middendorffiana* recovery rate was driven simply by variation in rate of emergence from the sediments. In contrast, we cannot positively rule out colonization from outside for No Good Lake because there was an upstream source for this lake. However in this case, the upstream source contained both *D. middendorffiana* and *H. shoshone*; yet to date, only *D. middendorffiana* has recovered in this lake.

If the delayed recovery in Knob Lake was in fact a consequence of a very small founding population, it is important to consider why the founding population was so much lower in this lake than in the other fish removal lakes. Variation in initial emergence from the sediments across lakes should be a function of factors that affect (1) rates of diapausing egg deposition before fish introduction (e.g., lake productivity and temperature), (2) rates of egg bank depletion via hatching, predation, and degradation (e.g., temperature and predator densities), and (3) rates of egg bank burial (via sedimentation, which could be positively related to lake productivity), and duration of fish residence (De Stasio 1989; Parker et al. 1996). Of these, the last three might help to explain why Knob Lake seemed to have many fewer emerging *Daphnia* than other experimental lakes at the time of fish removal. Knob Lake is relatively warm and productive and had the longest period of fish residence of the four lakes

(Table 1), suggesting that egg bank depletion/burial could have proceeded further in this lake.

For *Hesperodiaptomus* in the Rocky Mountains, variation in egg bank size among lakes has been attributed to differences among lakes in the presence of the amphipod *Gammarus lacustris*, an egg predator (Parker et al. 1996). In contrast, amphipods are rare in Sierra Nevada alpine lakes (Knapp et al. 2001b) and do not occur in Humphreys Basin, and there were no obvious differences in benthic invertebrate assemblages among our experimental lakes (Knapp and Sarnelle unpubl. data). Thus, we suspect that egg bank depletion for both species was simply a function of hatching, degradation, and burial during long periods of fish residence.

The failure of *H. shoshone* to recover in any of the experimental lakes leads us to modify previous conclusions about the reassembly of alpine zooplankton assemblages after fish eradication (Knapp et al. 2001b). In the latter study, we concluded, on the basis of a broad-scale survey of lakes with relatively short fish residence times, that *H. shoshone* typically recovers after fish disappearance in the Sierra Nevada. It is clear from the current study, however, that *H. shoshone* does not always recover, and as a dominant member of the zooplankton assemblage in lakes that have never had fish (Knapp et al. 2001b), this failure is of major significance for reassembly. Failure to reassemble in Sierra Nevada zooplankton is congruent with observations in at least two Rocky Mountain lakes (Parker et al. 1996, 2001), but contrasts with observations in lowland lakes recovering from acidification (Locke et al. 1994; Keller et al. 2002). These differences could be related to habitat differences in the strength and duration of perturbations, the productivity of the lakes (lowland lakes have longer growth seasons, which might allow for larger egg banks), and the opportunities for dispersal among lakes (Stemberger 1995).

Several lines of evidence suggest that recovery failure of *Hesperodiaptomus* is likely to be a permanent condition in high-elevation lakes. With an egg bank depleted to the point where mate limitation or other factors prevent recovery, reestablishment must be initiated by overland dispersal or major flooding events (Stemberger 1995). The latter are largely confined to lowland areas, whereas most evidence suggests that freshwater calanoid copepods have a very limited ability to disperse overland, relative to other crustacean zooplankton (Proctor 1964; Boileau and Hebert 1991; Stemberger 1995; Jenkins and Underwood 1998; Parker et al. 2001). Experimental studies of overland colonization by zooplankton have found no evidence of calanoid invasion after 1–2 yr, despite the presence of nearby source populations (Jenkins and Bui-kema 1998; Cáceres and Soluk 2002). In contrast, representatives of all other major groups of metazoan zooplankton (rotifers, cladocerans, cyclopoid copepods) invaded within 8–13 weeks in these two studies. The combination of low rates of overland dispersal and the potential demand for high initial densities to overcome mate limitation leads us to suspect that, despite the ability of calanoid copepods to produce long-lived diapausing eggs (Hairston 1996; Parker et al. 1996), their successful recovery in alpine lakes after fish extirpation might sometimes require intentional reintroduction (McNaught et al. 1999).

We have shown that the probability of recovery after fish

eradication is lower for the calanoid copepod *H. shoshone* than for *D. middendorffiana*. One mechanism that could be driving this difference, but which has not been the focus of any previous investigation, is mate limitation of the dioecious copepod. Mate limitation is perhaps the simplest mechanism leading to Allee effects in sexually reproducing populations (Courchamp et al. 1999). Our calculations, which are based partly on observed recovery times of *D. middendorffiana*, suggest that the magnitude of such Allee effects could be very large, in the sense that founding population size must be several orders of magnitude larger for *H. shoshone* than for *D. middendorffiana* to allow for re-establishment (Fig. 1). To demonstrate that mate limitation is responsible for the reduced recovery probability of *H. shoshone*, an experiment in which initial stocking density is varied is essential. Given the range of stocking densities required, such a manipulation would likely need to be carried out at the whole-lake scale. We plan to initiate such an experiment in seven lakes within Humphreys Basin during 2003.

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