Sea Otter Population Structure and Ecology in Alaska

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History of Sea Otters in the North Pacific

Sea otters are the only fully marine otter. They share a common ancestry with the Old World land otters, but their route of dispersal to the New World is uncertain. The historic range of the species is along the northern Pacific Ocean rim, between central Baja California and the islands of northern Japan. Because they forage almost exclusively on bottom-dwelling marine invertebrates such as clams, snails, crabs, and sea urchins, they predominantly occur near shore. Their offshore distribution is limited by their diving ability; although they are capable of diving to more than 100 meters deep, most of their feeding takes place between the shoreline and depths of 40 meters. They are social animals, generally resting in protected bays or kelp forests in groups, commonly referred to as rafts. Because they are gregarious, possess a fine fur, and occur primarily near shore, they have been exploited by humans for as long as they have co-occupied coastal marine communities.

An adult male sea otter at rest. The hind flippers bear the color-coded tags used to identify individuals that are resighted.

During the late Pleistocene, glacial advances and retreats in the northern latitudes likely influenced genetic exchange within the sea otter's northern range. When the glaciers were at their maximum, ice sheets extended over large coastal areas, isolating sea otter populations and causing local extinctions. During periods of glacial retreat, sea otters likely recolonized the newly available habitats, allowing exchange of individuals and gene flow between populations.

Beginning in about 1750, sea otter populations underwent dramatic declines as a direct result of commercial harvest for their furs. Explorations by Vitus Bering led to the discovery of abundant sea otter populations in the Aleutian Islands. The early harvest, conducted by Russians with enslaved Aleut hunters, began in the eastern Aleutians. Eventually the harvest became multinational and contributed significantly to the exploration and settlement of the North Pacific coastline by Europeans. There were two distinct periods of harvest—one reaching its peak about 1800 and averaging about 15,000 per year and a second about 1870, averaging about 4,000 per year. The causes for this harvest pattern are unknown, but it may represent two distinct periods of overexploitation separated by a brief period of population recovery.

By 1890 the species had been eliminated throughout most of its range, persisting in small numbers at 13 isolated locations in California, Alaska, and Russia. The number of sea otters that survived the fur trade is unknown, but available data suggest that some remnant populations may have been as small as a few dozen individuals. In 1911, sea otters were afforded protection under the International Fur Seal Treaty, and populations apparently responded by gradually increasing in abundance. The rates of population recovery varied among locations, averaging 9% annually and ranging from 6 to 13%. The population at Amchitka Island in the central Aleutians had the highest growth rate among those surviving, apparently reaching carrying capacity by about 1950.

Efforts to aid the recovery of the species into the vast unoccupied habitats between California and Prince William Sound began in 1965. Sea otters from Amchitka and Prince William Sound were translocated to Oregon, Washington, British Columbia, and several locations in southeastern Alaska. With the exception of Oregon, these translocations have resulted in the establishment of successful colonies. Population growth rates of translocated sea otters have been significantly greater than among remnant populations, averaging 21% and ranging from 18 to 24%. We don't know why the growth rates of the remnant and translocated populations are so different, but it may be partly because of the abundant food and space available at the translocated sites.

