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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.

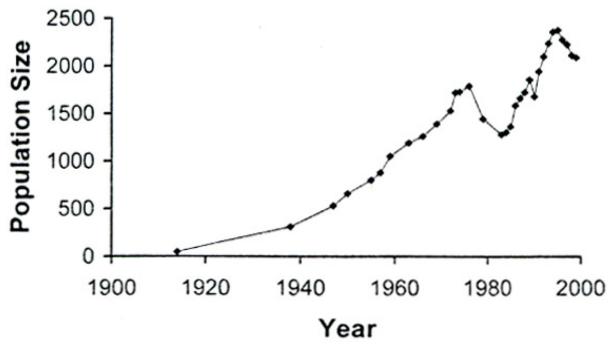


Figure 1. Abundance of California sea otter population from 1911 through 1999. Data from 1982 onward are counts made during annual spring surveys. Earlier data from counts and estimates using a variety of methods. The 1914 data point is uncertain although the population was very small at that time.

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.

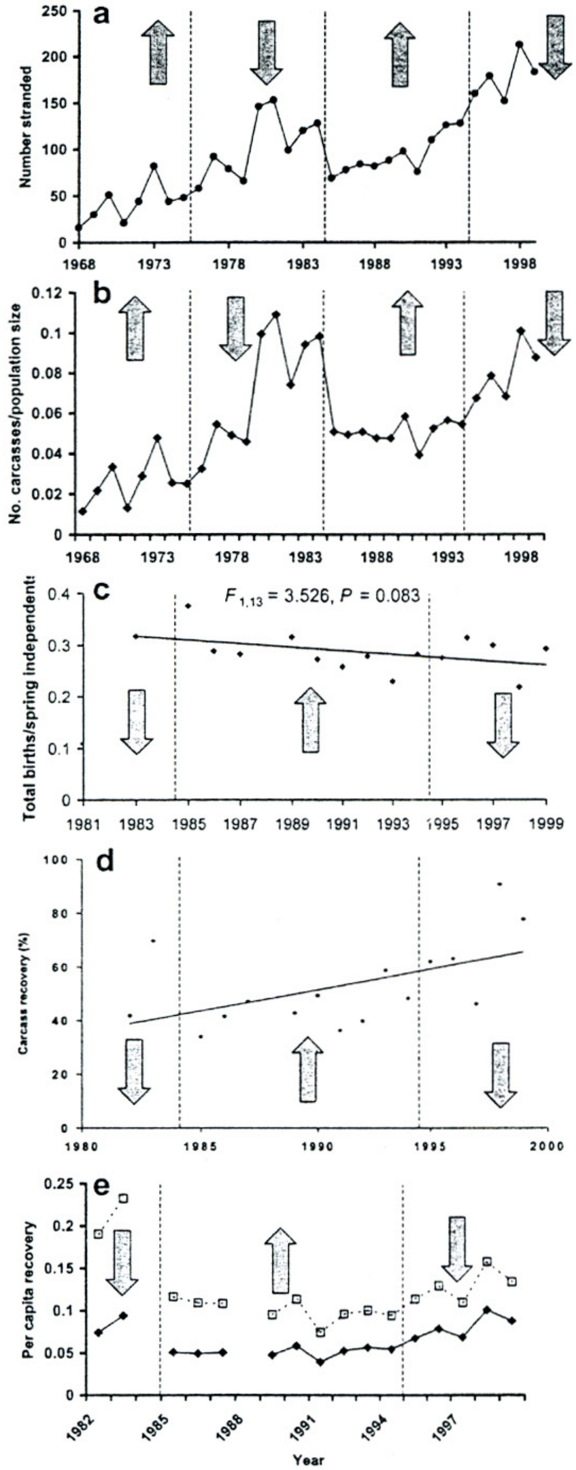
The salvage data are consistent with this explanation. The per capita number of recovered beach-cast carcasses increased during the 1976–1984 and 1995–1999 declines (Fig. 2b). This trend is partially explained by an increased carcass recovery rate of 1.56% per year since 1983 ($F_{1,14} = 45.36$, $P < 0.001$), 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
1968 1973 1978 1983 1988 1993 1998
c
$F_{1,13}$ = 3.526, P = 0.083
Total births/spring independents
0.4
0.3
0.2
0.1
0
1981 1983 1985 1987 1989 1991 1993 1995 1997 1999
d
Carcass recovery (%)
100
80
60
40
20
0
1980 1985 1990 1995 2000
e
Per capita recovery
0.25
0.2
0.15
0.1
0.05
0
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).

