Growth and Equilibrium in Sea Otter Populations

James A. Estes

Journal of Animal Ecology, Volume 59, Issue 2 (Jun., 1990), 385-401.

Journal of Animal Ecology (1990), **59,** 385–401

GROWTH AND EQUILIBRIUM IN SEA OTTER POPULATIONS

BY JAMES A. ESTES

United States Fish and Wildlife Service, Institute of Marine Sciences, University of California, Santa Cruz, California, 95064, U.S.A.

SUMMARY

(1) Counts through time were compiled for five sea otter (*Enhydra lutris*) populations in the north-east Pacific Ocean that were below equilibrium density: Attu Island, south-east Alaska, British Columbia, Washington State, and central California. Similar data were obtained from the equilibrium density population at Amchitka Island in 1971 and 1986.

(2) Shorelines of Attu and Amchitka islands each were divided into forty-five segments, within which lineal (length of shore at mean higher high water) and areal (mean higher high water to the 10-fathom (18·3-m) depth contour) measures were made of the amount of habitat.

(3) Rate of increase for the four northern populations was 17–20% year^{-1}. Density- or size-dependent changes in rate of increase could not be demonstrated for any of these populations. The California population, in contrast, has undergone three apparent growth phases: the early 1900s to the mid-1970s when it increased about 5% year^{-1}; the mid-1970s to the mid-1980s when it declined about 5% year^{-1}; and the mid-1980s to 1988 when it increased about 7% year^{-1}. An exponential growth model accounted for 92–98% of the variation in counts through time in all cases.

(4) Population increase at Attu Island was achieved largely by range expansion as opposed to increased density. Range expansion in lineal and areal habitat occurred at 11% and 13% year^{-1}, respectively; neither rate was lower ($P > 0{\cdot}25$) than the observed rate of increase in numbers of animals counted.

(5) Despite similarities in island size and physical environment, the most conservative estimates of population density at Amchitka Island were $> 3\times$ greater than maximum density estimates for Attu Island.

(6) Surveys of Amchitka Island from the mid-1930s through the mid-1980s indicate that the population increased to a peak in the 1940s; declined abruptly thereafter; and subsequently increased to a new and higher equilibrium in the 1960s, where it has since remained.

(7) These population data, together with information on sea otter foraging and benthic community structure at Attu and Amchitka islands, suggest that multiple population equilibria exist in this system, emanating from complex trophic interactions low in the food web. I hypothesize that the lower population equilibrium is achieved largely or exclusively on an invertebrate diet consisting principally of herbivorous sea urchins. When unregulated by sea otter predation, the rocky benthos is deforested by sea urchin grazing. As growing otter populations compete increasingly for food, grazing intensity declines and the system shifts to one dominated by kelp beds, in turn leading to increased production, a shift in habitat structure, and population increases of kelp bed fishes.

Apparently this new food resource elevates the sea otter population to a higher and more stable equilibrium.

INTRODUCTION

The intrinsic rate of increase is '. . . the exponential rate at which a population with a stable age distribution grows when no resource (e.g. food, space, shelter and water) is in short supply' (Caughley 1977: 53). Few direct measures of intrinsic rate of increase are available for large mammals in natural environments. This is mainly because: (i) large mammals typically are long-lived and have low birth rates (Eisenberg 1981), thus requiring many years for significant population increases to occur; (ii) human-related disturbances often confound the data; (iii) population status in relation to equilibrium density is uncertain; and (iv) gains or losses from emigration or immigration are unknown.

Sea otters (*Enhydra lutris* Linnaeus) in the North Pacific Ocean provide unusual opportunities to measure population growth. Overhunting in the eighteenth and nineteenth centuries fragmented populations and nearly exterminated the species (Kenyon 1969). Surviving populations were legally protected in 1911, most of these subsequently increased, and several appear to have reached equilibrium levels. The sea otter's habitat in these remote regions probably remains largely free from human disturbances. Furthermore, due to the sea otter's dependence on shallow benthos for food (Kenyon 1969; Estes, Jameson & Johnson 1981), their tendency to be gregarious and rather sedentary (Garshelis & Garshelis 1984; U.S. Fish & Wildlife Service 1987), and the deep, wide passes separating many of the oceanic islands around which they live (Kenyon 1969), much of the species' natural range remains unoccupied. Finally, interactions between sea otters and nearshore communities are well understood (VanBlaricom & Estes 1988).

In the early 1960s a small population became re-established at Attu Island (Jones 1965), westernmost of the Aleutian archipelago. Sea otters were reintroduced to south-east Alaska, British Columbia, and Washington State during the late 1960s and early 1970s (Jameson *et al.* 1982). A remnant population also survived in central California (Kenyon 1969). These populations were sufficiently far away from one another, and from other populations, that subsequent changes in their abundance and distribution must have resulted largely or exclusively from intrinsic births and mortalities.

Here I report long-term changes in these populations. I first compare rate of increase among the populations at Attu Island, south-east Alaska, British Columbia, Washington State, and central California. Next, I illustrate temporal changes in the distribution and density of sea otters at Attu Island. Finally, I compare sea otter densities between Attu Island (population below equilibrium) and Amchitka Island (population at or near equilibrium). From these population data, and information on sea otter diets and food web interactions, I develop a hypothesis to explain relationships between the chronology of population change and population status relative to equilibrium density. I will suggest that in some areas the effects of sea otter predation is to enhance, rather than to depress, their equilibrium population density.

METHODS

Population surveys at Amchitka and Attu islands

Surveys at Attu Island began in 1932 (Kenyon 1969). These were done by various observers and methods. Thereafter, I counted otters from a 5·2-m skiff. Large groups of

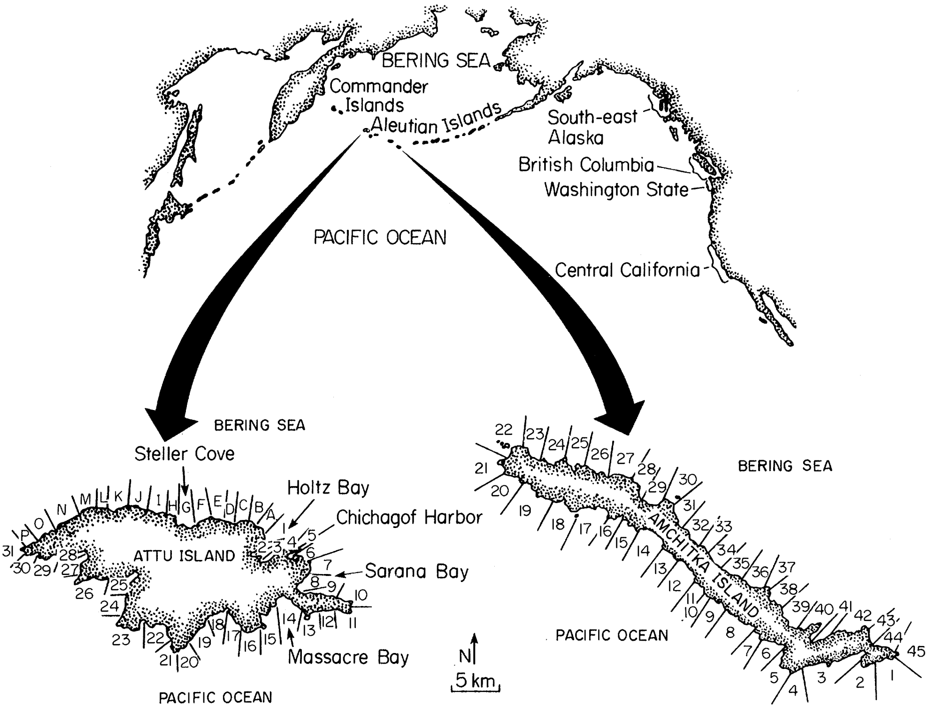

Fig. 1. The North Pacific Ocean showing locations of study populations and place names referred to in the text. The boundaries of coastal segments within which sea otters were counted are shown on the inserts of Amchitka and Attu islands.

