Population Demographics and Genetic Diversity in Remnant and Translocated Populations of Sea Otters

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Abstract: *The effects of small population size on genetic diversity and subsequent population recovery are theoretically predicted, but few empirical data are available to describe those relations. We use data from four remnant and three translocated sea otter (*Enhydra lutris*) populations to examine relations among magnitude and duration of minimum population size, population growth rates, and genetic variation. Mitochondrial (mt)DNA haplotype diversity was correlated with the number of years at minimum population size ($r_s = -0.741$, $p = 0.038$) and minimum population size ($r_s = 0.709$, $p = 0.054$). We found no relation between population growth and haplotype diversity, although growth was significantly greater in translocated than in remnant populations. Haplotype diversity in populations established from two sources was higher than in a population established from a single source and was higher than in the respective source populations. Haplotype frequencies in translocated populations of founding sizes of 4 and 28 differed from expected, indicating genetic drift and differential reproduction between source populations, whereas haplotype frequencies in a translocated population with a founding size of 150 did not. Relations between population demographics and genetic characteristics suggest that genetic sampling of source and translocated populations can provide valuable inferences about translocations.*

Demografía Poblacional y Diversidad Genética en Poblaciones Remanentes e Introducidas de Nutrias Marinas

Resumen: *Los efectos de un tamaño poblacional pequeño en la diversidad genética y la subsecuente recuperación son predecidas teóricamente, pero hay pocos datos empíricos viables para describir estas relaciones. Utilizamos datos de cuatro poblaciones remanentes y tres introducidas de nutrias marinas (*Enhydra lutris*) para examinar relaciones entre la magnitud y la duración de un tamaño poblacional mínimo, tasas de crecimiento poblacional y variación genética. La diversidad de haplotipos (mt)DNA mitocondriales estuvo correlacionada con el número de años al tamaño poblacional mínimo ($r_s = -0.741$, $p = 0.38$) y con el tamaño poblacional mínimo ($r_s = 0.709$, $p = 0.54$). Encontramos que no existió relación entre el crecimiento poblacional y la diversidad de haplotipos, aunque el crecimiento fue significativamente mayor en las poblaciones introducidas comparado con las poblaciones remanentes. La diversidad de haplotipos en poblaciones establecidas a partir de dos fuentes fue mayor que en una población establecida a partir de una sola fuente y fue mayor que en sus respecitvas poblaciones fuente. Las freqcuencias de haplotipos en poblaciones introducidas de tamaños de fundación de 4 y 28 difirieron de lo esperado, indicando deriva génica y reproducción diferencial entre poblaciones fuente, mientras que frecuencias de haplotipos en una población introducida con tamaño de fundación de 150 no difirió. Las relaciones entre demografía poblacional y características genéticas sugieren que los muestroes de poblaciones fuente e introducida pueden proveer inferencias valiosas referentes a las introducciones.*

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Introduction

A fundamental concern in resource conservation and management is the loss of biological diversity, expressed as species diversity at the ecosystem level or genetic diversity at the species level (i.e., declines in genetic diversity or increasing interpopulation variance in gene frequencies; Shaffer 1981; Lande 1988; Leberg 1990). A common approach to conserving species diversity and mitigating declines in abundance is the establishment or augmentation of populations through translocation (Griffith et al. 1989; Leberg 1993; Wolf et al. 1996).

Strategies regarding the selection of source populations, numbers of individuals, and habitat requirements have been suggested (Shaffer 1981; Leberg 1990; Wolf et al. 1996). But translocations frequently result in small founding population sizes (i.e., population bottlenecks; Griffith et al. 1989; Wolf et al. 1996), which, if sustained over several generations, may result in reduced genetic variation (Nei et al. 1975; Lande & Barrowclough 1987; Frankham 1996). The potential effects of reduced population size and subsequent inbreeding include reduced fecundity and survival, which have been observed in captive (Ralls et al. 1979; Ballou & Ralls 1982; Ralls et al. 1988) and wild (Westemeier et al. 1998) populations.

