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Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there?

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Abstract

The size of Steller sea lion populations in the Gulf of Alaska and Aleutian Islands was estimated by applying life table statistics to counts of pups and adults (non-pups) at rookery sites. Total population size was 5.10 times the number of pups counted or 3.43 times the number of adults counted. Only 55% of the adult population return to rookeries during the summer. Data compiled from published and unpublished sources for all 39 major rookeries in Alaska suggest that the total number of Steller sea lions (including pups) rose from 250 000 to 282 000 between the mid 1950s and the mid 1970s. Since 1980 it has decreased by over 70% (roughly 5% per year) to about 76 000 animals in 1992. Most of the decline took place in the Aleutian Islands and Kodiak region. However since 1989, the population decline appears to have slowed or stopped within two subareas of these large regions—the eastern Aleutians and western Gulf of Alaska. Increases have been occurring in the smaller populations of southeast Alaska. It is not known why these changes have occurred.

Introduction

The Steller sea lion (*Eumetopias jubatus*) ranges from the Channel Islands, off southern California, around the Pacific Rim to northern Japan, with most of the world population breeding between the central Gulf of Alaska and the western Aleutians (Scheffer, 1958; Schusterman, 1981; King, 1983; Loughlin *et al.*, 1984). Sea lions generally mate, give birth and care for their pups at rookeries, and rest and moult at haulouts. There are 39 major rookeries (Fig. 1) and over 250 haulouts in Alaska (Loughlin *et al.*, 1992), of which most are on remote and exposed rocks and islands.

In the mid 1970s, it became apparent that something was amiss among Alaskan sea lions in the eastern Aleutians when surveys counted 50% fewer animals than in previous decades (Braham *et al.*, 1980). Declines were not noted elsewhere in the Aleutians (Fiscus *et al.*, 1981) until the early 1980s (Merrick *et al.*, 1987), at which time they were also observed in the central and western Gulf of Alaska (Merrick *et al.*, 1987).

In response to the population declines in Alaska, the Steller sea lion was listed in 1990 as a *threatened* species under the US Endangered Species Act (NMFS, 1992). In 1995, the National Marine Fisheries Service proposed managing the population as two separate stocks—an eastern (*threatened*) population and a western (*endangered*) population (NMFS, 1995). The boundary between the two stocks occurs along the Yakutat region of Alaska (east of 144°W—near Prince William Sound) and corresponds to a break in the genetic distribution of haplotypes (Bickham *et al.*, 1996) as well as the distribution of breeding sites (Fig. 1).

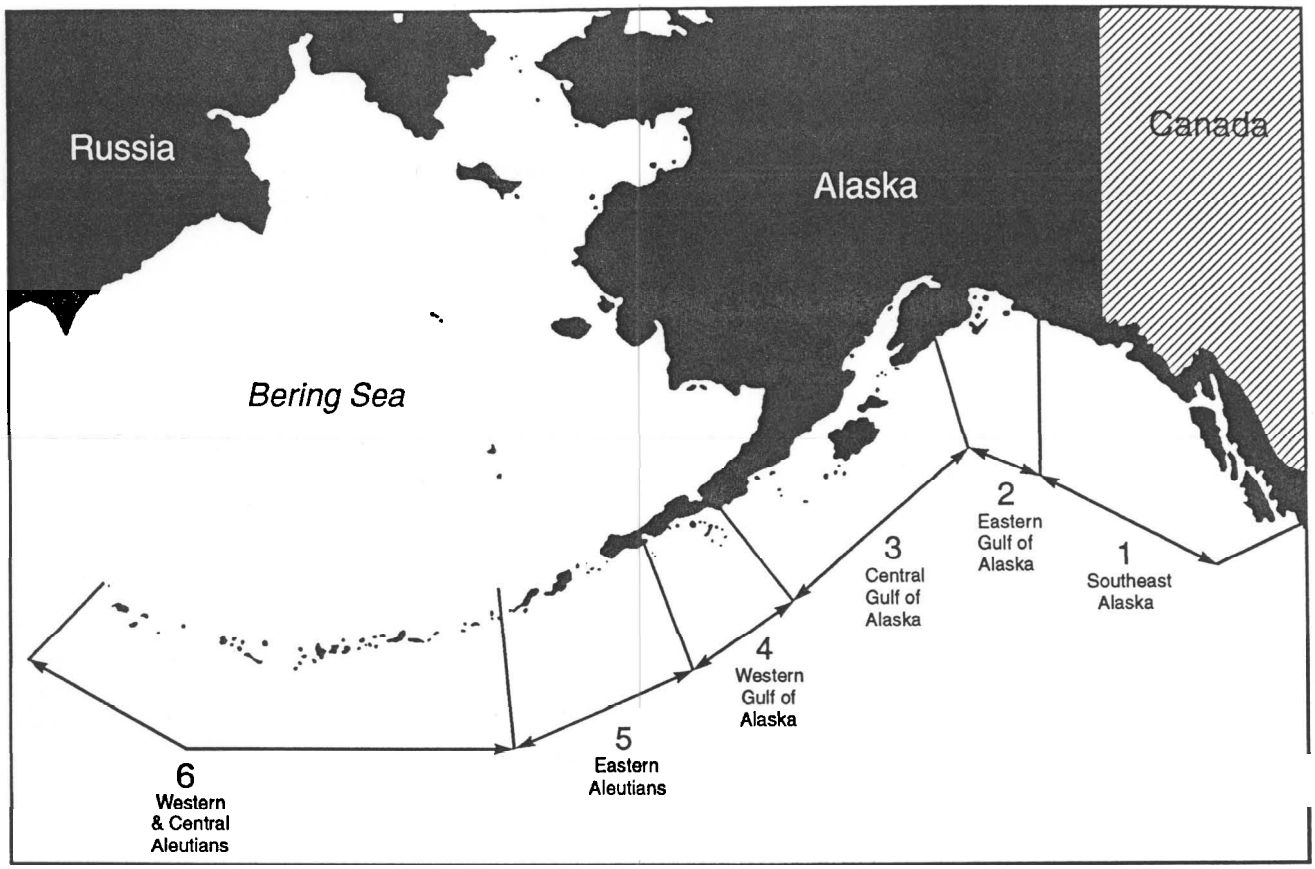
Linear regression of index counts[1] suggested an overall population decline of 52% between 1956–60 and 1980 (Merrick *et al.*, 1987). More recent surveys in 1989 indicated that the declines continued unabated (Loughlin *et al.*, 1992). Declines have also been reported in Russia (Perlov, 1991), but not in Canada or in southeastern Alaska (Bigg, 1985; Loughlin *et al.*, 1992).

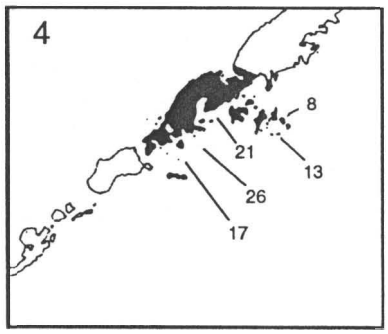
In Alaska, Steller sea lions have been counted sporadically from planes, boats, and on foot since 1956. Typically, counts of pups and adults have been made in the summer when most animals are ashore. Such counts serve as an index of population size and are the primary means of monitoring overall changes in abundance.