animals and extensive areas of shallow habitat were counted from shore or offshore islets using 10 × binoculars and a 50–80 × telescope.

Surveys were conducted during calm weather from mid-June to mid-August. The shoreline of Attu was divided into forty-five contiguous segments (Fig. 1). An inshore transect was established parallel to shore along the seaward margin of kelp beds. When possible, an offshore transect about 0·5–1 km further to seaward was run on the return trip. Each otter sighted was scored by coastal segment, inshore or offshore transect, and whether it was an independent or female with pup. I used similar methods at Amchitka Island in 1971 and 1986.

Surveys of other populations

Sea otter populations in south-east Alaska and the State of Washington were surveyed by methods similar to those described above (Jameson *et al.* 1982, 1986; Johnson *et al.* 1983; K. Pitcher, unpublished). Fixed-wing aerial surveys were used in British Columbia (Bigg & MacAskie 1978; MacAskie 1984, 1987). Several aerial and shore-based counting techniques have been used in California (United States Fish & Wildlife Service 1987; Estes & Jameson 1988). I use only the number of otters counted in the following analyses.

Data analysis

Annual rates of change in abundance or range were estimated from the exponential growth equation, $N_t = N_0 e^{rt}$, where N_t = population count or range in year t, N_0 = population count or range in some earlier year 0, and r = annual rate of increase. Because sea otters reproduce throughout the year, I did not calculate annual rate of increase as $e^r - 1$. Linear regressions on ln (counts) versus time were done to obtain the best fit to exponential population change, and to compare changes among populations. Power of the test ($1-\beta$, where β = probability of Type 2 error) that $r=0$ was estimated by the methods of Gerrodette (1987: 1367, eqn (20)), with α = (probability of Type 1 error) = 0·05, r = observed annual rate of increase, and CV (coefficient of variation) = 0·13 (determined from seven replicate aerial surveys of the California population; J. A. Estes, unpublished). I used a one-way analysis of covariance (ANCOVA) to test the hypothesis that growth rates were similar among populations (Zar 1974), and a Student–Newman–Keuls (SNK) multiple range test to evaluate significant differences among specific populations.

Rates of change in population size were calculated for all pairwise combinations of dates for which surveys were done. I use these data, and the patterns of residual variation around the best-fit line, to evaluate temporal deviations from perfect exponential changes in population counts.

Population densities were measured at Attu and Amchitka islands. I used lineal (shoreline distance at mean higher high water) and areal (sea surface between mean higher high water and the 10-fathom (fm) (= 18·3-m) [Attu and Amchitka Island] or 20-fm (= 36·6-m) [Attu Island] depth contour) measures of sea otter habitat. (The 36·6-m contour for Amchitka Island was unavailable.) Both the 18·3 and 36·6-m contours were used because the depth limit of the sea otter's habitat is uncertain. Measurements were made with a digitizer from United States Coast and Geodetic Survey Oceanographic charts (Attu Island) and United States Army Gunnery charts (Amchitka Island). All measurements were done twice, from which % differences were calculated as (maximum − minimum)/minimum. To determine if shoreline or area is a better predictor of sea otter density, counts at Attu and Amchitka were regressed against both variables (using the most recent survey data in each case). To test the hypothesis that population growth is achieved by range expansion, density vs. time was compared with number counted vs. time for the Attu population. To test the hypothesis that growing and equilibrium populations have similar densities, I compared density measures between Attu and Amchitka islands.

RESULTS

Population increase

If data obtained by the same methods at each site are used, sea otter population counts at Attu Island, south-east Alaska, British Columbia, and the State of Washington have increased at 17–20% year^{-1} (Table 1, Fig. 2). Exponential increase explained 93–96% of the total variation in numbers in each population (Table 1). Even though the statistical tests for significant increases by populations in south-east Alaska and British Columbia lacked power, these populations must have increased by at least the indicated rates because their initial sizes are known.

Rate of increase differed among the five populations ($F=9{\cdot}06$, $P<0{\cdot}005$, d.f. = 4,22). Population counts in California increased at a lower rate than at Attu Island ($P<0{\cdot}001$), south-east Alaska ($P<0{\cdot}001$), British Columbia ($P<0{\cdot}005$), and Washington State ($P<0{\cdot}001$), whereas none of the latter four rates differed significantly (SNK test). Trends in counts of the California population differed during several time periods. From 1914, when the population was estimated to contain about 50 individuals, to 1976, when a

TABLE 1. Rates of increase in counts of sea otter populations

Location	Dates	Number of surveys	Annual rate of increase (R)	r^2	Pups: independent	$P(R=0)$	Power $(1-\beta)$
Attu Island	1965–86	10	0·259	0·94	NA	$<0{\cdot}0005$	$>0{\cdot}999$
	1975–86	8	0·172	0·96	0·34	$<0{\cdot}0005$	$>0{\cdot}999$
South-east Alaska	1975–87	3	0·176	0·93	0·20	$0{\cdot}05<P<0{\cdot}01$	0·802
British Columbia	1977–87	3	0·177	0·93	NA	$0{\cdot}1<P<0{\cdot}25$	0·802
Washington State	1978–87*	5	0·230	0·96	NA	$0{\cdot}005<P<0{\cdot}005$	$>0{\cdot}999$
	1978–87	5	0·206	0·92	0·09	$0{\cdot}01<P<0{\cdot}025$	$>0{\cdot}999$
Central California	1914–76	14	0·055	0·96	NA	$<0{\cdot}0005$	$>0{\cdot}999$
	1938–76	13	0·044	0·98	NA	$<0{\cdot}0005$	0·996
	1976–83	4	−0·050	0·96	NA	$0{\cdot}01<P<0{\cdot}025$	0·136
	1983–87	5	0·078	0·96	0·16	$0{\cdot}001<P<0{\cdot}005$	0·496

NA, data not available.
* Count made in 1987 by Washington Game Department, using aerial and shore-based surveys.

maximum of 1789 individuals was counted, the increase was about 5·5% per year. Although an exponential fit is quite good during this period ($r^2=0{\cdot}96$), the residual variation does not appear randomly distributed around the regression. This is largely due to the 1914 estimate of 50 individuals, which could be low because it is little more than a guess. From 1938 to 1976, population counts increased about 4·4% per year. The exponential fit of this line is excellent ($r^2=0{\cdot}98$), although the residual variation suggests a declining growth rate after about 1960. Based on four spring surveys from 1976 to 1983, the population declined ($F_{1,2}=44{\cdot}76$; $P<0{\cdot}025$) about 5% per year. Counts obtained in five spring surveys from 1983 to 1987 increased 7·8% per year. The exponential fit is again good ($r^2=0{\cdot}96$) and the rate of increase significant ($F_{1,3}=75{\cdot}57$; $P<0{\cdot}005$). Because the three periods of increase and decline in counts of the California population were selected a posteriori to provide the best fit, changes in population trends may not have been as sharply punctuated as Fig. 2 indicates.

