

STOCK STRUCTURE OF SEA OTTERS (*ENHYDRA LUTRIS KENYONI*) IN ALASKA

C. S. GORBICS

U.S. Fish and Wildlife Service,
2730 Loker Avenue West, Carlsbad, California 92008, U.S.A.
E-mail: carol.gorbics@fws.gov

J. L. BODKIN

Alaska Biological Science Center,
U.S. Geological Survey
1011 East Tudor Road, Anchorage, Alaska 99503, U.S.A.

ABSTRACT

Sea otters in Alaska are recognized as a single subspecies (*Enhydra lutris kenyoni*) and currently managed as a single, interbreeding population. However, geographic and behavioral mechanisms undoubtedly constrain sea otter movements on much smaller scales. This paper applies the phylogeographic method (Dizon *et al.* 1992) and considers distribution, population response, phenotype and genotype data to identify stocks of sea otters within Alaska. The evidence for separate stock identity is genotypic (all stocks), phenotypic (Southcentral and Southwest stocks), and geographic distribution (Southeast stock), whereas population response data are equivocal (all stocks). Differences in genotype frequencies and the presence of unique genotypes among areas indicate restricted gene flow. Genetic exchange may be limited by little or no movement across proposed stock boundaries and discontinuities in distribution at proposed stock boundaries. Skull size differences (phenotypic) between Southwest and Southcentral Alaska populations further support stock separation. Population response information was equivocal in either supporting or refuting stock identity. On the basis of this review, we suggest the following: (1) a Southeast stock extending from Dixon Entrance to Cape Yakataga; (2) a Southcentral stock extending from Cape Yakataga to Cape Douglas including Prince William Sound and Kenai peninsula coast; and (3) a Southwest stock including Alaska Peninsula coast, the Aleutians to Attu Island, Barren, Kodiak, Pribilof Islands, and Bristol Bay.

Key words: distribution, genetics, management unit, phenotype, phylogeographic, population response, stock, sea otter, *Enhydra lutris*, Alaska.

Sea otters (*Enhydra lutris*) once inhabited coastal waters of Alaska in most ice-free areas, from southeast Alaska northward through Prince William Sound, Kenai peninsula, Alaska peninsula, Kodiak Archipelago, Aleutian Islands, Bristol Bay, and the Pribilof Islands (Kenyon 1969). Wide expanses of

deep ocean between islands of the north Pacific and the Asian and North American mainlands, as well as periods of glacial advance and retreat likely restricted movements of sea otter historically (Kenyon 1969, Pielou 1991). Further limits to movements are likely imposed by social and behavioral attributes that result in relatively small home ranges (Riedman and Estes 1990). Contemporary Alaska sea otter distribution is discontinuous with areas of unoccupied habitat. These discontinuities reflect both natural barriers such as wide and deep ocean passages and remnant effects of 18th and 19th century fur harvest reductions.

Sea otters in Alaska have generally been managed as a single population of the subspecies (*E. l. kenyoni*). Observed lack of population expansion into certain areas and genetic differences suggest that groups of otters within Alaska are likely not presently panmictic and may be functioning to some degree as independent populations or "stocks."

The Marine Mammal Protection Act (16 U.S.C. 1361) defines "population stock" or "stock" as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature." A stock has been further defined as a demographically significant unit that is relatively isolated and separated from other stocks such that there is little or no intermixing or that the overall population is not panmictic (Perrin and Brownell 1994). Both of these definitions may be applicable to sea otter populations in Alaska, based on spatial isolation and potentially limited (or no) genetic exchange among "stocks."

The concept of biologically meaningful units below the species level is widely accepted by resource professionals and include terms such as subspecies (recognized by the International Code of Zoological Nomenclature), populations, evolutionarily significant units (ESU) (used as a designation under the Endangered Species Act), management units, and stocks (Ryder 1986; Moritz 1994a, b; Perrin and Brownell 1994; Cronin 1996; Britten *et al.* 1997). Most definitions of groupings below the species level include some level of reproductive isolation, as well as genetic distinction. Management units have been defined as populations with divergent allele frequencies, independent of phylogenetic distinction (Moritz 1994a, Cronin 1996). We have adopted the recommendation of Moritz (1994a) and use the term "stock" as synonymous with management unit, as defined by genetic data. In addition to genetic data, other types of information (*e.g.*, morphology, distribution, behavior, and physiology) can be useful in defining population stocks (Cronin 1993).

Dizon *et al.* (1992) suggest four categories of information that may be used to study stock structure: (1) geographic distribution, (2) population response, (3) phenotype, and (4) genotype. A large body of data exists in each of these four categories that can be used to define sea otter stocks in Alaska. We use the phylogeographic method suggested by Dizon *et al.* (1992) and applied by Loughlin (1997) to Steller sea lions (*Eumetopias jubatus*) to evaluate stock identity of sea otters within Alaska. The purpose of this paper is to examine evidence of potential biologically meaningful boundaries for contemporary sea

otter stocks in Alaska, and to discuss the relevance of stock identity to sea otter management and conservation in Alaska.

