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Comparative Demography of Sea Otter Populations

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Population trends are poorly documented and demographic information is typically lacking for many carnivorous mammals. The sea otter (*Enhydra lutris*) has a well known history of decline and recovery, and while many other species have declined as precipitously, few have recovered so spectacularly. Generally speaking, northern populations (remnants within the range of *E. l. lutris* and *E. l. kenyoni*) have recovered at high rates while recovery of the southern sea otter (*E. l. nereis*), which is listed as legally threatened under the Endangered Species Act (ESA), has progressed more slowly. Our purpose is to contrast trends in abundance and demographic patterns between southern (California) and northern (Washington, British Columbia, Alaska, and Asia) sea otter populations. Specifically, we provide (1) a brief review of the main findings to date; (2) a summary of ongoing and planned studies; and (3) recommendations for future research. A more detailed account of these and other issues concerning the conservation and management of sea otters is provided in the U.S. Fish and Wildlife Service's Recovery Plan for the California Sea Otter (U.S. Fish and Wildlife Service 1996).

Summary of past research

Demographic information on sea otters comes from several sources. Population monitoring programs have been conducted mostly by state and federal agencies. Information on reproduction and mortality comes from work conducted by scientists from state and federal agencies, academia, and the private sector. Although there have been several long-term monitoring programs, most information on population trends, and much of what is known about reproduction and mortality, comes from the *post hoc* assembly of data that were collected for other purposes. In some cases recognition of patterns is confounded by the different methods used in existing research. More recently, there has been a concerted effort to apply consistent techniques in studies of reproduction and mortality in different parts of the sea otter's range. Nonetheless, varying conditions and purposes of work in different areas have inevitably influenced the comparability of available data.

Trends in abundance

The earliest comprehensive reports of status and trends in sea otter populations were written by Barabash-Nikiforov (1947) and Lensink (1960). Karl Kenyon's (1969) monograph summarized information through the mid-1960s and reports by Rotterman and Simon-Jackson (1988), Riedman and Estes (1990), and Estes (1991) provide the most recent updates.

By the early 1900s sea otters had been hunted to near extinction throughout their range (Lensink 1960). When prohibition against further take was enacted in 1911, a dozen known colonies remained, none of which are thought to have contained more than several hundred individuals (Kenyon 1969). These colonies recovered at varying rates in the ensuing decades, although not in unison. The sea otter population at Amchitka Island in the western Aleutian archipelago was one of the first to recover, apparently reaching equilibrium numbers by the late 1930s or early 1940s. In other areas recovery lagged behind by as much as a half century.

Sea otters were hunted to extinction in several isolated areas of the Aleutian archipelago and along the west coast of North America between eastern Prince William Sound and central California. They were reestablished in the late 1960s and early 1970s to southeast Alaska, British Columbia, and Washington via relocations (Jameson et al. 1982), and in the mid-1960s a small colony naturally recolonized Attu Island, western-most of the Aleutians (Jones 1965). The subsequent growth of these colonies has been documented through repeated surveys. These data are informative because (1) founding population sizes are known in all cases; (2) each area was surveyed using consistent methods; and (3) the populations are sufficiently isolated that movement among populations is unlikely to have affected their population growth rates. All 4 populations increased at 17-20% per year, which is near the sea otter's theoretical maximum rate of increase, r_{max} (*sensu* Cole 1954), based on known or estimated values of key life history parameters (Estes 1990). Furthermore, these growth trajectories have shown no indication of density compensation, even though the population in southeast Alaska contained greater than 1500 individuals at the time of the last survey. However, the most recent information from Washington (R. Jameson, unpublished) indicates that the population growth rate there has declined somewhat in the past few years.

Although there has been less consistency in the census techniques used to survey California sea otters, this population clearly has grown more slowly than the northern populations. Except for the mid-1970s to the early 1980s, when the California sea otter declined (Estes 1990) in apparent response to incidental mortality in a coastal set net fishery (Wendell et al. 1985), the rate of increase has consistently been about 5% per year. This comparatively low rate of increase, coupled with its small size, limited range, and concern over possible catastrophic losses from oil spills, led the U.S. Fish and Wildlife Service to list the California sea otter population as threatened under the ESA in 1977.