The ability of wild populations to recover from population bottlenecks may be impaired by the effects of reduced genetic variation (Wayne 1995), although this generality has been questioned (Caro & Laurenson 1994). Westemeier et al. (1998) documented reduced fecundity and genetic diversity following a long-term population decline in the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*). Alternatively, high genetic diversity was maintained during a brief bottleneck in the greater one-horned rhinoceros (*Rhinocerous unicornis*; Dinerstein & McCracken 1990). Despite numerous theoretical treatments of the effects of bottlenecks on genetic variation and fitness (e.g., Lande 1994; Mills & Smouse 1994; Frankham 1995), few empirical examples from natural populations are available that have quantified relations between genetic diversity and population demography or that have evaluated the effects of translocations on genetic diversity and drift.

Mitochondrial DNA (mtDNA) is a useful genetic marker because of its relatively high levels of variation among individuals, both within and among populations. As such, it has been particularly effective in elucidating patterns of intraspecific population structuring (Avise et al. 1987; Moritz 1994; Avise 1995). Uniparental (matrilineal) and haploid transmission mean that mitochondrial effective population size is considerably smaller than that expected for nuclear genes, increasing sensitivity to genetic drift (Moritz 1994). These characteristics make mtDNA particularly appropriate for tracing recent evolutionary history, including colonization or translocation events and population bottlenecks (Wilson et al. 1985).

Sea otters (*Enhydra lutris*) provide an excellent opportunity to study relations between population demographics and genetics in a large, long-lived mammal. The near extirpation of sea otters by fur hunters in the nineteenth century left 11 small, isolated populations that have persisted (Kenyon 1969). In addition, three translocations of sea otters resulted in viable populations (Riedman & Estes 1990; Fig. 1). Because remnant and translocated populations have remained reproductively isolated during recovery, we were able to examine the effects of small population size, resulting from either overharvest or translocation, on genetic variation and population demographics. Ge-

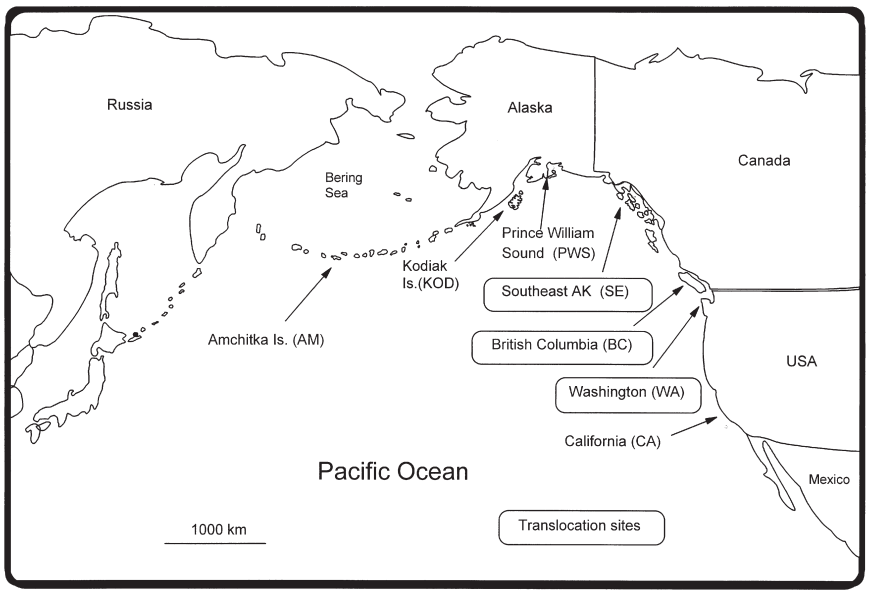

*Figure 1. Locations of remnant and translocated sea otter (*Enhydra lutris*) populations sampled.*

netic markers were further used to characterize the magnitude of potential founder events and genetic drift that may have resulted from differential survival or reproductive success of females used in translocations from multiple sources.

Studies using allozymes (Rotterman 1992; Lidicker & McCollum 1997), mtDNA (Sanchez 1992; Cronin et al. 1996), and multilocus minisatellites (Scribner et al. 1997) found geographically separate sea otter populations to be differentiated genetically, although there was little evidence of phylogeographic structuring (Scribner et al. 1997). Large differences among remnant populations in nuclear and mtDNA gene frequency reflect the lack of gene flow since population reductions or drift in gene frequencies due to population bottlenecks. Remnant populations separated by large geographic distances frequently shared haplotypes, suggesting recent common ancestry and historic gene flow (Cronin et al. 1996). Levels of genetic diversity varied greatly among remnant populations but apparently were not related to contemporary population sizes (Scribner et al. 1997).