METHODS

We used a hierarchical classification scheme to define four categories of stocks (following Dizon *et al.* 1992). Category I stocks are separated from others not only by genetic distances, but also by geographic distances. The stocks are effectively reproductively isolated from each other. Category II stocks also exhibit genetic differences, but have weaker geographic separation. There may be some or significant geographic overlap, but critical differences in genetics, behavior, morphology, or a combination indicate reproductive isolation to some degree. Category III stocks are characterized by little genetic differentiation, but still show a high degree of reproductive isolation through geographic separation either through true allopatry or strict parapatry. Category IV stocks have extensive gene interchange and no subdivision by geographic barriers. Populations in this category appear panmictic.

In the classification scheme four decision criteria are evaluated to imply reproductive isolation and stock identity and to assign categories: geographic distribution, population response, phenotype, and genotype. These criteria serve as "proxies" or indirect measures of reproductive isolation (or lack) since we are unable to directly measure reproductive isolation. Geographic distributional data (designated "a" in the classification scheme) include information pertaining to all aspects of abundance, migration, pollutant and parasite loads, and other data that provide information about the population movements relative to geographical space and time. These data largely define whether there are geographical barriers within the population distribution and whether they are physically isolated or not. Population response data (designated "b") include information on all aspects of demography (age at sexual maturity, fecundity, growth rate, and mortality). Phenotypic data (designated "c") include primarily morphological differentiation. Morphological differences between two or more stocks strongly suggest limited gene flow among these populations. These differences may also represent underlying genetic differences. The genotypic category (designated "d") includes unique genotypes, significant gene frequency differences, or genetic distances which indicate that gene flow among two populations is restricted, implying reproductive isolation. Genetic differences are considered to be the most unequivocal for differentiating intraspecific structure (Dizon *et al.* 1992, Dizon and Perrin 1997, Woodley 1997).

The four decision criteria are evaluated to determine if each provides evidence of lumping or splitting putative stocks. The population would then be designated by phylogeographic category and decision criteria, for example, I bc/abcd. Letters that appear on both sides of the solidus (bc) indicate where information is equivocal; letters on the right side of the solidus only (ad) indicate where information supports splitting into multiple stocks. Letters on the left side of the solidus only would indicate where information does not



Figure 1. Current and historic distribution of sea otters in Alaska. The width of the coastal band is illustrative and does not correspond to available habitat. Areas shown as vacant have very low densities or rare occurrences of sea otters based on most recent survey information. Locations of remnant populations: (1) Rar Islands, (2) DeLarof Island, (3) Bristol Bay, (4) Sandman Reefs, (5) Shumagin Islands, (6) Kodiak Islands, (7) Prince William Sound (see footnote 2).

support splitting into multiple stocks. Missing letter abbreviations would signify lack of data.

This classification scheme does not include consideration of socioeconomic and political factors. Additionally, Dizon *et al.* (1992) note that arguments for classification must be made with the knowledge that information is constantly being updated and that intraspecific populations themselves are dynamic and, therefore, classifications are subject to change over time. This is particularly relevant in Alaska as some populations are growing rapidly (*e.g.*, southeast Alaska; Bodkin *et al.* 1999) while another is undergoing rapid decline (*e.g.*, southwest Alaska; Estes *et al.* 1998).

RESULTS

Distributional Data

Present distribution—Extirpation of sea otters throughout Alaska resulted in seven small remnant populations in southcentral and southwestern Alaska that provided the nuclei for recolonization. Translocations in the late 1960s resulted in the establishment of a population within southeast Alaska, including Yakutat (Bodkin *et al.* 1999). Although range expansion has occurred throughout much of Alaska, there are still areas of suitable habitat which remain unoccupied, primarily in the southeast region (Fig. 1).

Surveys conducted throughout Alaska during the past several decades provide a reasonably complete and current image of sea otter distribution in Alaska (Kenyon 1969, Riedman and Estes 1990, Burn 1994).^{1,2} Sea otters are

¹ DeGange, A. R., D. C. Douglas, D. H. Monson and C. M. Robbins. 1994. Surveys of sea otters in the Gulf of Alaska in response to the Exxon Valdez oil spill. Exxon Valdez oil spill damage assessment project final report (Marine Mammal Study 6). Available from Alaska Resources Library and Information Services, 3150 C Street, Suite 100, Anchorage, AK 99503.

² Gorbics, C. S., J. L. Garlich-Miller and S. L. Schliebe. 1998. Alaska marine mammal stock assessments 1998. Sea otters, polar bear and walrus. Unpublished draft report. Available from U.S. Fish and Wildlife Service, Marine Mammals Management, 1011 East Tudor Road, Anchorage, AK 99503.

nearly continuous in their distribution along shorelines from Attu island in the western Aleutians to the Alaska Peninsula, including Kodiak Island, although in many areas sea otters are rare. Distances up to 230 km separate suitable sea otter habitat among several of the island groups of the Aleutians, certainly limiting exchange of individuals. A break in distribution occurs within Cook Inlet between the Alaska Peninsula and the Kenai Peninsula where densities are currently low. From Cook Inlet, sea otters are continuously distributed from Kachemak Bay, along the southern Kenai Peninsula to Prince William Sound and south to Cape Suckling. Sea otters are rare between Cape Suckling and Yakutat. Sea otters occur within Yakutat Bay and in southeast Alaska where they are currently found primarily along the outer coast.

