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POPULATION GENETIC STUDIES OF THE SEA OTTER (*ENHYDRA LUTRIS*): A REVIEW AND INTERPRETATION OF AVAILABLE DATA

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ABSTRACT

Current information about the utility of genetic markers for estimating population structuring in sea otters (*Enhydra lutris*) is reviewed. Analyses of spatial population structuring with biochemical and molecular genetic markers are discussed in the context of the species' ecology and history of exploitation. Studies that used a diversity of genetic markers including allozymes, mitochondrial DNA (mtDNA), and multilocus minisatellites revealed that geographically separated populations of sea otters are highly differentiated, though little evidence for phylogeographic structuring was suggested. Analyses of population relationships based on mtDNA haplotype frequency distribution suggested that populations can be separated into four major groups: (1) California; (2) Prince William Sound, Alaska; (3) Kodiak Island, Alaska, and islands of the Aleutian archipelago, including the Commander Islands; and (4) the Kuril Islands. Populations from locales separated by large geo-

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graphic distances often shared haplotypes, suggesting recent common ancestry and some degree of *historical* gene flow. The large differences among populations in nuclear and mtDNA gene frequency suggested strong constraints on *contemporary* gene flow and/or considerable drift in gene frequencies due to population bottlenecks. No evidence for microgeographic structuring was noted. Levels of genetic diversity within populations varied greatly across the species range but were not related to contemporary estimates of population size.

Genetic markers have become an important source of empirical data for a diversity of applied and basic research issues. Increasing attention has been focused on ecological, demographic, and evolutionary factors that mold observed associations between genotypes and geographic distributions (Avise 1989). Spatial distributions and depths of genealogical topologies have provided strong evidence linking contemporary population structure to historical processes (Avise *et al.* 1987).

Sea otters (*Enhydra lutris*), though the subject of considerable ecological research and conservation efforts, have not been studied in great detail with genetic markers. The few studies which have been conducted to date have been instrumental in addressing a diversity of issues pertaining to species taxonomy, population biology, and the effects of human exploitation. The objectives of this review are to provide a synopsis of genetics data for sea otters and a general summary of the species' ecological characteristics and historical population fluctuations. Population genetics data must be interpreted within the context of natural history, historical exploitation, and recovery.

Background

The sea otter (*Enhydra lutris*) historically occurred across the Pacific Rim from Baja California, Mexico, to Hokkaido, Japan (Fig. 1; also see Kenyon 1969). Historical harvests by indigenous peoples of the North Pacific possibly resulted in local extinctions (Simenstad *et al.* 1978). During the nineteenth century sea otters were hunted to near extinction. Commercial harvests, which began in the middle of the 1800s, were halted by international treaty in 1911. At that time the species was probably reduced to less than 1% of an estimated preharvest abundance of several hundred thousand individuals (Riedman and Estes 1990).

Remnant populations of sea otters, each probably numbering less than a few hundred individuals, survived in California; southcentral Alaska; the Aleutian, Commander, and Kuril Islands; and the Kamchatka Peninsula. These few individuals provided the basis for recovery of the species. Presently, more than 100,000 sea otters occur throughout approximately 75% of their historical range (Bodkin *et al.* 1994). Immigration into vacant habitats has resulted in the reoccupation of the entire Aleutian and Kuril archipelagos, the Alaskan Peninsula, and southcentral Alaska.

In addition, otters have been translocated into unoccupied areas, further contributing to the species' recovery. Hundreds of otters from Amchitka Island