The end of the sea otter fur trade was indicated by harvests of <48 per year from 1906 to 1910 (Lensink 1962; Kenyon 1969). Although accurate estimates of size are not available for all remnant populations, anecdotal information and surveys suggest that few (<100) individuals per location remained at the time they were legally protected in 1911 (Lensink 1962; Kenyon 1969). Surveys of abundance were not generally undertaken until populations became conspicuous, usually consisting of several hundred or more individuals. Moreover, remnant populations displayed different demographics during their recovery (Fig. 2).

In the 1960s and 1970s, translocations of otters from Amchitka Island and Prince William Sound, Alaska (source populations), to unoccupied habitat in southeast Alaska, British Columbia, and Washington were conducted to aid the species' recovery (Jameson et al. 1982; Fig. 3). Accurate data are available on numbers of animals moved and on the timing and rates of recovery of translocated populations (Bigg & MacAskie 1978; Jameson et al. 1982; MacAskie 1987; Estes et al. 1989; Estes 1990; Bodkin et al. 1994; Agler & Kendall 1995).

Our objectives were to test for relations among genetic diversity and measures of population demographic characteristics: time at minimum population size, minimum population size, and population growth rates. We used mtDNA haplotype frequencies to evaluate possible genetic drift and differential contributions by females of

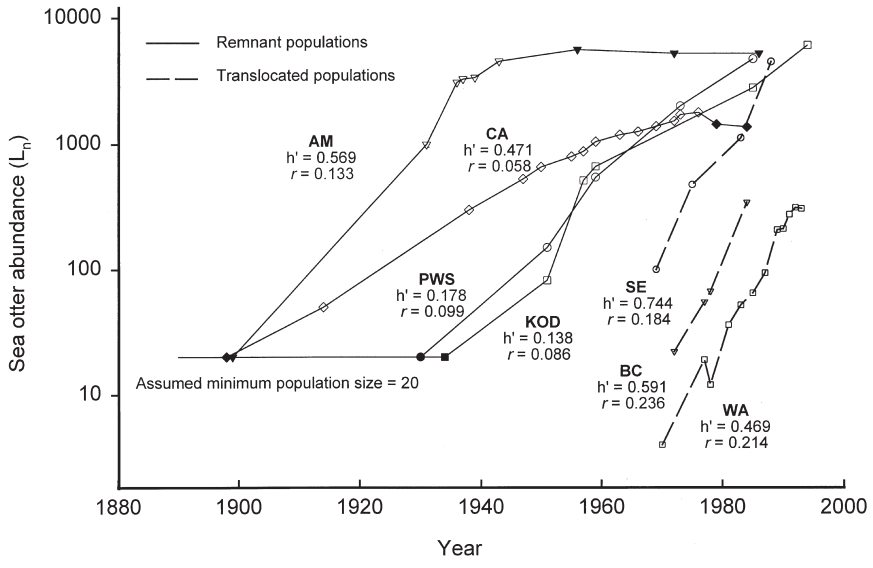

Figure 2. Growth curves and haplotype (h′) diversities for four remnant sea otter populations, Amchitka (AM), California (CA), Kodiak (KOD), and Prince William Sound (PWS), and three translocated sea otter populations, British Columbia (BC), Southeast Alaska (SE), and Washington (WA), based on post-release surveys. Open symbols indicate data used in calculating growth rates. Sources for population data are AM: Dufresne (1931 Sea otter in Aleutian bird reservation Memorandum, Alaska Department of Fish and Game, Juneau), Kenyon (1969), Estes (1990); CA: Bryant (1915), Bool-ootian (1961), Estes and Jameson (1983), Wendell et al. (1986), Estes et al. (1994); KOD: Lensink (1962), Simon-Jackson et al. (1986), U.S. Fish and Wildlife Service (1011 E. Tudor Road, Anchorage, Alaska); PWS: Lensink (1962), Pitcher (1975), Irons et al. (1988); BC: Bigg and MacAskie (1978), MacAskie (1987); SE: Jameson et al. (1982), Agler and Kendall (1995); WA: Jameson et al. (1982), Bodkin et al. (1994).

