POPULATION ECOLOGY - ORIGINAL PAPER

Limits to genetic bottlenecks and founder events imposed by the Allee effect

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Abstract The Allee effect can result in a negative population growth rate at low population density. Consequently, populations below a minimum (critical) density are unlikely to persist. A lower limit on population size should constrain the loss of genetic variability due to genetic drift during population bottlenecks or founder events. We explored this phenomenon by modeling changes in genetic variability and differentiation during simulated bottlenecks of the alpine copepod, *Hesperodiaptomus shoshone*. Lake surveys, whole-lake re-introduction experiments and model calculations all indicate that *H. shoshone* should be unlikely to establish or persist at densities less than 0.5–5 individuals m^{-3}. We estimated the corresponding range in minimum effective population size using the distribution of habitat (lake) sizes in nature and used these values to model the expected heterozygosity, allelic richness and genetic differentiation resulting from population bottlenecks. We found that during realistic bottlenecks or founder events, >90% of *H. shoshone* populations in the Sierra Nevada may be resistant to significant changes in heterozygosity or genetic distance, and 70–75% of populations may lose <10% of allelic richness. We suggest that ecological constraints on minimum population size be considered when using genetic markers to estimate historical population dynamics.

Introduction

The Allee effect, viewed broadly, is a decrease in population growth rate as population density declines (inverse density-dependence), resulting from mechanisms such as mate limitation, obligate cooperation, and group-based antipredator strategies (Allee et al. 1949; Odum 1959; Courchamp et al. 1999). A specific consequence of strong inverse density dependence is the existence, in some cases, of a critical population density, the density below which population growth rate is negative (Courchamp et al. 1999). In effect, critical density represents a minimum population density, and depending on habitat size, a minimum population size, because at lower densities both the persistence of established populations and the establishment of new populations will be unlikely. To date, most discussions of the Allee effect have focused on issues relating to the establishment of invasive species (Lewis and Kareiva 1993; Veit and Lewis 1996; Leung et al. 2004), population decline and recovery of endangered species (Kuussaari et al. 1998; Lamont et al. 1993; Forsyth 2003) or collapsed populations of harvested taxa (Myers et al. 1995; Liermann and Hilborn 1997; Gascoigne and Lipcius 2004). Here, we draw attention to an unappreciated connection between critical density, a phenomenon drawn from population dynamics, and loss of genetic diversity in small populations, a phenomenon drawn from population genetics.

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By constraining the minimum effective population size, the Allee effect should constrain the genetic outcome of bottleneck events. Here we define a bottleneck event as a severe decrease in population size or the founding of a new population by a small number of colonists. Theory predicts that for sufficiently severe bottlenecks, the change in gene frequency depends only on the effective population size during the bottleneck and the duration of the bottleneck, because genetic drift overwhelms selection in small populations (Nei et al. 1975; Maruyama and Fuerst 1985). Because many populations rebound rapidly from small size, with threatened and endangered species a notable exception, the minimum effective population size sustained during a bottleneck event largely determines the genetic makeup of the post-bottleneck population, affecting both the absolute genetic variation remaining and the degree of genetic divergence from the pre-bottleneck population's genetic state (Nei et al. 1975; Wade and McCauley 1988).

The theoretical and empirical literature tends to focus on extreme bottlenecks with very small effective population sizes. The minimum effective population size in theoretical analyses is often ten or fewer individuals (Nei et al. 1975; Pannell and Charlesworth 1999; Whitlock and McCauley 1990; Leberg 2002). Empirical work, especially on species of conservation concern, has confirmed both the occurrence and the genetic impact of such extreme bottlenecks (Le Page et al. 2000; Robichaux et al. 1997; Glenn et al. 1999). As a result, it is typical for observations of very low genetic variability in natural populations or high genetic divergence between populations to be automatically ascribed to genetic drift associated with severe population bottlenecks. In effect, most analyses of genetic variability and genetic differentiation via drift contain an implicit assumption that the population could have established or recovered from an arbitrarily small size; one or two individuals in the case of asexual or sexual species, respectively. This assumption affects not only direct assessments of population bottlenecks, but also analyses that use genetic differentiation to infer other processes such as migration (Boileau et al. 1992; Ramstad et al. 2004). If the minimum effective population size determined by the Allee effect is relatively large, as suggested for some species such as sexually reproducing zooplankton (Gerritsen 1980), conch (Stoner and Ray-Culp 2000) and several insects (Hopper and Roush 1993; Berggren 2001; Liebhold and Bascompte 2003), bottlenecks or founder events may result in little loss of genetic variability via drift.