A more detailed analysis of population change was obtained by calculating rates of increase or decline from all pairwise combinations of counts. Although any single rate obtained by this method should be cautiously interpreted, changes in rates of increase are indicated by the rows and subdiagonals of the matrices of these values (Appendix I). Matrix rows provide rates of change beginning with the date at the row's left, and ending with the date at the top of the column. The matrix subdiagonal indicates rates of change between any two sequential surveys. Trends in rate of change can be determined by regressing sequential values against time. Although I could not reject the hypothesis of no significant trends in population growth rates, the power of the test was low.

Population birth rate

The number of pups counted per independent sea otter ranged from 0·09 for Washington State to 0·34 for Attu Island (Table 1). These calculations only include surveys that followed the presumed seasonal birth peak for each population (i.e. April/May surveys in California following the February/March birth peak, and July/August surveys in Alaska and Washington State following the May/June birth peak). The California population also was surveyed during October/November. When 'small pups' counted during the autumn surveys were added to total pups counted the previous spring,

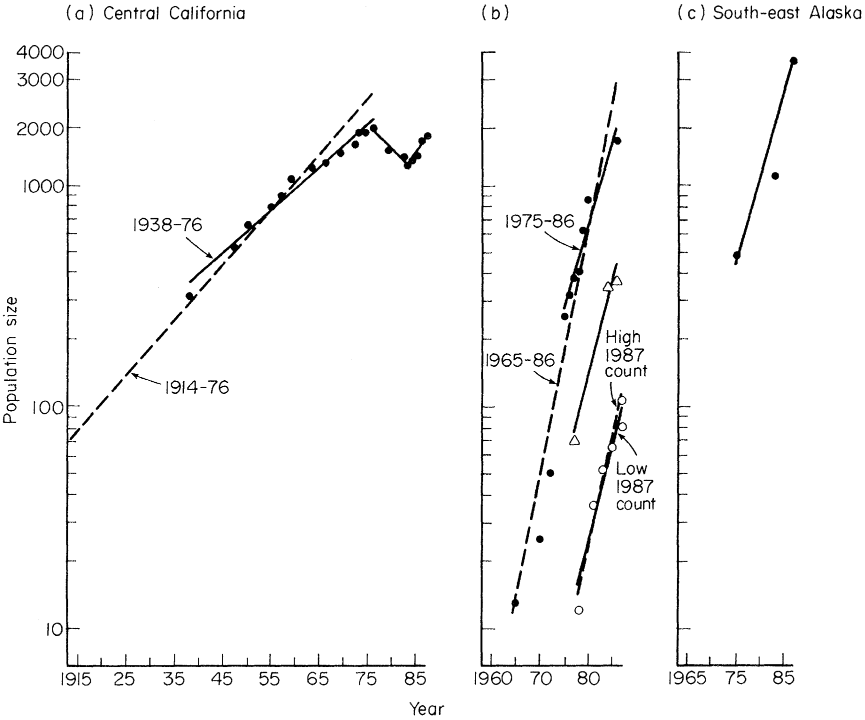

FIG. 2. Trends in population counts of sea otters from (a) central California, (b) Attu Island (●), British Columbia (△), and Washington State (○), and (c) south-east Alaska. The lines in each plate are least squares best fits of ln population size vs. time (years) for the indicated time intervals. Data for central California (a) were divided into three periods, based on an a posteriori examination of apparent trends. The dashed line in (a) is the best-fit line for data gathered from 1914–76; the solid line represents the same analysis, omitting the 1914 data point. Data for Attu Island (b) were similarly analysed for the period 1965–86 (- - -) and 1975–86 (——). The solid line fit for the Washington State surveys (b) represents data gathered by similar methods; the dashed line fit uses a higher count, obtained in a second 1987 survey by the Washington Department of Fisheries and Wildlife (E. Bowlby, unpublished).

the pup/independent ratio increased to about 0·25. This is a more accurate estimate of population birth rate in California, because few pups remain with their mothers for more than 7 months (Wendell, Ames & Hardy 1984; Siniff & Ralls 1988), and pups categorized as being 'small' based on their size, pelage, and behaviour are mostly <3 months old (Payne & Jameson 1984).

In total, 2742 sea otters were counted at Attu Island in areas and times when both inshore and offshore transects were run; 98% (2675) of these were counted on inshore transects. Pup/independent ratios were 0·39 and 0·16, respectively, for inshore and offshore transects (normal approximation to binomial test of equal proportions, $z = 17{\cdot}3$, $P < 0{\cdot}001$).

Sea otter habitat at Attu and Amchitka islands

Attu and Amchitka islands probably offer potentially similar environments for sea otters. Each island is bathed by the same major ocean currents (McAlister & Favorite 1977), and the common marine organisms are similar (J. A. Estes, personal observation).

Table 2. Trend analyses for rate of change vs. time in sea otter populations at Attu island, south-east Alaska, Washington State, and central California. Linear regressions were run for rates shown in the matrix subdiagonals (Appendix 1) (x_{ij}) versus times given at the top of column j. Power was estimated from Gerrodette (1987), with $\alpha = 0{\cdot}05$ and $CV = 0{\cdot}13$

Area and dates	Regression slope (b)	E	d.f.	$P(b=0)$	Power ($1-\beta$)
Attu Island (1965–86)	−0·0094	0·681	1,8	$0{\cdot}25 < P < 0{\cdot}5$	0·099
(1975–86)	−0·018	0·439	1,5	$0{\cdot}5 < P < 0{\cdot}75$	0·133
Washington State (1978–87)	−0·034	3·193	1,2	$0{\cdot}1 < P < 0{\cdot}25$	0·089
South-east Alaska (1969–78)	0·022	2·095	1,1	$0{\cdot}25 < P < 0{\cdot}5$	0·044
Central California (1938–76)	−0·001	1·925	1,11	$0{\cdot}1 < P < 0{\cdot}25$	0·052
(1976–83)	0	0	1,1	$P > 0{\cdot}9995$	0·027
(1983–87)	0·006	0·065	1,2	$0{\cdot}75 < P < 0{\cdot}9$	0·034
(1914–87)	−0·001	1·486	1,18	$0{\cdot}1 < P < 0{\cdot}25$	0·038

Table 3. Measures of shoreline and benthic area $< 18{\cdot}3$ m at Attu and Amchitka islands

	Attu Island	Amchitka Island
Number of coastal segments	45	45
Mean segment length (range) km	7·83 (2·78–22·67)	5·83 (1·63–11·87)
% variation in segment length measurements ($\bar{x}$)	3·1	3·4
Total shore length (km)	367·8	262·1
Mean segment area (range) km^2	3·16 (0·89–10·19)	3·12 (1·06–7·65)
% variation in segment area measurements ($\bar{x}$)	3·9	1·9
Total benthic area $< 18{\cdot}3$ m depth (km^2)	148·2	140·97
Benthic area $< 18{\cdot}3$ m (km^2)/shore length (km)	0·22	0·29

Exposed rocky coasts typify both islands. Total shore lengths and areas of benthos < 18·3-m depth also are similar (Table 3).