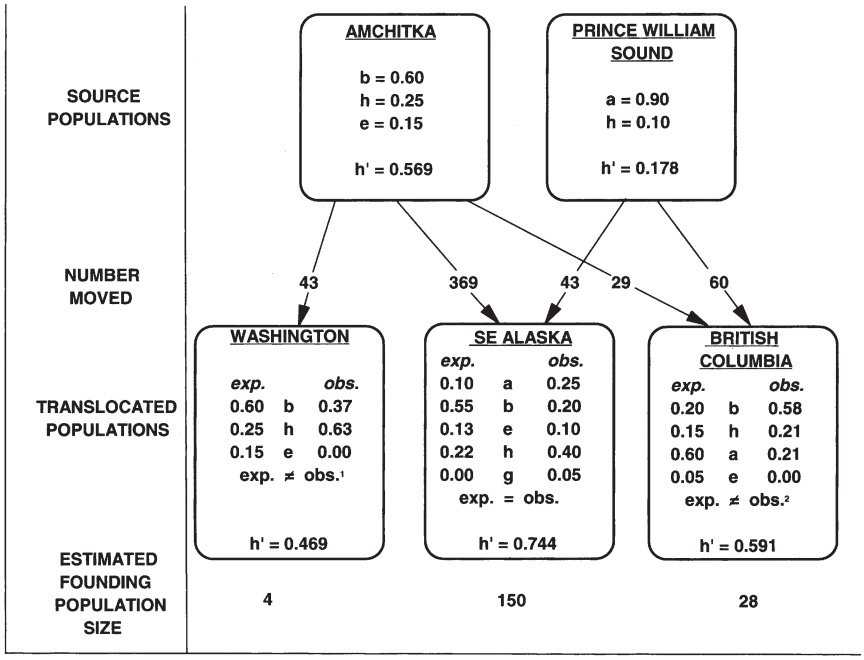

Figure 3. Observed and expected estimates of haplotype frequency (lower case), haplotype diversity (h′), and otter numbers moved from source populations. Haplotype frequency estimates from source populations are taken from Cronin et al. (1996) and founding population sizes from Estes et al. (1989). In the Washington population, observed haplotype frequencies differed significantly from those expected ($\chi^2 = 8.94$, p = 0.01). In the British Columbia population, observed haplotype frequencies differed from those expected ($\chi^2 = 7.18$, p = 0.06).

different sources in translocations. We compared population growth rates between source and translocated populations. We present our findings relative to conservation efforts for other species that may be undergoing declines and where translocations may be considered a management option.

Methods

Study Areas

We obtained tissue samples and population data from remnant populations at Amchitka Island (AM), the Kodiak (KOD) Archipelago, and Prince William Sound (PWS), Alaska, and California (CA), and from translocated populations in British Columbia (BC), Washington (WA), and southeast Alaska (SE) (Figs. 1 & 3). The 1969–1972 BC translocation consisted of 29 sea otters from AM and 60 from PWS; the 1965–1969 SE translocation consisted of 369 otters from AM and 43 from PWS; the 1969–1970 WA translocation consisted of 43 otters from AM (Jameson et al. 1982). Founding sizes for translocated populations are from Estes et al. (1989) and were calculated by extrapolating growth regressions back in time to 1 year after translocation.

Demographic Analyses

We used published and unpublished counts or estimates to calculate contemporary growth rates for each remnant and translocated population. In calculating population-specific growth rates, we consistently used either actual counts or estimates of abundance. Annual growth rates (r) were calculated by regressing the natural logs of survey counts or population size estimates ($\log_n(x)$) over time. For the AM population we used survey data from 1931 to 1943 for estimating the growth rate because growth likely declined as carrying capacity was initially reached after 1943 (Estes 1990). Because of the anomalous growth characteristics after 1976 in CA, we used only abundance estimates from 1914 to 1976 to calculate a growth rate. From this, we extrapolated back from the earliest estimate or count of population size to a point in time when the population equaled 20 (assumed minimum population size) or to the year 1890 (assumed point in time of minimum population size, based on harvest records; Lensink 1962). We assumed a minimum size of 20 for all remnant populations based on data from CA, where 32 animals were present in 1914.