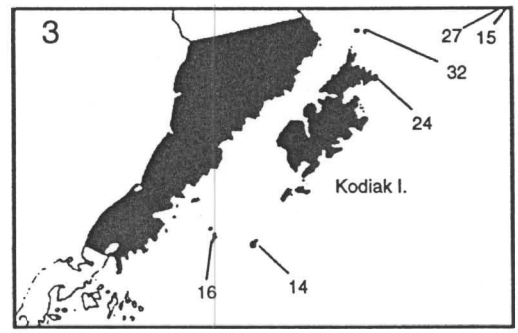
There have been few attempts to estimate the actual number of Steller sea lions in Alaska (Kenyon & Rice, 1961; ITG, 1978; Loughlin *et al.*,

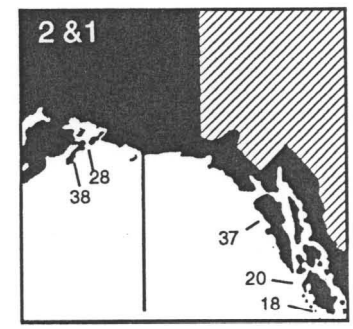
†Deceased.

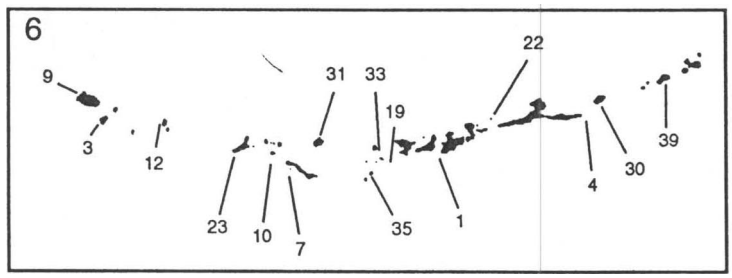
[1]Index or trend sites are those that have been selected from the overall database because they have been counted in each major survey period. Index counts provide a measure of relative population size and trend.

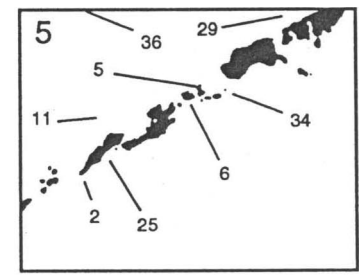












1.6 Adak	7.6 Amchitka	13.4 Chernabura	20.1 Hazy	26.4 Pinnacle Rock	33.6 Tag
2.5 Adugak	8.4 Atkins	14.3 Chirikof	21.4 Jude	27.3 Pye (Outer)	34.5 Ugamak
3.6 Agattu	9.6 Attu	15.3 Chiswell	22.6 Kasatochi	28.2 Seal Rocks	35.6 Ulak
4.6 Agligadak	10.6 Ayugadak	16.3 Chowiet	23.6 Kiska	29.5 Sea Lion Rock	36.5 Walrus
5.5 Akun	11.5 Bogoslof	17.4 Clubbing Rocks	24.3 Marmot	30.6 Seguam	37.1 White Sisters
6.5 Akutan	12.6 Buldir	18.1 Forrester	25.5 Ogchul	31.6 Semisopochnoi	38.2 Wooded
		19.6 Gramp Rock		32.3 Sugarloaf	39.6 Yunaska

Figure 1. Steller sea lion rookeries in the six study areas of the Gulf of Alaska and Aleutian Islands (adapted from Merrick *et al.*, 1988, and Loughlin *et al.*, 1992). The geographic split between eastern and western stocks is shown by the line separating Areas 1 and 2. Number prefixes of names designate the rookery; suffixes identify the areas in which the rookeries are found.

1984; 1992). Typically, only estimates of relative abundance are reported from index sites counted simultaneously in all regions and years surveyed. As a result, the coarsely aggregated census data do not provide detailed information about population sizes and trends.

The following examines the census counts of adults and pups made at rookeries in 6 areas of the Gulf of Alaska and waters surrounding the Aleutian Islands (Fig. 1). A life table analysis is applied to the available census data to estimate the total population size of Steller sea lions from 1956–1992 to obtain a better resolution of when and where changes in population size occurred.

Steller sea lion biology

Males begin to come ashore at rookeries in mid May, and remain on land until mid July (Gisiner, 1985). The females arrive shortly after the males and give birth to a single pup within 3 days of being on land. Pups are born from late May to early July, with the peak of pupping occurring in June (Scheffer, 1945; Pike & Maxwell, 1958; Mathisen *et al.*, 1962; Gentry, 1970; Pitcher & Calkins, 1981; Bigg, 1985). Females stay with their pups for the first 5 to 13 days after birth then go to sea to feed (Sandegren, 1970). Feeding trips generally last for less than 24 hours and usually occur at night every 1 to 3 days (Spalding, 1964; Fiscus & Baines, 1966; Gentry, 1970; Sandegren, 1970; Merrick *et al.*, 1988). Pups generally nurse for a year and are weaned before the next breeding season, although some pups may maintain a bond with their mother for up to 3 years. Young sea lions (1–3 years old) are often seen suckling adult females at rookery and haulout sites (Gentry, 1970; Sandegren, 1970; Calkins & Pitcher, 1982). Adults and dependent young remain on or near rookeries until October, dispersing to haulouts for the remainder of the year.

Not all sea lions use rookeries during the summer. A portion of the population remains on haulouts year round (Loughlin *et al.*, 1992).

Seasonal variation in numbers of sea lions at rookeries is similar wherever they breed (Bigg, 1985). Typically, the number is lowest in December and highest after pupping in July before the adults disperse (Aumiller & Orth, 1980; Smith, 1988). Sea lions continue to use haulout sites during the winter months and do not undertake extensive migrations like some pinnipeds. However, males may disperse further north than females (D. Calkins, pers. comm.), and tagged subadults have been sighted up to 1500 km from where they were marked (Calkins & Pitcher, 1982).

Tagging studies suggest that sea lions return to their birth sites as they become sexually mature (Calkins & Pitcher, 1982). This phenomenon is well documented in northern fur seals (Kenyon & Wilke, 1953) and suggests that each sea lion rookery may be a somewhat distinct breeding stock. Further support for the genetic uniqueness of rookery populations comes from recent DNA studies (Loughlin, 1994; Bickham *et al.*, 1996).

Methods

Evaluation of numbers and trends

Numbers of pups and adults[2] counted at rookeries between 1956 and 1992 were obtained from both published and unpublished sources (Kenyon & Rice, 1961; Kenyon, 1962; Mathisen & Lopp, 1963; Braham *et al.*, 1980; Fiscus *et al.*, 1981; Calkins & Pitcher, 1982; Withrow, 1982; Bigg, 1985; Byrd, 1989; Merrick *et al.*, 1987; 1988; 1990; 1991; 1992; Loughlin *et al.*, 1984; 1986; 1992; Sease *et al.*, 1993). Original data sources were used whenever possible, because errors were noted in a few published data summaries. In general the data are sparse.

Early counts of Steller sea lions in the 1950s and 1960s were made visually on site and from scrutinizing photographs taken in conjunction with sea otter surveys done over many months (Kenyon & Rice, 1961; Kenyon, 1962; Mathisen & Lopp, 1963). Sea lion surveys through the 1970s and 1980s were designed to ensure the largest number of animals observed ashore by counting during midday at the peak of the breeding season in June and July (Braham *et al.*, 1980; Fiscus *et al.*, 1981; Calkins & Pitcher, 1982; Withrow, 1982; Bigg, 1985; Merrick *et al.*, 1987; 1988; 1990; 1991; Loughlin *et al.*, 1984; 1986; 1992).

Although sea lions haul out at predictable places and are relatively easy to count, there is always some uncertainty about the number of animals that are at sea and not counted. Numbers of animals counted on land may be affected by tides, weather, visibility, time of day and time of month, among other factors (Withrow, 1982). Thus, sea lion counts are not estimates of total population size but are minimum estimates of the number of animals using a particular site. At face value they serve as relative indices of population size and trends in abundance.