Physical features of the habitat of the sea otter contribute to isolation of populations from each other. The sea otter uses a relatively narrow band of coastal habitat generally bounded by the shoreline and waters to 100 m in depth (Kenyon 1969). The physical feature separating sea otters between Yakutat and Prince William Sound is approximately 125 km of vacant coastal habitat observed during a 1995 survey.³ The physical feature constraining movement of sea otters between the Kenai Peninsula and the Alaska Peninsula is approximately 100 km of open water across Cook Inlet with maximum water depth approximately 100 m. The physical feature separating sea otters between the Kenai Peninsula and the Kodiak Archipelago is approximately 70 km of open water with maximum water depth approximately 200 m (with the Barren Islands half-way between). Sea otters were absent in the waters of southeast Alaska from the beginning of the 20th century to the late 1960s. Although no sea otters migrated into this area from either the north or the south, a translocation of over 400 animals in the late 1960s resulted in the establishment of the population that resides there today.

Movements—Sea otters exhibit complex movement patterns related to habitat characteristics, social organization, and reproductive biology. It is likely that movements differ among populations depending on whether a population is at or near carrying capacity or has access to unoccupied suitable habitat into which it can expand (Riedman and Estes 1990). Most research into sea otter movements has been conducted where unoccupied habitat is available to dispersing animals. For example, dominant adult males in California generally occupy and defend relatively small territories which vary seasonally between summer-fall (4.03 km²; 1.1 km of coastline) and winter-spring (7.8 km²; 2.16 km of coastline) occasionally moving relatively long distances to male aggregations (average = 80.1 km; maximum = 150 km) (Jameson 1989). Females generally occupy home ranges larger than male territories, but do not exhibit similar routine long distance movements (maximum <20 km), and

³ Doroff A. M., and C. S. Gorbics. 1998. Sea otter surveys of Yakutat Bay and adjacent Gulf of Alaska coastal areas—Cape Hinchinbrook to Cape Spencer 1995–1996. Final report on Contract No. OCS Study MMS 97–0026 to Minerals Management Service, Anchorage, Alaska. 49 pp. Available from U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK.

thus have lifetime home ranges considerably smaller than adult males.⁴ Early research in the Aleutian Islands by Lensink (1962) and Kenyon (1969) also found that males have larger home ranges than females and described the female sea otter's home range as including 8–16 km of contiguous coastline. Adult male home ranges in Prince William Sound are from 4.6 to 11.0 km² and adult female home ranges are from 1.0 to 4.8 km² (Garshelis and Garshelis 1984). In Prince William Sound a telemetry study documented movements of adult males up to 100 km between male areas and breeding areas (Garshelis and Garshelis 1984). Additional telemetry studies on juveniles in Prince William Sound,⁵ adults (males and females) along the Alaska Peninsula⁶ and adults (males and females) in the Kodiak Archipelago⁷ documented movements typically of 50 km or less. Comparable data are not available from other areas in Alaska.

Although seasonal and lifetime home ranges suggest limited movements, sea otters can move much greater distances when translocated. In California such translocated animals returned 318 km from release sites back to capture sites (Ralls *et al.* 1992). In Alaska a female treated and then released after the *Exxon Valdez* oil spill traveled 400 km from her release site (Monnett *et al.* 1990).

Although sea otters are somewhat constrained by the 100-m depth profile, they can navigate some distance over deep water. Sea otters have traveled distances of up to 50 km over water deeper than their maximum foraging depth, traveling from San Nicolas Island to the mainland along southern California. However, this was after translocation.⁷ Similar travel, but unrelated to translocation, was documented by Bodkin *et al.* (2000) from Medny to Bering Island in the Commander Islands of Russia. Thus, 50 km may approximate the distance over open, deep water that constrains interisland movement.

Contaminants—Contaminant levels in sea otters are variable, likely reflecting point sources over small geographical scales. High levels of PCB and DDT have been found near military installations in the Aleutians (Bacon 1994, Jarman *et al.* 1996, Giger and Trust 1997), but were low or undetectable in Prince William Sound⁸ and southeast Alaska (Estes *et al.* 1997). Comprehensive studies to address large geographic variation in contaminant levels are not available.

⁴ Ralls, K., T. Eagle and D. B. Siniff. 1988. Movement patterns and spacial use of California sea otters. Pages 33–63 in D. B. Siniff and K. Ralls, eds. Final Report on Contract No. 14-12-001-3003, Population status of California sea otters. Minerals Management Service, Los Angeles, CA.

⁵ J. L. Bodkin, unpublished data.

⁶ Monnett, C., L. M. Rotterman, D. B. Siniff and J. Sarvis. 1988. Movement patterns of western Alaska peninsula sea otters. Final report to Minerals Management Service (OCSEAP research unit 688), Anchorage, AK. 51 pp.

⁷ Rathbun, G. B., J. A. Estes and R. L. Brownell, Jr. 1989. Reintroduction of sea otters to San Nicolas Island, California. Page 51 in Proceedings of the Eighth Biennial Conference on the Biology of Marine Mammals. (Abstract).

⁸ C. S. Gorbics, unpublished data.

Population Response Data

Population growth rates—Population growth rates vary among locations studied in Alaska. For example, estimated growth rates are 22% for southeast Alaska, 10% for Prince William Sound, 8% for Kodiak, and 13% for Amchitka (Estes 1990; Bodkin *et al.* 1999, 2000).⁵ Generally, translocated populations have demonstrated growth rates approaching 20%, while remnant populations vary from 8% to 13% (Bodkin *et al.* 1999). It is likely that variation in growth rates among populations reflects population status relative to differences in habitat suitability and potentially available resources, rather than intrinsic differences among geographically separate populations.