We tested for relations of three population variables—years at minimum number, minimum number, and population growth rate—to haplotype diversity among the seven populations we sampled with Spearman's rank correlation. We examined the sensitivity of our correlations by varying the minimum population size from 10 to 40 (holding year at minimum constant) and varying the assumed year at minimum from 1870 to 1910 (holding minimum number constant) in a sensitivity analysis. Years at the minimum population size were the number of years between 1890 and the year in which we estimated that population size equaled 20.

Genetic Analyses

Muscle or blood samples were obtained from the three translocated sea otter populations and the remnant (source) populations from which they were derived.

Source populations were AM (n = 20) and PWS (n = 31) (Fig. 3), and translocated populations were BC (n = 19), SE (n = 20), and WA (n = 24). We obtained tissues from two additional remnant populations, CA (n = 20) and KOD (n = 14) (Fig. 1), for which historical survey data are available.

Genomic DNA was extracted with standard methods involving either SDS (sodium diodecyl sulfate), proteinase-k digestion, and phenol-chloroform extraction (Sambrook et al. 1989) for muscle, or phenol-chloroform-methylene chloride extraction for blood (Cronin et al. 1994). Polymerase chain reaction (PCR) was used to amplify four segments of mtDNA by methods described in Cronin et al. (1996). To identify haplotypes, restriction enzymes were used to digest each of the four segments of mtDNA (ND1, 19 enzymes; ND3/4, 18 enzymes; ND5/6, 13 enzymes; 12S-16S, 10 enzymes) from each sampled population (Cronin et al. 1996). Haplotypes were defined from composite restriction-fragment patterns for enzymes showing variable fragment patterns (Lansman et al. 1981). Remnant population haplotypes are from Cronin et al. (1996).

We evaluated potential genetic drift and differential female reproductive contributions between source populations used in translocations by comparing observed to expected haplotype frequencies. We estimated expected frequencies in translocated populations using proportional contributions of source populations from translocation records and current haplotype frequencies from source populations. Haplotype diversities (h') were calculated from the number of haplotypes and their frequency in each population (Nei 1987).

Results

Demographic Analyses

We used estimated founding population sizes for translocated sea otter populations of 28 (BC), 150 (SE), and 4 (WA) from Estes et al. (1989; Fig. 2). Using contemporary growth rates (Fig. 2) and extrapolating back in time from the first survey date, we estimated that the four remnant populations were at the assumed minimum population size of 20 in 1898 (CA), 1899 (AM), 1930 (PWS), and 1934 (KOD), respectively. Estimated population growth rates were significantly higher in translocated populations ($\bar{x}$ = 0.21, range = 0.18 - 0.24) compared to remnant populations ($\bar{x}$ = 0.09, range = 0.06 - 0.13) (students $t = -5.258$, $p = 0.003$; Fig. 2).

Genetic Analyses

Haplotype frequencies in translocated populations differed significantly from expected in WA ($\chi^2 = 8.94$, $p = 0.01$) and were marginally significant in BC ($\chi^2 = 7.18$, $p = 0.06$), but were not different in SE ($\chi^2 = 7.09$, $p = 0.13$) (Fig. 3). One haplotype (g) found in SE was not identified in the source populations (AM or PWS) or in any other sampled population. Because the WA population was established from a single source (AM) and estimated founding population size was low (4), changes in haplotype frequency may be attributed to genetic drift. Discrepancies between observed and expected haplotype frequencies in the translocated BC population are likely due to disproportional contributions of the two source populations. For example, although PWS contributed twice the number of individuals to the BC population as did AM, the b haplotype, documented only in the AM source population, was observed in much greater frequency than expected, suggesting that AM females contributed disproportionally to population growth following translocations.

Haplotype diversities in remnant populations ranged from 0.138 at KOD to 0.569 at AM (Fig. 2) and averaged 0.338 (Cronin et al. 1996). Haplotype diversities in translocated populations ranged from 0.469 at WA to 0.744 at SE (Fig. 3) and averaged 0.601. Haplotype diversity generally was higher in translocated populations, although the difference between mean values from remnant and translocated populations was not significant ($t = 2.57$, $p = 0.12$); however, power (0.24) of the test was low.