The coastal segments within which sea otters were counted at Attu and Amchitka islands were similar in number, average shore length, and average area < 18·3-m depth (Table 3). Average difference between the two shore length measures was 3·1% for Attu and 3·4% for Amchitka. Average measurement differences of segment area < 18·3-m depth were 3·9 and 1·9% for Attu and Amchitka, respectively.

Population abundance at Amchitka Island

Using methods similar to those employed at Attu, surface-based sea otter surveys were conducted for parts of Amchitka Island in 1972 and 1986. Although I have never surveyed the entire coast of Amchitka from the surface, I have conducted aerial surveys of the entire island, and determined the ratios of surface-based to aerial counts using the two methods simultaneously in small coastal segments (Estes 1977). Based on survey methods used at Attu, I estimated the Amchitka population in three ways: (i) by multiplying island-wide aerial counts and the average surface to ground ratio; (ii) by extrapolating otter densities obtained in the surface counts from Amchitka to total island habitat; and (iii) by dividing the number of otters counted in surface surveys by the proportion of the total counts made in the surface-survey areas during island-wide aerial surveys.

During 1972 at Amchitka Island, I made ten replicate counts of four areas, first from the air and immediately thereafter from shore (Estes 1977). Surface counts averaged 1·96 × greater than the simultaneous aerial counts. Multiplying the average of three island-wide aerial counts completed at Amchitka in 1972 (3832, see Table 2 in Estes 1977) by 1·96 provides an estimate of 7511 sea otters.

I visited Amchitka Island during June/July 1986 and made surface counts in two areas, one on the Bering Sea coast (Fig. 1, segments 33–38) and one on the Pacific Ocean coast (segments 2–6). Together these areas comprised 17·3% of the total shoreline, and 25·8% of the total benthos $< 18{\cdot}3$ m. I counted 676 otters in segments 33–38, and 685 otters in segments 2–6. Extrapolated to the total shore length and total benthic area $< 18{\cdot}3$ m at Amchitka Island, these data provide estimates of 7855 and 5267 sea otters, respectively. Dividing the 1986 surface counts at Amchitka by the proportion of the total aerial counts made in these same areas in 1972—0·239 on 23 August; 0·206 on 25 August; 0·260 on 11 September—gives estimates of 5245–6597 sea otters. Although each estimation procedure has certain drawbacks or untestable assumptions, the data suggest that sea otter abundance at Amchitka Island did not change substantially between 1972 and 1986. Henceforth, I will use 5245 as the estimate for Amchitka Island because it provides the most conservative comparison with Attu Island.

Range expansion at Attu Island

Sea otters probably were extinct in the Near Islands by the beginning of the twentieth century. None were seen in a 1960 survey of these islands nor were any seen in several prior surveys (Kenyon 1969). Otters were first seen again in the Near Islands in 1965 (Jones 1965): seven were counted near Chichagof Harbor, four near Steller Cove, and two in Massacre Bay (Fig. 1). Twenty-five were counted at Attu in 1970, all near Chichagof Harbor (Sekora 1973). In July 1972 I visited Chichagof Harbor and counted fifty otters; more may have inhabited nearby areas that were not surveyed.

In 1975 I surveyed the entire coast of Attu and counted 254 sea otters between Holtz and Sarana bays (Fig. 1). Subsequent range expansion occurred by progressive spreading in both directions around the island (Fig. 3). From 1975 to 1986, shore length and benthic area $< 18{\cdot}3$-m depth occupied by sea otters increased at 0·11 and 0·13 year^{-1}, respectively, neither of which was significantly less than the rate of increase in number of animals counted. (Shore length: $t = 0{\cdot}283$, $P < 0{\cdot}75$, d.f. = 10. Area: $t = 0{\cdot}368$, $P < 0{\cdot}75$, d.f. = 10.) By 1986 most of Attu's coast was reoccupied by sea otters.

Population densities at Attu and Amchitka islands

Although sea otter population counts at Attu Island increased > 17% per year from 1975 to 1986, growth was achieved largely by range expansion rather than increased density (Fig. 3). Of the twenty-three coastal segments occupied by sea otters during > 2 survey years (segments I–14, Fig 1), in only four (H, 2, 11 and 12) did the number of animals counted increase significantly (test criterion: $\ln \text{sea otter no.} = a + b[\text{time}]$, $P[b = 0] < 0{\cdot}05$). Otter numbers in those segments that contained most of the population in 1975 (numbers 5–8) remained fairly constant, although large fluctuations occurred in several