Pups are a measure of herd productivity and are counted separately from adults. It is generally accepted that pups, which do not leave the rookery during their first two months of life, provide a better index of population size and trend than do counts of adults (Berkson & DeMaster, 1985). To date, the best estimates of pup production are from spook counts (where adults on rookeries are forced

[2]Adults or nonpups include both immature (juvenile) and mature animals.

Table 1. Numbers of Steller sea lions counted in Alaska in 1991 (from Merrick *et al*, 1992). Pup estimates for rookeries not counted in 1991 are from counts made in 1990 or 1992 (from Merrick *et al.*, 1991 and Sease *et al.*, 1993).

Area	No. of rookeries	Adults			Pups	Total counted
		Haulout	Rookery	Total		
1. Southeast Alaska	3	3663	5786	9449	4164	13 613
2. Eastern Gulf of Alaska	2	3592	1220	4812	657	5469
3. Central Gulf of Alaska	5	3044	4671	7715	4083	11 798
4. Western Gulf of Alaska	4	2106	3235	5341	1993	7334
5. Eastern Aleutian Islands	7	1810	3481	5291	2531*	7822
6. Central and Western Aleutians	15	16 672	7216	13 888	5493**	19 381
All regions	35	20 887	25 609	46 496	18 921	65 417

*Includes an estimated 356 pups at Ogchul and Sea Lion Rocks.
**Includes an estimated 417 pups at Attu.

into the water and the remaining pups counted); however, spook counts tend to be costly and disrupt the rookery. Pups can also be counted visually from shore or from photographs, but pups can be missed if hidden behind rocks and other animals.

Life table estimation of population size

The total sea lion population (pups+adults) was estimated for each of the 6 sea lion areas (Fig. 1) by applying life table statistics (Bigg, 1985; Loughlin *et al.*, 1992) to rookery counts made primarily during the months of June and July. Tabulated counts are contained in Appendix 2 of Trites & Larkin (1992). The physical boundaries for each of the six study areas were based on proximities of rookeries to one another and by the similarity of population trends at individual sites (Merrick *et al.*, 1987).

A mathematical model (Trites, 1996) with survival and reproductive rates taken from York (1990) and Calkins & Pitcher (1982), produced a simulated population consisting of 21.54% pups and 78.46% non-pups (25.04% adult males and 53.42% adult females). The total size of the simulated population was 4.64 times the number of pups born ($4.64 = 0.2154^{-1}$). Similarly, the number of pups born was 0.27 times the number of adults ($0.27 = 21.54 \times [25.04 + 53.42]^{-1}$). Thus we extrapolated the size of the Gulf of Alaska sea lion population from the numbers of pups and adults counted at rookeries during aerial and shore surveys.

The number of pups observed in the wild is a minimum estimate of the actual number born in a given year. For example, a census conducted in June fails to account for pups born in July. Similarly, a July census misses pups that died and those that have left the rookery. Pups hidden behind rocks or other sea lions are another complication. We, therefore, applied a 10% correction factor to all recorded pup counts to account for dead pups or those not yet born. Thus, in years when pups were counted at all rookeries of a given area,

$$\textit{Total population} = 1.10 \times 4.64 \times \textit{pups counted} = 5.10 \times \textit{pups counted}. \quad (1)$$

As with pups, the number of adults counted at a rookery is a minimum estimate of the total number present (unless the site is also being used as a haulout). For example, some lactating females are at sea during censuses, while other sea lions may not use rookeries at all during the breeding season. This is confirmed by a range-wide census in 1991 which counted 45% of observed adults at haulout sites (Table 1). During this census, 20 887 adults were counted at haulouts, and 25 609 adults and 18 921 pups were at rookeries (Table 1); for a total of 65 417 animals. These figures imply that the size of population was at least 2.55 times larger than the numbers of adults counted at the rookeries (i.e. 2.55=65 417/25 609). The actual population is of course larger because some animals are at sea during the census.

Assuming that pups do indeed make up 21.54% of the population (see above), the total population in 1991 should have numbered 87 841 (i.e. 18 921/0.2154). This is 22 424 more animals than were counted (Table 1) and suggests that one-third or 33% of the adult population was at sea during the census (cf. Loughlin *et al.*, 1992). Thus the total population (including animals at sea and on haulouts) can be derived from

$$\textit{Total population} = 3.43 \times \textit{adults counted}, \quad (2)$$

where adults are only those non-pups counted at rookeries, 3.43=87 841/25 609, and total population includes all non-pups alive plus the number of pups born.

We estimated total population size by applying Eqs 1 and 2 to the sum of all rookery counts of pups or adults made in a given area. In years when

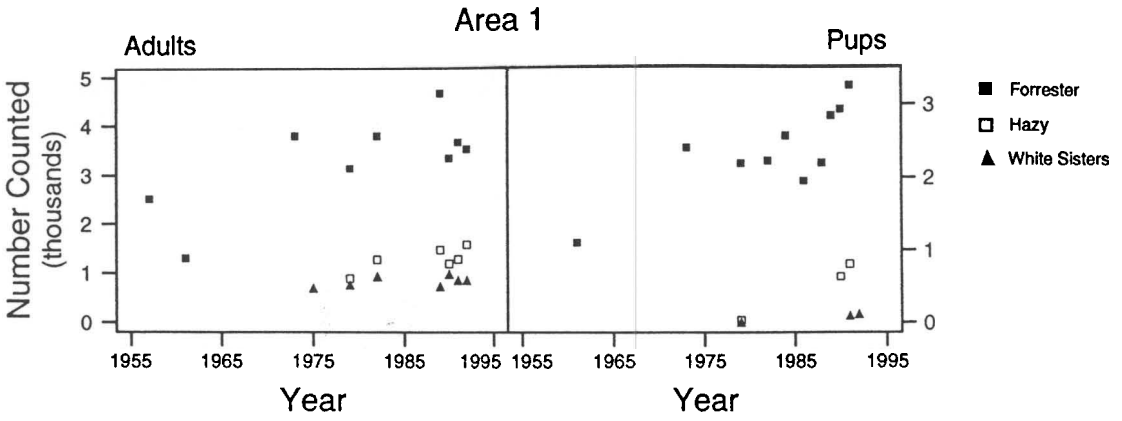


Figure 2. Numbers of adults and pups counted in Area 1 on three rookeries: White Sisters, Hazy Island, and Forrester.

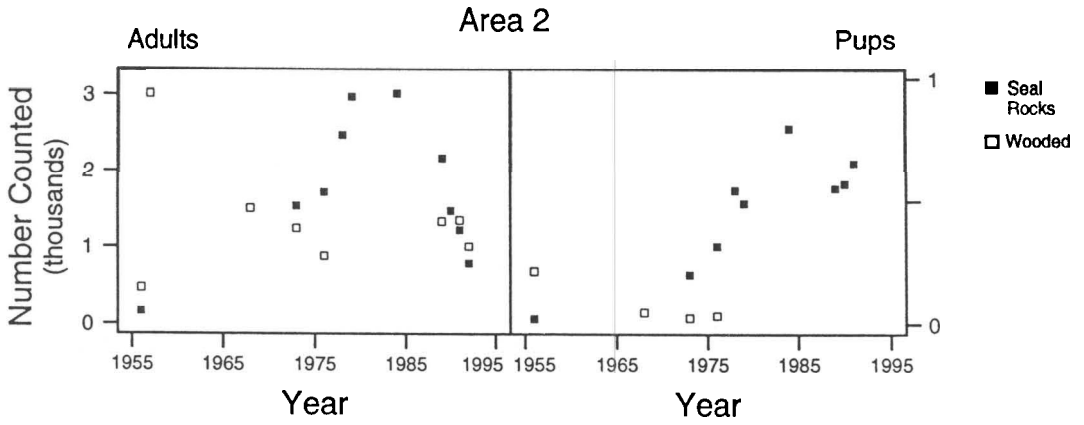


Figure 3. Numbers of adults and pups counted in Area 2 on two rookeries: Seal Rocks and Wooded Island.

counts were made at all but one or two rookeries, we interpolated the number present on missed rookeries from the counts made in adjoining years. No estimates were made when insufficient rookeries were surveyed.