The two translocated populations (SE and BC) founded from multiple source populations had haplotype diversities that exceeded those of both of their source populations (AM or PWS; Fig. 3). The higher haplotype diversities in populations with two sources and the presence of haplotypes from each source indicate reproductive success by females from each source. Haplotype diversity in the WA population (0.469), founding size of four, was 18% lower than in the single-source population (AM, 0.569) from which it was founded. Among the remnant sea otter populations, haplotype diversity was relatively low at KOD and PWS, where populations remained at minimum levels for many generations (Fig. 4). Haplotype diversity was higher at AM and CA, where duration at minimum population size was estimated at about one generation (8–9 years).

Correlation Analyses

Haplotype diversity was negatively correlated with the amount of time a population spent at the assumed minimum number ($r_s = -0.741$; $p = 0.038$) and positively correlated with the minimum population size ($r_s = 0.709$, $p = 0.054$). There was no significant relation between estimated population growth rates and haplotype diversity ($r_s = 0.53$, $p = 0.18$).

In the sensitivity analysis, both variables remained significantly correlated with h' at an assumed minimum population size of 10 (years at minimum, $r_s = -0.81$, $p = 0.025$; minimum number, $r_s = 0.741$, $p = 0.038$). At an

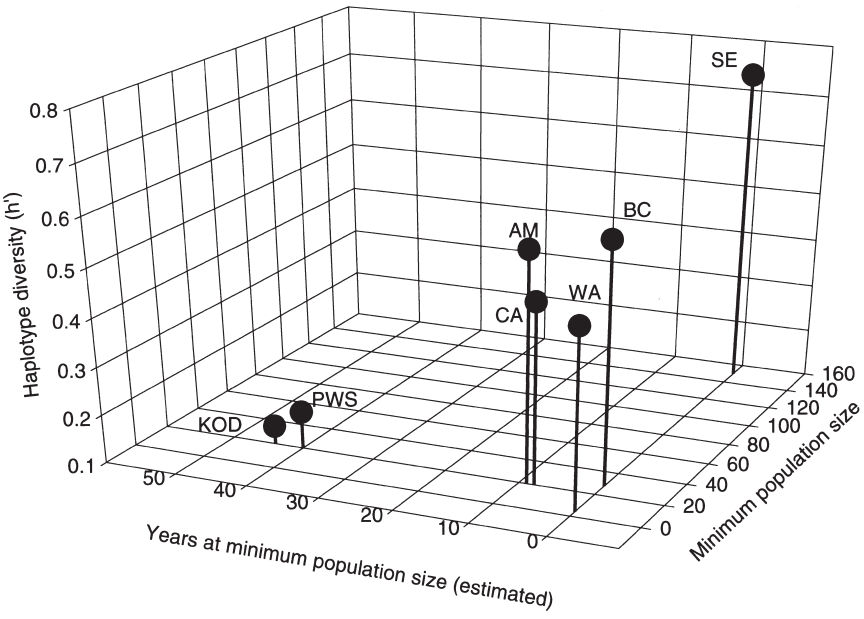

Figure 4. Plot of years at estimated minimum population size (x-axis) and estimated minimum population size (z-axis) against haplotype diversity (y-axis). Both minimum population size and years at minimum population size were significantly correlated with haplotype diversity (r_s = 0.709 and −0.741, respectively). Abbreviations are explained in Fig. 2 legend.

assumed minimum population size of 40, only years at minimum remained correlated with h' ($r_s = -0.778$, $p = 0.025$). At an assumed year at minimum of 1870 (minimum size of 20), both variables remained significantly correlated with h' (years at minimum, $r_s = -0.741$, $p = 0.038$; minimum number, $r_s = 0.709$, $p = 0.054$). At an assumed year at minimum of 1910, both variables remained correlated with h' (years at minimum, $r_s = -0.802$, $p = 0.025$; minimum number, $r_s = 0.775$, $p = 0.025$).

Discussion

The effects of small population sizes on genetic diversity and the subsequent effects of reduced genetic diversity on fitness in wild populations have been poorly documented. Our empirical results provide support for theoretical work that suggests that persistent population bottlenecks will result in reduced genetic variation. Although we found reduced genetic variation to be correlated with both the time a population spends at minimum population size and the minimum population size, we detected no apparent relation between genetic diversity and population growth rates.

The lack of data on the history of remnant populations required us to make assumptions about the year when remnant populations reached their minimum number and about the number of individuals at that time. Years at minimum remained negatively correlated with genetic diversity in all four sensitivity scenarios, whereas minimum number remained positively correlated with diversity in three of the four scenarios. We acknowledge that site-specific histories of exploitation and recovery likely varied among remnant populations. Given our results, however, haplotype diversity is correlated with and may be used in a comparative sense as an indicator of population bottlenecks.