Because the Allee effect is a function of population density, habitat size is integral to predicting minimum possible population size, and thus the change in genetic variability and divergence, for species subject to an Allee effect. We present a quantitative analysis of how habitat size influences the loss of genetic diversity and the increase

in genetic divergence in diaptomid copepods, a group of organisms potentially subject to strong Allee effects driven by mate limitation. These planktonic crustaceans can only reproduce sexually (unlike cladocerans such as *Daphnia*) and have limited mobility in the potentially gigantic habitat of a lake or ocean. These constraints should create a minimum critical density below which the probability of encountering a mate is too low for a population to persist (Gerritsen 1980). Field data confirm the existence of mate limitation in diaptomid copepods (Kramer et al. 2008), and there is observational and experimental support for the existence of a critical density (Sarnelle and Knapp 2004; Parker et al. 1996; McNaught et al. 1999; Kramer et al. 2008). Copepod critical density can be estimated from information on body size, swimming speed and reproductive characteristics (Gerritsen 1980; Sarnelle and Knapp 2004; Kiørboe 2006). Because diaptomid copepods live in lakes and ponds, we can also easily define and quantify habitat sizes in nature. We use this information to assess the relationship between habitat size and the genetic impact of bottleneck events and suggest that Allee effects should be considered when analyzing population genetic data of copepods and other species with analogous characteristics.

Materials and methods

Our analysis focuses on *Hesperodiaptomus shoshone*, a large (>2 mm) diaptomid copepod that occurs in alpine lakes in the Sierra Nevada and the Rocky Mountains from Colorado to British Columbia. *H. shoshone* is univoltine, produces only diapausing eggs, and is highly susceptible to eradication by fish introduction (Knapp et al. 2001; Kramer 2007). Fish introductions have resulted in the absence of *H. shoshone* from a large number of lakes it had previously occupied, even though fish are no longer present in many cases (Knapp and Sarnelle 2008).

Sarnelle and Knapp (2004) estimated the critical density of *H. shoshone* to be 0.5–5 m^{-3} using a simple, random-encounter model of copepod mating (Eq. 6 in Gerritsen 1980), and a range of values for maximum daily population growth rate ($R = 1.05$–1.50 from Allan 1976) and length of reproductive season (60–120 days). Gerritsen's (1980) relatively simple model was used, rather than a more realistic, highly parameterized model (such as in Kiørboe 2006), because we have no information about several aspects of *H. shoshone* life history needed for complex models, most notably the hatching rate from resting eggs and the mortality rate of juvenile copepods. Basing the estimate of critical density on a wide range of maximum R in effect incorporates variation in these unknown demographic rates. Further, the range of maximum growth rates used is conservatively high given an observed daily growth

rate of 1.005 for a newly established population of *H. arcticus*, a closely related large, alpine copepod (McNaught et al. 1999). Most importantly, an estimated critical density of 0.5–5 m^{-3} is reasonably congruent with the results of a recent experimental reintroduction of *H. shoshone* [which suggested a critical density of 0.2–3 m^{-3} (Kramer et al. 2008)], with the lowest observed *H. shoshone* densities in established populations (6 m^{-3}, Sarnelle and Knapp 2004), and with an estimate based on quantitative observations of *H. shoshone* mating behavior (0.6–1.3 m^{-3}, Kramer 2007).

Critical density multiplied by habitat size (in this case lake volume) gives the minimum number of individuals necessary for a population to establish and persist. The range of relevant habitat sizes was determined using the surface area and maximum depth of 169 *H. shoshone*-containing lakes, which constituted a representative sample of *H. shoshone* habitat in the Sierra Nevada (R. Knapp, personal communication). We estimated mean depth from maximum depth with the regression equation: mean depth = 0.782 + 0.315 × maximum depth (R^2 = 0.77), which is based on 2,345 northern US lakes spanning a range of maximum depths similar to the Sierra Nevada lakes (P. Soranno, personal communication). Volume was then estimated as surface area × mean depth.

