hen Steller sea lions (Eumetopias jubatus) were being considered for listing as endangered or threatened under the U.S. Endangered Species Act (ESA) in the late 1980s, there was no evidence to support geographic stock separation for the species. Consequently, the species was listed as threatened throughout its range even though sea lion populations in some areas were not at low levels or declining. A significant management issue resulting from the ESA listing of the Steller sea lion is the impact the Act's protective measures are having on commercial fisheries, particularly the fisheries for Pacific salmon and North Pacific groundfish.

The ESA prohibitions on the take of listed species require the National Marine Fisheries Service (NMFS) to consider management actions that reduce or eliminate take and which presumably enhance the probability of a species' recovery. In the case of the Steller sea lion, because of the animals' interactions with commercial fishing activities, those management actions can restrict the time and area of fishery openings, reduce allowable harvests, or curtail fishing in areas that are designated under the ESA as critical habitat for Steller sea lions. Although Steller sea lions in the United States are managed currently as a single population regardless of their geographic derivation, if separate stocks were to be identified and managed separately, local or regional management could be implemented based on the dynamics of local or regional Steller sea lion populations.

This article examines information obtained before and after the Steller sea lion's original listing under the ESA to determine if sufficient

The Steller Sea Lion: Two Discrete Stocks?

data now are available to distinguish discrete stocks. The analysis employs a phylogeographic approach, using information on distribution, genotype, phenotype, and population response to define a stock. The analysis provides evidence which suggests the existence of two discrete stocks of Steller sea lions, an eastern and western stock geographically separated at approximately long. 144°W. Studies of mitochondrial DNA (mtDNA) provide the strongest evidence of this geographic stock separation. Analysis of population demography also support the thesis, while tagging and branding studies suggest that Steller sea lions are reproductively faithful to their birth sites and that immigration rates are low.

Introduction

The breeding range of the Steller sea lion extends from the Kuril Islands and Okhotsk Sea, eastward through the Aleutian Islands and Gulf of Alaska, and then south to Año Nuevo Island off central California (Fig. 1). The number of sea lions throughout the range declined by over 60% from about 300,000 in the 1960s to about 116,000 in 1989, the year the National Marine Mammal Laboratory (NMML) coordinated the first range-wide survey. The second range-wide survey in 1994, also coordinated by the NMML, indicated a further overall decline: however, the survey indicated also that the number of animals

was not declining in the area from southeastern Alaska through Oregon.

The historical center of sea lion abundance is the Gulf of Alaska and eastern Aleutian Islands. Within that area, Steller sea lions have been most abundant between the Kenai Peninsula and Kiska Island (Kenai-Kiska) (Fig. 1). Counts of animals on rookeries and haul-out sites within the Kenai-Kiska area have been used to monitor sea lion status and trends in Alaska. These counts indicated a rapid decline in abundance between the 1970s and 1989 and have continued to show a decline but at a slower rate from 1989 to 1995 (Fig. 2). As yet, the cause(s) for the decline has not been identified.

Population dynamics

The demography of Steller sea lions in southeastern Alaska differs from the demography of sea lions in other areas of Alaska. The southeastern Alaska population has declined only slightly, whereas those populations to the west have declined substantially. In 1995, NMML scientists conducted a population viability analysis (PVA) using the number of pups and adults counted from 1975 to 1993 at Alaskan rookeries and found that the probability of extinction of the Steller sea lion was much less for the southeastern Alaska region (about 0.1 at 100 years) compared with other parts of the state (about 0.9 at 100 years). Whether these differences in probability of extinction are genotypic differences or rather represent manifestations of different abiotic or biotic factors affecting the local populations is unknown.

A cluster analysis of the rates of change in adult numbers ob-



Figure 1. The map depicts the range of Steller sea lions. Arrows indicate rookeries and the shaded areas represent the approximate distribution of sea lions when at sea. The Kenai Peninsula-Kiska Island area is also shown.

served at rookeries in Alaska during 1975-94 found consistent aroupings of rookeries with common trends. These groupings ranged from couplets of adjacent rookeries (within 37 km of each other, e.g., Marmot Island and Sugarloaf Island in the Gulf of Alaska) to groupings of five or more sites spread over several hundred kilometers (e.g., Sugarloaf Island to Atkins Island). The implication of these groupings. which persisted through periods of population stability and decline. is that shared environmental features such as prey resources or oceanographic conditions may affect rookery demographics. Pup counts at separate rookeries will be examined using cluster analysis in the near future.