Estimated total population sizes for each of the six Alaska regions (1956–92) were fit with local regression models (loess) that assumed normally distributed errors with constant variances (Cleveland *et al.*, 1993). Diagnostic residual plots were used to select the optimum fraction of data for smoothing. Assumptions concerning the distribution of errors were checked using normal probability plots. Pointwise 95% confidence intervals were calculated for all regressions as outlined in Cleveland *et al.* (1993).

Results

Estimates of population size by area

The number of pups and adults counted by rookery, year, and area are shown in Figs 2–6. Total population size, calculated using Eqs 1 and 2, and estimates of population trends are shown in Figs 8 and 9.

In general, there was a good correspondence between population estimates derived from the pup and the adult counts (Fig. 8; for Areas 1, 3, 4, 5 and 6 combined: paired $t_{26} = -1.634$, $P = 0{\cdot}114$). The only significant exception was in Area 2 where the adult based estimates exceeded the pup based estimates by about 80% (paired $t_9 = 5.540$, $P < 0{\cdot}001$). Greater confidence was placed upon population estimates derived from pup counts in Area 2 because pups do not leave the rookery during the first few months after birth, and adult numbers can vary considerably if mature animals are away from the rookery or immature animals are using the rookery as a haulout. In the other five areas the local regression models were fit to the combined—pup and adult derived—estimates (Fig. 8).

Area 1. There are 3 major rookeries and 5 major haulout sites in southeastern Alaska (Fig. 1). The largest rookery is Forrester Island. The two other rookeries, White Sisters and Hazy Island, used to be classified as haulouts until the late 1970s when some of the females using these sites began giving birth. Since then, there has been a steady increase in pup production on these former haulouts (Fig. 2).

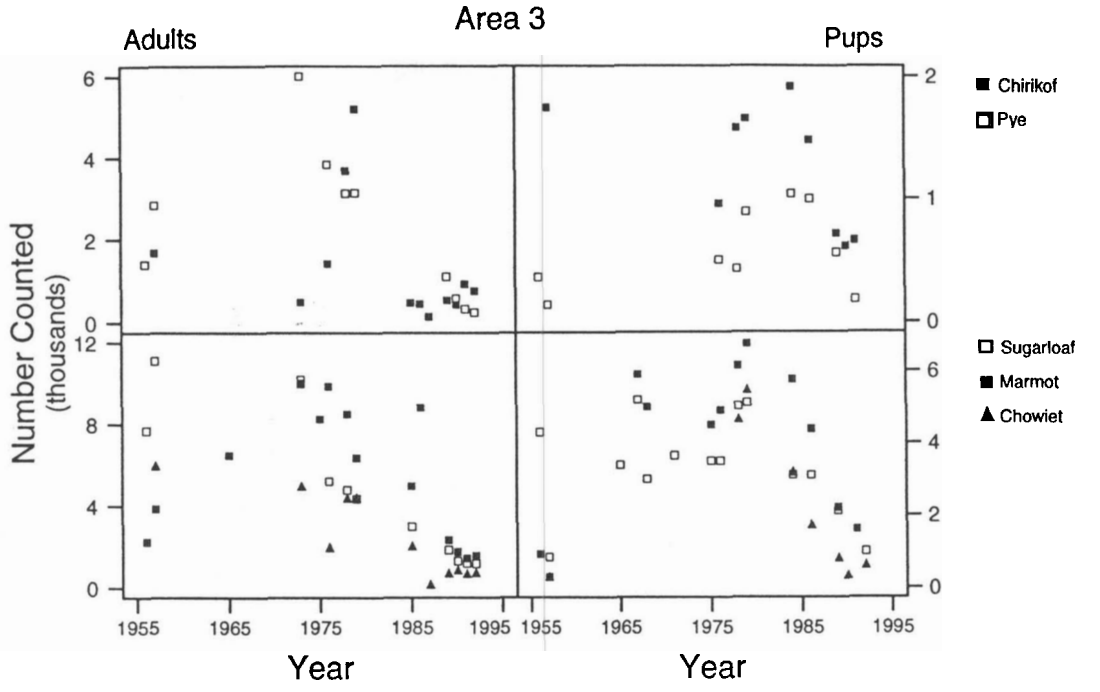


Figure 4. Numbers of adults and pups counted in Area 3 on five rookeries: Chowiet, Marmot, Sugarloaf, Chirikof, and Pye.

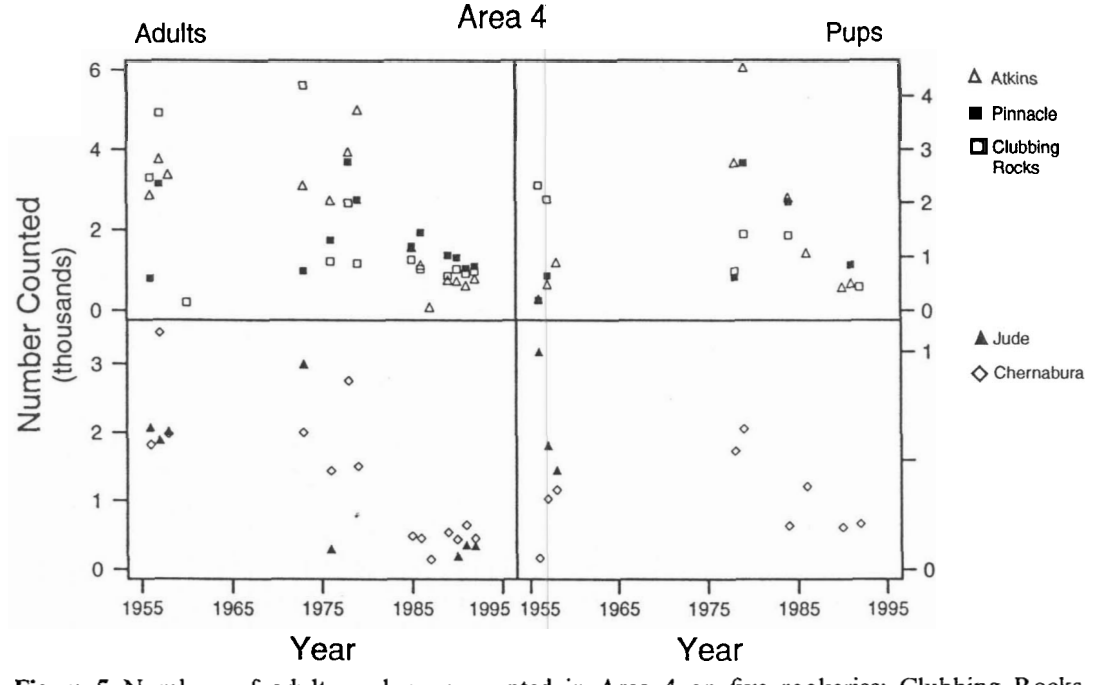


Figure 5. Numbers of adults and pups counted in Area 4 on five rookeries: Clubbing Rocks, Pinnacle, Atkins, Jude, and Chernabura.

The total number of sea lions (pups and adults) in Area 1 was estimated by multiplying the total count of pups or rookery adults by their respective correction factors (Eqs 1 and 2). From 1980 to 1992 we assumed the annual increase in pup production at Hazy Island and White Sisters was approximately linear when field estimates were unavailable (Fig. 2). Prior to this time, we assumed that pups were born only on Forrester Island. Total numbers of adults counted at rookeries in Area 1 did not include those made at White Sisters, and did not include counts from Hazy Island before 1983.