adult females typically remain in the center of the range where otters have exploited resources for many years, and otters generally lose weight before dying of disease, we reasoned that mass/length ratios for adult female carcasses that died from trauma might be a more sensitive indicator of nutritional limitation to the population. A weakly significant ($P = 0.057$) decline in mass/length ratios for these female carcasses through time is evident, even though sample sizes are small (Table 2). Levels of subcutaneous fat were recorded beginning in 1992. The percentages of otter carcasses with no or scant levels of subcutaneous fat has remained virtually unchanged (61.6 in 1992–1994; 62.6 in 1995–1999).

Shark kills—The number of shark-mortalities has varied considerably among years (from 3 to 33 carcasses retrieved). Overall, the number of shark-bitten carcasses (expressed as a proportion of the population) appears to have increased through time (Fig. 3), especially during the periods of population decline (Table 2). This latter pattern is statistically significant ($F_{3,28} = 3.033$, $P = 0.046$). An unusually large number of carcasses with shark bites were recovered in 1999.

Seasonal and Geographical Patterns of Mortality

Carcasses were recovered throughout the year though the highest numbers were obtained in spring and summer (Fig. 4). Overall, 51.4% of the carcasses were recovered between April and August compared to an expected 41.7% recovery during this period if mortality rate were seasonally uniform. The monthly distributions of carcass recoveries differed significantly among the four time periods (χ^2, 33 df = 78.8, $P < 0.001$), with elevated spring/summer recovery rates being more pronounced during the periods of population decline than they were during the periods of population increase.

Annual per capita stranding rate varied from a low of 0.03 in the area between Cayucos and Seaside to a high of 0.23 in the area north of Seaside (Table 3). There are no clear trends through time for any of the three areas.

Discussion

Population trends prior to 1982 (Fig. 1) are potentially confounded by variable survey methods and estimation techniques.[4] The resulting uncertainty, together with the limited data available for 1976–1984, has brought into question the magnitude and even the validity of the apparent decline during this period. Two lines of reasoning indicate that a decline indeed occurred. A substantially elevated mortality rate from entanglement in fishing gear was reported during the late 1970s and early 1980s,[2] and the resumption of population growth coincided with restrictions to the fishery (Estes 1990). Furthermore, a population decline between 1976 and 1984 is the most reasonable explanation for the trend discrepancy between the 1938–1976 and 1984–1995 periods.

Although a consistent survey method has been used since 1982, the recent population decline might also be explained as a methodological artifact because

[4] Wendell, F. E., R. A. Hardy and J. A. Ames. 1986. A review of California sea otter, *Enhydra lutris*, surveys. Technical Report No. 51. 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.

Table 2. Summary statistics of cause of death in California sea otter carcasses by time period. Bold numbers indicate periods of population decline. Statistical tests for significant variation among times periods provided on the right. Sample sizes shown in italics.

	Time period							
Cause of death (% of carcasses)	1968–1975	1976–1984	1985–1994	1995–1999	Test	df	Test statistic	P
By category					Crosstabulation	9	$\chi^2 = 187.43$	$\ll 0.001$
No. strandings	*334*	*940*	*940*	*891*				
Human	6.29	**6.60**	9.89	**1.91**				
Natural	6.29	**4.26**	18.40	**18.41**				
Shark	12.87	**7.55**	8.40	**9.20**				
Unknown	74.55	**81.60**	63.30	**70.48**				
Sample size	*31*	*222*	*213*	*228*				
Uncertain, no trauma	9.28	**23.62**	22.66	**25.59**	Chi-square	3	$\chi^2 = 6.85$	0.077
By age					Crosstabulation	9	$\chi^2 = 35.2$	$\ll 0.001$
Sample size	*317*	*913*	*903*	*876*				
Pups	26.18	**29.17**	28.13	**29.11**				
Subadults	23.66	**16.67**	14.95	**14.16**				
Adults	35.65	**45.83**	43.3	**44.06**				
Aged	14.51	**8.33**	13.62	**12.67**				
By sex (pups excluded)								
Sample size	*292*	*701*	*680*	*700*				
Males	59.25	**52.78**	52.35	**57.57**	Crosstabulation	3	$\chi^2 = 7.30$	0.063
Females	40.75	**47.22**	47.65	**42.43**				
From disease (fresh carcasses only)	nd	nd	38.60	**34.76**	Chi-square	1	$\chi^2 = 0.36$	0.549
Sample size			*127*	*233*				
From shark bites (No/Pop size)	0.00296	**0.00554**	0.00422	**0.00755**	1-way ANOVA	3,28	$F = 3.033$	0.046
Sample size	*43*	*71*	*79*	*82*				

Table 2. Continued.