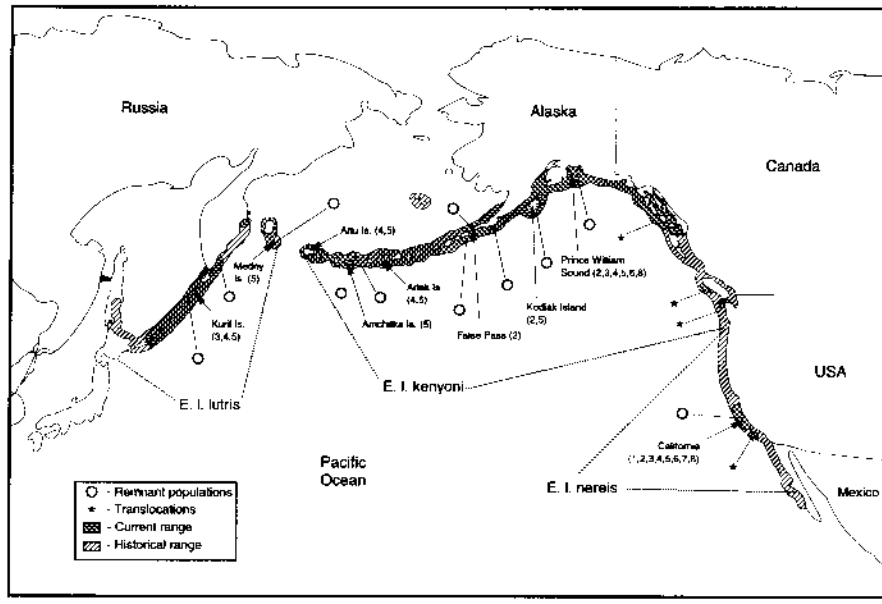

Figure 1. Historical and contemporary range distribution for the sea otter (*Enhydra lutris*). Numerals refer to studies in Table 1.

were moved to Oregon, Washington, British Columbia, and southeastern Alaska (Jameson *et al.* 1982). Sea otters from Prince William Sound, Alaska, were also released in southeastern Alaska. More recently, sea otters from coastal California were translocated to San Nicolas Island off the California coast (Riedman and Estes 1990). Two additional translocations, of sea otters from Amchitka Island into vacant habitats in Oregon and the Pribilof Islands, were unsuccessful.

Population bottlenecks and subsequent movements from remnant populations (either by natural dispersal or translocation) undoubtedly have contributed to present patterns of genetic variation within and among populations.

Available data suggest very low survival rates among translocated individuals; founding populations contain only several to a few dozen individuals (Estes 1989). Data collected following the translocations suggested that population growth rates may be quite low for a relatively long period before maximum growth rates ($R_{max} = 0.20$) are reached.

Sea otters inhabit shallow coastal areas and are most commonly observed in waters less than 30 m deep (Garshelis and Garshelis 1984, Riedman and Estes 1990). Offshore distribution is probably limited by diving physiology, because maximum dive depth is approximately 100 m (Newby 1975). Constraints posed by available foraging habitat restrict sea otters to a relatively narrow band of water extending offshore to a distance related to seafloor bathymetry. Gene flow among populations is thus limited to linear, shallow-water coastal habitats, or to relatively short distances of open water between suitable hab-

itats. Sea ice limits sea otter distribution in the north (Lensink 1962, Kenyon 1969); factors limiting southern range distribution are relatively unexplored but may be related to water temperature (Riedman and Estes 1990).

Available data suggest that sea otters are capable of rather long-distance movements (> 300 km; Ralls *et al.* 1991) and that movements of tens of kilometers are normal (Garshelis and Garshelis 1984). However, little data exist about the degree of philopatry exhibited by sea otters. Such data may be useful in predicting the rate of gene flow among populations and may provide additional criteria for establishing conservation plans or management units.

Sea otters are gregarious and tend to aggregate in areas that offer abundant benthic prey and resting sites (Lensink 1962, Kenyon 1969). Their high energy requirements (Lensink 1962, Kenyon 1969, Costa and Kooyman 1982), make long-distance travel for foraging unlikely. Resting and foraging behaviors have been observed to occur in close proximity (100–200 m; Lensink 1962). There is some evidence that protected areas are important for resting and foraging during inclement weather, particularly for females with dependent offspring (Lensink 1962).

