FIVE

Reexamination of the Life Table for Northern Fur Seals with Implications about Population Regulatory Mechanisms

TIM SMITH
TOM POLACHECK

INTRODUCTION

Fur seal *(Callorhinus ursinus)* populations in the north Pacific have periodically been subjected to intensvie harvesting since the 1700s (Lander and Kajimura, 1976). Several breeding areas are currently used, with apparent segregation of the animals into separate breeding populations (Kenyon et al., 1954). The best known of these populations is that occupying the Pribilof Islands in the Bering Sea. This population has been the subject of intensive scientific study and harvest management since 1911, as a result of a treaty between Japan, Canada, U.S.S.R., and the United States (Roppel and Davey, 1965). The population was at an extreme low point in abundance in 1911, when only about 70,000 pups were born annually. Following 1911 the population increased, and currently approximately 300,000 pups are born annually (Lander and Kajimura, 1976). The fur seals occupy beaches on the Pribilof Islands during the summer months, where pupping and breeding occur. Males establish and defend harems. Initially the treaty terminated all harvesting, but since 1918 a large proportion of the males between the ages of 2 and 6 have been harvested each year under the assumption that they are "surplus" in the sense that they are not necessary for the maintenance of the population.

A series of studies since 1954 (Kenyon et al., 1954; Scheffer, 1955; Nagasaki, 1961; Chapman, 1961, 1964, 1973) have described, elaborated on, and tested the hypothesis that this population is regulated in size by density through changes in the survival rate of young animals (see also Chapter 10). In addition, a lesser number of studies (Ichihara, 1971; Bulgakova, 1971) have tested this same hypothesis for breeding populations in the western Pacific Ocean. These studies are based on results of research programs by the treaty nations.

In this chapter we review the available information on reproductive and survival rates of Alaska fur seals in the late 1950s, when the population was thought to be in equilibrium, and present a life table for the population for this period. Noting that the population was apparently increasing at about 8%/year when it was at low abundance (see Chapter 10), we calculate the nature and magnitude of changes in the life table implied in the general density-dependent hypothesis.

This examination of the implied changes in the life table was suggested by our review of the hypothesis that vital rates are changing in response to population density (Smith and Polacheck, 1981). We found that in most cases the available data do not support the general hypothesis of density-dependent changes. Furthermore, even if the changes suggested in earlier interpretations of the data are real, the magnitude of these changes is insufficient to account for the high rate of increase in population size observed during the early part of this century. Thus, one objective of this chapter is to determine the magnitude of the changes in vital rates that we would expect given this high rate of increase. We then consider if the absence of evidence for such change is reasonable in view of the quantity of data that have been collected.

The information available for the Pribilof Island fur seal herd is most complete for St. Paul Island, where approximately 80% of pups are born each year. Because information from St. George Island is less complete, whenever possible we will consider only the St. Paul data, although parallel trends have been observed on both islands.

BACKGROUND

The data for this work come from the commercial harvest of 2 to 6-year-old males (Figure 1) and from the national scientific research programs. The research programs have fluctuated widely in scope and have encompassed many aspects of the biology of fur seals. The principal information from these programs relevant to this Chapter are (1) the counts of pups born from 1911 to