Reproductive characteristics—Age at first reproduction, reproduction rate for mature females, and reproductive synchrony vary among regions and among studies within regions (Table 1). Reproductive characteristics may vary with population status in some species (Riedman and Estes 1990), although Jameison and Johnson (1993) concluded that no evidence presently exists to suggest such a relationship in sea otter populations.

Survival rates—Annual survival rates among adult male and female sea otters are generally high, based on evidence from California, Prince William Sound, the Aleutian Islands, and Kodiak populations (Table 1).⁶ Females have higher survival rates when compared to males in all geographic areas considered. Annual survival rates of juveniles may be more sensitive to environmental conditions than adult survival rates (Eberhardt and Siniff 1977, Hanks 1981). Postweaning survival rates have been evaluated within the California, Prince William Sound and Aleutian Island populations (Table 1). Variation in juvenile survival rates are likely related to population status (and resource availability) or interannual variation, rather than geography (Bodkin and Ballachey 1996).

Phenotypic Data

Skull size—Wilson *et al.* (1991) examined 20 skull characteristics of 304 adult sea otters from throughout the species range to revise the taxonomy of the species. While sample sizes were too small to identify population structuring within Alaska, significant differences were observed among California, Alaska, and Russia populations. We recently examined 10 skull characteristics from 26 sea otters from southwest Alaska (Amchitka Island) and 42 from southcentral Alaska (Prince William Sound) (Table 2). Exact ages of specimens measured were not known but included only adults. Mean male trait sizes were significantly larger than females for all traits. Four of 10 male trait sizes from Amchitka otters were significantly greater than those from Prince William Sound. Seven of 10 female trait sizes from Amchitka otters were significantly greater than those from Prince William Sound. In none of the 20

⁵ Eberhardt, L. L., and D. B. Siniff. 1988. Population model for Alaska Peninsula sea otters. Report on Contract No. 14-12-001-30033 to Minerals Management Service, Anchorage, Alaska. ix + 94 pp.

Table 1. Reproductive and survival characteristics of sea otters by geographic location.

Region/ study location	Age at first repro- duction	Reproduction rate for sexually mature females	Reproductive synchrony	Adult survival rate		Post-weaning juvenile survival rate	
				Female	Male	Female	Male
Southcentral/ Prince William Sound	2 ^a	84% ^a	April ^b	93% ^a	79% ^b	21% ^c	8% ^c
Southwest/ Aleutian Islands	4 ^b	56%–71% ^d	May ^b	96% ^f	not available	89% ^{e,g,h}	51% ^{e,g,h}
Southwest/Kodiak	3 ^{c,d}	88% ^{e,f}	May–June ^a	92% or 94% ^m	not available	18% ⁱ	sexes combined ^b
California	2	83% ^b	May ^b	89%–96% ^a	86%–91% ^a	sexes combined ^b	not available
	3 ^f	94% ^e	none ^g	89%–91% ⁱ	52%–61% ⁱ	58% ^j	sexes combined
		93% ^f	January–March and late summer to early fall ⁱ	93% ^m	72% ^m		
		90% or 94% ^l	none ^l				
		90%–107% ^l					

^a Bodkin *et al.* 1993
^b Garshelis *et al.* 1984
^c Kenyon 1969
^d see footnote 11 on page 641
^e Monson and DeGange 1995
^f Jameson and Johnson 1993
^g Monnett *et al.* 1991
^h Monson 1995
ⁱ Siniff and Ralls 1991
^j Riedman *et al.* 1994
^k see footnote 12 on page 641
^l see footnote 13 on page 641
^m see footnote 7
ⁿ Monnett 1988
^o see footnote 10 on page 641
^p see footnote 4

Table 2. Skull size comparison for adult male and female sea otters from southwest Alaska (Amchitka, $n = 26$) and southcentral Alaska (Prince William Sound (PWS), $n = 42$). Differences between sexes and regions evaluated using two-way ANOVA (GLM, SAS Institute, Cary, NC) with Bonferroni adjustment for alpha ($\alpha = 0.05/10$ (number of tests)). Significant differences where $P < 0.005$ indicated in bold, $P < 0.008$ in italics. Sizes measured to the nearest 0.1 mm.

Skull trait	Males		Females	
	Southwest/ Amchitka mean (CV)	Southcentral/ PWS mean (CV)	Southwest/ Amchitka mean (CV)	Southcentral/ PWS mean (CV)
mandible length	90.9 (3.4)	88.1 (3.0)	87.8 (2.7)	83.3 (3.2)
mandibular condyle length	28.5 (4.9)	27.5 (6.0)	27.5 (4.3)	25.0 (6.9)
condylabasal length	<i>134.7 (2.6)</i>	<i>131.1 (2.7)</i>	130.0 (2.3)	124.5 (2.8)
premaxilla-auditory bulla foramen	101.5 (2.9)	96.7 (3.4)	97.8 (2.4)	91.9 (3.1)
premaxilla-parietal crest	130.5 (3.4)	125.8 (2.0)	127.1 (2.6)	120.2 (2.1)
occipital condyle-opposing paroccipital process	75.4 (4.1)	76.6 (2.9)	72.8 (3.1)	71.5 (3.5)
posterior lacerate foramen-opposing paroccipital process	64.7 (4.3)	65.7 (3.4)	62.5 (2.4)	61.7 (3.4)
pterygoid process foramen-opposing zygomatic/jugal suture	70.8 (4.0)	71.3 (3.5)	68.7 (3.1)	66.1 (3.8)
ventral orbit length	39.1 (2.9)	36.6 (4.0)	36.3 (6.4)	34.5 (4.0)
dorsal orbit length	55.4 (2.7)	53.9 (3.6)	52.6 (4)	51.8 (3.0)

comparisons were Prince William Sound mean trait sizes significantly greater than measures from Amchitka otters. Levels of variation in trait sizes were similar between Amchitka and Prince William Sound. These results demonstrate significant differences in sea otter skull size between southwest Alaska and southcentral Alaska, although the cause of the differences is unknown.