Cause of death (% of carcasses)	Time period 1968–1975	1976–1984	1985–1994	1995–1999	Test	df	Test statistic	*P*
Mass (kg)/Length (cm)—adults only					2-way ANOVA			
Sample size	*72*	*197*	*355*	*318*	Time	3,934	$F = 4.489$	0.004
Males	*0.1972*	0.1903	0.1907	0.1824	Sex	1,934	$F = 413.33$	<0.001
Females	0.1409	0.1440	0.1401	0.1352	Sex × Time	3,934	$F = 0.619$	0.603
Sample size	*13*	*22*	*24*	*25*				
Females (with trauma)	0.1565	0.1540	0.1533	0.1340	1-way ANOVA	3,81	$F = 2.607$	0.057

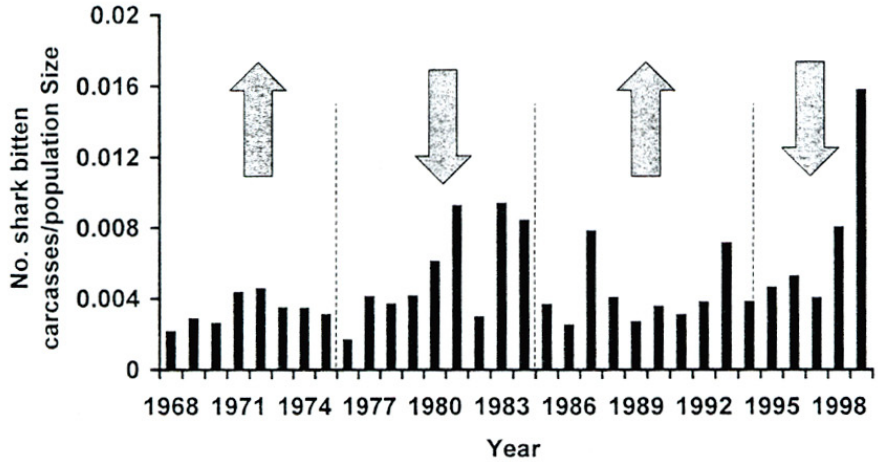

Figure 3. Number of beach cast sea otter carcasses for which shark attack was the certain or likely cause of death. Data plotted as number of carcasses/population counts or estimates (Fig. 1) for corresponding years.

the range of the population has expanded during this time; recently colonized habitat is surveyed from the air; and approximately 30% fewer otters are seen from the air than from the ground (CDFG, unpublished data). However, this explanation is unlikely. The highest percentages of otters counted from the air (over 30% of the total count each year) were obtained from 1993 to 1995 whereas the percentages of otters counted from the air since the population decline began in 1995 have ranged between 14% and 26% (USGS, unpublished data). Furthermore, a subset of the survey data from the central part of the range, an area that has been counted by the same procedures since 1982, also indicates a decline in abundance from 1995 to 1999.

The theoretical maximum rate of population growth (r_{max}, Cole 1954) for sea otters is about 20% per year, based on an age of first reproduction of 3 yr, a longevity of 15 yr, and a female fertility rate of 0.5 female young/adult female/year (Estes 1990, Riedman and Estes 1990). A number of sea otter populations, including those in Washington State, British Columbia, southeast Alaska, and the western Aleutian Islands have achieved sustained periods of population increase at r_{max} (Estes 1990), although several of the remnant populations appear to have recovered at somewhat lower rates (Bodkin *et al.* 1999). The California sea otter population, in contrast, has not increased at more than about 5% per year through most of the 20th century, during which time there also were at least two periods of decline—the mid-1970s to the early 1980s and the mid- to late 1990s (Fig. 1). Both the interpopulation discrepancies in λ and the more subtle changing trends within the California population appear to be driven largely by variation in mortality (Riedman *et al.* 1996, Monson *et al.* 2000*a*).