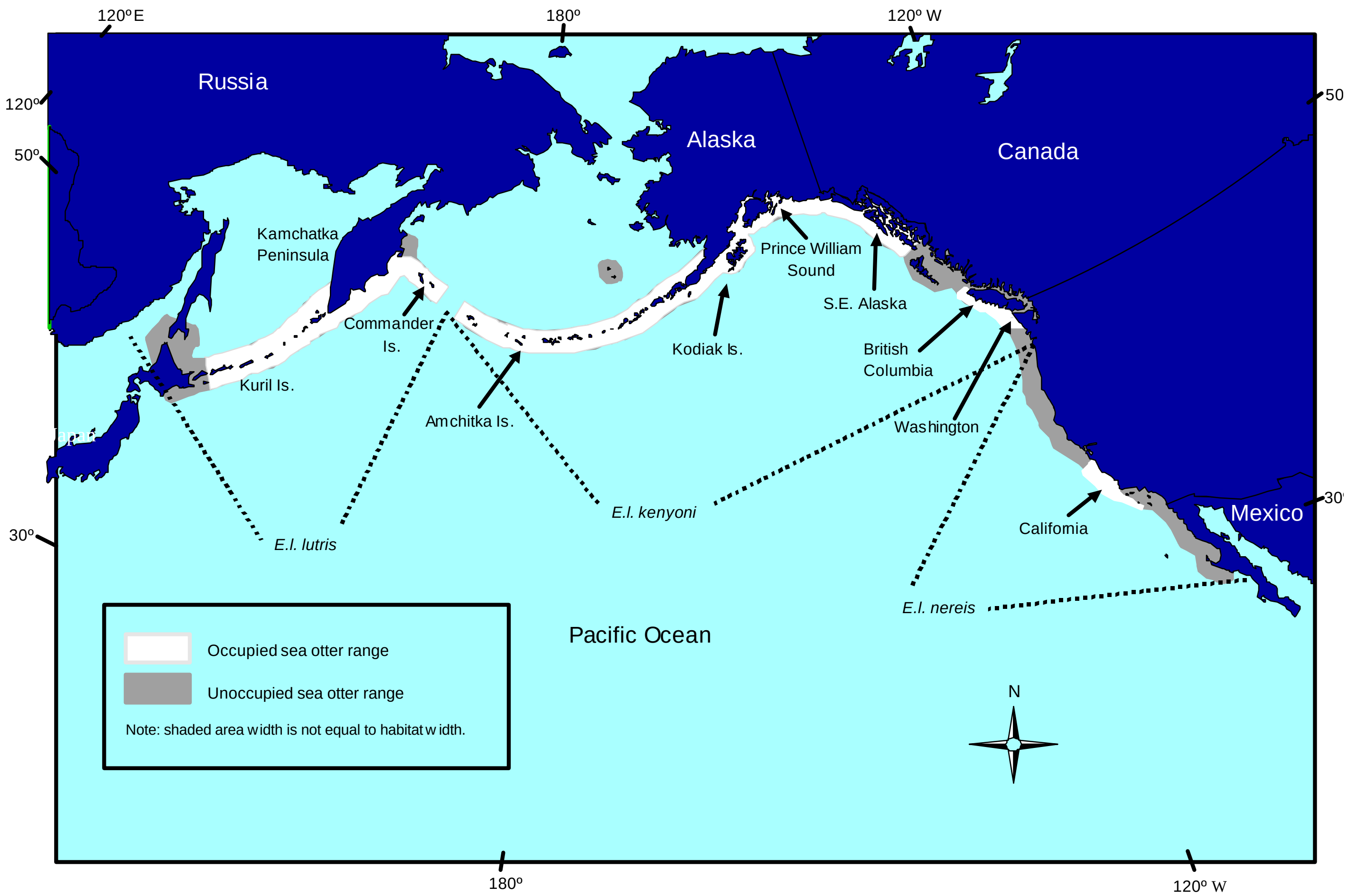
The varying patterns of sea otter population decline and recovery provide a unique and powerful tool for studying the effects of historic reductions on populations, as well as how populations respond to varying environmental conditions. During the past decade, using molecular genetics, researchers have been trying to understand how sea otter populations might differ throughout the North Pacific and what effects population reductions and recovery have had on population genetics. Also, as a result of the varying degree of recovery among isolated populations, we have the opportunity to contrast life history attributes (such as condition, reproduction, and survival) among populations throughout their range. These contrasts may be useful in developing methods to assess the status of populations where traditional methods of surveying abundance are difficult and expensive.