The key link in examining the relationship between minimum population size and population genetics is the effective population size. Changes in gene frequency due to drift are determined by effective population size rather than census population size (Wright 1931), and fluctuations in population size, skewed sex ratios and variance in reproductive success act to reduce the effective population size (Wright 1938). We used life history data and several assumptions to develop a simple, deterministic estimate of the effective population size of *H. shoshone* populations at the critical density. We assume population size during the bottleneck remains at the minimum to be maximally conservative, and that the sex ratio of *H. shoshone* is 1:1 (Kramer 2007). Therefore, any reduction in effective population size is due to variance in reproductive output.

We expect high variance in reproductive success because the low encounter rate at critical density will lead to zero reproductive output in the majority of individuals. To estimate the number of individuals that do contribute offspring to the next generation, we use the clutch size (mean = 16.02, SD = 4.18) measured for *H. shoshone* stocked into mesh enclosures in four lakes (Kramer et al. 2008), and the conservative assumption that successful individuals (male and female) are able to mate twice, with each of these females producing two clutches during the reproductive season. Our aim is to err towards overestimating variance in reproductive success by assuming all reproduction is contributed to by a somewhat

unrealistically limited pool of individuals, but is somewhat offset by an assumption of zero variance in reproduction among successful pairs. Based on the assumptions above, we can estimate the minimum number of reproducing individuals (N_r) necessary to maintain population size at the critical density as follows:

$$N_r = \frac{\text{habitat size} \times \text{critical density}}{\text{clutch size} \times \text{\# of clutches/pair}}$$
$$= \frac{\text{habitat size} \times \text{critical density}}{16 \times 2} \quad (1)$$

We also conservatively assume 100% hatching success and zero mortality before reproduction. Effective population size (N_e) is then estimated as (Wright 1938):

$$N_e = \frac{4N_r - 2}{2 + \text{Var}(k)}, \quad (2)$$

where $\text{Var}(k)$ is the variance among all adults in the number of gametes contributed to the next generation.

We consider bottlenecks that last for 1–10 generations. Longer bottlenecks are unlikely for *H. shoshone* and diaptomid copepods in general (Sarnelle and Knapp 2004; McNaught et al. 1999). McNaught et al. (1999) found population growth to be exponential, with natural population density nearly attained in only four generations (following reintroduction at a density of 1.5 individuals m^{-3}). Short bottleneck duration is also a likely scenario for any species with high reproductive rates not subject to habitat loss, harvest or other external forces.

The ranges of bottleneck duration and minimum effective population size estimated above are used to examine how two measures of genetic variability and two measures of genetic divergence are affected by bottlenecks in populations subject to Allee effects. Change in genetic variability is estimated by heterozygosity, perhaps the most widely used measure for the maintenance of genetic variation, and allelic richness, which is much more sensitive to changes in population size (Nei et al. 1975; Nei 1987). For simplicity and to be consistent with previous analyses (Nei et al. 1975), we estimate change in heterozygosity and allelic richness as a proportion of the variation present before the bottleneck. We calculate both measures as in Nei et al. (1975), using the same initial levels of genetic variability (see "Discussion"). The proportion of heterozygosity retained during a bottleneck has an analytical solution (Nei et al. 1975):

$$\frac{H_b}{H_I} = \left(1 - \left(\frac{1}{2 \times N_e}\right)\right)^t, \quad (3)$$

where H_b is heterozygosity at the end of the bottleneck, H_I is initial heterozygosity, and t is the duration of the bottleneck in generations. The proportion of allelic richness retained was estimated using the simulation method of Nei et al. (1975).

To represent genetic divergence we consider Nei's genetic distance (D) because it allows us to consider two currently or historically linked populations (Chakraborty and Nei 1977). We estimate D between two populations, where one is founded by a random sample from a second population that is at mutation–drift equilibrium, using the infinite alleles model as in Eq. 21 from Chakraborty and Nei (1977). We also consider F_{ST}, which measures the overall genetic similarity of a group of populations, following the assumptions for the migrant pool model and a small number of colonists as in Eq. 1 from Wade and McCauley (1988). Under this model F_{ST} measures the genetic differentiation among a group of populations founded from a single source population (Wade and McCauley 1988). This model was selected because it is the only formulation that does not require parameters, such as migration, which do not enter into our other analyses. Initial levels of variability were the same as for the heterozygosity and allelic richness calculations.