Several patterns of mortality stand out as being unique to California sea otters, the most striking of which is the high percentage (42% of all carcasses) of prime-age adults (approximately 3–10 yr old) in the beach-casts. A large percentage of prime-age adult sea otters occurred in the beach-cast carcasses following the *Exxon Valdez* oil spill (Monson *et al.* 2000*b*), and the precipitous, recent decline of sea otters in western Alaska (reportedly from increased killer whale

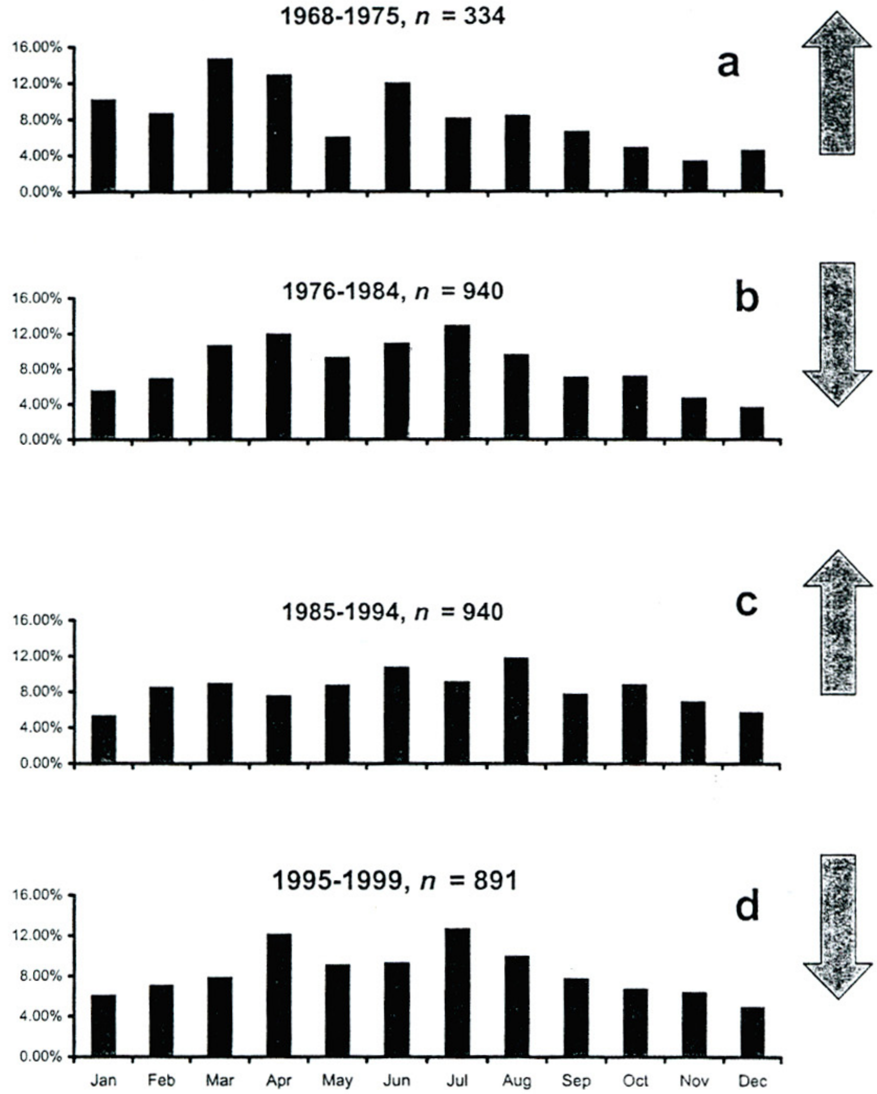

Figure 4. Monthly patterns of number of beach-cast sea otter carcass retrieved in California from 1968 to 1999. Data sorted by periods of population increase (panels a and c) or decline (panels b and d).

predation; Estes *et al.* 1998) was driven by elevated mortality rates of all ages. Otherwise, mortality rate is normally low in presenescent adult sea otters and this is reflected by the low percentage of prime-age adults in beach-cast carcasses (Kenyon 1969, Bodkin *et al.* 2000, Monson *et al.* 2000*a*) from other regions.