Population Structure in Sea Otters

The molecular-level population structure of modern sea otters likely reflect the combined influences of long-term natural processes and recent human harvests. Several factors historically restricted gene flow within the sea otter population. One is the relatively small home ranges of sea otters. Although sea otters have been known to travel as much as a few hundred kilometers, they tend to stay close to home, with home ranges that average a few tens of kilometers of coastline. This, in conjunction with a essentially linear population that extends over nearly 20,000 km, tends to limit the exchange of genetic material over long distances. In addition, long distances between island groups in the Aleutian archipelago and periodic advances of glacial ice sheets would serve to restrict the movements of sea otters, further limiting gene flow. More recently, overexploitation through commercial harvests has severely reduced sea otter distribution and abundance. By 1900, probably no more that several hundred sea otters persisted in 13 widely separated locations between California and the Kuril Islands of Russia. The long distances between most neighboring populations (for example, California and Prince William Sound) almost certainly prevented gene flow among remnant populations since late in the commercial fur harvest.

The reductions in distribution and abundance, or bottlenecks, consist of two components. One is the magnitude of the reduction, or how few animals persisted. The other is the duration of the bottleneck, or how long the population stayed at or near the minimum population size. Both of these factors can reduce genetic diversity, with implications for individual and population fitness. Since about 1990 we have been studying sea otter population genetics. Our goal has been to improve understanding of how populations might differ relative to location within their remnant range and what the potential effects of the recent human-induced population bottlenecks might be.

Our studies of sea otter genetics using the maternally inherited mitochondrial DNA show that populations separated by large distances share common genes, indicating a recent common ancestry and some degree of gene flow prior to 1750. We identified at least four major groups that generally correspond to the three recognized subspecies of *Enhydra lutris* (*E.l. lutris*, *E.l. kenyoni*, and *E.l. nereis*), based on cranial morphology. The molecular genetics work identified two populations within the *E.l. kenyoni* subspecies, one from Prince William Sound and another from Kodiak and westward through the Aleutian Archipelago. The results also indicated that the Commander Island population was more closely related to the Aleutian population than to the Kuril population (*E.l. lutris*). We found large differences in mitochondrial DNA among contemporary populations, indicating restricted gene flow or drift because of the recent population bottlenecks. In more recent work we have looked at factors other than genetics to identify potential population structuring within Alaska. Based on population distributions and physical characteristics, as well as genetic



Sea otter distribution in the north Pacific Ocean, illustrating the geographic distribution of the three subspecies in Alaska.

data, at least three stocks are evident in Alaska: southeast Alaska, Prince William Sound, and from Kodiak westward through the Aleutian archipelago.

Our ability to overharvest sea otters has been clearly demonstrated. Because sea otters in Alaska continue to be harvested for their furs, it is important to manage those harvests in a sustainable manner. To avoid overexploitation, sea otters must be managed on a geographic scale compatible with their well-known behavioral and reproductive biology. For example, had the average annual harvest of sea otters between 1750 and 1900 (about 3000–6000) occurred evenly throughout their range, it is likely there would have been no detectable decline in their overall abundance by 1900. However, because the harvest systematically progressed across relatively small portions of their range, the species was nearly hunted to extinction.

Translocating individuals is an increasingly common tool for aiding in the recovery of wildlife populations that have been reduced or eliminated from portions of their historic range. Between 1965 and 1972, 544 sea otters were moved from Amchitka Island and Prince William Sound to vacant habitat in Washington (43), British Columbia (89), and southeast Alaska (412). Because of mortality and emigration following translocation, the estimated founding population sizes were 4, 28, and 150, respectively. British Columbia and southeast Alaska received sea otters from both parent populations, while Washington received otters only from Amchitka.