Sea otters are polygynous. The species' breeding ecology may greatly influence the effective number of breeding adults, as well as group size and composition (Loughlin 1980, Garshelis and Garshelis 1984, Jameson 1989). Sea otters tend to segregate into separate male- and female-dominated areas. Females generally occupy specific areas throughout the year, along with dependent offspring and territorial males. Adult males establish territories in areas where females are found; they defend these territories from other males. Other males tend to aggregate in large groups, occasionally numbering several hundred individuals, in areas separate from female-dominated areas. Male aggregations consist of a high proportion of younger males and may be the result of territorial males forcing younger individuals into suboptimal areas or to the edge of the population range. Males may make regular large-scale movements (> 100 km) from breeding areas to male aggregation areas (Garshelis and Garshelis 1984, Jameson 1989). In many instances, territorial males return to the same territories year after year.

Several direct lines of evidence suggest some degree of population genetic structuring. First, considerable variation in morphology has been described across the species' range, resulting in the recognition of three subspecies (Wilson *et al.* 1991). Second, mass extirpation of populations to 11 remnant locations (Fig. 1) of small population size (*e.g.,* the Prince William Sound and California populations are believed to have been reduced to < 50 individuals) and the small estimated size of translocated populations suggest a high probability of genetic drift in allele frequency. Furthermore, aspects of the species' behavioral ecology and population dynamics increase the likelihood of bottleneck effects. On the basis of the polygynous mating system and estimated adult sex ratio, Ralls *et al.* (1983) estimated that effective population size was about one-fourth the actual population size. Third, otters generally do not disperse over great distances, and habitat is constrained to shallow coastal

regions. Finally, discontinuities in habitat may effectively preclude gene flow among certain areas (*e.g.*, among island groups of the Aleutian archipelago).

Population Genetic Structure

Few data have been published about using biochemical or molecular genetic techniques to address questions of spatial population structuring or levels of genetic variability for sea otters. The studies conducted to date (Table 1) encompass much of the historical range of the species (Fig. 1) and address questions related to subspecific status, spatial genetic variation, and intrapopulation levels of genetic variability.

The earliest studies (Lidicker and McCollum[2]) used allozyme electrophoresis to describe levels of heterozygosity in sea otters from California and Alaska. The authors found 5 of 30 loci (16.7%) to be variable. Multilocus heterozygosity was estimated to be 6.0%. No rare or private alleles were found, and all alleles were present in both Alaskan and California populations. Limited sample sizes for the Alaskan population precluded statistical comparisons of allele frequencies. The authors contend that the only bottleneck effect on the California population was the possible loss of rare alleles. From historical data on population numbers, recruitment, and demographic composition, Ralls *et al.* (1983) concluded that the California population in all likelihood retained 77% of prebottleneck levels of genetic variability.

In recent years several additional biochemical and molecular studies have been conducted. Analyses have been based on a variety of different techniques—allozymes (Rotterman 1992); mitochondrial DNA (Sanchez 1992, Cronin *et al.* 1996, Bodkin *et al.* 1992[3], Koepfil and Wayne[4]); VNTR microsatellites (Koepfil and Wayne[4]); multilocus minisatellites (Fain and Sanchez[5]). Results differ somewhat among studies, principally in the degree of genetic variation found (Table 1).

Rotterman (1992) conducted an electrophoretic survey of 208 sea otters from three Alaskan locales (Prince William Sound, Kodiak Island, and the Alaskan Penninsula) and the California population (Fig. 1). Forty-one allozyme loci were used in the analysis. Three loci (7.3%) were variable, and heterozygosities were low (mean $H = 0.021$). Only two loci revealed sufficient levels of variability to be used in spatial analyses. Genetic distances (Nei, 1978) among populations were low (0.001–0.006). Significant differences in allele frequency among the four populations were found for each variable locus (F_{st}

[2] Lidicker, W. Z., and F. C . McCollum. Genetic differentiation of sea otter populations. 4th Biennial Conference on the Biology of Marine Mammals, San Francisco, CA. 14–18 December 1981.

[3] Bodkin, J., B. Ballachey and M. A. Cronin. 1992. Mitochondrial DNA analysis in the conservation and managment of sea otters. U.S. Fish & Wildlife Research Bulletin 92–37.

[4] K. Koepfil and R. Wayne, Department of Biology, University of California, Los Angeles 90024, personal communication, September 1994.