Demographic patterns

The strikingly different growth rates between sea otter populations in California and more northern regions is attributable to different demographic schedules. That is, the populations differ in some aspect of their age-specific probabilities of reproduction, survival, or some combination thereof. Differences in mortality are thought to be the main factor explaining divergent rates of population growth, as explained below.

Most females conceive and give birth for the first time at age 3, and since the lengths of gestation and post-partum dependency are each about 6 months, females that successfully wean their pups reproduce on roughly an annual cycle

(Jameson and Johnson 1993; Riedman et al. 1994). Females usually come into estrous within a few days of separating from their pup. Therefore, when pups are lost prematurely, the reproductive cycle is shortened. Although most pregnancies probably are carried to term, many post-partum losses occur shortly after birth. Despite this, age of first reproduction and the age-specific probability of females giving birth appear to be largely invariant among populations, irrespective of whether they are increasing, at or near equilibrium, or in decline (Jameson and Johnson 1993; Bodkin et al. 1993; Monson and DeGange 1995; Monson et al., unpublished manuscript; Tinker and Estes, unpublished data).

In contrast to reproductive rates, age-specific mortality schedules vary considerably among sea otter populations. Maximum longevity of wild sea otters is about 20 years (Bodkin, unpublished data). Beach-cast carcasses are rarely found in areas where populations are growing rapidly, and most of those that are recovered are aged (Kenyon 1969). This observation, and the analysis of population growth potential based on life history data indicate that very low mortality between birth and senescence is the rule in populations that are increasing at rates near r_{max} (Estes 1990). In contrast, the age-specific mortality schedule of resource-limited populations, such as those at Amchitka Island or western Prince William Sound, features an increased probability of mortality among dependent and recently weaned juveniles. Therefore, the age-structure of beach-cast carcasses from resource-limited populations is bimodal, with peaks at the very young and old age classes. Mortality rates of individuals between about 3 and 8 years are very low, regardless of population status. A third pattern, in which probability of mortality is relatively high for all post-weaning ages, produces a carcass age structure similar to that of the living population. This pattern was seen following the *Exxon Valdez* oil spill (Bodkin et al. 1993) and is also typical of the California population (Pietz et al. 1988). The reason for this mortality pattern is still poorly understood, although there appear to be a wide range of possible causes.

Ongoing and planned research

Population monitoring of sea otters in California and Washington is part of the U.S. Department of the Interior's research program, and is expected to continue indefinitely. Elsewhere, population surveys probably will be done opportunistically, or as the need arises.

A large-scale comparative study of sea otter demography and behavior was initiated in the early 1990s. This project is being conducted as a series of 2 to 3 year studies of populations that are either small and growing rapidly or large and at or near equilibrium density. Similar methods, centered on information obtained from a sample of individuals equipped with surgically implanted radio transmitters, are used in each study. Information on diet, activity-time budgets, distribution and movements, reproductive success, and mortality is being gathered. In addition, surveys of pre-determined coastal segments are conducted at monthly intervals to obtain samples of beach-cast carcasses, and to determine trends in abundance and reproduction. There is ongoing or recently completed field research at Amchitka and Adak islands (populations near equilibrium density), and Shemya Island and Washington State (growing populations). A similar study is planned for California where the data will be added to those obtained in the 1980s by Siniff and Ralls (1988). The ultimate goals of this program are to relate population status to demographic and behavioral patterns, and in particular to better understand the status and factors limiting growth of the California population.

Conclusion and recommendations

The above-described activities will form an empirical backbone for the long-term conservation and management of sea otters. Continued population monitoring is probably the most fundamental need, although information on demography and behavior is also necessary if there is to be any hope of understanding the observed trends. Three additional areas of research could enhance this goal.