We used founding population data (the number of individuals and the duration at the minimum number) and mitochondrial DNA data from remnant and translocated sea otter populations to examine the effects of population bottlenecks on genetic diversity and subsequent population growth rates. We found that genetic diversity is negatively correlated with the length of time a population remained at a minimum number (the longer the population remained small, the less genetic diversity) and positively correlated with the minimum population size (the larger the minimum population size, the greater the genetic diversity). Although we found higher population growth rates in translocated populations, we also found that growth rates were not correlated with genetic diversity. Translocated populations have exhibited higher average growth rates (21% per year) than remnant sea otter populations (9% per year), and translocations with two sources resulted in increased genetic diversity. Despite the dramatic population bottlenecks, caused by both harvests and translocations, we have been unable to identify negative effects, in terms of population growth rates, caused by loss of genetic diversity in contemporary sea otter populations.

Population Ecology

Reproductive Rates

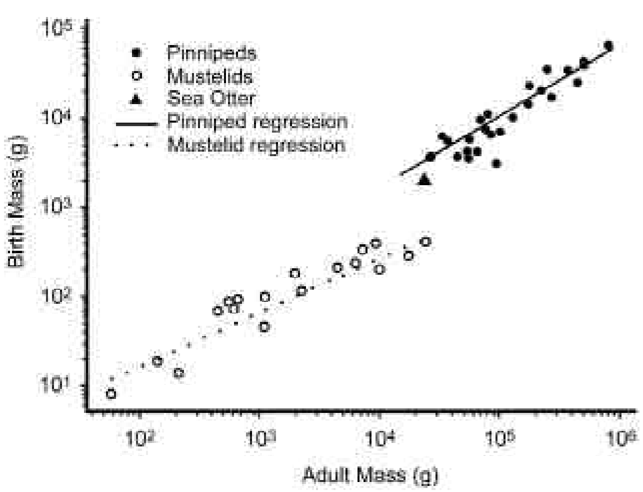
We found that age-specific sea otter birth rates are nearly constant throughout their range, regardless of food and space availability. A small proportion of females have their first pup at two years of age, about 50% first reproduce at the age of three, and most females have produced a pup by the age of four. After their first pup, successful adult females generally have one pup per year, with the annual reproductive rates for mature females holding at 85–90%. If a pup dies before it is weaned, the female usually breeds again within days of losing her pup. There is some indication that females over 12–15 years of age may have fewer pups.

The overall reproductive potential of sea otters is primarily limited by the litter size of one. The birth of one “large” pup that can survive in the harsh environment into which it is born appears to be a necessary adaptation to life in the sea. The trait of a single offspring is one the sea otter shares with all other completely marine mammals (cetaceans, pinnipeds, and sirenians), as opposed to all other mustelids, which give birth to multiple young. In fact, European land otters living along the coast tend to have smaller litters than their inland counterparts, possibly because of the harshness of the environment and the limited availability of protected den sites along the coast. This suggests a pathway for the evolution of this trait. That is, as litter size decreased, pup size likely increased. Fewer and larger pups allowed ancestral sea otters to exploit more-exposed dens and less-hospitable stretches of coast than their larger-litter cousins that needed den sites that were more protected. As this trend continued, ancestral sea otters would have occupied increasingly hostile environments until they were able to actually give birth at sea, away from the protection of the den. At this point a single young was the most a mother could possibly protect and raise, leading to larger and larger single pups, with the rate of multiple births becoming less and less common over time. But it also allowed sea otters to occupy the entire coastline at high densities, regardless of the availability of land-based den sites.