Results

The sample of lakes inhabited by *H. shoshone* in the Sierra Nevada range from 77 to 7.3×10^6 m^3, with a median volume of 1.3×10^5 m^3 (Fig. 1). The corresponding range of minimum effective population size for a minimum population density of 0.5 m^{-3} is 2.4–2.4 $\times 10^5$ individuals, or 1.2–1.2 $\times 10^5$ pairs, with a median effective
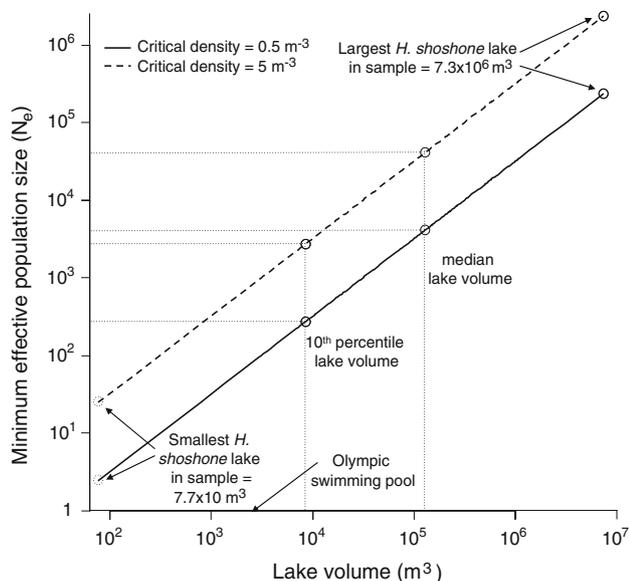

Fig. 1 The expected relationship between lake volume and minimum effective population size for a representative sample of *Hesperodiaptomus shoshone* populations in the Sierra Nevada ($n = 169$) at a critical density of 0.5 or 5 m^{-3}. The tenth percentile and median lake sizes are indicated

population size of 4.1×10^3 (Fig. 1). With a critical density of 5 m^{-3} the lower limit on effective population size for similarly sized habitat is 10 times higher.

The proportion of the original heterozygosity retained in a bottlenecked population rises rapidly as habitat size increases from the minimum habitat size (Fig. 2). It asymptotes at a small habitat size, with over 90% of the original variability retained in habitats larger than 1,500 m^3, even for the lowest critical density and longest bottleneck duration considered (Fig. 2). This size is exceeded by 97.5% of the *H. shoshone* habitat in the Sierra Nevada (Fig. 1). At the median habitat size, >99% of heterozygosity is retained for all combinations of critical density and bottleneck duration. Not surprisingly, similar retention percentages for allelic richness require much larger habitat size (Fig. 3). What is important to note is that even our most extreme scenario, consisting of a ten generation bottleneck at the critical density of 0.5 m^{-3}, results in over 90% retention of the original alleles in roughly 65% of the sample of *H. shoshone* lakes (Fig. 3). Higher critical densities rapidly increase retention, leading to the expectation of 90% retention for 90% of populations when the critical density is 5 m^{-3} and the bottleneck lasts for ten generations (Figs. 1, 3). For the median habitat size, 93–99% of allelic richness is retained for the combination of parameters considered.

The pattern for genetic distance is similar to the pattern seen in heterozygosity (Fig. 4). D cannot be strictly interpreted as a percentage difference between two populations, but in this case a value of 0.1 is roughly equal to 90% identity of alleles between the two populations (Nei 1987). For our most extreme scenario, habitats larger than 4,500 m^3 result in $D < 0.1$. This includes over 90% of Sierra Nevada *H. shoshone* habitat. Genetic distance of a median size habitat from its founding population is <0.01.

