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CAUSES OF MORTALITY IN CALIFORNIA SEA OTTERS DURING PERIODS OF POPULATION GROWTH AND DECLINE

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ABSTRACT

Elevated mortality appears to be the main reason for both sluggish growth and periods of decline in the threatened California sea otter population. We assessed causes of mortality from salvage records of 3,105 beach-cast carcasses recovered from 1968 through 1999, contrasting two periods of growth with two periods of decline. Overall, an estimated 40%–60% of the deaths were not recovered and 70% of the recovered carcasses died from unknown causes. Nonetheless, several common patterns were evident in the salvage records during the periods of population decline. These included greater percentages of (1) prime age animals (3–10 yr), (2) carcasses killed by great white shark attacks, (3) carcasses recovered in spring and summer, and (4) carcasses for which the cause of death was unknown. Neither sex composition nor the proportion of carcasses dying of infectious disease varied consistently between periods of population increase and decline. The population decline from 1976 to 1984 was likely due to incidental mortality in a set-net fishery, and the decline from 1995 to 1999 may be related to a developing live-fish fishery. Long-term trends unrelated to periods of growth and decline included a decrease in per capita pup production and mass/length ratios of adult carcasses over the 31-yr study. The generally high proportion of deaths from infectious disease suggests that this factor has contributed to the chronically sluggish growth rate of the California sea otter population.

Key words: California sea otter, *Enhydra lutris nereis*, mortality, population trends, salvage of beach-cast carcasses.

Once-abundant sea otter (*Enhydra lutris*) populations were reduced to a few scattered remnants by the Pacific maritime fur trade (Kenyon 1969). After protection in 1911, the remnant population in central California gradually increased and expanded its range (Riedman and Estes 1990). This population was listed as Threatened in 1977 under the U.S. Endangered Species Act because of its small size, limited distribution, slow growth rate, and vulnerability to oil spills. There are now more than 2,000 California sea otters, distributed along roughly 500 km of coastline from Half Moon Bay in the north to Government Pt. in the south. The population remains below a provisional threshold for delisting (Ralls *et al.* 1996).

Two sources of long-term information on the California sea otter population are periodic counts of the living animals and salvage records from beach-cast carcasses. The counts indicate a gradual increase since 1911, punctuated by two periods of more recent decline (Fig. 1). One such decline, which occurred from approximately 1976 to 1984, was probably caused by increased mortality from entanglement in fishing nets. After restrictions were imposed upon the fisheries, population growth resumed until about 1994 when again the number of otters began to decline (Fig. 1). The cause or causes of this latter decline, which continued through at least 1999, remain uncertain. The salvage program was initiated in 1968 and by the end of 1999 included data on 3,105 sea otter carcasses.[1] The current status of the population is unclear because the population counts since 1999 do not show a clear trend.

In this paper we use the population counts and salvage data to assess trends in abundance and associated patterns of mortality in the California sea otter population from 1968 through 1999. First, we explore possible reasons for the declines, including artifacts due to survey methodology, redistribution, decreased fecundity, and increased mortality. This analysis indicates that while various survey artifacts may have contributed to the apparent declines, both declines were real, and increased mortality was the likely cause. We next examine the salvage database for patterns indicative of specific kinds of mortality, including entrapment in fishing gear, infectious disease, starvation due to depletion of food resources, and predation. Seasonal and geographical patterns of sea otter mortality in California are also

[1] Reviews of sea otter mortality using these data are available for the periods from 1968 to 1974 (Morejohn, G. V., J. A. Ames and D. B. Lewis. 1975. Post mortem studies of sea otters, *Enhydra lutris*, in California. California Fish and Game, Marine Resources Technical Report 3.) and from 1968 to 1993 (Pattison, C. A., M. D. Harris and F. E. Wendell. 1997. Sea otter, *Enhydra lutris*, Mortalities in California, 1968 through 1993. California Fish and Game, Marine Resources Division Administrative Report 97-5.). Both documents can be obtained from California Department of Fish and Game, 1451 Shaffer Road, Santa Cruz, CA 95060.