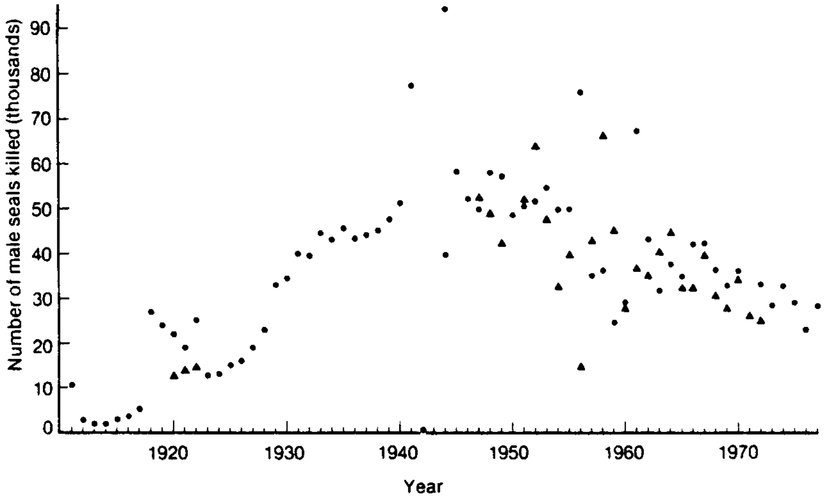

Figure 1 Number of male seals killed on St. Paul Island in the annual harvests, by year (●) and by year class (▲), from NPFSC (1961, 1969, 1971, 1975) and NMFS (1978).

1924, (2) the counts of harem and idle bulls since 1911, (3) the determination of the age of the kill of males from tooth layers since 1947, (4) the pelagic samples of seals from 1958 to 1961, (5) the estimates of numbers of pups born since 1961, and (6) the numbers of pups found dead on the beaches each summer since 1911. These data are described in detail in Smith and Polacheck (1981), and in papers referenced therein. A brief description of the use we make of each of these sources of data follows.

Direct counts of pups on rookeries were made from 1911 to 1924, varying from counts on all rookeries to counts on a sample of the rookeries. Useful estimates or counts are available only for the years shown in Figure 2.

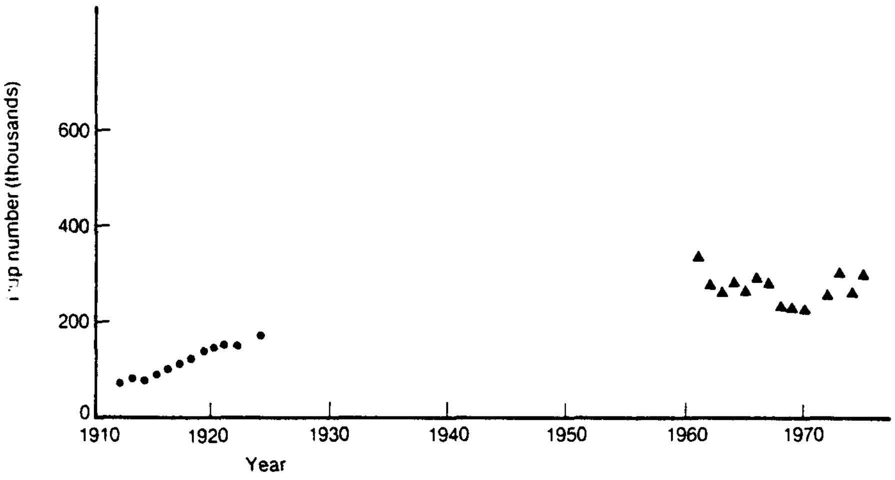

Figure 2 Counts (●) and estimates (▲) of the number of pups born on St. Paul Island, from Lander and Kajimura (1976).

The numbers of adult males on the rookeries, by reproductive class, have been estimated each year since 1912 (Figure 3). The most reliable data are available for the number of males actually holding harems, termed "harem masters." Fewer accurate data are also recorded for the number of adult males not holding harems, termed "idle bulls." The changes in abundance of harem and idle males provide the only measure of the numbers of males escaping the harvest, although uncertainties about survival rates make this difficult to interpret quantitatively.

The determination of age is accomplished by counting ridges on the surface of the teeth (Scheffer, 1955) and by counting layers inside the teeth (Anas, 1970). Age has been determined using these methods for a sample of the animals killed in the harvest since 1947. This permits estimation of the total numbers of males killed from each class, providing estimations of year class strength of males for ages 2 to 6. The estimates of total male kill by year class since 1947 are shown along with the annual kills of males in Figure 1.