The relationship between habitat size and F_{ST} shows populations in habitats > 500 m^3 have very low F_{ST} (Fig. 5). We include F_{ST} because of its popularity as a measure of genetic differentiation, especially for researchers estimating migration from genetic data. At the same time, it is less than ideal for our purposes due to its more restrictive, and less applicable, assumptions of the relationship between populations. The F_{ST} shown (Fig. 5) is that expected among populations when those populations are founded by the same number of colonists from a single mixture of potential colonists. In addition, these populations grow to a large size in a single generation. The most we can safely draw from this is that all the populations must be very small in order for very short bottlenecks to substantially increase the amount of genetic variance distributed among populations. F_{ST} is further discussed below.
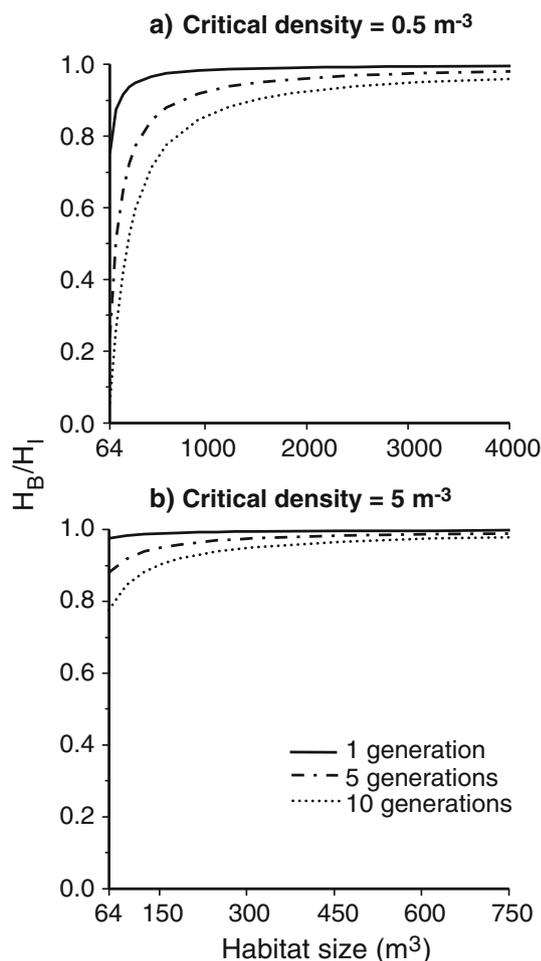
Fig. 2 The expected ratio of post-bottleneck heterozygosity (H_B) to initial heterozygosity (H_I) as impacted by habitat size and duration of the bottleneck for **a** a critical density of 0.5 individuals m^{-3}, **b** a critical density of 5 individuals m^{-3}. Bottleneck duration is the number of generations over which a population is at its minimum effective population size. A habitat of volume 64 m^3 is the largest habitat in which effective population size can decline to one male and one female when the critical density = 0.5 m^{-3} and is roughly equivalent to the minimum habitat size observed in the Sierra Nevada populations (77 m^3)

Fig. 3 The proportion of original allelic richness retained after a population bottleneck as influenced by habitat size and bottleneck duration for **a** a critical density of 0.5 individuals m^{-3}, **b** a critical density of 5 individuals m^{-3}. Bottleneck duration is the number of generations over which a population is at its minimum effective population size. Estimates were produced using the simulation technique of Nei et al. (1975). Initial effective population size = 4×10^6, mutation rate = 10^{-8}, number of iterations = 5,000