[5] Fain, S. and M. Sanchez, U.S. Fish & Wildlife Service Forensics Laboratory, Ashland, OR 97520, personal communication, September 1994.

Table 1. Literature pertaining to genetic analyses of sea otters (*Enhydra lutris*).

Study[a]	Reference	*N*	Genetic marker	Technique	Objectives	Levels of genetic variation: Within pop.	Levels of genetic variation: Between pop.
1	Ralls *et al.* 1983	—	Theory	Simulation	Genetic variation	—	—
2	Rotterman 1992	208	Allozymes	SGE[b]	Spatial variation	Low	Low
3	Sanchez 1992	86	mtDNA	Southern blotting[c]	Spatial variation	Moderate	Moderate
4	Bodkin *et al.* (see text footnote 2)	97	mtDNA	PCR-RFLP[d]	Stock ID variation	Moderate	Moderate
5	Cronin *et al.* 1996	167	mtDNA	PCR-RFLP[d]	Spatial variation	Moderate	Moderate
6	Fain and Sanchez (see text footnote 4)	23	VNTR	Multilocus minisat.[e]	Social structure	Moderate	Moderate
7	Koepfil and Wayne (see text footnote 3)	unk	VNTR	Microsat.[f]	Stock ID	Low	Low
			mtDNA	Sequence	Systematics	Low	Low
8	Lidicker and McCollum (see text footnote 1)	unk	Allozymes	SGE[b]	Genetic variation	Moderate	—

[a] See Figure 1 for locations of studies.
[b] Starch-gel electrophoresis.
[c] DNA-DNA hybridization of total genomic DNA probed with sea otter mtDNA.
[d] Restriction fragment analysis of PCR-amplified regions of the mitochondrial genome.
[e] Jeffreys *et al.* (1985*a*, *b*) polycore minisatellite repeat.
[f] Dinucleotide, simple-sequence microsatellite loci.

values for Ada and Pgm-1 were 0.263 and 0.165, respectively; $P < 0.05$). No relationship between degree of interpopulation allele frequency difference and geographic proximity was observed. Interpopulation genetic relationships were not reflective of subspecific status. For each locus, the California population was more genetically similar to some Alaskan populations than Alaskan populations were to one another.

Results from studies with mtDNA were generally concordant. In many instances samples were shared across studies (*e.g.*, Cronin *et al.* 1996, Sanchez 1992, Bodkin *et al.* 1992[3], Koepfil and Wayne[4], Fain and Sanchez[5]). Each study found haplotypes characterized in California to represent a monophyletic group. Haplotype frequency distributions differed significantly among populations in each study. Although little phylogeographic structuring was suggested, analyses based on population haplotype frequencies generally supported the present subspecific classifications of Wilson *et al.* (1991).

Sanchez (1992) surveyed variation throughout the entire mitochondrial genome. Eighty-six otters from three populations (California; Prince William Sound, Alaska; and Kuril Islands; Fig. 1) representing each of the three recognized subspecies were surveyed by means of restriction fragment analysis. Eighteen restriction enzymes were employed in the analysis, and 94 restriction fragments were resolved. Eight closely related haplotyes were characterized (P range 0.077–0.595). Sanchez found that geographically separated populations of sea otters were highly differentiated in mtDNA haplotype frequency distribution, although haplotypes were not site-specific. There was no evidence of subpopulation structuring within Prince William Sound or California. Nucleotide and haplotype diversities varied greatly among populations but were not related to contemporary estimates of population size. From the limited sequence divergence among extant mtDNA lineages, the lack of phylogeographic structuring, and the co-occurrence of haplotypes in geographically disjunct populations, Sanchez concluded that recent common ancestry, high gene flow, and greatly reduced evolutionarily effective population sizes were suggested.