From 1958 to 1974, age and reproductive condition were determined for females collected pelagically. Samples of reasonable size were obtained by U.S. researchers from 1958 to 1961 and are used here to estimate reproductive and survival rates.

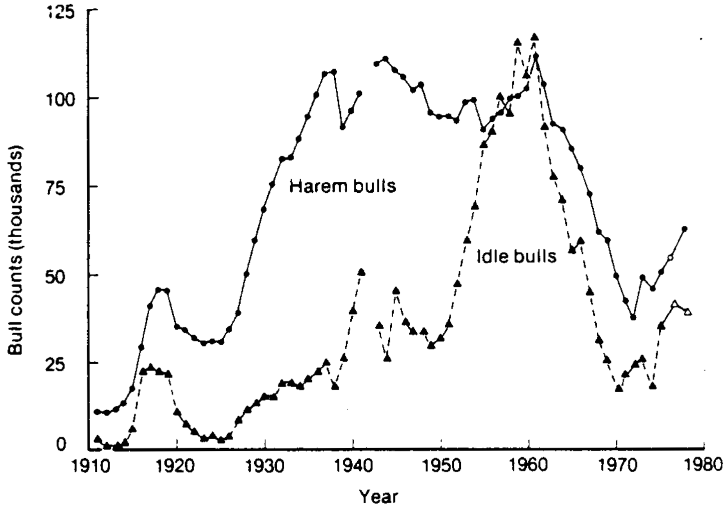

Figure 3 Counts of harem and idle bulls for St. Paul Island, from 1911 to 1977, from Lander and Kajimura (1976) and NMFS (1978).

Starting in the late 1940s pups were tagged in an attempt to estimate the number of pups born. Recovery information was based on the subsequent kill of males at ages 2 through 6. The estimates obtained from this procedure are not considered to be reliable (Chapman, 1964). Starting in 1961, estimates of the numbers of pups born were made based on marking pups by shearing a patch of fur, and subsequently recovering marked individuals in the same summer (Chapman and Johnson, 1968). These latter estimates are considered reliable and are shown in Figure 2 along with the earlier counts of pups born.

The number of pups found dead on the beaches prior to their leaving land in late summer had been estimated for a number of years since 1911. These counts are thought to represent nearly all the mortality occuring on land. They are useful in determining if the survival of pups on land has changed with increased population.

In analyzing these data we use standard statistical procedures for significance tests (Snedecor and Cochran, 1967) and follow Seber (1973) for estimating survival rates. In addition, we make use of discrete life-table analyses, following Mertz (1971) and Leslie (1945).

FEMALE SURVIVAL RATES

Previous Estimates

Survival rates of adult females have been estimated variously, based primarily on the age composition of pelagic samples taken in 1952 and from 1958 to 1961. Chapman (1961) estimated an average rate of 0.79 (rounded to 0.80) based on the age composition of the 1958-1960 U.S. pelagic samples. Nagasaki (1961) analyzed the pelagic samples from the United States for 1958, from the Japanese research program for 1952 and 1958, and the age structure of the females harvested on the Pribilof Islands in 1956 and 1957. He concluded that the sampling biases were such that". . . it is almost impossible, in the present state of study, to calculate accurate mortality rate by age based on the observed age-composition of catches". Chapman (1964) analyzed the U.S. pelagic samples for the years 1958 to 1961 combined, and estimated age-specific survival rates as the ratios of the "adjusted" numbers of each successive pair of ages. The "adjusted" numbers were obtained by fitting a Gompertz curve to the observed age distribution for seals at age 8 and older. This had the effect of smoothing the data and allowing extrapolation along this curve to ages less than 8. However, the fit of the smoothing curve to the observed numbers at each age is not very good with a systematic overestimation of the observed numbers sampled for ages 8 to 15.