The estimated sea lion population in southeast Alaska (assuming that Forrester Island has always been the major rookery) increased from less than 100 in the 1920s (Rowley, 1929) to 350 in 1945 (Imler & Sarber, 1947), and 2500 in 1957 (Mathisen & Lopp, 1963). The population rose markedly

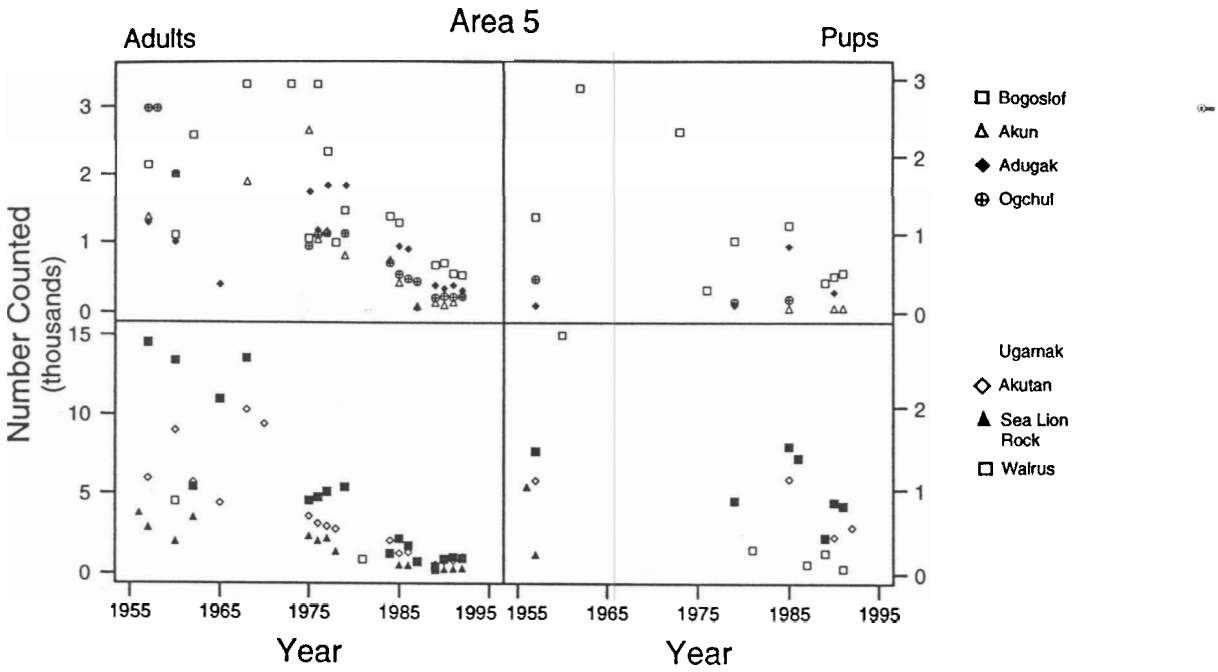


Figure 6. Numbers of adults and pups counted in Area 5 on eight rookeries: Cape Morgan, Ugamak, Sea Lion Rock, Adugak, Ogchul, Bogoslof, and Akun. Walrus Island is part of the Pribilof group in the Bering Sea.

through the 1960s and 70s (Fig. 2) and was estimated at about 19 000 in 1992 (Fig. 8). Forrester Island is currently the largest rookery in the world. However, most of the recent population growth in southeast Alaska appears to be occurring at Hazy Island (Fig. 2).

Area 2. The sea lion population in Prince William Sound is the smallest of all six areas in the Gulf of Alaska (Fig. 1). The region consists of 2 rookeries and 5 major haulouts (Loughlin *et al.*, 1992). In July of 1956, most of the 234 pups counted by Mathisen & Lopp (1963) were born on Wooded Island (Fig. 3). Twenty years later, the bulk of the breeding population was on Seal Rocks (Fig. 3), possibly because the 1964 earthquake changed the topographies of the two islands (Sandegren, 1970; Calkins & Pitcher, 1982).

At Wooded Island, over 200 pups were born in 1956 (Fig. 3), but less than 50 were counted in subsequent survey years (1968, 1973 and 1976). On Seal Rocks, the numbers of pups increased from 21 in 1956 to almost 800 in 1984, although numbers of adults have declined since 1980.

Counts of pups from both rookeries were pooled to estimate total population size in the Prince William Sound region. However, estimates based on adults were only calculated for Wooded Island before 1969, and from Seal Rocks after 1969, to reflect the change in rookery location.

Total numbers of sea lions present in Area 2 during the 1950s and 1960s were approximately 1000 individuals (based on pup counts). The population increased from the early 1970s to the mid 1980s, peaking at about 3500 animals (Fig. 8). More recent surveys suggest that the Prince William Sound breeding population size consisted of approximately 3000 animals in 1992.

Estimates of sea lion density in Area 2, based on pup counts, were considerably lower than estimates derived from adult counts (Fig. 8). For example, the adult-based estimates during the 1950s through 1970s suggest there were about 5000 sea lions present, in contrast to the 1000 we estimated were actually there. Although the adult-based estimates always exceed the pup-based estimates, the differences appear to have diminished through the 1980s. This suggests that many of the adults counted in Area 2 were not part of this breeding population and were not born in this area. In fact, many of the young males and females hauled out and counted in Area 2 probably originate from larger populations to the west (i.e. Area 3).

Area 3. Historically, more sea lions were concentrated among the 5 rookeries and 13 major haulouts near Kodiak Island than anywhere else in Alaska (Fig. 1). A sixth rookery, Chiswell, appears to be no longer used as a breeding site, and was not included with counts from other sites after 1972. Pup production on Marmot and Sugarloaf Islands (once the two largest rookeries in Alaska) suggests that the population increased over two periods of time: 1956–67 and 1973–78 (Figs 4 and 8). Overall, the