Cronin *et al.* (1996), in the most extensive molecular survey to date, surveyed 167 individuals from eight populations, including representatives from each of the three recognized subspecies (Fig. 1). Samples were obtained from live-captured animals (blood) and from carcasses (muscle tissues). The authors used restriction fragment analysis of PCR-amplified DNA from four regions of the mitochondrial genome (ND1, ND4, ND5/6, and 12S-16S ribosomal RNA; approximately 8.2 kb). Nine closely related haplotypes were documented (P range 0.04%–0.41%). Phylogenetic analyses revealed the haplotypes to be grouped into two major clades. There was little concordance between the phylogenetic relationship among haplotypes and their geographic distribution. Two haplotypes, however, were only found in California, lending further support for the monophyly of the California population.

Sea otter populations differed significantly in haplotype frequency. Analyses of population relationships based on haplotype frequency distributions suggested that sea otter populations can be separated into four major groups: (1)

California; (2) Prince William Sound, Alaska; (3) Kodiak Island, islands of the Aleutian chain, and Medny Island of the Commander Islands; and (4) the Kuril Islands. Each group had between one and three unique haplotypes. Haplotype diversities varied greatly (range 0.181–0.600), with the lowest diversity in Prince William Sound and the highest on Adak and Amchitka Islands in the Aleutian archipelago.

Bodkin *et al.* 1992[3] surveyed 97 animals from six populations (including samples from five of the populations surveyed by Cronin *et al.* 1996), using restriction fragment analysis of PCR-amplified mtDNA. However, these authors analyzed an additional population in southeastern Alaska which was derived from transplanted animals originating in Prince William Sound and the Aleutian Islands. Interestingly, this translocated population had the highest haplotype diversity and contained haplotypes found exclusively in ancestral source populations. Over all populations, nine closely related haplotypes were resolved. Two haplotypes were unique to California, and one haplotype was found only in the Kuril Islands.

In contrast to the moderate levels of variation resolved with mtDNA restriction fragment analyses, Koepfil and Wayne[4] found relatively little variation in a survey with sequence analysis. For sequence analysis of 350 bp of the mtDNA control region, Koepfil and Wayne used 98 sea otters from six populations representing each of the three recognized subspecies. They found five haplotypes that differed from one another by only one to three base pairs. Two haplotypes were unique to California, and one haplotype was predominantly found in sea otters from Prince William Sound, though this same haplotype was also the most common, being represented in all three populations surveyed from the Aleutian Islands and Medny Island. Sequence data could not be analyzed phylogeographically because of the low number of variable nucleotide sites, but some populations (*e.g.*, California and Medny Island) could be distinguished according to haplotype frequency. Analyses of VNTR microsatellite data are ongoing and may provide a valuable source of information about spatial variation in the species.

Fain and Sanchez[5] used four multilocus VNTR probes (Jeffreys probes 33.15 and 33.6 [Jeffreys *et al.* 1985*a*, *b*] and human minisatellite probes CMM101 and MS1) to address questions of macrogeographic population structuring, levels of genetic variability within locales, and interindividual relationships. Twenty-three individuals from the three populations surveyed by Sanchez (1992) were analyzed. Results are based on the average portion of fragments of homologous size which are shared among individuals within and between populations (*i.e.*, band-sharing coefficients; Lynch 1990).

Significant differences among populations were documented for all pairwise population comparisons (*e.g.*, $F' = 0.245$ to 0.488 for one multilocus marker, 33.15). Several fragments within the multilocus profiles were found to be fixed within each population but lacking in other populations. Average band sharing among individuals within each population was generally quite high ($S_x =$ 0.68–0.75 for 33.15). Average band sharing among individuals within the California population (0.74) was significantly higher than for interindividual

comparisons within the Prince William Sound population. Interestingly, the highest within-population band-sharing values were observed from the Kuril Islands (0.75), though the five individuals surveyed were obtained from four separate islands. Differences in band-sharing coefficients among the three populations could simply reflect low population sample sizes. Alternatively, the values could reflect higher gene correlations among individuals, either from inbreeding or common ancestry relative to low remnant effective population numbers.

Discussion

Population genetics data for sea otters must be interpreted in the context of natural history, history of exploitation, declines in numbers and distribution, and recent recolonization. Observations made in recent times may not reflect characteristics of pre-exploited populations. Current population number, distribution, movements, and behavioral and reproductive ecology are related in part to recent population expansion and recolonization. Most populations are not in equilibrium, either demographically or genetically.