Body size—Average lengths and masses of sea otters vary between California and Alaska with the Alaska average somewhat larger (Roest 1973). However, size of Alaska sea otters varies with geographic location and some Alaska sea otters weigh less than California sea otters (Riedman and Estes 1990). Although phenotypic differences such as body size may suggest limited gene flow or represent underlying genetic differences, these differences may instead be related to variation in the status of populations. Sea otters in expanding populations with lower densities may be larger or in better condition (based on mass-length ratio) than those in equilibrium populations with higher densities (Kenyon 1969, Monson *et al.* 2000).

Genotypic Data

A number of studies have used genetic data to analyze spatial population structuring in some part of the sea otter's range. Genetic techniques used included allozymes (Rotterman 1992), mitochondrial DNA (mtDNA) (Sanchez 1992, Bodkin *et al.* 1992, Cronin *et al.* 1996, Bodkin *et al.* 1999), and multilocus minisatellites (Scribner *et al.* 1997). All of these studies looked at differences among the three subspecies of sea otters (southern sea otter, *Enhydra lutris nereis*; Alaska sea otter, *Enhydra lutris kenyoni*; and *Enhydra lutris lutris*).

Assessment of genetic distinctions within the Alaska subspecies have had varying results. One study did not find sufficient allozyme variation¹⁰ to conclude that the Alaska sea otters could be subdivided into stocks. However, Scribner *et al.* (1997) argue that the technique used in this study¹⁰ considered allozyme loci with low levels of variation which detracts from its utility as a tool for analysis of stock identification. The use of this technique for stock identity of marine mammals is uncommon.

Other studies using mtDNA analysis identified ten different mtDNA ge-

¹⁰ Rotterman, L. M., and C. M. Monnett. 1991. Mortality of sea otter weanlings in eastern and western Prince William Sound, Alaska, during the winter of 1990–1991. *Exxon Valdez* oil spill damage assessment project final report (Marine Mammal Study 6-18). Available from Alaska Resources Library and Information Services, 3150 C Street, Suite 100, Anchorage, AK 99503.

¹¹ Schneider, K. B. 1973. Reproduction in the female sea otter. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-17-4, Progress Report. 36 pp.

¹² Udevitz, M. S., B. E. Ballachey and D. L. Braden. 1996. A population model for sea otters in western Prince William Sound. *Exxon Valdez* oil spill restoration project final report (project 93043-5). Available from Alaska Resources Library and Information Services, 3150 C Street, Suite 100, Anchorage, AK 99503. 34 pp.

¹³ Monnett, C., and L. M. Rotterman. 1992. Mortality and reproduction of female sea otters in Prince William Sound, Alaska. *Exxon Valdez* oil spill damage assessment project final report (Marine Mammal Study 6-13). Available from Alaska Resources Library and Information Services, 3150 C Street, Suite 100, Anchorage, AK 99503.

notypes in sea otters throughout their range; six of these were found in Alaska sea otters (Table 3) (Sanchez 1992, Bodkin *et al.* 1992, Cronin *et al.* 1996, Bodkin *et al.* 1999). The frequency distribution of these genotypes differed among the five geographic areas considered (Russia, southwest Alaska, southcentral Alaska, southeast Alaska, and California) (Table 3). Bodkin *et al.* (1992) and Cronin *et al.* (1996) concluded that sea otters within three areas we are considering—southeast Alaska, Prince William Sound (southcentral Alaska), and Kodiak-Aleutians Islands (southwest Alaska)—were separate stocks. We determined that mtDNA haplotype frequency distributions varied significantly among these three areas (log likelihood ratio test, $P = 0.001$). Additionally, haplotype frequencies in southeast Alaska (a translocated population) differed significantly from parent population haplotype frequencies (Bodkin *et al.* 1999).

Genetic differences identified in Bodkin *et al.* (1992, 1999) and Cronin *et al.* (1996) could reflect a recent restriction in gene flow (or a more recent divergence of genotype variability) among geographic areas due to the local extirpation of sea otters by hunters in the 18th and 19th centuries, or reflect genetic drift, resulting from small population sizes. Alternatively, historical divergence due to changes in distribution and local extirpation caused by glaciation and other habitat changes over longer time periods could result in observed differences. Cronin *et al.* (1996) concluded that frequencies of genetic haplotypes are distinct enough between Prince William Sound and the Kodiak-Aleutian Islands to suggest that these groups were somewhat differentiated even before the effects of the 18th and 19th century harvests.