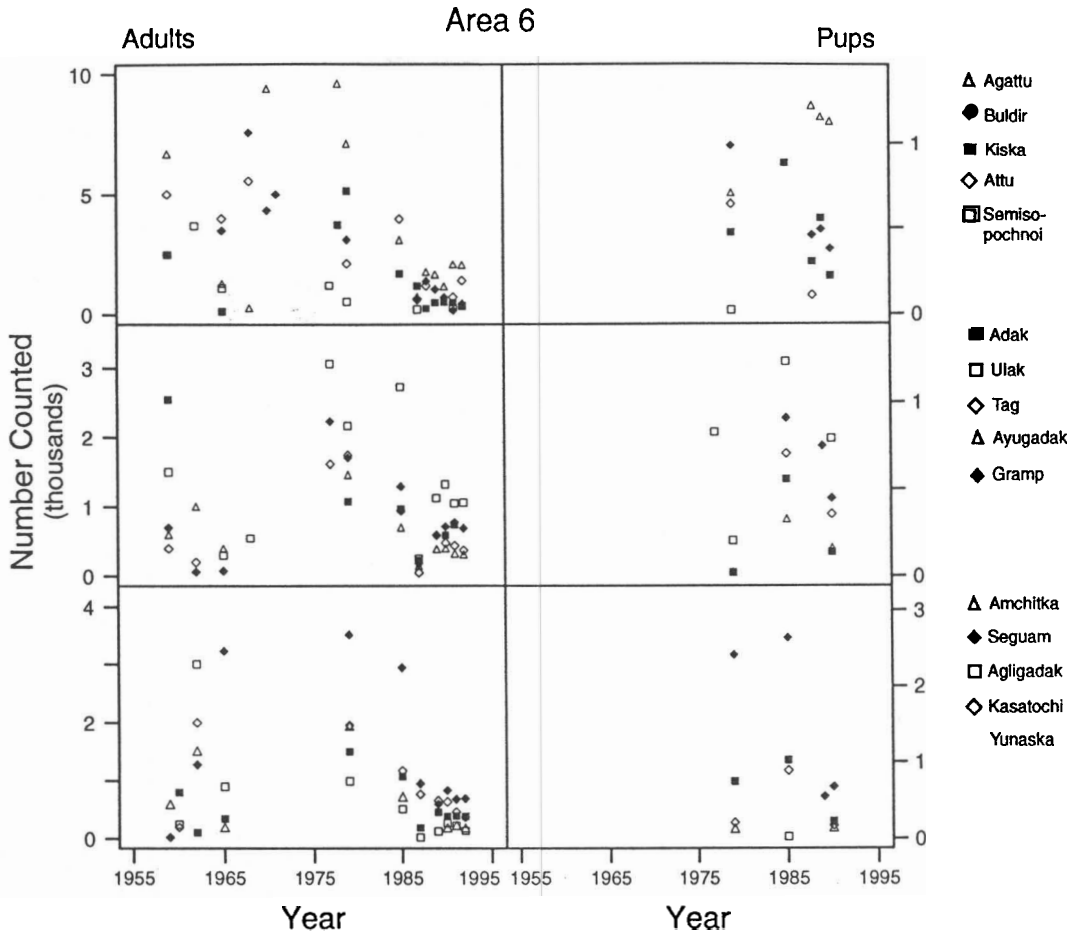


Figure 7. Numbers of adults and pups counted in Area 6 on fourteen rookeries: Attu, Agattu, Buldir, Cape St Stephens, Lief Cove, Ayugadak, Semisopochnoi, Ulak, Tag, Gramp Rock, Kasatochi, Agligadak, Seguam, Yunaska.

total number of sea lions in Area 3 apparently increased from 63 000 to 74 000 during the first period, and from 72 000 to 83 000 during the second. However, after 1980, the population declined precipitously and is currently estimated at approximately 11 000 animals (1992 level).

Area 4. There are 4 rookeries and 7 major haulouts in the western Gulf of Alaska (Fig. 1). A fifth rookery, Jude, appears to be no longer used as a breeding site and was not included with counts from other sites after 1972. Pup and adult counts (Fig. 5) suggest there were about 32 000 sea lions in Area 4 during the late 1950s (Fig. 8). By the late 1970s, the population had risen to 38 000. The model suggests a linear increase over this 20-year period with extremely wide confidence intervals due to the lack of data (Fig. 8). However, pup and adult counts made consistently over the past decade indicate the total population declined from 38 000 in 1979, to 9000 in 1992 (Fig. 8).

Area 5. There are 7 rookeries and 5 major haulouts in the eastern Aleutians (Fig. 1). An eighth rookery shown in Fig. 1, Walrus Island, is part of the Pribilof Islands group in the Bering Sea. Many of the adults at Walrus Island likely originate from the eastern Aleutians. Adult and pup counts were regularly made in the eastern Aleutians between 1957 and 1992 (Fig. 6). They suggest the population increased from 73 000 in 1956 to 85 000 in 1966 (Fig. 8). A gradual decline in numbers began in the mid 1960s. By 1992, approximately 12 000 animals remained.

Area 6. The central and western Aleutian Islands contain 15 rookeries and 7 major haulouts (Fig. 1). Limited data suggest that the population increased between 1959 and the mid 1970s (Figs 7 and 8). However, sporadic counts of pups made since 1977 indicate a declining population (Fig. 7). Counts of adults, also obtained sporadically since 1959, suggest that the central and western Aleutian population began declining in the late 1970s or early 1980s (Fig. 7).

Because there are so many rookeries in Area 6, and because different sites were counted in different years, it is difficult to accurately reconstruct the

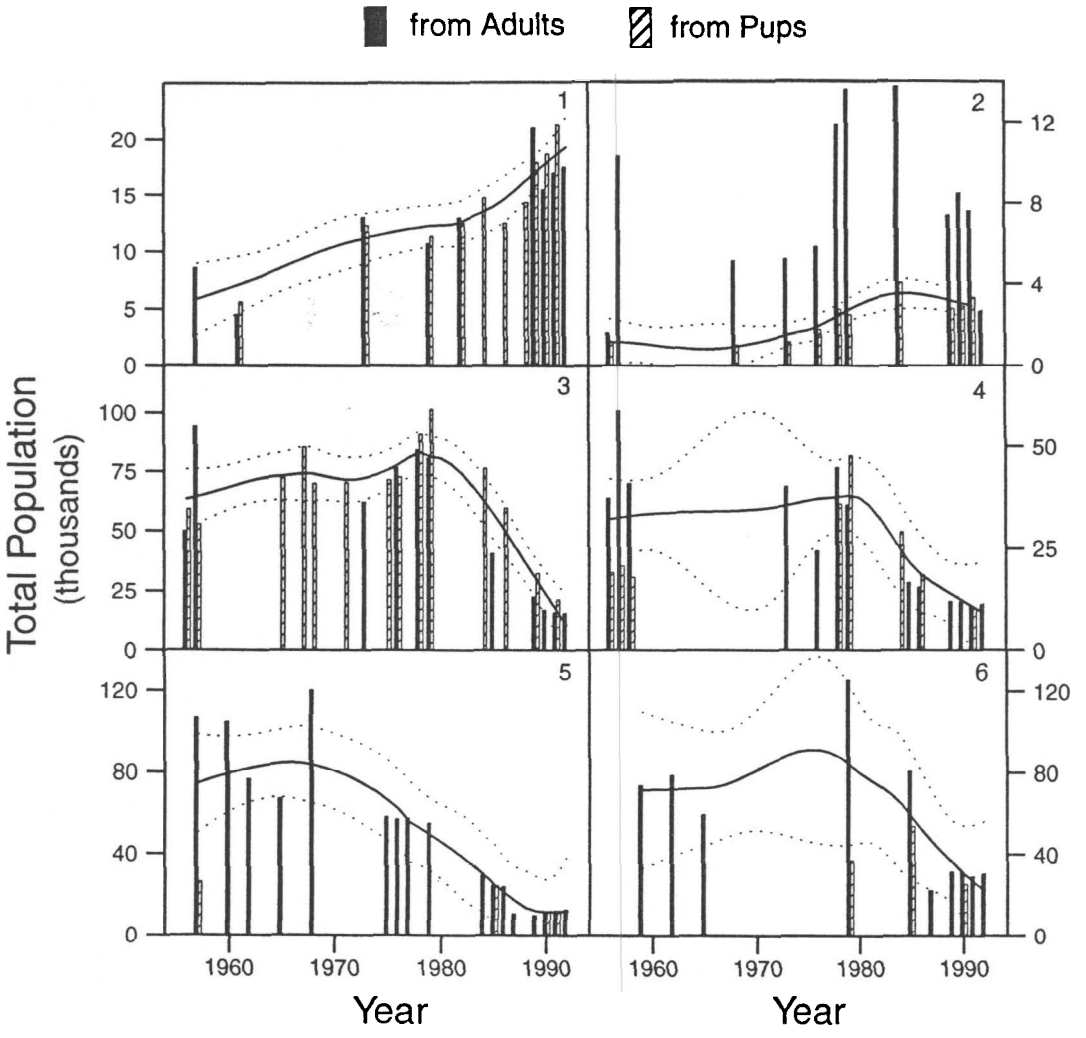


Figure 8. Total population size in Areas 1–6 estimated from pup counts and adult counts. The data were fit with a local regression (solid line) with pointwise 95% confidence intervals (dashed lines). Correlation coefficients and spanning fractions for each of the 6 areas were: Area 1—$r^2=0.83$, $f=0.55$; Area 2—$r^2=0.91$, $f=0.60$; Area 3—$r^2=0.84$, $f=0.50$; Area 4—$r^2=0.59$, $f=0.50$; Area 5—$r^2=0.77$, $f=0.50$; Area 6—$r^2=0.52$; $f=0.80$. Note differences in y-axes scales.

total number of sea lions present in this region. Based on the local regression models fit to the adult derived estimates, the population consisted of approximately 71 000 animals during the early 1960s, and 91 000 in 1975 (Fig. 8). The more recent pup and adult counts suggest the population numbered about 22 000 in 1992.