Massive extirpations over the species range were followed by a period of rapid population growth and recolonization. Under these conditions, one prediction would be that at a macrogeographic level, large differences in population gene frequency would exist due to population fragmentation and genetic drift resulting from low remnant population numbers. Little spatial variation would be expected over short geographic distances, because individuals would presumably be derived from the same small founding population.

Each genetic marker employed revealed that on a macrogeographic level (across subspecies and large geographic distances) sea otter populations are highly divergent. Analyses based on low inter- *vs.* intrapopulation band-sharing coefficients and disparities in allozyme and mtDNA haplotype frequency distributions show that populations are highly differentiated genetically. The three mtDNA studies (Sanchez 1992, Cronin *et al.* 1996, Koepfil and Wayne[3]) support the monophyly of the California population. The large differences among populations in nuclear and mitochondrial gene frequency suggest strong constraints to gene flow and/or considerable drift in gene frequencies due to population bottlenecks. Limited sequence divergence among all extant mtDNA haplotypes, and the lack of phylogeographic concordance strongly suggest that populations are evolutionarily recently derived from a common ancestral source and are characterized by low evolutionary effective population size. Not all populations have reached a state of reciprocal monophyly. Populations from locales separated by large geographic distances often share the same haplotypes, suggesting recent common ancestry and some degree of historical gene flow.

The utility of any genetic marker for detecting population structuring or population differences depends on the levels of variation observed (Nei 1987, Leberg 1992). Comparisons of results across the studies described above highlight several important differences among the markers. Most of the studies

cited surveyed many locations. But results of the allozyme analysis (Rotterman 1992), in terms of subspecific and interpopulation relationships, generally are not supported by the other molecular studies.

Low levels of variation at the allozyme loci surveyed detract from their utility as a tool for macro- or microgeographic analyses of spatial population structuring. Results from the mtDNA studies (Sanchez 1992, Bodkin *et al.* 1992[3], Cronin *et al.* 1996), and analyses of other nuclear genetic markers (multilocus DNA fingerprints; Fain and Sanchez[5]) also revealed comparatively low levels of intrapopulation variation, consistent with past declines in population numbers and distribution. Genetic variability may have been lost as the result of population bottlenecks caused either by rapid and prolonged reduction in effective population size, or by reintroductions of few founding individuals. Many of the referenced studies either directly or indirectly have addressed questions of genetic diversity (Table 1).

Research Needs

Estimates of the degree of genetic differentiation among populations and of genetic variation within populations have been used for inferences about the ecology and evolutionary history of natural populations (*e.g.*, Nevo *et al.* 1984). Genetic analyses have provided a genetic basis for systematic classification of sea otters (*e.g.*, monophyletic relationships of California relative to other Pacific Rim populations) and for spatial structuring at the macrogeographic level (Cronin *et al.* 1996). Further genetics research could address a number of applied and basic issues pertaining to the species' behavioral ecology, colonization (both natural and *via* translocations), and microgeographic population structuring. Population genetic data could be used to address the following issues:

(1) The exploitation of sea otter populations is not regulated at present, and Alaska is considered to be one management unit. Harvest is not currently proportional to estimates of local abundance. Sampling conducted on a microgeographic scale may provide an effective means of discriminating among local populations. Systematic sampling along the linear habitats of occupied coastal areas may aid in estimating the levels of, and barriers to, gene flow.

(2) The effects of historical bottlenecks (in terms of extensive, indiscriminate harvest during the last century, and success of translocations) have not been addressed. Highly polymorphic genetic markers (*e.g.*, VNTR minisatellite and microsatellite loci) may prove extremely important for investigating the effects of population bottlenecks and the success of translocation efforts.

(3) Highly polymorphic genetic markers may be extremely useful for investigating sea otter social structure.

(4) Contemporary estimates of population levels of genetic variability and interpopulation genetic structuring are presumed to be largely a function of historical exploitation and subsequent recovery. Analyses of samples from historical populations (*e.g.*, museum specimens) may provide valuable information on "natural" population genetic characteristics and the species' ecology.

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