The seasonal pattern of beach-cast carcass recoveries in California is also unusual. Most natural deaths in other regions occur during late winter and early spring (Kenyon 1969, Bodkin *et al.* 2000), probably due to the accumulated rigors of winter weather conditions. Rarely are beach-cast carcasses found during other times of the year. In California, however, beach-cast carcasses are recovered throughout the year, with the highest numbers in spring through late summer, normally a period of mild weather.

Table 3. Summary of sea otter population counts, number of annual strandings, and per capita stranding rate for California from 1983 to 1999. Data segregated into 3 main areas. Periods of population decline shown in bold.

	North End of Range to Seaside			Seaside to Cayucos			Cayucos to South End of Range		
Year	Spring count	No. of documented strandings	Documented strandings per capita	Spring count	No. of documented strandings	Documented strandings per capita	Spring count	No. of documented strandings	Documented strandings per capita
1983	52	26	0.50	1,108	60	0.05	117	34	0.29
1984	55	24	0.44	1,119	69	0.06	129	35	0.27
1985	54	14	0.26	1,201	38	0.03	106	17	0.16
1986	93	36	0.39	1,384	33	0.02	109	9	0.08
1987	78	32	0.41	1,436	37	0.03	147	15	0.10
1988	80	17	0.21	1,534	41	0.03	111	24	0.22
1989	109	29	0.27	1,540	29	0.02	207	30	0.14
1990	136	26	0.19	1,329	37	0.03	215	34	0.16
1991	195	25	0.13	1,446	30	0.02	300	23	0.08
1992	249	28	0.11	1,601	40	0.02	251	42	0.17
1993	287	50	0.17	1,539	38	0.02	413	38	0.09
1994	217	37	0.17	1,732	47	0.03	410	44	0.11
1995	188	56	0.30	1,696	61	0.04	493	43	0.09
1996	331	61	0.18	1,670	40	0.02	277	78	0.28
1997	227	52	0.23	1,643	35	0.02	359	65	0.18
1998	246	83	0.34	1,388	79	0.06	480	51	0.11
1999	273	78	0.29	1,336	45	0.03	481	64	0.13
	$\Sigma = 2,870$	$\Sigma = 674$	0.23	$\Sigma = 24,702$	$\Sigma = 759$	0.03	$\Sigma = 4,605$	$\Sigma = 646$	0.14

The key to understanding the overall depressed growth and periods of decline in the California sea otter population, therefore, appears to lie with understanding the cause of death in prime-age animals and the reason so many of these animals die during the summer. Because the California sea otter occurs near the species' southern range limit, elevated summer mortality might be related to thermal intolerance. This explanation seems unlikely given that the coldest water temperatures and highest rates of production in central California coincide with spring/summer upwelling. Nor is it evident why starvation- or disease-induced mortality should be more prevalent during summer. Increased net, pot, and trap fishing occurs during this period,[5] probably because of the more favorable weather conditions. Although there are striking differences in carcass age composition and seasonal mortality patterns between California sea otters and those elsewhere, dissimilarities within California between periods of population growth and decline are more subtle. Even though the demographic parameters measured from the carcass record differed significantly between the periods of population growth and decline, our statistical power also was high due to large sample sizes. The important question is whether or not these differences are biologically significant. They may be, as preliminary modeling studies suggest that even modest shifts in mortality can account for the observed rates of change during periods of population increase and decline.[6]

While further work is needed to properly evaluate the demographic significance of the carcasses record, several tentative conclusions can be drawn from our analyses. The proportion of fresh carcasses that died from infectious disease did not differ before and after 1995, thus indicating that an increased incidence of infectious disease is not responsible for the recent population decline. However, infectious disease, including acanthocephalan peritonitis, protozoal encephalitis, bacterial infections from external wounds (primarily *Streptococcus*), and valley fever (Coccidioidomycosis) were the proximate cause of death in more than 40% of the fresh carcasses (Thomas and Cole 1996), and Lafferty and Gerber (2002) reported that the proportion of the population found dead on the beach in any given year is positively correlated with the proportion of deaths caused by acanthocephalan peritonitis. Parasites and microbes for which the sea otter is not a natural host are mostly responsible for these diseases,[7] thus raising the question of whether infectious disease in the California sea otter should be considered as a natural phenomenon. Indeed, recent studies by Miller *et al.* (2001) suggest that organisms associated with humans and domesticated animals are significant contributors to disease-related mortality in sea otters. Thus, while our preliminary analyses do not indicate that changes in infectious disease are responsible for the four periods of growth and decline since 1968, infectious disease may well be an

[5] Personal communication from Marine Fisheries Statistical Unit, California Department of Fish and Game, 4665 Lampson Avenue, Suite C, Los Alamitos, CA 90720.