CLASSIFICATION AND CONCLUSIONS

Synthesis of available data suggests that sea otters in Alaska can be classified into at least three distinct stocks, two of which fall into a category II ab/abcd status (southcentral and southwest) and one which falls into a category I bc/abcd (southeast) based on the Dixon *et al.* (1992) classification. The stocks identified are (1) the southeast Alaska stock extending from Dixon Entrance northward to Cape Yakataga; (2) the southcentral Alaska stock extending from Cape Yakataga westward to Cape Douglas including Prince William Sound and the Kenai peninsula coast; and (3) the southwest Alaska stock including the Alaska Peninsula coast, southward and westward along the Aleutians to Attu Island including Barren Islands, Kodiak Archipelago, Pribilof Islands, and Bristol Bay (Fig. 1). Significant genetic and phenotypic differences evident within the population of sea otters in Alaska provide evidence for these classifications. For the southcentral and southwest stocks, we conclude that the available information on distribution and movement ("a"), and population responses ("b"), are equivocal and support neither lumping or splitting, whereas the information on phenotypic differences ("c"), and genotypic differences ("d") support splitting. For the southeast stock, the available information on population responses ("b") and phenotypic differences ("c") are equivocal and

Table 3. mtDNA genotype distribution and frequency among Alaska stocks and throughout sea otter range (Cronin *et al.* 1996, Bodkin *et al.* 1999) ($P < 0.001$).

Stock	Genotypes											<i>n</i>
	F	E	H	B	A	G	I	J	D	C		
Alaska—Southwest Stock	0.01	0.07	0.29	0.63								75
Alaska—Southcentral Stock		0.10	0.40	0.10	0.90							31
Alaska—Southeast Stock			0.54	0.20	0.25	0.05						20
Russia				0.10			0.34	0.02				41
California									0.35	0.65		20

support neither lumping or splitting, whereas the information on distribution and movement ("a") and genotypic differences ("d") supports splitting.

By far, the strongest evidence for separate stock identity is the mtDNA studies of Bodkin *et al.* (1992, 1999) and Cronin *et al.* (1996). The current constrictions in sea otter distribution at the proposed stock boundaries between the southeast and southcentral stocks further support the concept of limited gene flow between stocks. The location of the boundary between the southcentral and southwest stocks between the southern Kenai Peninsula and Kodiak Archipelago (Fig. 1) is estimated. Additional genetic analysis may provide further resolution regarding the location.

The population structure of sea otters in Alaska has changed radically from their historic and likely continuous distribution of previous centuries, to near extirpation at the turn of the past century due to human exploitation, to the current expanded abundance and distribution due to world-wide protection from widespread hunting. Evaluation of genetic variability provides strong evidence that at least the southcentral and southwest stocks were differentiated even before population fragmentation resulting from exploitation by humans, suggesting long-term phylogenetic structuring. The historic southeast population was eliminated through overharvest, and the present southeast stock originated from translocations from the southwest and southcentral stocks. Therefore, we are unable to suggest how this stock may have been historically related to the other stocks. We acknowledge that there is likely some limited dispersion, particularly at the boundary between the southcentral and southwest stocks based on occasional observations of animals traversing this area, however, the genetic differences indicate that dispersal is limited to such an extent that interbreeding is currently, and was historically, rare.

Several factors we considered—growth rates, various reproductive characteristics, and survival rates—may vary among stocks not because of lack of genetic exchange, but because of varying population status among geographic areas. We believe these factors reflect how a population is responding to short-term changes in the environment such as resource availability and population density. For example, the high population growth rates observed in the southeast stock likely reflect an abundance of both food and space resources, as opposed to genetic differences (Bodkin *et al.* 1999). For this reason, we considered these factors equivocal in evaluating stock differences. Alternatively, the differences in sizes of sea otters between southwest and southcentral are not readily explained by differences in resource availability because both populations were considered to be at or near equilibrium at the time of the data collection (Estes 1990, Bodkin *et al.* 2000).

As sea otters continue to be harvested throughout Alaska, or as unexpected events occur such as the decline of sea otters in the Aleutian Islands possibly due to increased predation, managers must consider population status, physical habitat features, and life history features on scales appropriate to sea otter movement and dispersion capabilities. The sea otter population in the north Pacific in 1750 consisted of an estimated 200,000–300,000 animals. Their near extirpation resulted from an average annual reported harvest of less than

1.5%, probably well below a sustainable yield (Kenyon 1969). Depletion occurred not simply because of excessive harvest, but because of a systematic overharvest from small geographic areas relative to the range of the population. Exchange of animals between harvested and unharvested areas was constrained by the limited movements exhibited by sea otters.

It is possible that the stock structure of sea otters in Alaska will change during the next century. As abundance and distribution continue to increase in portions of the state, geographic isolation may be reduced, and dispersal between present day stocks may begin. Alternatively, as populations contract due to changes in predation, hunting, or other factors, geographic isolation may increase and new limits on dispersion may develop. The measurable factors which currently separate the stocks will likely shift and change and should be reflected in future estimates of genetic distinction and distribution. It is also possible that additional data from within each region could identify further population structuring.

ACKNOWLEDGMENTS

This work was supported by the U.S. Fish and Wildlife Service, Marine Mammals Management and the U.S. Geological Survey, Alaska Biological Science Center. Contributions by D. Burn, K. Kloecker, L. Comerci, J. Miller, D. Cramer, B. Kelly, L. Holland-Bartels, T. Loughlin, D. Monson, and G. Garner helped in the development of the paper. The authors are also grateful for the suggestions from two anonymous reviewers.