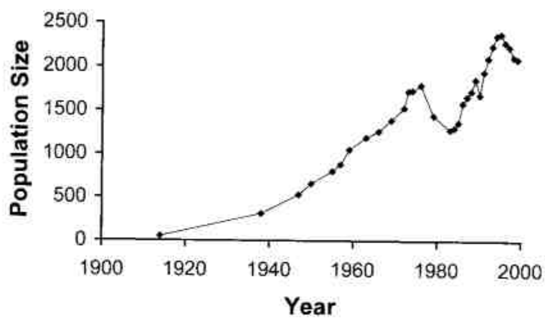


Figure 1. Abundance of California sea otter population from 1911 through 1999. Data from 1982 onward are counts made during annual spring surveys. Earlier data from counts and estimates using a variety of methods. The 1914 data point is uncertain although the population was very small at that time.

considered in these analyses. Finally, we discuss ways in which mortality patterns in California sea otters differ from those of sea otters in Alaska and Russia.

Methods

Survey Methods

A variety of methods have been used over the years to assess population size of California sea otters. Standardized survey procedures were adopted in 1982. These involve counting the population twice annually—during late spring and early autumn—from shore in road-accessible stretches of coastline and from fixed-wing aircraft in the remaining areas. Counts are typically conducted from morning through early afternoon on days with light winds and clear air. The road-accessible shoreline is divided into segments that can each be counted in several days. Ten to twelve teams of two observers conduct the shore-based surveys. Each team is responsible for counting all sea otters in a particular segment, which is done by progressing from one end of the segment to the other. Counts are made using binoculars and spotting scopes from convenient promontories. Dependent young are categorized as small or large depending on size and development. The estimated probability of detection in the shore-based surveys is 0.95, although this declines at distances beyond about 850 m (Estes and Jameson 1988). Three observers and a pilot conduct the aerial counts by flying transects parallel to shore and spaced approximately 400–800 m apart, at an air speed of 90 nmi/h (165 km/h), and at an elevation of 65 m. Our analyses are based on the assumption that detection probabilities from these methods have remained constant since 1982.

Salvage Methods

In 1968 the California Department of Fish and Game (CDFG) began cataloging stranded sea otter carcasses. A network of people has continued this effort to the present. Basic information about stranded sea otters—date of recovery, sex,

Table 1. Cause of death categories assigned to beach cast California sea otter carcasses.

Category
Natural
shark-bite (certain)
shark-bite (probable)
lacerated
dependent pups and immatures with no trauma
dependent pups and immatures with trauma
females with mating wounds
dead pups with mothers
other natural causes including disease and parasites
Anthropogenic
shot (certain)
shot (probable)
killed in research operations
other direct human causes (*e.g.*, boat strike, entanglement in fishing lines, fishing pots, oil)
drowned in fishing nets
Other
uncertain with trauma
uncertain with no trauma apparent
unknown

age-class (pup, immature, subadult, adult and aged adult based primarily on total length and tooth eruption and wear), recovery location, and cause of death—has been obtained since 1968. Carcass assessment protocols, including definitions of terms and code descriptions are provided by Pattison *et al.*[1] Cause of death is assigned to one of 16 categories (Table 1). Fields for amount of subcutaneous fat, presence of tarry feces (an indication of enteritis), age estimated from a sectioned first premolar (Garshelis 1984), results of radiographs, and tissue samples were added in 1992. Fields for condition of teeth, nose wounds on females (a male sea otter bites the female on the nose during mating), amount of white fur or grizzle (correlated with age), and presence and relative amounts of intestinal and peritoneal acanthocephalan parasites were added in 1994.

Since 1992, sea otter carcasses recovered in fresh condition, and those from otters stranding alive but dying shortly thereafter, were examined by veterinary pathologists at the U.S. Geological Survey's (USGS) National Wildlife Health Center in Madison, Wisconsin, the California Department of Fish and Game's Marine Wildlife Care and Veterinary Research Center in Santa Cruz, California, or at the University of California at Davis.