Evidence for the Stationarity of the Age Structure

The age distribution of the female seals collected in the pelagic samples by U.S. research vessels is given in Table 1. In order to obtain unbiased estimates of survival rates, the age distribution of the female fur seal population must be stationary (i.e., constant size for the population and with constant proportions in each age class), and the sampling must be representative across the age classes for which survival estimates are made. General demographic theory states that if the population has been at a constant size for a certain period of time, the age structure will approach constant proportions from year to year.

It appears that the population probably reached a maximal, and perhaps constant, size in this century during the late 1940s and early 1950s. This is suggested by (1) the relatively constant annual kill of males between 1944 and 1955, (2) the declining rate of increase in the annual kills between 1930 and 1944, (3) the relatively constant counts of harem master bulls between about 1938 and 1961, and (4) the relatively constant counts of idle males between 1943 and 1951. These are all measures of the male segment of the population, but they suggest that the female segment was likewise relatively constant in size. The harvesting practices were relatively stable from the early 1920s until the early 1950s (Roppel and Davey, 1965).

The conclusion of an approximate constant size is brought into doubt by data for the kill from each year class, which are available since 1947 (Figure 1). The fluctuations in these numbers suggest that the number of seals at ages 2 to 5 in successive year classes varied considerably during this period; this might induce nonstationarity in the age distribution. The fluctuations in the kill by year class in the 1950s are also reflected in the annual kills of males (Figure 1). Similar variations in the annual kills are not seen prior to 1956 (disregarding the war years), which suggests that year class strength may not have affected age structure stationarity prior to the 1950s. Moreover, whereas the numbers killed by year class from 1947 to 1953 are consistent with the hypothesis of constant size, the data from 1954 and 1971 suggest a general but variable decline. It should be noted that the harvesting regime for males changed somewhat starting in the mid- to late 1950s as the annual catches began to decline (Roppel and Davey, 1965). However, these changes do not seem to explain the decline. This apparent decline, if real, should not have affected the age structure for the older animals between 1958 and 1961.

Table 1 Number of Female Seals by Age Class Collected by U.S. Researchers, by Year

Age	1958	1959	1960	1961	1958-1961
3	39	43	18	84	184
4	42	93	36	96	267
5	70	114	55	68	307
6	99	118	45	62	324
7	103	143	66	95	407
8	102	164	105	107	478
9	81	108	144	114	447
10	97	96	129	112	434
11	113	98	136	82	429
12	134	76	106	71	387
13	110	56	120	76	362
14	92	70	107	67	336
15	71	87	67	68	293
16	56	69	53	55	233
17	36	36	46	24	142
18	22	27	23	25	97
19	14	16	19	10	59
20-22	5	17	12	9	43

By 1958, when the first pelagic samples used here were taken, any irregularities in the age structure caused by the increase in size of the population since 1911 should have diminished to inconsequential levels if the population had approached a constant size. This was checked and confirmed by examination of the predicted age structures from a simulation model of population size. This model, described by Smith and Polacheck (1981), is structured around single-species density-dependent concepts. It assumes variously that fecundity, juvenile survival, and adult survival change with density such that the model mimics the observed growth of the population as reflected in the male harvest and, where available, the numbers of pups born. There are slight biases toward understimation in survival rates calculated from such simulated age structures for the late 1950s.

An additional complication in the representativeness of the pelagic samples is that substantial numbers of females of several age classes were killed beginning in 1956, in a management effort to reduce the numbers of pups born and thereby increase the survival of pups to age 3. The effect on the age structure of this harvesting was explored by further examination of the simulation model described above. The calculations were extended through 1961 with the age structure of the harvest of females from 1956 to 1961 incorporated into the model. The simulated age structures suggest that no effect of this harvest would have been observable for animals age 11 and older through 1961. Furthermore, the age structure probably did not show any effect of this harvesting for animals older than 8 in 1958, 9 in 1959, and 10 in 1960. The lack of effects for these ages is attributable to a combination of the magnitude and age structure of the female harvest.