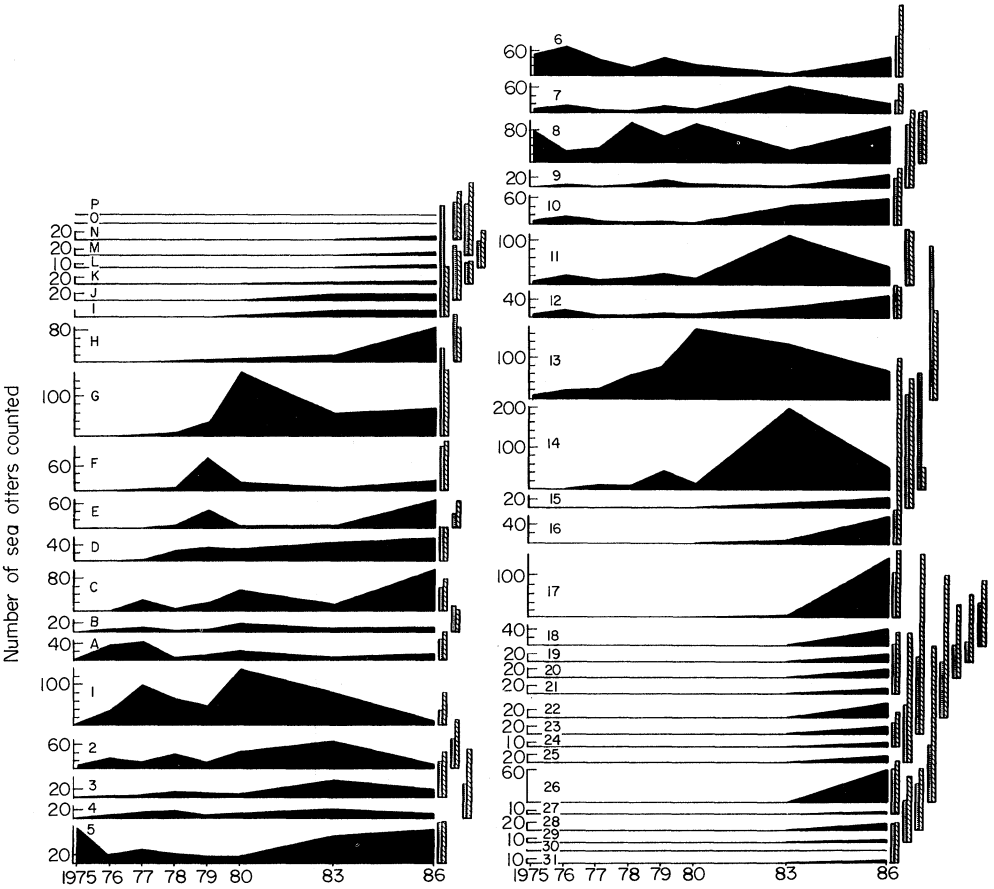

FIG. 3. The number of sea otters counted, by coastal segment, at Attu Island 1975–86. Segment numbers or letters given at the left of each panel correspond with areas shown in Fig. 1. The founding population was first established near Chichagof Harbor (segments 5 and 6). Thus, the pattern of range expansion to the east along the Bering Sea coast, and then west along the Pacific coast, is seen by reading down from segment 6, and to the west along the Bering Sea coast by reading up from segment 5. Histograms to the right of each plate show the expected number of sea otters for each segment, given the population density at Amchitka Island (assuming a total population of 5245 (the lowest estimate), mean = 37·2 otters km^{-2} < 18·3-m and 20·0 otters km^{-1} of coast at MLW) and the segment's benthic area (dotted bars) or length of coast (dashed bars). The time axis of each segment is aligned with the base of its corresponding histogram.

other segments. Abundance peaks seldom exceeded the minimum density at Amchitka Island (Fig. 3). Based on coast length and benthic area < 18·3-m depth respectively, only two and four of the twenty-three segments at Attu with otters present in more than two surveys ever had counts exceeding those expected on the basis of average Amchitka Island density, and only 0 and 1 segments sustained such counts. (I define 'sustained' as ⩾ half the total number of counts.)

Island-wide changes in population density at Attu Island were estimated by defining population ranges for each survey year (Fig. 3), summing shore lengths or benthic areas < 18·3-m depth from the coastal segments within these ranges (Fig. 1), and then dividing

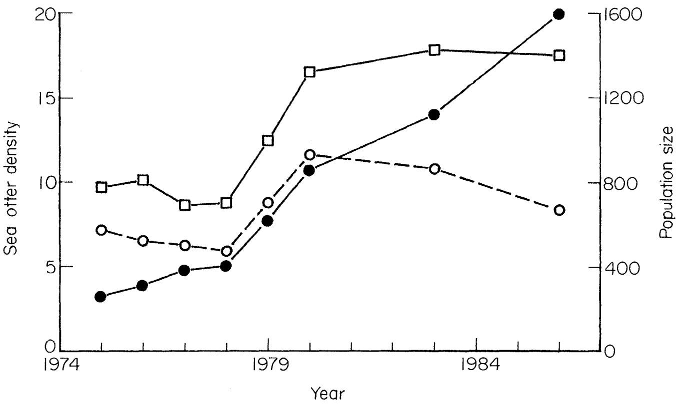

FIG. 4. Temporal changes in sea otter population density and size at Attu Island 1975–86. Density estimates (□ = number per area < 36·6m; ○ = number per length of shore) were obtained from population counts and measures of the amount of habitat within the range of animals counted. Changes in population size (● = survey counts) during the same time period are shown for comparison.

the population counts by both lineal and areal habitat measures. Based on these measures, from 1975 to 1986 lineal and areal population densities increased 1·2 × and 1·6 ×, respectively (Fig. 4). During this same period, population size increased 6·2 × (Fig. 4).

Similar population data and habitat measures from Amchitka Island indicated a substantially greater density of sea otters. Using comparable measures of habitat, even the most conservative density estimate for Amchitka Island was > 3 × greater than the maximum estimate for Attu Island.

To summarize, sea otter population growth at Attu Island occurred mainly by range expansion rather than by increasing density within areas of established range. Otter counts within coastal segments seldom showed significantly increasing trends, seldom increased beyond that expected for an equilibrium population (Amchitka Island), and were almost never sustained at those expected levels.

DISCUSSION

Sea otters probably were distributed nearly continuously from the northern Japanese archipelago to central Baja California before humans hunted them to the brink of extinction during the eighteenth and nineteenth centuries (Kenyon 1969). Many of the otter's invertebrate prey increased in their absence (Estes & VanBlaricom 1985). More recently, fisheries and habitat destruction no doubt depressed prey populations in some areas. Nonetheless, most of the North Pacific Ocean is well suited for the recovery of sea otter populations, providing habitat in which space and food are abundant and human-related disturbances are absent or minimal. This situation is unusual among lutrine species, most of which continue to decline because of hunting, pollution, and habitat destruction (Mason & Mcdonald 1986).

Rate of increase

The recovery patterns of five sea otter populations indicates similarities, as well as perplexing differences. Populations at Attu Island, south-east Alaska, British Columbia, and Washington State, although spanning a broad geographic range and a likely variety of habitats, all have increased between 17 and 20% per year. This probably is near the maximum rate of increase (r_m) for the species. r_m can be estimated from life-table data using Cole's (1954) equation:

$$1 = e^{-r_m} + b^{-r_m a} - be^{-r_m(w+1)}$$

where a is the age of first reproduction, b is the annual birth rate of females, and w is the age of last reproduction. For sea otters, females first reproduce at 3–4 years (Eberhardt & Siniff 1977); assuming an even sex ratio at birth (Kenyon 1969; Schneider 1972, 1973) female reproductive rates are about 0·43–0·45 year^{-1} (Eberhardt & Siniff 1977: Siniff & Ralls 1988; R. J. Jameson & A. M. Johnson, unpublished.); and maximum female longevity is about 15 years (Siniff & Ralls 1988). These parameter estimates provide estimates of r_m of 19·6–23·7% year^{-1}, which are similar to the observed values.

These rates of increase are higher than those previously reported for sea otter populations (Kenyon 1969), and although it is possible that they have been supplemented by immigration, I think this unlikely for the following reasons. (i) Although long distance ($>$ 100 km) movements commonly occur in sea otters (Garshelis 1983; Siniff & Ralls 1988; Jameson 1989), individuals rarely disperse beyond the ranges of their established populations other than to colonize adjacent unoccupied habitats when populations are expanding. (ii) If population growth was being enhanced by immigration, it is unlikely that the augmentation would produce similarly high rates of increase in all four populations. (iii) The observed rates reported here are within the theoretical maximum for this species, although these require a pre-senescence mortality rate of near zero.