Analysis of Salvage Data

To detect relationships between mortality patterns and population trends, we collapsed the 16 mortality categories (Table 1) in the database into four broad groupings: human, natural, shark, and unknown. The "human" category contains otters that died from unequivocal human impacts, including shootings, boat strikes, or drownings in nets or other fishing gear. The "natural" category contains otters that died from certain kinds of trauma (*e.g.*, mating injuries), emaciation, disease, gastrointestinal conditions (such as duodenal impaction, hemorrhagic gastritis, and intussusception), infections, and tumors. Some of these causes of mortality are not necessarily independent of human influences and may well be related to deteriorating water quality, elevated contaminants, and other as yet poorly understood dimensions to the ecology of disease-causing microbes and parasites that are affected by domesticated animals, land-use practices, and a myriad of other possible factors associated with the high human population density in coastal California. The "shark" category contains otters that were certainly or probably killed by shark bites and the "unknown" category contains all otters for which the cause of death could not be determined. Most of the animals in this latter category were in various states of decomposition.

We then sorted the collapsed data into four time periods: two when the population was increasing, 1968–1975 and 1985–1994, and two when it was decreasing, 1976–1984 and 1995–1999. These periods were chosen based on surveys of the living population (Fig. 1) and annual carcass recoveries (Fig. 2a, b). We also sorted the data by month of recovery to evaluate seasonal patterns in the number of beach-cast carcasses. Because population trends during the boundary years between these chosen periods (1975 and 1976, 1984 and 1985, 1994 and 1995) were more ambiguous, all of our analyses were conducted with and without information from these years. Similar results were obtained from both analyses and only those done on the full data set are reported herein.

We were able to conduct more detailed analyses on the data from 1982 to 1999, when population surveys were conducted using the standardized methods described above. To estimate the annual number of sea otter deaths during this period, we first estimated the minimum number of recruits each year by summing the number of dependent pups counted during spring and autumn population surveys. Because the time from birth to weaning and the time between spring and autumn surveys are each about six months (Riedman *et al.* 1996, Monson *et al.* 2000*a*), few dependent pups were double-counted in the spring and fall surveys. The probability of mortality from birth to weaning is about 0.5, most of which occurs within the first month of life (Siniff and Ralls 1991, Riedman *et al.* 1996). Therefore, about half of the animals born are recruited into the population of independent sea otters, which for a stationary population must equal the number of deaths. The population was not stationary during the period of our analysis. We therefore also estimated the annual increment (or decrement) of population change as the product of population size (determined from the survey results) and annual rate of population change (estimated as the slope of the linear best-fit between ln population size and time). The number of sea otter deaths each calendar year from 1982 to 1999 was then estimated by subtracting the increment or adding the decrement of population change to the estimated number of recruits, as specified above. Annual carcass recovery rates were estimated as the number of carcasses retrieved divided by the estimated number of deaths.

To determine if there was large-scale spatial variation in the pattern of carcass recovery, we sorted the 1982–1999 data into three areas: south of Cayucos, Cayucos to Seaside, and north of Seaside. We estimated the annual per capita recovery rate for each of these areas as the number of carcasses recovered during a calendar year divided by the number of animals counted during the spring-range-wide population surveys that same year.

Results

General Causes of Population Declines

Possible explanations for the survey declines are, either singly or in combination, (1) survey artifacts, (2) movement of otters outside the survey area, (3) reduced fertility, or (4) increased mortality. Survey artifacts cannot account for the declines (see Discussion). It also is unlikely that large numbers of otters have moved out of the survey area as these would have been observed and reported. While the per capita pup count (based on ground count areas only) declined somewhat ($F_{1,13} = 3.526$, $P = 0.083$) from 1982 to 1999, neither the overall trend nor the distribution of residuals correspond with the patterns of population growth and decline during this period (Fig. 2c). Hence, the recent decline, like its predecessor, appears to have been caused largely by increased mortality.