Discussion

Our analyses show that habitat size can have a very large influence on the potential for loss of genetic variation and increase of genetic divergence resulting from population bottlenecks. A likely conservative scenario is to assume actual minimum densities are closer to 0.5 m^{-3} and that bottleneck duration is close to the three to four generations suggested by past observation (Boileau et al. 1992; McNaught et al. 1999). Under this scenario colonization events in 70–75% of *H. shoshone* habitat would result in <10% loss of allelic richness (Fig. 3). Furthermore, over 90% of *H. shoshone* populations are resistant to significant changes in heterozygosity or genetic distance (Figs. 2, 4).
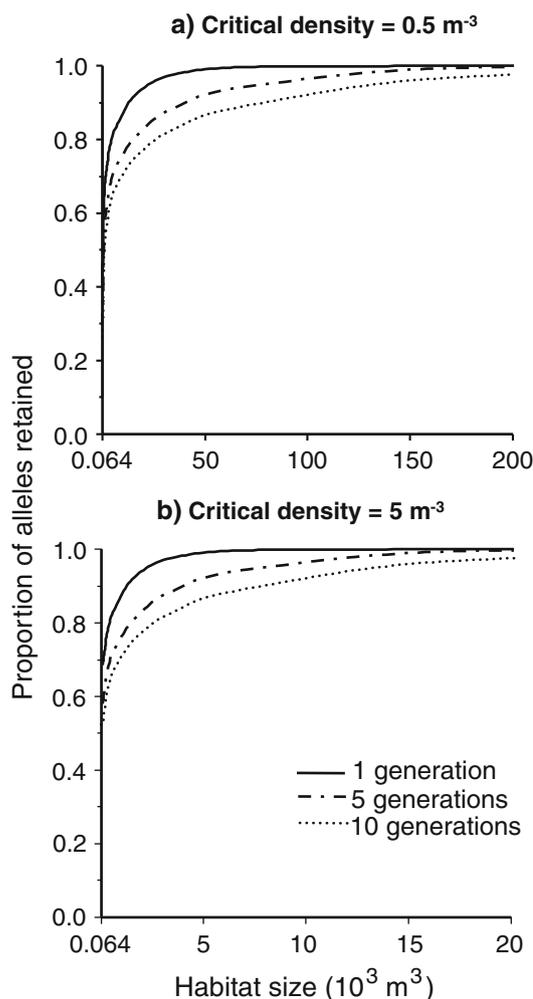
This is a very different outcome than expected under the common assumption that there is no lower limit to population size.

Recovery and establishment events can take different forms in *H. shoshone* populations. Because *H. shoshone* produce diapausing eggs, "colonists" can enter the lake (i.e., the water column) from the egg bank, as well as from other lakes, although the modes and rates of diaptomid colonization across lakes are largely unknown. If *H. shoshone* has been extirpated from the water column for many generations, the egg bank can become depleted, and colonization from the egg bank will be limited (Knapp and Sarnelle 2008). In this paper, the terms "recovery" and "colonization" are used synonymously and assume a
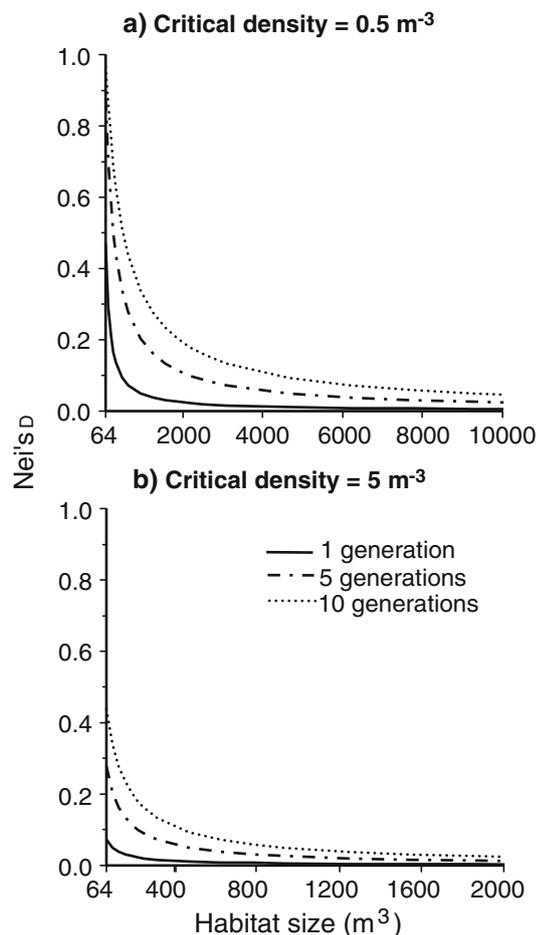
Fig. 4 Expected Nei's distance (*D*) for a population founded at the critical population density from a founding population at mutation–drift equilibrium as influenced by habitat size and duration of the bottleneck for **a** a critical density of 0.5 individuals m^{-3}, **b** a critical density of 5 individuals m^{-3}. Expected *D* calculated as in Eq. 21 from Chakraborty and Nei (1977) with effective population size = 4×10^6 and mutation rate = 10^{-8} in the founding population. Bottleneck duration is the number of generations over which a population is at its minimum effective population size