Tagging and branding

Tagging and branding studies have been used to examine the

Steller sea lion's migratory and foraging behavior as well as natal site fidelity. In 1975 and 1976. Alaska Department of Fish and Game (ADF&G) biologists branded 7.046 Steller sea lion pups at six rookeries in the Gulf of Alaska. Brands were designed to indicate rookery and year of birth. Since then, observers throughout the Gulf of Alaska and southeastern Alaska have reported substantial numbers of young, immature, branded sea lions throughout Alaska. Some sea lions had moved over 1,500 km from the branding site: young, immature animals were also reported in the Gulf of Alaska that were tagged as pups in British Columbia. Generally, yearlings and young animals 1-4 years of age dispersed over great distances.

Satellite telemetric studies were conducted by NMML during the past decade in both summer and winter on young-of-the-year and adult female Steller sea lions. These studies indicate that the marked animals forage from a central place and return to that place at the end of the trip, which may last from hours to months. The rookery is part of the central place, but the central place may also include adjacent haul-out sites and perhaps a nearby rookery. Though the sea lion's winter foraging range is great, telemetric data have shown that most animals return to the tagging location and not to another far-off site.

Steller sea lions tagged by NMFS scientists in the Aleutian and Kuril Islands and by Russian scientists on the Kamchatka Peninsula dispersed in similar ways (Fig. 3). These studies indicated that sea

lions dispersed less as they became sexually mature and tended to spend substantially more time near their birth sites when older. NMML scientists branded 800 pups (424 female, 376 male) with individual numbers at Marmot Island in 1987 and 1988, but the size of the colony declined rapidly afterwards (through August 1994) so, to date, only 21 of the 424 females have been seen as adults. Of the 21 resighted females, all were observed as adults on Marmot Island; 2 were seen without pups at Marmot Island in 1992 and then with pups at nearby Sugarloaf Island in 1994.

Branded males have been sighted as subadults in many parts of the range. An animal marked at Rogue Reef in Oregon was resighted at Marmot Island, Alaska; a male branded at Marmot Island in 1977 was resighted at Ugamak Island in the eastern Aleutian Islands in 1985: Marmot Island males are commonly seen in southeastern Alaska in winter. Whether these males will return to their islands of birth to obtain a territory and reproduce (usually by 9 or 10 years of age) is expected to be known in the next 3 years as they become physically and sexually mature. Once males are physically capable of obtaining a territory, they generally return to the same territory in successive years, sometimes for as many as 7 years.

Based on resightings of tagged Steller sea lions, it appears that they are faithful to their birth site and that they generally return there to breed, like other otariids. Although such resightings do not conclusively demonstrate natal site fidelity, they do suggest that site fidelity is a strong instinctive behavior. ADF&G biologists reported that nearly 80% of the branded sea lions that they

sighted at Sugarloaf Island in 1976-77 were branded there as pups in 1975-76. They also reported that of 15 recognizably branded females that gave birth at Marmot Island and Sugarloaf Island, only 1 gave birth at a rookery which was not its birth site. Less than 10% of the females marked by the NMML have been documented to breed elsewhere. In all cases, the females bred at rookeries that were near their birth site and that were part of the group identified in the cluster analysis mentioned above using rates of population change. Because of these trends in site fidelity, genetic exchange between rookeries may be low. Consequently, the level of migration or gene flow occurring between putative population stocks (e.g., from Prince William Sound to southeastern Alaska) may be small. If gene flow between stocks is one or two females per generation, which is not unreasonable, it could be sufficient to promote genetic isolation.

Genotypic data

Studies of mtDNA provide the strongest evidence for stock separation in Steller sea lions. NMML biologists in collaboration with Texas A&M biologists examined a segment (approximately 450 nucleotide base pairs) of the mtDNA control region from 224 Steller sea lion pups sampled at rookeries in Oregon, most of Alaska, and the Kamchatka Peninsula and Commander Islands. Russia. A phenetic analysis and distance matrix were also produced. The study found nucleotide variability at 29 sites, which defined 52 haplotypes which were further grouped into eight maternal lineages. There was no common haplotype that predominated throughout the range, but many haplotypes occurred at low frequency. Cluster analysis indicated that these lineages may be subdivided into two genetically differentiated populations, including an eastern population (Oregon and southeastern Alaska) and a western population (Prince



Figure 2. Counts of adult and juvenile Steller sea lions at rookeries and haulout sites in the Kenai-Kiska area during June 1975-94.

William Sound and west). The average percent sequence divergence among the 52 haplotypes was 1.7% (range 0.4-3.8%). Nucleon diversity estimates for six of the eight populations combined was h = 0.927, suggesting high levels of genetic diversity. Further, calculated gene flow estimates (*N_cm*), indicate about 9.5 females per generation migrating to a nearby rookery (the movement between stocks, as suggested above, is much lower).

Similar mtDNA analysis were conducted by University of California scientists on skin samples from 11 Steller sea lions from Año Nuevo Island, California, resulting in seven haplotypes, six of which were identical to those identified from southeastern Alaska and Oregon. One haplotype was unique to Año Nuevo Island.