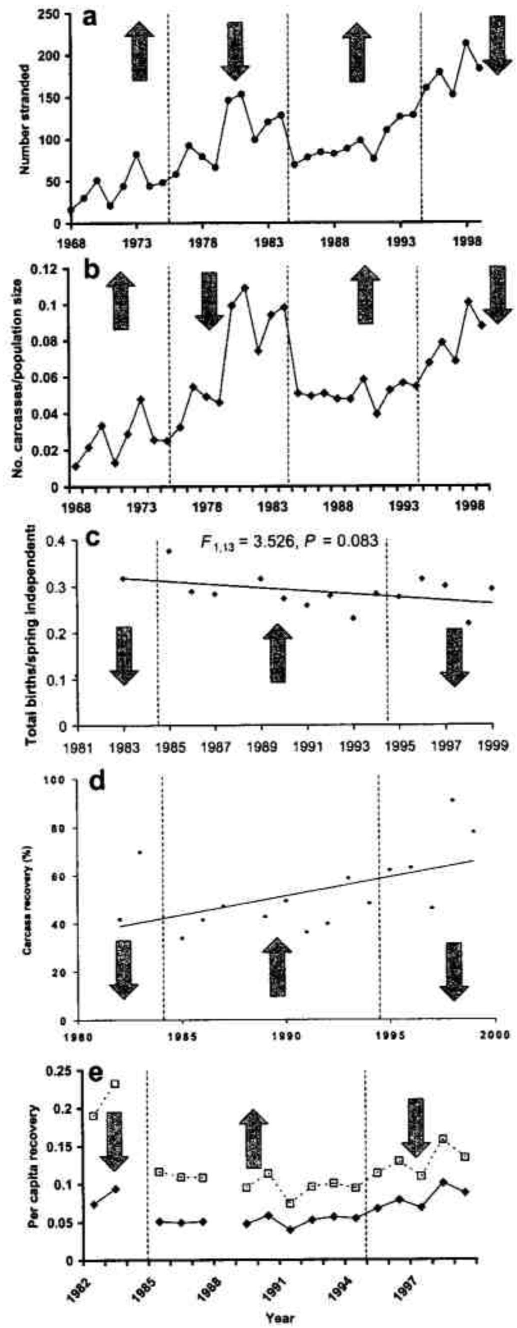
The salvage data are consistent with this explanation. The per capita number of recovered beach-cast carcasses increased during the 1976–1984 and 1995–1999 declines (Fig. 2b). This trend is partially explained by an increased carcass recovery rate of 1.56% per year since 1983 ($F_{1,14} = 45.36$, $P < 0.001$), for a total of 26% (Fig. 2d). However, even when per capita recoveries are adjusted for this change, elevated carcass recovery rates are seen during the periods of population decline (Fig. 2e).

While the 1976–1984 decline is believed to have resulted from elevated incidental mortality in the net fisheries[2] (Estes 1990), reasons for the more recent decline are less certain. Proposed explanations include entrapment in fishing gear, disease, starvation, and attacks by great white sharks (*Carcharodon carcharias*). Each of these should produce associated patterns in the carcass database between periods of population increase and decline if the carcasses provide a representative sample of mortality. We sought to evaluate these explanations in the analyses described below.

Mortality Patterns in Periods of Population Growth and Decline

The proportions of carcasses in the four mortality groups differed significantly among time periods (Table 2). There are several apparent reasons for this, including a small number of human-caused mortalities after 1995, increased natural mortality after 1985, a high incidence of shark mortality from 1968–1975, and elevated numbers of carcasses for which cause of death was unknown during the periods of population decline. Age composition of the carcasses also differed significantly through time, mainly due to relatively large numbers of subadults and small numbers of adults in 1968–1975. The mass/length ratio of adult carcasses decreased significantly through time, especially in males (2-way ANOVA, Table 2). However, the sex/time interaction was not statistically significant and the mass/length ratio of female carcasses that died from acute trauma (presumably representing healthier animals) also declined significantly through time (1-way ANOVA, Table 2). Neither the sex ratio (from 1968 through 1999) nor the pro-