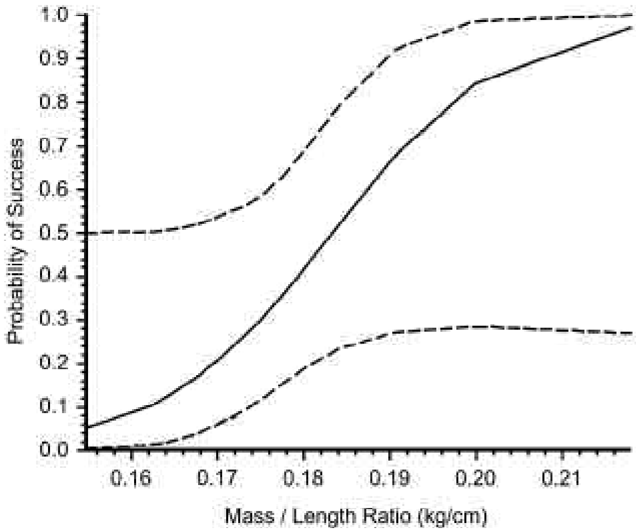
Survival Rates

In contrast to reproductive rates, post-weaning survival rates appear to be dramatically affected by food availability. Sea otter populations living with an abundance of food have relatively high survival rates in all age classes, with especially high survival for juveniles. However, long-established populations with limited food resources have a different survival rate pattern. Survival rates from weaning through the first year of life are generally low but variable. Survival for the middle age classes is uniformly high, and survival rates in the older age classes decline rapidly with age. Juvenile survival appears to be the primary mechanism of population regulation in undisturbed sea otter populations.

Pre-weaning pup survival appears to depend on the age and condition of the mother at the time of birthing—pups of healthier, more experienced mothers are more likely to survive. Female sea otters must spend extensive amounts of time grooming and nursing their newborn pups, keeping them warm and dry on their chest or hauled out on rocks. This necessarily restricts the amount of time they can spend foraging for food themselves.



The relationship between mean adult female mass and mean birth mass (mean litter size × mean pup mass) for 26 species of marine mammals (pinnipeds) and 19 species in the otter family (mustelids). Sea otters are much closer to the pinniped group than to the mustelid group. The pinniped data are from Lee et al. (1991), and the mustelid data are from Parker (1990) and Nowak (1991).



The relationship between weaning success and female mass/length ratio at capture for sea otters at Amchitka Island, Alaska from 1992 to 1994. The solid line represents the average, and the dashed lines represent the confidence intervals.

A female in poor condition will not be able to restrict her feeding time to the extent a female in good condition can, and her pup will be exposed to longer periods in the water and less grooming and nursing. The result is poorer pup survival during the first few weeks of life, the period during which most pre-weaning pup mortality occurs.

This effect may be exaggerated during winter, when conditions are particularly harsh. In sea otter populations with limited food resources, pups born in winter are more likely to die soon after birth. Because the female generally breeds soon after losing her pup, her next pup will likely be born during spring or early summer, when the pup will have a better chance to survive. After a 5- to 7-month period of dependency, she will wean the pup, breed again, and have another pup about a year after the birth of the previous pup.

Thus, even though some females may produce and successfully wean pups at any time of year, the environmental effects on pre-weaning pup survival, along with a reproductive cycle of approximately one year, tend to produce and maintain peak pupping periods in the spring and early summer. The breadth and peak of the pupping period depend on the severity of winter weather conditions and the general availability of food. If food is abundant (as in newly occupied habitat) or seasonal conditions are fairly uniform (as in the more southerly latitudes), pupping peaks may be absent, variable, or very broad, depending on chance environmental events. In the northern latitudes of the sea otter's range in Alaksa, because of strong seasonal differences in environmental conditions, there tends to be a sharp peak in pupping in spring, although pups can be born during any month.

Conclusion

The twentieth century was a period of recovery from near-extirpation for sea otters throughout the North Pacific Ocean. The presence of populations in varying stages of recovery has provided unique opportunities to study the response of sea otters to population bottlenecks and the changing ecological conditions they encounter following recovery. As we enter the twenty-first century, we find sea otter populations in southeast Alaska still expanding into previously unoccupied habitat and demonstrating rapid growth. Other populations, such as in Prince William Sound, appear to be relatively stable. However, throughout the Aleutian Archipelago and much of the Alaska Peninsula, we have seen dramatic declines in sea otter abundance over the past decade. This situation will continue to provide opportunities to study how sea otters respond to, and recover from, population declines.

Suggestions for Further Reading

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