Changes in population size in the Gulf of Alaska and Aleutians

The total sea lion population in the Gulf of Alaska and Aleutian Islands appears to have increased from 250 000 animals in the mid 1950s, to 282 000 in 1975 (Fig. 9a). Since then, it has declined by over 70% (roughly 5% per year). Approximately 76 000 animals remained in 1992.

A slightly different picture emerges when changes in population size are considered on a region by region basis (Fig. 9b). For example, approximately 70% of the decline in Alaska since 1978 can be attributed to Areas 3 and 6. While the four largest populations (Areas 3–6) have declined, increases in abundance have occurred in Area 1 since the mid 1950s. In Area 2, the smallest of the Gulf populations, numbers of pups born increased in the late 1980s while numbers of adults declined.

Sea lion populations between the Eastern Gulf (Area 3) and the Western Aleutians (Area 6) did not begin to decline at the same time. The first to decline were those in Area 5, beginning in the mid 1960s. This was followed by Area 6 (1975), Area 4 (1978) and Area 3 (1979). In 1992, the total Alaskan population numbered approximately 76 000 (Fig. 9), of which 19 000 (25%) belonged to the eastern population (Area 1) and 57 000 (75%) formed the western population (Areas 2–6; Fig. 10).

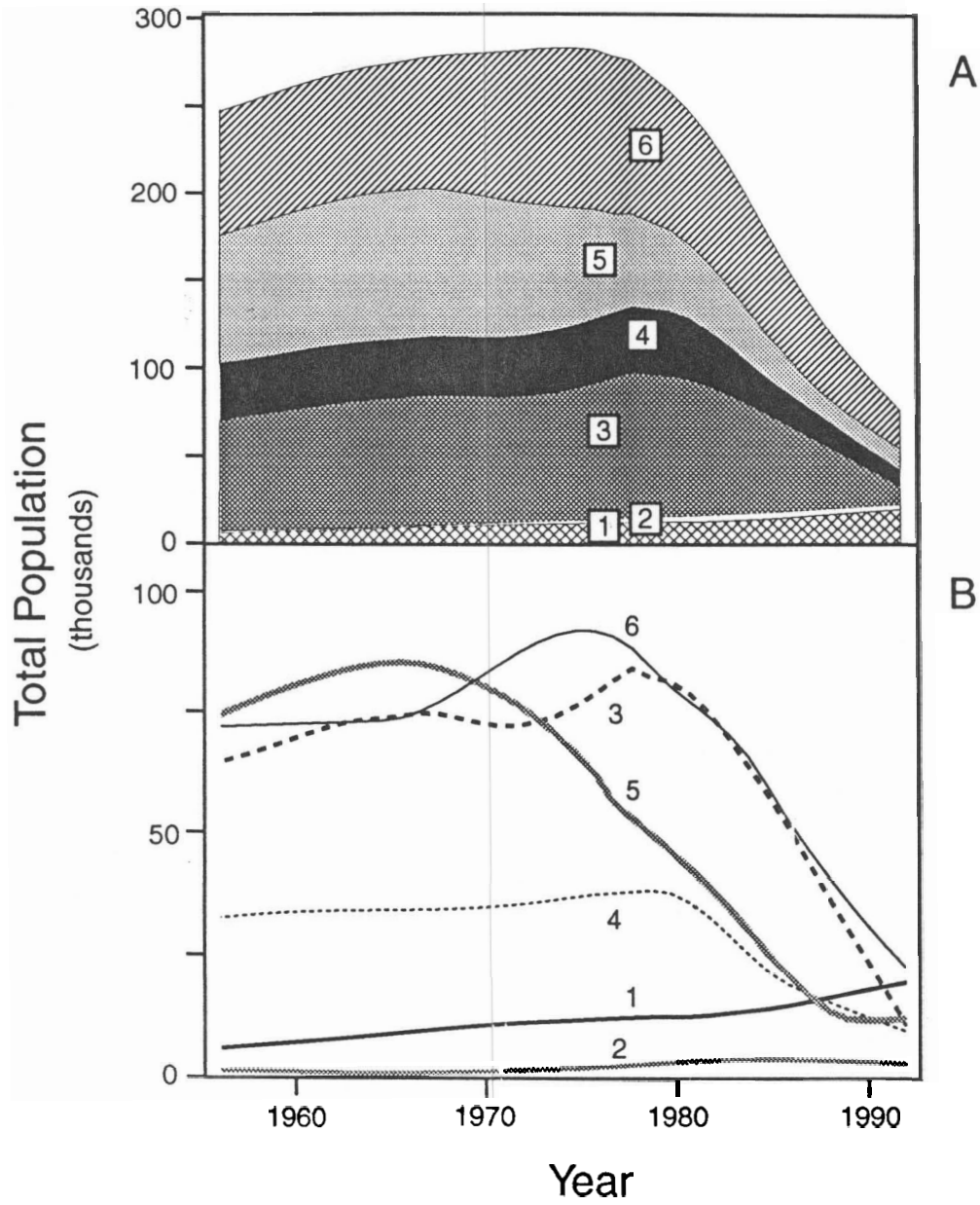


Figure 9. Estimated number of sea lions by area in the Gulf of Alaska and Aleutian Islands (from Fig. 8).

Discussion

Some have incorrectly inferred from sea lion counts made at index sites that the population has been declining since counts were first made in the late 1950s and early 1960s. This conclusion appears to be based on previous analyses that have fitted linear regressions to as few as 3 point estimates of population size made between the 1950s and 1980s (e.g. Fig. 2 of Merrick *et al.*, 1988). Index counts include only the few years and sites that were simultaneously surveyed. They exclude considerable census information and can only reflect the relative difference between the current population and previous levels. Their selective use does not infer when the declines began.

We attempted to use all of the available census data to estimate total population sizes and assess rookery trends. Our results confirm the findings of Braham *et al.* (1980) that the sea lion decline first began in the mid 1960s in the eastern Aleutians (Area 5). Declines in Areas 3, 4 and 6 began later, between 1975 and 1979. Overall, the total sea lion population in the Gulf of Alaska and Aleutian Islands appears to have been relatively large and stable throughout the 1950s, 60s and 70s. Since 1980, sea lions have declined rapidly, except in southeastern Alaska and Prince William Sound (Areas 1 and 2).