[6] Tinker, M. T., J. A. Estes and D. F. Doak. 2000. Development of a spatially explicit population model to assess potential population impacts associated with translocation of sea otters from south of Pt. Conception. Final Report for Friends of the Sea Otter. 40 pp. Document can be obtained from U.S. Geological Survey, Center for Ocean Health, 100 Shaffer Road, University of California, Santa Cruz, CA. 95060.

[7] Personal communication from Kevin Lafferty, U.S. Geological Survey, Channel Islands Field Station, Marine Science Institute, University of California, Santa Barbara, CA 93106.

important factor for the overall depressed rate of population growth in California sea otters during the 20th century.

Per capita pup counts declined by about 5% from 1982 to 1999 (Fig. 2c). While this trend is not statistically significant, it does indicate a modest decline in productivity. Whether that decline was caused by reduced fertility, elevated postpartum mortality, or both is unclear, although studies done in the 1980s and early 1990s (Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman *et al.* 1996) reported high levels of fecundity, with over 90% of adult females giving birth each year. The co-occurring trend of decline in mass to length ratios in carcasses of adult males and adult females with trauma hints at elevated nutritional stress through time. In this regard, a decline in the quality or abundance of food could have occurred for a variety of reasons, including prey depression by the otters themselves. Otters have inhabited the areas from which most of the carcasses are retrieved (Seaside northward and Cayucos southward) for many years. Both 24-h activity budgets (Ralls and Siniff 1990) and forging data (Ralls *et al.* 1995) collected during the 1980s suggested that at least some age-sex classes might be subject to nutritional stress. Together, these trends indicate that conditions in central California have become less favorable for the survival and reproduction of sea otters over the past several decades. Nonetheless, measures of productivity and body condition do not correspond well with the periods of population decline and increase, thus suggesting that these shorter-term changes have other causes.

The summer increase in proportion of retrieved carcasses was most pronounced during periods of population decline, thereby indicating that elevated summer mortality is responsible for the declines. The conclusion that the 1976–84 decline was likely due to entanglement in a then-growing set-net fishery (Estes 1990) is based on the large number of otters that died in the fishery,[2] and the fact that the population began to increase again shortly after the fishery was restricted to deeper water. Similar increases in mortality incidental to commercial fisheries may be responsible for the recent population decline. This idea is supported by the facts that captive otters readily enter pots that are used in a shallow water live fish fishery (USGS and Monterey Bay Aquarium, unpublished data), reported landings in this fishery increased substantially from 1995 to 1999 (Fig. 5a), and annual carcass recoveries and reported landings are significantly correlated (Fig. 5b).

Even though a great deal of information is available from the large number of beach-cast sea otter carcasses that have been salvaged over the 31-yr period of our analysis, the high proportion of dead otters that were not recovered, and the high proportion of recovered carcasses for which cause of death was unknown make the database difficult to interpret. We conservatively estimate that some 40%–60% of the sea otter deaths that occurred between 1982 and 1999 were not recovered as beach-cast carcasses. Failure to recover more of the carcasses was due in part to regional variation in the probability of recovery (Table 3). Furthermore, the extent to which beach-cast carcasses provide a representative sample of mortality is uncertain. Clearly, pups are underrepresented in the sample. Also, sick or moribund animals may be more likely to come ashore than those that are drowned and discarded by fishers at sea because weakened animals tend to haul out, whereas drowned and discarded ones (at least those drowned in gill nets at depth) usually sink.[2] The large proportion of carcasses for which the cause of death was unknown adds further uncertainty to a population-level assessment of