Fig. 5 Expected genetic differentiation (F_{ST}) for a group of identical populations founded at the critical density from a single source population as influenced by habitat size for critical densities of 0.5 and 5 individuals m^{-3}. See Wade and McCauley (1988)

depleted egg bank or no egg bank at all. Another possibility, probably more common, is that *H. shoshone* populations become greatly reduced or even eliminated from the water column for a much shorter time, then reestablish readily from a well-stocked egg bank. This type of recovery precludes the genetic signature of a bottleneck event. More generally, the presence of an egg bank results in overlapping generations (Hairston et al. 1995) and a larger effective population size than for a similar-sized, univoltine population lacking diapausing eggs (Nunney 1993).

If *H. shoshone* populations can often recover from lower densities than we have estimated, the genetic impact of population bottlenecks will obviously be increased.
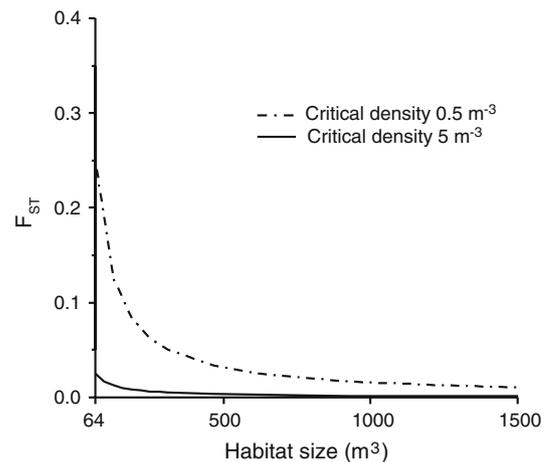
Therefore, it is important to examine the potential for bias in our assumptions about copepod population dynamics and genetic structure. A criticism of the Gerritsen (1980) model is that some copepod species are known to use chemical signals to detect mates (Katona 1973; Doall et al. 1998; Nihongi et al. 2004; Kiørboe and Bagøien 2005), which would decrease the minimum density relative to a random diffusion model. A reduction in critical density would also be achieved by behaviors that increase local density of copepods (Buskey et al. 1996; Tsuda and Miller 1998). While we do not rule out these influences, several lines of empirical evidence are congruent with a critical density in the range 0.5–5 m^{-3} (see "Materials and methods"). Our conservative assumptions about reproduction in estimating effective population size likely offset any over-estimation of critical density based on a random encounter model. Specifically, we have assumed that all eggs produced are viable, all hatch the next year and no juveniles die before reproducing. The assumption of 100% hatching success is the most obviously conservative assumption since large numbers of eggs are known to remain dormant in the sediments. We were also extremely conservative in assuming that males and females are able to reproduce twice in a season. Multiple clutches are common in good years (Kramer 2007), but a single pair producing two clutches in a low-density population should be rare because *H. shoshone* must mate before each viable clutch (Watras and Haney 1980) and the probability of mating at all would be very low.

Finally, our estimates of *D* and loss of allelic richness are dependent on the initial levels of variability present in the pre-bottleneck population. Increased variability results in larger *D* and increased loss of allelic richness when other

parameters are held constant. For our analysis, we used the same initial parameters as Nei et al. (1975) and Chakraborty and Nei (1977) for their hypothetical fruit fly population. We thought this suitable since we are also considering invertebrate populations with high carrying capacities and rapid population growth. This similarity makes our results directly comparable with these earlier analyses, which were the first to quantify the major impact that severe population bottlenecks have on the genetics of a population. Additionally, we could find no reported values for average effective population size or mutation rate for nuclear genes in freshwater copepods which would be more directly applicable to our calculations.

Given the limits the Allee effect should impose on the genetic outcome of population bottlenecks and colonization events, it seems crucial to consider habitat size in making inferences from genetic data. For example, genetic information has been used to infer population structure and phylogeography in arctic copepods (Boileau and Hebert 1988; Boileau et al. 1992). These studies found significant genetic differentiation among nearby ponds, suggesting very low migration, which seemed inconsistent with the ponds' proximity (Boileau and Hebert 1988). This paper and subsequent analyses (Boileau and Hebert 1991; Boileau et al. 1992) led the authors to suggest a model in which very rapid initial growth rates, with carrying capacity reached in five generations or less, retain genetic differences resulting from genetic drift due to founder events, despite migration between populations.