The data suggest the rate of population decline may be slowing in the 1990s. This impression (Fig. 9a) is partly due to the population increases that

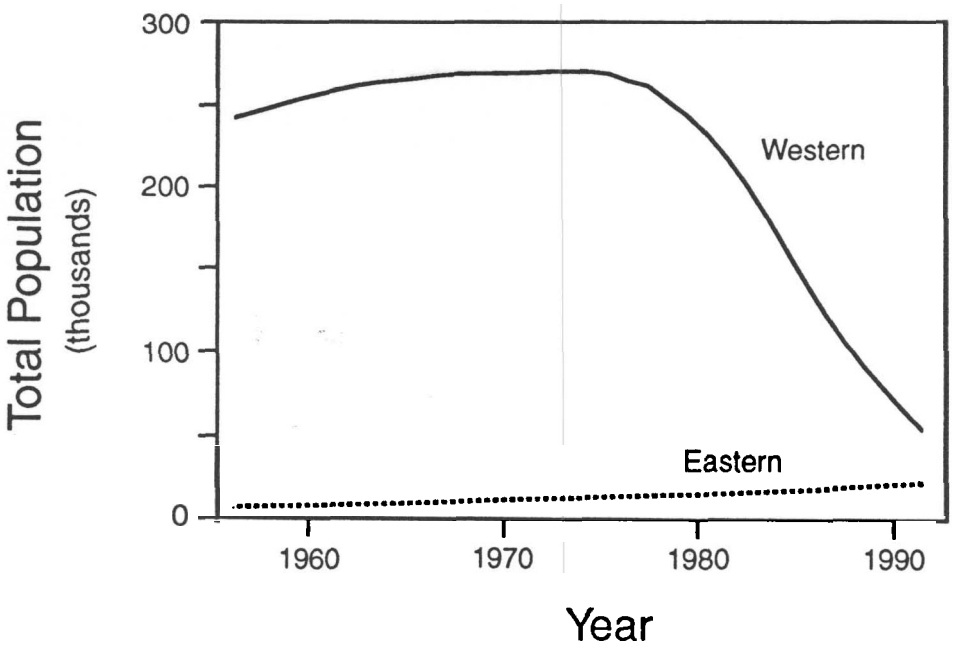


Figure 10. Estimated number of sea lions in the eastern (Area 1) and western (Areas 2–6) stocks of Alaska.

have been occurring in the eastern stock (Area 1—Southeast Alaska). Close inspection of the population trends of each region of Alaska (Figs 9b and 10) reveals that the overall western stock (Areas 2–6) continues to decline at a rate of about 5% per year, but that within two of the subareas—the Western Gulf and Eastern Aleutians (Areas 4 and 5)—the decline may have stopped. Counts of adult and juvenile Stellers observed at rookery and haulout trend sites from 1989 to 1994 are consistent with this claim (see Table 9 of Merrick, 1994). Index site data further suggest the decline may have also stopped in the western Aleutian Islands (Merrick, 1994). Further census data will be needed, however, to substantiate whether these positive changes are longterm or merely temporal.

Kenyon & Rice (1961) estimated there were 183 000 adult Stellers in the Gulf of Alaska and Aleutian Islands in the late 1950s. Other surveys of different Alaskan rookeries and haulouts made sporadically through the 1960s and 1970s suggest that the population in Alaska exceeded 200 000 animals in the early 1970s and was near the maximum level attainable within the ecological limits of the sea lion's habitat (ITG, 1978). These estimates are similar to those we present. From 1974 to 1980 the size of the Alaskan population was estimated at over 196 000 nonpups (Loughlin *et al.*, 1984). In 1989, the estimate was 81 000 nonpups (Loughlin *et al.*, 1992). By contrast our estimates suggest there were 220 000 Stellers from 1974 to 1980 (280 000 if pups are included) and approximately 88 000 nonpups (112 000 including pups) in 1989 (Fig. 9).

The accuracy of our population estimates relies on three major assumptions: the stability of the life table, the precision of the correction factors, and the accuracy and consistency of the counts.

Using a single life table assumes the fraction of pups in the population was constant from 1956 to 1992. This assumption may be reasonable for years prior to 1980 because the life table was calculated from samples collected near Kodiak Island during a period of relative population stability (1975–78). However, population estimates through the 1980s may be too high if the population decline was caused by an increase in mortality of young during their first year of life. Numbers of pups at birth would account for a higher proportion of the total population size if such a change occurred in the life table. For example, if juvenile survival decreased by 10–20% as hypothesized by York (1994), the population estimates derived from Eqs 1 and 2 would have to be reduced by 8–16%.

Eqs 1 and 2 also assume that counts underestimated the number of pups and adults using a site by 10% and 33% respectively, and that the correction factors are the same in all regions. Changing these assumptions directly alters the estimated population size by the same magnitude (i.e. if no correction factor was used, the population would be respectively 10% and 33% lower than shown in Figs 8 and 9). It is also possible that pup counts might overestimate an expanding population while adult counts overestimate one that is declining. Such possibilities might mean that population trend can be inferred from the ratio of adults to pups.

A number of other potential sources of error could also affect the accuracy of the extrapolated population estimates. For example, counts of pups and nonpups were made only once at each rookery, and not always by the same observer or with the same methods (e.g. surveys have been done from the air, water and shore). Estimates of variability due to weather, tide, disturbance, time of day, season, and other factors were also not available (Loughlin *et al.*, 1992). However, replicate surveys in the 1990s have shown low count variations (coefficients of variation were in the order of 10–15% for individual sites and much lower for the sum across sites; A. York, pers. comm.).

The available data indicate that the Alaskan Steller sea lion population was smaller in the 1950s than in the 1970s. Others have suggested that even lower numbers were present during the early part of the century compared to the mid 1950s (ITG, 1978). Such conclusions are based on the census counts from the 1950s and 1960s that may not be reliable (R. Merrick, pers. comm.) because some were done during times of reduced sea lion abundance (e.g. March), and some used undocumented methods, such as counting pups from photos. We used counts made between June and September (with the exception of a few early counts in Area 6), and feel that the available data are reliable and support the conclusion that sea lion populations were smaller in the 1950s than in the 1960s. Our conclusions are also supported by anecdotal reports from individuals who observed the sparse Steller population of Marmot Island in the 1940s increase through the 1950s to become the world's largest breeding population in the mid 1960s (D. Pearson, pers. comm., Kodiak, AK).

The stabilization in numbers of sea lions in the Gulf of Alaska from the late 1960s to late 1970s can be attributed to the direct effect of incidental capture in fishing gear, the shooting of sea lions and the harvesting of adults and pups (Trites, 1997). However, these factors explain only a small portion of the recent population decline, from 1980 to the present.

The reason for the decline of Steller sea lions in Alaska remains unknown (Hoover, 1988; Lowry & Loughlin, 1990; NMFS, 1992; Pascual & Adkison, 1994). Their disappearance could possibly be due to the removal of food resources by commercial fisheries (Alverson, 1992), although, nutritional stress could be occurring through natural changes in the ecosystem. Other causes, such as diseases, parasites, predation, and pollution must also be kept in mind as possible contributing factors.

The decline in sea lion numbers through the 1980s is not an isolated case. There have been declines in Alaskan populations of harbour seals and northern fur seals. Northern fur seals, numbering over 2 million in the early 1950s, are currently less than half of their former abundance on the Pribilof Islands (Lander & Kajimura, 1982; York & Hartley, 1981; Trites & Larkin, 1989; Trites, 1992). On Tugidak Island (near Kodiak Island), harbour seals declined by 85% between 1976 and 1988 (Pitcher, 1990). Limited data from other regions of Alaska also indicate that declines of harbour seal populations have occurred since the mid 1970s in the southeastern Bering Sea and Prince William Sound (Pitcher, 1990; Hoover, 1994).

The world population of Steller sea lions has declined by more than two-thirds since 1980. Declines have been reported in Russia and California, with the most significant drops occurring in the central portion of the Steller's range, the Gulf of Alaska and Aleutians. The only place where Steller sea lions appear to be thriving is in Oregon, British Columbia, and southeast Alaska.

Drawing upon all of the available census data provides the best possible understanding of when and where changes in population abundance occurred in Alaska. They suggest, for example, that the Steller sea lion population was not stable before it began to decline, and that the overall population decline began in the late 1970s. Such conclusions, based on careful consideration of the dynamics of different regions and of individual rookeries may potentially offer new insights into why the Steller sea lion has declined throughout most of its range.

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