Virtually no allozyme variation has been detected by protein electrophoresis perhaps because of limited geographic sampling. Blood and tissues from 157 sea lions were collected in the Gulf of Alaska during 1975-77 by ADF&G scientists. They studied 32 loci of which 4 exhibited rare alleles. No geographic variation was apparent except for a possibly weak differentiation of animals in Prince William Sound.

Phenotypic data

Animals from potentially separate stocks may differ in physical size. Analysis of pup mass from the Aleutian Islands (n=350), the Gulf of Alaska (n=411), southeastern Alaska (n=538), and Oregon (n=245) obtained during 1987-94 indicates that a cline in pup mass exists. Aleutian Island pups were significantly heavier than pups from the Gulf of Alaska and southeastern Alaska, and pups from Oregon weighed less than pups from any part of Alaska. ADF&G biologists found that agespecific axillary girth, standard length, and weight were all less during the 1980s than for animals collected during the 1970s. These data support the hypothesis that the decline in sea lion numbers may be linked to prey resources but provide no supporting data on geographic variation in size. Age-specific size in different geographic locations has not been compared (other than for pups) because of insufficient data.

Population responsed data

Significantly higher levels of haptoglobin were found in Steller sea lion blood samples from the Aleutian Islands than in blood samples from animals in southeastern Alaska. Haptoglobin is an acute phase blood protein that binds with hemoglobin to form a stable complex. Haptoglobin levels increase in association with tissue injury or other such stress (e.g., infection, trauma, inflammation). The higher levels found in the Aleutian Island samples suggest that higher levels of injury or trauma may exist there compared with southeastern Alaska.

Beta-endorphin levels in blood were analyzed from 30 sea lions collected in the central Gulf of Alaska. Beta-endorphins are morphine-like peptides produced by brain and pituitary tissue. They have an analgesic property, which may influence the behavior and physiology of wild animals. However, no significant differences were found for beta-endorphin levels among sampled animals. The geographic area sampled may have been too small to detect geographic variation in beta-endorphin levels. Existing data on the timing of the breeding cycle and reproductive behavior show no significant differences across the range.

Potential areas of research

Parasites or groups of parasites have been used as biological tags to differentiate populations. The lungworm Parafilaroides decorus may infect Steller sea lions only in California. Sufficient samples have not been found from areas outside California to support a definitive conclusion. But intraspecific morphological variation among Steller sea lions may account for some of the lungworm species originally reported from these sea lions. This area of research has the potential for providing further evidence for the existence of stock separation, but additional work is needed to determine if Steller sea lions from different parts of their range can be differentiated by their parasites.

Determination of the levels of contaminants (organochlorine pesticide residues, polychlorinated biphenals, and heavy metals)also may be useful for discriminating between populations. There are at present no studies that compare pollutant levels in Steller sea lions from different parts of the range or that suggest that pollutants are indicative of separate sea lion stocks.

Conclusion

A synthesis of available data suggests that Steller sea lions qualify as a Category II population; according to the definition of Dizon et al. (1992), Category II populations require "...that two (or more) populations/putative stocks coexist with total sympatry or with extensive geographical overlap or be weakly defined in parapatry. Geographically there would be no reason not to manage them together, but critical differences in behavior, morphology, genetics, or some combination of these indicate reproductive isolation to some degree." The strongest



Figure 3. Suggested preliminary dispersal scheme of Steller sea lions from birth to 4 years of age that were marked as pups at Russian rookeries.

evidence for stock separation is the mtDNA studies which indicate that an eastern and a western stock exist with the division at about Prince William Sound. However, NMML biologists recommend additional genetic analysis using protein electrophoresis and nuclear DNA. Additional stocks may be identified in Russia and the Commander Islands once the entire area is sampled. The differences observed in population dynamics and the site groupings resulting from the cluster analysis further supports the notion of limited gene flow among rookeries (and stocks). Tagging and branding studies show that Steller sea lions are reproductively faithful to their birth sites and

that fewer than 10% emigrate. The large amount of mixing away from rookeries during the nonbreeding season is potentially confounding but may not result in interbreeding between animals from the two areas. The differences noted in pup weights is tantalizing and suggests the need to finish cranial morphometric studies for which most of the measurements have been completed. Haptoglobin studies also provide intriauing results supporting the two-stock concept for Steller sea lions and should be pursued.

In closing, NMML biologists recommend that Steller sea lions be managed as two stocks, an eastern stock that includes all animals east of Cape Suckling, Alaska (long. 144°W; Fig. 1), and a western stock, which includes all animals at and west of Cape Suckling. When sufficient data are available, particularly on the genotype of Steller sea lions in the Kuril Islands, recognition of additional stocks may be appropriate.

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