[2] Wendell, F. E., R. A. Hardy and J. A. Ames. 1985. Assessment of the incidental take of sea otters, *Enhydra lutris*, in gill and trammel nets. Technical Report 54. Marine Resources Branch, California Department of Fish and Game, Sacramento, California. Document can be obtained from California Department of Fish and Game, 1451 Shaffer Road, Santa Cruz, CA 95060.


a
Number stranded
250
200
150
100
50
0
1968
1973
1978
1983
1988
1993
1998
b
No. carcasses/population size
0.12
0.1
0.08
0.06
0.04
0.02
0
c
Total births/spring independents
$F_{1,13}$ = 3.526, P = 0.083
0.4
0.3
0.2
0.1
1981 1983 1985 1987 1989 1991 1993 1995 1997 1999
d
Carcass recovery (%)
100
80
60
40
20
1980 1985 1990 1995 2000
e
Per capita recovery
0.25
0.2
0.15
0.1
0.05
1982 1985 1988 1991 1994 1997
Year

portion of fresh carcasses that died from infectious disease (1992–1999) varied significantly among periods of population increase and decline (Table 2). In the following sections we present these data in the context of expectations from the various hypothesized reasons for population change.

Entanglement in fishing gear—Because it is very difficult to identify drowning as a cause of death in most instances,[3] we reasoned that otters drowning because of entanglement in fishing gear would be included in the general mortality category of "unknown" and especially "uncertain, with no obvious trauma." Overall, 72% of the carcasses died of unknown causes (Table 2). The percentage of otter carcasses that died of unknown causes was 7.1% greater during the periods of population decline than during the periods of population increase. The proportions of carcasses in the category of "uncertain, with no obvious trauma" also differed significantly among time periods and were greatest during the periods of population decline. However, this latter analysis is strongly influenced by a particularly low value for the 1968–1975 period (Table 2).

Disease—The percentage of carcasses identified as dying from natural causes, including infectious diseases and complications from parasite infestations, increased after 1984. However, there was no marked increase in the proportion of carcasses that died of natural causes from 1995 to 1999, when the population was declining, compared to 1985–1994, when the population was increasing (Table 2). Detailed necropsies on fresh carcasses began in 1992. The percentage of these otters dying of disease, while large, also did not differ significantly between the 1992–1994 and 1995–1999 periods (Table 2).

Nutritional limitation—If nutritional limitation were in part responsible for changing population trends over the past 30 yr, this might be reflected by reduced mass/length ratios (Monson *et al.* 2000*a*) and lessened amounts of subcutaneous fat. Overall, the mass/length ratios of adult otter carcasses declined through time although this pattern was most evident in males (Table 2). Because

[3] Personal communication from Melissa Miller, California Department of Fish and Game, 1451 Shaffer Road, Santa Cruz, CA 95060.

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Figure 2. Temporal patterns of reproduction and mortality in California sea otter, 1968–1999. Vertical dashed lines mark breaks between periods of population increase and decline (indicated respectively by upward and downward block arrows). Note data missing for 1984 and 1988 in some panels because fall population surveys were not conducted and thus total pup production could not be estimated. (a) Number of recovered beach-cast carcasses; (b) per capita recovery rate of beach-cast carcasses, obtained by dividing numbers in panel (a) by abundance estimates in Fig. 1; (c) per capita pup production, obtained by dividing sum of number of dependent sea pups counted during spring and autumn surveys by number of independent otters counted during spring surveys (only data from shore survey areas included); (d) estimated percentage of deaths in independent sea otters retrieved as beach-cast carcasses, obtained by dividing number of beach cast carcasses by total number of pups counted in spring plus fall surveys (line is linear regression); (e) estimated per capita recovery rate (solid symbols, solid line), adjusted for increasing carcass recovery rate over time (open symbols, dashed line) by dividing estimated recovery rates by estimated proportion of deaths retrieved as beach-cast carcasses (obtained from linear regression in panel d).