LITERATURE CITED

- BACON, C. E. 1994. An ecotoxicological comparison of organic contaminants in sea otters (*Enhydra lutris*) among populations in California and Alaska. M.S. thesis, University of California, Santa Cruz, CA. 56 pp.
- BODKIN, J. L., AND B. E. BALLACHEY. 1996. Monitoring the status of the wild sea otter population: Field studies and techniques. *Endangered Species Update*. University of Michigan, School of Natural Resources and Environment. 13(12):14-19.
- BODKIN, J. L., B. E. BALLACHEY AND M. A. CRONIN. 1992. Mitochondrial DNA and the conservation and management of sea otters. *Research Information Bulletin*, U.S. Department of the Interior 37:1-3.
- BODKIN, J. L., D. MULCAHY AND C. J. LENSINK. 1993. Age-specific reproduction in female sea otters (*Enhydra lutris*) from southcentral Alaska: Analysis of female reproductive tracts. *Canadian Journal of Zoology* 71:1811-1815.
- BODKIN, J. L., B. E. BALLACHEY, M. A. CRONIN AND K. T. SCRIBNER. 1999. Population demographics and genetic diversity from remnant and reestablished populations of sea otters (*Enhydra lutris*). *Conservation Biology* 13:1378-1385.
- BODKIN, J. L., A. M. BURDIN AND D. A. RYAZANOV. 2000. Age and sex specific mortality and population structure in sea otters. *Marine Mammal Science* 16:201-219.
- BRITTEN, H. B., B. R. RIDDLE, P. F. BRUSSARD, R. MARLOW AND T. E. LEE JR. 1997. Genetic delineation of management units for the desert tortoise, *Gopherus agassizii*, in northeastern Mojave desert. *Copeia* 3:523-530.
- BURN, D. M. 1994. Boat-based surveys of sea otters in Prince William Sound. Pages 61-80 in T. R. Loughlin, ed. *Marine mammals and the Exxon Valdez oil spill*. Academic Press, San Diego, CA.

- CRONIN, M. A. 1993. Mitochondrial DNA in wildlife taxonomy and conservation biology: Cautionary notes. *Wildlife Society Bulletin* 21:239-248.
- CRONIN, M. A. 1996. Systematics, taxonomy, and the Endangered Species Act: The example of the California gnatcatcher. *Wildlife Society Bulletin* 25:661-666.
- CRONIN, M. A., J. L. BODKIN, B. E. BALLACHEY, J. A. ESTES AND J. C. PATTON. 1996. Mitochondrial-DNA variation among subspecies and populations of sea otters (*Enhydra lutris*). *Journal of Mammalogy* 77:546-557.
- DIZON, A. E., AND W. F. PERRIN. 1997. Report of the Molecular Genetics of Marine Mammal Workshop. Pages 3-48 in A. E. Dizon, S. J. Chivers and W. F. Perrin, eds. *Molecular genetics of marine mammals*. Special Publication Number 3, Society for Marine Mammalogy, Lawrence, KS.
- DIZON, A. E., C. LOCKYER, W. F. PERRIN, D. P. DEMASTER AND J. SÉSSON. 1992. Rethinking the stock concept: A phylogeographic approach. *Conservation Biology* 6:24-36.
- EBERHARDT, L. L., AND D. B. SIFF. 1977. Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada* 34:183-190.
- ESTES, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* 59:385-401.
- ESTES, J. A., C. E. BACON, W. M. JARMAN, R. J. NORSTROM, R. G. ANTHONY AND A. K. MILES. 1997. Organochlorines in sea otter and bald eagles from the Aleutian archipelago. *Marine Pollution Bulletin* 34:486-490.
- ESTES, J. A., M. T. TUNICER, T. M. WILLIAMS AND D. E. DOAK. 1998. Killer whale predation on sea otters linking oceanic and nearshore systems. *Science* 282:473-476.
- GARSHELIS, D. L., AND J. A. GARSHELIS. 1984. Movements and management of sea otters in Alaska. *Journal of Wildlife Management* 48:665-677.
- GARSHELIS, D. L., A. M. JOHNSON AND J. A. GARSHELIS. 1984. Social organization of sea otters in Prince William Sound, Alaska. *Canadian Journal of Zoology* 62:2648-2658.
- GIGER, M., AND K. A. TRUST. 1997. Tissue concentrations of elemental and organochlorine compounds in sea otters from two Aleutian Islands in Alaska. USFWS Technical Report WAES-TR-97-01, Anchorage, AK. 11 pp.
- HANKS, J. 1981. Characterization of a population condition. Pages 47-73 in C. W. Fowler and T. D. Smith, eds. *Dynamics of large mammal populations*. John Wiley and Sons, New York, NY.
- JAMESON, R. J. 1989. Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science* 5:159-172.
- JAMESON, R. J., AND A. M. JOHNSON. 1993. Reproductive characteristics of female sea otters. *Marine Mammal Science* 9:156-167.
- JARMAN, W. M., C. E. BACON, J. A. ESTES, M. SIMON AND R. J. NORSTROM. 1996. Organochlorine contaminants in sea otters: The sea otter as a bio-indicator. *Endangered Species Update*, University of Michigan, School of Natural Resources and Environment 13(12):20-22.
- KENYON, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* Number 68:1-352. Bureau of Sport Fisheries and Wildlife, Washington, DC.
- LENSINK, C. J. 1962. The history and status of sea otters in Alaska. Ph.D. dissertation, Purdue University, Purdue, IN. 165 pp.
- LOUGHLIN, T. R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. Pages 159-171 in A. E. Dizon, S. J. Chivers and W. F. Perrin, eds. *Molecular genetics of marine mammals*. Special Publication Number 3, Society for Marine Mammalogy, Lawrence, KS.
- MONNETT, C. 1988. Patterns of movement, postnatal development and mortality of sea otters in Alaska. Ph.D. dissertation, University of Minnesota, Minneapolis, MN. 134 pp.
- MONNETT, C., L. M. ROTTERMAN, C. STACK AND D. MONSON. 1990. Post release monitoring of radio-instrumented sea otters in Prince William Sound. Pages 400-420