Our results support previous theoretical work regarding the relative effects of magnitude and duration of population bottlenecks on genetic diversity (Nei et al. 1975; Ralls et al. 1983; Lande & Barrowclough 1987; Leberg 1990; Leberg 1992). In two translocated sea otter populations with estimated founding sizes of 28 (BC) and 4 (WA), we observed high growth rates ($r = 0.232$ and 0.184, respectively), and high haplotype diversities (0.469 and 0.591, respectively). Moreover, population growth appeared to occur within a few years following translocation at all three sites. The two populations exhibiting the slowest growth rates (0.086, KOD and 0.099, PWS) are also the populations that experienced the longest time at minimum population size and the lowest genetic diversity ($h' = 0.138$ and 0.178, respectively). In contrast, AM and CA remained at minimum population sizes for brief periods (<10 years) and displayed high genetic diversity ($h' = 0.569$ and 0.467, respectively) but still demonstrated relatively slow growth rates (0.133 and 0.058). Because all remnant populations likely had small founding population sizes, but only KOD and PWS had long periods at minimum population sizes, our results indicate that reduced haplotype diversity is apparently related most to bottleneck duration.

Monitoring gene frequencies may help identify reproductive contributions from translocations of more than one source. Differences in observed haplotype frequencies can result from genetic drift, differential survival, or reproductive success among source populations. Expected haplotype frequencies were estimated based on

frequencies in source populations and the number of sea otters from different sources. Observed haplotype frequencies indicate that, in both multi-source translocations, both sources contributed to the success of the translocation. When founding size was small (BC), however, contributions were apparently disproportional, whereas when founding size was large (SE), contributions appeared proportional (Fig. 3).

Haplotype diversity provides an additional measure of the success of translocations. We observed a lower haplotype diversity in the single-source translocation and higher haplotype diversities in two-source translocations. Although source populations were geographically disjunct, genetically distinct (Scribner et al. 1997), and presumably reproductively isolated, we found no influence of outbreeding depression on translocation success or population growth rates. Although we did not detect a relation between haplotype diversity and fitness, as measured by population growth, significant differences in growth were detected between remnant and translocated populations.

Understanding factors affecting growth is important in conservation and management, particularly because growth rates affect population bottlenecks. The cause(s) of the differences in growth rates between remnant and translocated populations are unknown. The high growth rates observed in translocated populations likely reflect abundant prey availability. In the absence of sea otters, many nearshore invertebrate prey species respond through increased abundance and size (Ebert 1968; VanBlaricom & Estes 1988; Riedman & Estes 1990; Estes & Duggins 1995), providing conditions for optimum growth following translocation. This supports conclusions of others (Griffith et al. 1989; Leberg 1993; Wolf et al. 1996) who emphasized that appropriate habitat is an important determinant of population growth rates following bottlenecks.

The cause(s) of the lower growth rates we observed in remnant populations are unclear. Kenyon (1969) found most reported harvests after 1911 to be from the KOD to PWS region, and Lensink (1962) reports the illegal take of sea otter pelts from KOD and PWS in the 1920s and 1930s. Assuming small remnant population sizes, additional harvest mortality would result in reduced recovery rates. The low growth rate in CA, particularly after 1976 (Wendell et al. 1986; Estes et al. 1994), has been attributed to incidental mortality in net fisheries. It appears likely that continued human-related mortality contributed to the reduced growth rates observed in remnant populations, despite the legal protection extended to the sea otter in 1911, thereby extending both the magnitude and duration of bottlenecks.

Translocations are a management tool to aid in recovery and restoration of reduced or extirpated populations. Such efforts may be improved by concurrent monitoring of genetic markers and population growth characteristics. Our results indicate that haplotype diversity in translocated populations may be maintained or enhanced through several mechanisms, including (1) minimizing the magnitude and duration of population bottlenecks, (2) using large numbers of individuals from multiple sources, (3) reducing post-translocation mortality, and (4) selecting optimum habitat. Genetic data from source and translocated populations should allow further inferences about relations between genetic characterizations and population demographics.

Acknowledgments

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