Several pinniped species may have r_m values similar to sea otters. Northern elephant seals (*Mirounga angustirostris*) in California may have increased 17·9% year^{-1} (Chapman 1981), although Cooper & Stewart (1983) estimated a lower rate of 14·5% year^{-1}. As Cooper & Stewart (1983) point out, extensive dispersal and immigration of northern elephant seals, especially primiparous females (Reiter, Panken & Le Boeuf 1981), make populations difficult to define and accounts for rates of increase as high as 40–50% year^{-1} in some local colonies. A rate of increase of 16·8% year^{-1} for antarctic fur seals (*Arctocephalus gazella*) was reported by Payne (1977). The high rates of increase observed in both these species probably resulted because their populations, having been reduced to low levels, were protected and permitted to recover in environments where resources were not limiting. Rates of increase reported for other pinnipeds are somewhat less (Bonner 1975; Smith 1975; Chapman 1981), although values of r_m calculated from life-table data (Schmitz & Lavigne 1984) tend to be several per cent year^{-1} higher than the maximum observed values reported above.

Similar rates of increase among the four sea otter populations in Alaska, British Columbia, and Washington State suggests further that these populations are similar demographically. Thus, the variation (from 0·09 to 0·34) in pup: independent ratios across these populations (Table 1) is a paradox. One explanation for these differences is that the populations are demographically different. High fecundities are accompanied by high mortalities, but these balance to produce constant population growth rates. I consider this possibility unlikely. Only the pup counts at Attu Island were high enough to account for growth rates of 17–20% per year. The pup: independent ratio of 0·09 for

Washington State is impossibly low, and the ratio of 0·20 for south-east Alaska allows for virtually no mortality. A second possibility is that season and/or seasonality of births differs among these populations. Surveys of each population were timed to follow presumed seasonal birth peaks. If timing of the birth peak varied among the populations, pup: independent ratios derived from the counts would not be comparable. Furthermore, even if all surveys were done at the same time of year relative to a birth peak, the results would not be comparable unless births were similarly aggregated in time. An unbiased measure of pup production is possible only when births are sufficiently synchronous that all of the young can be counted in a single, properly timed, survey. Although highly synchronous births occur in many species of pinnipeds (Cooper & Stewart 1983) and ungulates (Sinclair 1977), births occur throughout the year in sea otters (Kenyon 1969; Siniff & Ralls 1988). Lower pup: independent ratios would be recorded for populations with less seasonally synchronous births. A third possibility is that the spatial distribution of births varies among these populations, and that areas of high or low pup production were not uniformly sampled in the surveys. There is some evidence for this possibility from Attu Island, where higher pup counts were obtained on inshore than offshore transects. However, the proportion of the population counted offshore at Attu Island (2%) was so small that it is hard to imagine significant numbers of non-reproductive animals were not seen in offshore areas. Counts are needed of independents and recently born pups, taken at frequent time intervals (at least once a month and preferably more often) from several different areas, for each of the populations. Little can be inferred from sea otter pup counts without such information.

Counts of the California sea otter population have increased at a significantly lower rate than those for the other four populations. This cannot be a time- or size-dependent effect. The California population apparently has never grown at much more than about 5% year^{-1}, even early in this century (Appendix 1(E)). Furthermore, other populations have maintained uniformly high growth rates to sizes exceeding (south-east Alaska) or equalling (Attu Island) that estimated for the California population.

Reasons for the lower rate of increase in California are unclear, although possibilities include (i) a reduced birth rate, (ii) increased mortality rate, or (iii) emigration. Emigration is an unlikely explanation because extralimital sightings, although not uncommon, cannot account for the difference and there is no place along the west coast of North America where so many sea otters could have gone undetected. Whether birth rate of California sea otters is lower than in the other populations is uncertain (see above). Possible sources of mortality in California, not experienced by the four northern populations are: (i) human disturbance—roughly 100 otters year^{-1} have drowned in set nets (Wendell, Ames & Hardy 1986) and the recent growth resurgence (Fig. 2) followed set net restrictions in 1985; (ii) attack by great white sharks (*Carcharodon carcharias*)—about 10% of the sea otter carcasses salvaged range-wide, and over 30% of those salvaged north of Cypress Point were probable shark attack victims (J. A. Ames, unpublished); (iii) reduced habitat quality near the southern periphery of the species' range.

Equilibrium density

A population might be inferred to be at equilibrium with limiting resources (carrying capacity) if it were not increasing in number or density and if physical or biological disturbances were not limiting its further growth. Although the population at Attu has increased in number, this increase has been achieved largely by range expansion and population density has remained generally constant. This constant density through time could be interpreted as the carrying capacity were it not for the fact that the population at Amchitka Island also has reached and maintained a substantially higher density.

One possible explanation for the different population densities is that resource availability differs between Attu and Amchitka. Another possibility is that these islands have similar potential carrying capacities, but that present differences represent different stages of recovery from near extinction. I favour the latter explanation based on (i) population growth patterns at Attu Island, (ii) anecdotal information on population change at Amchitka Island, (iii) benthic community structure at Attu and Amchitka islands, and (iv) the diet of sea otters at Attu and Amchitka islands.

My suggested scenario is this: During the initial phase of population increase, sea otters feed mostly on benthic invertebrates (Estes, Jameson & Johnson 1981; Estes, Jameson & Rhode 1982). Food or space may be limiting resources within the established range, and a steady-state density may be achieved, but an equilibrium demography is not. The net increment between birth and mortality disperses into unoccupied habitat. Thus, a constant population density is maintained and population increase is achieved largely by range expansion. When the habitat is filled, dispersal into unoccupied areas is no longer possible and competition for food becomes severe (sea otters at Amchitka Island spend about 3 × more time feeding during daylight hours than they do at Attu Island (Estes, Jameson & Rhode 1982)). As prey abundance is reduced, the otters begin feeding on smaller, nutritionally poorer prey, with two important results. Mortality from starvation increases, especially among juveniles (Kenyon 1969) and, because of the consequent reduction in abundance of small sea urchins, the system shifts from one dominated by sea urchin barrens to one dominated by kelp beds (Estes, Smith & Palmisano 1978; Estes, Duggins & Rathbun 1989; J. A. Estes & D. O. Duggins, unpublished). This interaction, in turn, increases benthic habitat complexity and production (Duggins 1988; Duggins, Simenstad & Estes 1989), leading to increased densities of kelp bed fishes (Quast 1971a, b; Bodkin 1988; Ebeling & Laur 1988). In response to these habitat and food resource changes, the otter's diet switches from one largely comprised of invertebrates, to one dominated by fish (Kenyon 1969; Estes, Jameson & Johnson 1981). Sea otters probably are less able to limit fish than sea urchin populations, and with the elevated production and more diverse and persistent prey, the carrying capacity of sea otters becomes higher and more stable. Thus, by adding an indirect trophic interaction low in the food web, there has been a positive feedback between predator and prey abundance, rather than the generally assumed negative feedback system.