- in K. Bayha K. and J. Kormendy, eds. Sea otter symposium: Proceedings of a symposium to evaluate the response effort on behalf of sea otters after the T/V Exxon Valdez oil spill into Prince William Sound. Anchorage, Alaska. U.S. Fish and Wildlife Service, Biological Report 90(12). 485 pp.
- MONNETT, C., L. M. ROTTERMAN AND D. B. SINIFF. 1991. Sex-related patterns of post-natal development of sea otters in Prince William Sound, Alaska. *Journal of Mammalogy* 72:37-41.
- MONSON, D. H. 1995. Reproduction strategies in sea otters at Amchitka Island, Alaska. M.S. thesis, University of California, Santa Cruz, CA. 60 pp.
- MONSON, D. H., AND A. R. DEGANJE. 1995. Reproduction, preweaning survival and adult survival of sea otters at Kodiak Island, Alaska. *Canadian Journal of Zoology* 73:1161-1169.
- MONSON, D. H., J. A. ESTES, J. L. BODKIN AND D. B. SINIFF. 2000. Life history plasticity and population regulation in sea otters. *Oikos* 90:457-468.
- MORITZ, C. 1994a. Defining 'Evolutionary Significant Units' for conservation. *Trends in Ecology and Evolution* 9:373-375.
- MORITZ, C. 1994b. Applications of mitochondrial DNA analysis in conservation: A critical review. *Molecular Ecology* 3:401-411.
- PERRIN, W. F., AND R. L. BROWNELL, JR. 1994. A brief review of stock identify in small marine cetaceans in relation to assessment of driftnet mortality in the North Pacific. Report of the International Whaling Commission (Special Issue 15):393-401.
- PIELOU, E. C. 1991. After the ice age. University of Chicago Press, Chicago, IL.
- RALLS, K., D. B. SINIFF, A. DOROFF AND A. MERCURE. 1992. Movements of sea otters relocated along the California coast. *Marine Mammal Science* 8:178-184.
- RIEDMAN, M. L., AND J. A. ESTES. 1990. The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history. United States Fish and Wildlife Service, Biological Report 90(14). 126 pp.
- RIEDMAN, M. L., J. A. ESTES, M. M. STADLER, A. A. GILES AND D. R. CARLSON. 1994. Breeding patterns and reproductive success of California sea otters. *Journal of Wildlife Management* 58:391-399.
- ROEST, A. I. 1973. Subspecies of the sea otter, *Enhydra lutris*. Contributions in Science, Natural History Museum, Los Angeles County. No. 252. 17 pp.
- ROTTERMAN, L. M. 1992. Patterns of genetic variability in sea otters after severe population subdivision and reduction. Ph.D. dissertation, University of Minnesota, Minneapolis, MI. 227 pp.
- RYDER, O. A. 1986. Species conservation and systematics: The dilemma of subspecies. *Trends in Ecology and Evolution* 1:9-10.
- SANCHEZ, M. S. 1992. Differentiation and variability of mitochondrial DNA in three sea otter, *Enhydra lutris*, populations. M.S. thesis, University of California, Santa Cruz, CA. 101 pp.
- SCRIBNER, K. T., J. BODKIN, B. E. BALLACHEY, S. R. FAHN, M. A. CRONIN AND M. SANCHEZ. 1997. Population genetic studies of the sea otter (*Enhydra lutris*): A review and interpretation of available data. Pages 197-208 in A. E. Dizon, S. J. Chivers and W. F. Perrin, eds. Molecular genetics of marine mammals. Special Publication Number 3, Society for Marine Mammalogy, Lawrence, KS. 388 pp.
- SINIFF, D. B., AND K. RALLS. 1991. Reproduction, survival and tag loss in California sea otters. *Marine Mammal Science* 7:211-229.
- WILSON, D. E., M. A. BOGAN, R. L. BROWNELL, JR., A. M. BURDIN AND M. K. MAMINOV. 1991. Geographic variation in sea otters, *Enhydra lutris*. *Journal of Mammalogy* 72:22-36.
- WOODLEY, C. M. 1997. DNA-based identification of wildlife and marine species: What do you mean when you say "forensics." Pages 67-75 in A. E. Dizon, S. J. Chivers and W. F. Perrin, eds. Molecular genetics of marine mammals. Special Publication Number 3, Society for Marine Mammalogy, Lawrence, KS. 388 pp.

Received: 8 July 1999

Accepted: 28 November 2000