(1) Synthesize available data. A great deal of information already has been gathered on the abundance and trends of sea otter populations, and on the demography and behavior of individuals within these populations. Most of this information has not been published and some of it was obtained by people no longer working with sea otters. We recommend that all of the relevant demographic data be identified, assembled into a comprehensive data base, and analyzed and synthesized. At the very least, this will clarify what information is available and what more is needed.

(2) Population modelling. A rigorous analytical effort is needed to help field researchers focus their efforts on the most revealing populations, age and sex classes, and demographic/behavioral parameters. Properly done, population modelling can serve as a reality check for preconceptions and interpretations that have become accepted without benefit of rigorous analysis. For instance, we have argued that elevated mortality, as opposed to depressed reproduction, is responsible for the regulation of sea otter populations as they approach equilibrium density. While this argument is supported by the available data and may be correct, recent work on another carnivore species, the cheetah, suggests that a more careful look is needed. In the case of the cheetah, cub mortality is highly variable and this variation has been assumed to be responsible for the growth or decline of local populations (Caro and Laurenson 1994). However, iterated simulations of cheetah population trends using the available life history data show that observed levels of cub mortality have relatively little effect on population growth or decline, and that adult mortality is the likely causal variable (Crooks et al., in review). The case of the cheetah is relevant to sea otters because (a) we have also assumed that mortality of young animals is the major driving variable in population trends, and (b) sea otters, like cheetahs, come into estrous immediately after becoming separated from their young. Thus, it may be that elevated pup mortality, especially that which occurs shortly post-partum, produces an elevated rate of fecundity, in turn buffering the population against decline. Preliminary analyses of data collected from a declining population at Adak Island, Alaska suggest that variation in adult mortality rates may be a critical regulating factor in sea otter populations (Tinker and Estes, unpublished data).

(3) Develop a better understanding of linkages between sea otter population biology and community- and ecosystem-level processes. Ultimately, most population trends are driven by some aspect of the habitat. Food, predators, space, and other physical aspects of the habitat are common limiting factors for other species. Sea otters strongly depress their prey populations (Estes and VanBlaricom 1985; VanBlaricom and Estes 1988) and thus food limitation is often assumed to be the main factor regulating sea otter populations. While this is likely true, recent findings suggest that the interaction can take complex and unexpected forms. For instance, while organic carbon production from kelp beds may ultimately fuel the maintenance and growth of sea otter populations (Duggins et al. 1989; Estes 1990), poorly known relationships between coastal currents and prey recruitment appear to modulate the linkage between macroalgal-derived organic carbon production and sea otter abundance. These relationships, in turn, may explain why high density sea otter populations have persisted in some areas but not others (Estes and Duggins 1995; Estes 1996; Estes, unpublished data). Similarly, recent work at Amchitka Island has shown that episodic food subsidies from the oceanic realm can strongly influence the behavior and population biology of sea otters (Watt et al., submitted). Predation on newborn pups by bald eagles (Sherrod et al. 1975) or on adult sea otters by killer whales (Hatfield et al., in preparation) is another potentially important variable, and while predation may be negligible in many populations, it should not be overlooked. Finally, there is growing evidence that environmental contaminants may be responsible for reduced growth rates and declines of local sea otter populations (Estes et al., in press; see Jarman et al., this issue). These examples, while still equivocal, point out that any real understanding of the sea otter's demography must include community- and ecosystem-level interactions.

One broad goal of wildlife research is to develop strategies that help minimize the likelihood of extinction on relevant time scales. Except for the rare effects of environmental catastrophes, perspectives built around years or even decades are too short, especially for long-lived organisms like sea otters. Similarly, very long time scales (e.g., millennia) are too long to worry about because it is virtually impossible to forecast environmental, social, and political changes over these time scales. We should probably be concerned with developing conservation strategies for sea otters over periods of roughly 50 to 100 years. The sea otter's future appears bright at the moment, but one must be mindful of how misleading the short-term perspective can be. For instance, even 100 years ago a concerned resource manager would have viewed the prospects for grizzly bears or gray wolves in North America in much the same way as we view sea otters today. However, the ensuing century has demonstrated how wrong that perspective would have been, and how fragile species and populations can be over long periods of time.

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