Although I emphasize that this scenario is speculative, it has some supporting evidence. Surveys at Amchitka Island earlier in this century, when fish apparently were not being eaten in large amounts by sea otters, indicate the population peaked and declined at much lower numbers than presently exist there (Kenyon 1969; Estes 1981; Estes, Duggins & Rathbun 1989). A similar increase and decline has occurred at Medny Island, in the Commander Island group, although the otters there do not feed on fish and the otter population has remained at a low abundance following the decline (A. Zorin, personal communication). This evidence, while supportive, is certainly not definitive. Critical tests are forthcoming at Attu and Medny islands, where otter populations have recolonized all or most of the available habitat. Predictions of the scenario (i.e. the above described temporal covariation in community structure, sea otter foraging, and population density) can be evaluated by continuing to monitor the benthic habitat, behaviour, and population numbers of sea otters at those areas.

ACKNOWLEDGMENTS

I am grateful to R. Anthony, J. Bodkin, S. Brown, E. Faurot, R. Glinski, C. Harrold, D. Irons, M. Kenner, R. Mayer, D. Reed, C. Simenstad, G. VanBlaricom, J. Watson, R. Jameson and numerous others who assisted with field work; K. Pitcher for unpublished data from south-east Alaska; and C. Cooper, D. DeMaster, T. Gerrodette, M. Riedman, D. Siniff and G. VanBlaricom for comments on early drafts of the manuscript. Logistics was provided for work in the Aleutian Islands by the Alaska Maritime National Wildlife Refuge and the U.S. Coast Guard. Work was supported by the Fish and Wildlife Service, and National Science Foundation Grant No. DPP-8421362.

REFERENCES

Bigg, M. A. & MacAskie, I. B. (1978). Sea otters re-established in British Columbia. *Journal of Mammalogy*, **59,** 874–876.

Bodkin, J. L. (1988). Effects of kelp forest removal on associated fish assemblages in central California. *Journal of Experimental Marine Biology and Ecology*, **117,** 227–238.

Bonner, W. N. (1975). Population increase of grey seals at the Farne Islands. *Rapports et Proces-Verbaux des Reunions. Conseil International Pour L'Exploration de la Mer*, **169,** 366–370.

Caughley, G. (1977). *Analysis of Vertebrate Populations.* John Wiley & Sons, New York.

Chapman, D. G. (1981). Evaluation of marine mammal population models. *Dynamics of Large Mammal Populations* (Ed. by C. W. Fowler & T. D. Smith), pp. 277–296. John Wiley & Sons, New York.

Cole, L. C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology*, **29,** 103–137.

Cooper, C. F. & Stewart, B. S. (1983). Demography of northern elephant seals, 1911–1982. *Science*, **219,** 969–971.

Duggins, D. O. (1988). The effects of kelp forests on nearshore environments: biomass, detritus, and altered flow. *The Community Ecology of Sea Otters* (Ed. by G. R. VanBlaricom & J. A. Estes), pp. 192–201. Springer-Verlag, Berlin.

Duggins, D. O., Simenstad, C. A. & Estes, J. A. (1989). Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science*, **245,** 170–173.

Ebeling, A. W. & Laur, D. R. (1988). Fish populations in kelp forests without sea otters: effects of severe storm damage and destructive sea urchin grazing. *The Community Ecology of Sea Otters* (Ed. by G. R. VanBlaricom & J. A. Estes), pp. 169–191. Springer-Verlag, Berlin.

Eberhardt, L. L. & Siniff, D. B. (1977). Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada*, **34,** 183–190.

Eisenberg, J. F. (1981). *The Mammalian Radiations.* The University of Chicago Press, Chicago.

Estes, J. A. (1977). Population estimates and feeding behavior of sea otters. *The Environment of Amchitka Island, Alaska* (Ed. by M. L. Merritt & R. G. Fuller), pp. 511–526. TID-26712, National Technical Information Service, Springfield, Virginia.

Estes, J. A. (1981). The case of the sea otter. *Problems in Management of Locally Abundant Wild Mammals* (Ed. by P. Jewell & S. Holt), pp. 167–180. Academic Press, New York.

Estes, J. A., Duggins, D. O. & Rathbun, G. (1989). The ecology of extinctions in kelp forest communities. *Conservation Biology* **3,** 252–264.

Estes, J. A. & Jameson, R. J. (1988). A double-survey estimate for the probability of sighting sea otters in California. *Journal of Wildlife Management*, **52,** 70–76.

Estes, J. A., Jameson, R. J. & Johnson, A. M. (1981). Food selection and some foraging tactics of sea otters. *Worldwide Furbearer Conference Proceedings* (Ed. by J. A. Chapman & D. Pursley), pp. 606–641. Worldwide Furbearer Conference, Inc., Frostburg, Maryland.

Estes, J. A., Jameson, R. J. & Rhode, E. B. (1982). Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist*, **120,** 242–258.

Estes, J. A., Smith, N. S. & Palmisano, J. F. (1978). Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology*, **59,** 822–833.

Estes, J. A. & VanBlaricom, G. R. (1985). Sea-otters and shellfisheries. *Marine Mammals and Fisheries* (Ed. by J. R. Beddington, R. J. H. Beverton & D. M. Lavigne), pp. 187–235. George Allen & Unwin, London.

Garshelis, D. L. (1983). *Ecology of sea otters in Prince William Sound, Alaska.* Unpublished Ph.D thesis, University of Minnesota, Minneapolis.

Garshelis, D. L. & Garshelis, J. A. (1984). Movements and management of sea otters in Alaska. *Journal of Wildlife Management*, **48,** 665–678.

Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology*, **68,** 1364–1372.

Jameson, R. J. (1989). Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science*, **5**, 159–172.

Jameson, R. J., Kenyon, K. W., Johnson, A. M. & Wight, H. M. (1982). History and status of translocated sea otter populations in North America. *Wildlife Society Bulletin*, **10**, 100–107.

Jameson, R. J., Kenyon, K. W., Jefferies, S. & VanBlaricom, G. R. (1986). Status of a translocated sea otter population and its habitat in Washington. *Murrelet*, **67**, 84–87.

Johnson, A. M., Jameson, R. J., Schmidt, T. & Calkins, D. C. (1983). *Sea Otter Survey, Southeast Alaska, 1983*. United States Fish and Wildlife Service and Alaska Department of Fish and Game, Unpublished Report.

Jones, R. D. Jr (1965). Sea otters in the Near Islands, Alaska. *Journal of Mammalogy*, **46**, 702.

Kenyon, K. W. (1969). The sea otter in the eastern Pacific Ocean. *North American Fauna*, **68**, 1–352.

MacAskie, I. B. (1984). *Sea Otter Census, Vancouver Island, British Columbia 1984*. Whale Research Institute, Nanaimo, British Columbia, Unpublished Report.

MacAskie, I. B. (1987). Updated status of the sea otter (*Enhydra lutris*) in Canada. *Canadian Field-Naturalist*, **101**, 279–283.

Mason, C. F. & Macdonald, S. M. (1986). *Otters: Ecology and Conservation*. Cambridge University Press, Cambridge.

McAlister, W. B. & Favorite, F. (1977). Oceanography. *The Environment of Amchitka Island, Alaska* (Ed. by M. L. Merritt & R. G. Fuller), pp. 331–352. TID-26712, National Technical Information Service, Springfield, Virginia.