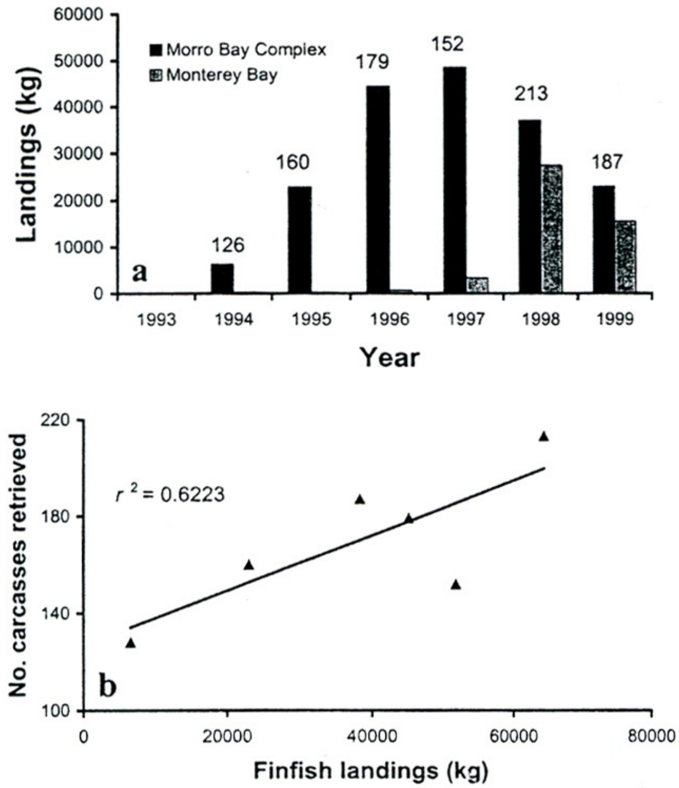

Figure 5. (a) Commercial finfish trap landings (gear code 21). Morro Bay complex includes Morro Bay and Port San Luis. Monterey Bay Area includes Monterey, Moss Landing, and Santa Cruz. Number of stranded sea otters shown above bars. (b) Annual number of sea otter carcass retrieved *vs.* annual finfish landings from fish traps. Line is least squares best fit.

mortality because cause of death could differ between the "knowns" and "unknowns." For instance, shark bite and shooting mortalities are highly diagnostic, even in extensively decomposed carcasses, whereas drownings and deaths from certain biotoxins are very difficult to diagnose, even in fresh carcasses. Yet another problem with interpreting the carcass record is that the proximate and ultimate causes of death may differ. For instance, animals weakened by poor nutrition or other factors may be more susceptible to infectious disease than those that are strong and healthy. These potential complications are nearly impossible to resolve from carcass records alone.

Despite the many uncertainties, the beach-cast carcass record for California sea otters provides insight into reasons for the slow growth and changing trends of the living population over the past 31 yr. While mortality caused by fishing gear may have contributed to the recent population declines, it is probably not responsible for the prolonged period of slow population growth during the 20th century because the causal fisheries developed too recently for that to be possible. Long-term declines in pup-to-adult and adult mass-to-length ratios indicate that conditions for sea otters in California are deteriorating. Chronically high levels of mortality from infectious disease also could be contributing to these long-term patterns because infectious disease was diagnosed as the cause of death in more than 40% of the fresh carcasses during the 1990s (Thomas and Cole 1996), there is no indication that this pattern has changed over time, and the population growth rate has been depressed throughout the 20th century. Conversely, neither reduced fecundity or body condition, nor elevated mortality from infectious disease appears to be responsible for the shorter periods of population decline.

Several areas of additional research could help clarify the main causes of mortality. One such need is for a comparative study of beach-cast carcasses from other populations. While the age-composition of beach-casts elsewhere is well known (Kenyon 1969, Bodkin *et al.* 2000, Monson *et al.* 2000*a*, *b*), the cause of death is not. It is important, in particular, to determine whether or not infectious disease is more common in California than elsewhere. While poorly known, infectious disease does occur in other sea otter populations and has been proposed as an important contributing factor to the sharp decline in sea otter numbers that occurred at Amchitka Island (in the Aleutian archipelago) during the 1940s (Rausch 1953, Kenyon 1969). A second area of research should focus on the living population of California sea otters, particularly current levels of fecundity and pup survival and the patterns and processes leading to death. This should include studies of disease in living animals and increased monitoring of fisheries that potentially threaten sea otters. Only with such information will it be possible to properly interpret cause of death from carcass records. Further modeling is needed to determine the extent to which subtle changes in mortality schedules indicated by the carcass record are capable of driving the observed dynamics of the population. Finally, we urge other investigators to more fully analyze the carcass database for the California sea otter. Our analysis is purposely broad and intended to identify only the most obvious patterns. An updated database is available from the authors.

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