Specifically, measured F_{ST} values suggested five or fewer individuals founded most of the populations (Boileau et al. 1992). The habitats surveyed ranged from large tundra ponds (volume = 20,166 ± 9,882 m^3) to small rock pools (volume < 50 m^3) (Boileau and Hebert 1988). The Allee effect would seem to make it improbable that five individuals could successfully colonize the large ponds. In support of the role of habitat size, measured gene frequency divergences for the large tundra ponds were consistently lower than for populations in much smaller rock pools in the same species (Boileau and Hebert 1988), suggesting less severe bottlenecks in the larger habitats. Our results highlight the fact that inclusion of very small habitats prone to severe bottlenecks could bias estimates of metapopulation-wide estimates such as F_{ST}. We suggest that the use of genetic statistics, and F_{ST} in particular, to estimate population size during colonization events in species subject to the Allee effect should acknowledge the ecological limitations on population growth.

Boileau and Hebert (1991) also identified an important additional force, colonization pattern, which interacts with the number of colonists to create the observed genetic pattern. They proposed that Arctic habitats were serially colonized and genetic distance built up as a small number of colonists from a previously colonized habitat successively filled each empty habitat (Boileau and Hebert 1991). The successive colonization events proposed by the authors would act very strongly to increase differentiation (Wade and McCauley 1988), especially in areas dominated by small pools. In the terms of our analysis, bottleneck duration is effectively extended by each subsequent colonization event, which could significantly increase genetic differentiation even when habitat is dominated by large lakes.

The potential of the Allee effect to maintain genetic variation and minimize differentiation has implications for both ecology and evolutionary biology. As in the arctic copepod example above, population genetics are being increasingly used to infer ecological processes such as migration and historical population size. Our example underscores the need for studies to directly consider minimum population size when analyzing genetic variation in species, such as copepods, thought to experience the Allee effect. Because the minimum effective population size can be dependent to a great degree on habitat size, bias will result if the distribution of habitat sizes sampled does not match the overall distribution of habitat size. The Allee effect creates differences in population genetic expectations that are dependent on ecology, and recognizing the potential impact of the Allee effect should allow ecologists to better understand their results and the ways in which model assumptions are violated in their analyses. Hopefully this will improve the accuracy of the inferences made using population genetics.

For evolutionary biologists, a relatively large lower limit on population size could reduce the likelihood of speciation according to some of the models that depend on genetic reorganization due to small population size and genetic drift (Wright 1931; Mayr 1963; Templeton 1980). A higher mean population size will decrease the influence of drift on the population's genetic makeup, presumably increasing the influence of natural selection. Fewer very small bottlenecks will also preserve more genetic variability on which natural selection can act. In several cases very low heterozygosity in wild populations has been attributed to severe historic bottlenecks (Nei et al. 1975; O'Brien 1994). Evidence for the Allee effect, and therefore larger critical population size, in species with very low genetic variability would suggest that other causes for low genetic variation might also need to be considered. However, it is also possible that genetic distances observed between populations of species subject to the Allee effect, such as the arctic copepods discussed above, could be the result of stochastic colonization success after a very large number of repeated dispersal events, each having a very low individual probability of success.

Our analysis suggests habitat size may play an important role in the population genetics of *H. shoshone,* as a

consequence of the Allee effect. Similar effects are possible in other taxa with minimum population sizes, such as conch (Stoner and Ray-Culp 2000), and several insects (Hopper and Roush 1993; Berggren 2001; Liebhold and Bascompte 2003). We are not suggesting that a species or population is immune to genetic drift or loss of genetic variability. Species with very large population size can harbor enormous genetic variability, and a reduction of population size, even if to a large absolute size, will cause some of that variability to be lost and increase the influence of genetic drift (Bucklin and Wiebe 1998). Rather, we suggest that Allee effects, caused by mechanisms such as mate limitation, impose limits on minimum population size that could have measurable and important consequences for population genetics. To our knowledge, these consequences have been ignored to date. Our results suggest that even modest limits on minimum population size can lead to substantially different genetic outcomes after bottleneck events.

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