Payne, M. R. (1977). Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London (B)*, **279**, 67–79.

Payne, S. F. & Jameson, R. J. (1984). Early behavioral development of the sea otter, *Enhydra lutris*. *Journal of Mammalogy*, **65**, 527–531.

Quast, J. C. (1971a). Fish fauna of the rocky inshore zone. *Nova Hedwigia*, **32**, 481–507.

Quast, J. C. (1971b). Estimates of the populations and the standing crop of kelp bed fishes. *Nova Hedwigia*, **32**, 509–540.

Reiter, J., Panken, K. J. & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Animal Behaviour*, **29**, 670–687.

Rotterman, L. M. & Simon-Jackson, T. (1988). Sea otter. *Selected Marine Mammals of Alaska. Species Accounts with Research and Management Recommendations* (Ed. by J. W. Lentfer), pp. 237–275. United States Marine Mammal Commission, Washington, D.C.

Schmitz, O. J. & Lavigne, D. M. (1984). Intrinsic rate of increase, body size, and specific metabolic rate in marine mammals. *Oecologia*, **62**, 305–309.

Schneider, K. B. (1972). Reproduction in the female sea otter. *Federal Aid in Wildlife Restoration Project W-17-4*, Project Progress Report, Alaska Department of Fish & Game, Anchorage.

Schneider, K. B. (1973). Reproduction in the female sea otter. *Federal Aid in Wildlife Restoration Project W-17-5*, Project Progress Report, Alaska Department of Fish & Game, Anchorage.

Sekora, P. (1973). *Aleutian Islands Wilderness Study Report*. A study conducted as a partial requirement of the Wilderness Act by the Bureau of Sport Fisheries and Wildlife. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Siniff, D. B. & Ralls, K. (1988). *Population Status of California Sea Otters*. Final Report to the United States Minerals Management Service, Contract Number 14-12-001-30033. Minerals Management Service, Los Angeles, California.

Sinclair, A. R. E. (1977). *The African Buffalo*. University of Chicago Press, Chicago.

Smith, T. G. (1975). Parameters and dynamics of ringed seal populations in the Canadian eastern Arctic. *Rapports et Proces-Verbaux des Reunions. Conseil International pour L'Exploration de la Mer*, **169**, 281–295.

United States Fish & Wildlife Service (1987). *Environmental Impact Statement. Proposed Translocation of Southern Sea Otters*. U.S. Fish & Wildlife Service, Ventura, California.

VanBlaricom, G. R. & Estes, J. A. (1988). *The Community Ecology of Sea Otters*. Springer-Verlag, Berlin.

Wendell, F. E., Ames, J. A. & Hardy, R. A. (1984). Pup dependency period and length of reproductive cycle: estimates from observations of tagged sea otters, *Enhydra lutris*, in California. *California Fish & Game*, **70**, 89–100.

Wendell, F. E., Hardy, R. A. & Ames, J. A. (1986). *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 & Game, Sacramento, California.

Zar, J. H. (1974). *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

(*Received 18 April 1989*)

APPENDIX 1

Annual rates of increase for sea otter populations at (A) Attu Island, (B) south-east Alaska, (C) British Columbia, (D) Washington State, and (E) central California. The *ij*th matrix element is the annual rate of change in number of sea otters counted from the year beginning at left of row *i* to the year ending at top of column *j*.

	Year ending										
Year beginning	1965	70	72	75	76	77	78	79	80	83	86
1965		0·13	0·19	0·30	0·29	0·28	0·27	0·28	0·28	0·25	0·23
1970			0·35	0·46	0·43	0·39	0·35	0·36	0·35	0·29	0·26
1972				0·54	0·46	0·41	0·35	0·36	0·36	0·28	0·25
1975					0·23	0·21	0·16	0·22	0·25	0·19	0·17
1976						0·19	0·12	0·22	0·25	0·18	0·16
1977							0·05	0·24	0·27	0·18	0·16
1978								0·43	0·38	0·20	0·17
1979									0·33	0·15	0·14
1980										0·09	0·10
1983	A										0·12

	Year ending			
Year beginning	1969	75	83	87
1969		0·03	0·07	0·12
1975			0·10	0·17
1983	B			0·30
1972		−0·05	0·11	0·09
1977			0·23	0·17
1984	C			0·02

	Year ending						
	1970	77	78	81	83	85	87
1970		−0·16	−0·20	−0·05	−0·01	0·01	0·02
1977			−0·46	0·16	0·17	0·15	0·16
1978				0·37	0·29	0·24	0·22
1981					0·19	0·15	0·15
1983						0·11	0·14
1985	D						0·17

APPENDIX (*cont.*)

Year ending

Year beginning	1914	38	47	50	55	57	59	63	66	69	72	73	74	76	79	82	83	84	85	86	87
1914		0·08	0·07	0·07	0·07	0·07	0·07	0·06	0·06	0·06	0·06	0·06	0·06	0·06	0·05	0·05	0·05	0·05	0·05	0·05	0·05
1938			0·06	0·06	0·06	0·05	0·06	0·05	0·05	0·05	0·05	0·05	0·05	0·05	0·04	0·03	0·03	0·03	0·03	0·03	0·03
1947				0·07	0·06	0·05	0·06	0·05	0·05	0·04	0·04	0·05	0·04	0·04	0·03	0·03	0·02	0·02	0·03	0·03	0·03
1950					0·04	0·04	0·05	0·05	0·04	0·04	0·04	0·04	0·04	0·04	0·03	0·02	0·02	0·02	0·02	0·02	0·02
1955						0·05	0·07	0·05	0·04	0·04	0·04	0·04	0·04	0·04	0·02	0·02	0·02	0·02	0·02	0·02	0·02
1957							0·09	0·05	0·04	0·04	0·04	0·04	0·04	0·04	0·02	0·02	0·01	0·01	0·02	0·02	0·02
1959								0·03	0·03	0·03	0·03	0·04	0·03	0·03	0·02	0·01	0·01	0·01	0·01	0·01	0·02
1963									0·03	0·03	0·03	0·04	0·03	0·03	0·01	0·01	0	0	0·01	0·01	0·01
1966										0·03	0·03	0·04	0·04	0·04	0·01	0	0	0	0	0·01	0·01
1969											0·03	0·05	0·04	0·04	0	0	−0·01	0	0	0·01	0·01
1972												0·12	0·07	0·04	−0·01	−0·01	−0·01	−0·02	−0·01	0	0·01
1973													0·01	0·01	−0·03	−0·03	−0·03	−0·03	−0·02	−0·01	0
1974														0·02	−0·04	−0·03	−0·04	−0·03	−0·02	−0·01	0
1976															−0·07	−0·05	−0·04	−0·04	−0·03	−0·01	−0·01
1979																−0·02	−0·04	−0·02	−0·01	0·01	0·02
1982																	−0·09	−0·02	0·01	0·04	0·04
1983																		0·06	0·06	0·08	0·08
1984																			0·05	0·10	0·08
1985																				0·14	0·10
1986	E																				0·05