New Estimates

Inspection of the data in Table 1 demonstrates that the samples are not representative of the animals in the younger ages as the proportions in each age class in the harvest show an increase with age up to the ages of 7 to 9 in all four years. There is considerable variability in the proportions observed in the age groups older than 8, however, which suggests the possible nonrepresentativeness of the samples between years. Following Seber (1973), the equality of the observed proportions between years within ages was tested with a chi-squared statistic. The test statistic for the data in Table 1 has a value of 122, with 36 degrees of freedom. As this is large ($p < 0.001$), there are likely some changes between years in the proportions within each age class. This could be the result of sampling biases between years or of nonstationarity of the age distribution.

The questions of the representativeness of the samples between years and the possibility of sample biases within years over the geographic areas sampled (Nagasaki, 1961) need to be investigated further. As the data are not readily available in a form that will allow such investigation at this time, and as these data have been used in the past (Chapman, 1961) to estimate survival rates, we have used them as presented, recognizing the need for more detailed investigation in order to better evaluate our results.

Owing to apparently changing survival rates with age, the most adequate estimator for survival for each age class is the ratio of numbers sampled at successive ages (Seber, 1973). Such estimates have not been presented elsewhere for the U.S. data, and are given here by year (Table 2) along with appropriate descriptive statistics (Seber, 1973). It is clear on inspection that the variability of the estimates increases markedly after approximately age 16, and that the samples are subject to high levels of variance in that they occasionally yield

Table 2 Survival (S) as Ratios of Observed Numbers of Females of Successive Ages in U.S. Pelagic Samples for Ages 8 to 20 by Year[a]

Age	S	$\bar{\sigma}$	C	r
		1958		
8	0.79	0.092	−0.0117	−0.55
9	1.20	0.680	−0.0144	−0.50
10	1.17	0.161	−0.0122	−0.50
11	1.19	0.152	−0.0073	−0.45
12	0.82	0.106	−0.0062	−0.50
13	0.84	0.118	−0.0070	−0.49
14	0.77	0.122	−0.0086	−0.50
15	0.79	0.141	−0.0091	−0.47
16	0.64	0.137	−0.0091	−.048
17	0.61	0.165	−0.0177	−0.49
18	0.64	0.218	−0.0097	−0.33
19	0.21	0.136	−0.0238	−0.45
20	0.33	0.385	—	—
		1959		
8	0.66	0.067	−0.0054	−0.53
9	0.89	0.125	−0.0095	−0.52
10	1.02	0.147	−0.0081	−0.47
11	0.78	0.119	−0.0075	−0.49
12	0.74	0.130	−0.0164	−0.57
13	1.25	0.224	−0.0222	−0.50
14	1.24	0.200	−0.0113	−0.44
15	0.79	0.128	−0.0060	−0.44
16	0.52	0.107	−0.0109	−0.53
17	0.75	0.191	−0.0165	−0.46
18	0.59	0.187	−0.0116	−0.39
19	0.31	0.160	−0.0875	−0.67
20	1.40	0.820	—	—
		1960		
8	1.37	0.122	−0.0092	−0.45
9	0.90	0.109	−0.0064	−0.52
10	1.05	0.130	−0.0077	−0.46
11	0.88	0.101	−0.0131	−0.55
12	1.13	0.151	−0.0124	−0.47
13	0.89	0.119	−0.0134	−0.45
14	0.63	0.098	−0.0121	−0.52
15	0.79	0.145	−0.0064	−0.51
16	0.87	0.175	−0.0189	−0.42
17	0.50	0.128	−0.0167	−0.55
18	0.83	0.256	−0.0280	−0.36
19	0.32	0.148	−0.0286	−0.62
20	1.00	0.578	—	—

Table 2 (continued)

Age	$\hat{S}$	$\hat{\sigma}$	C	r
		1961		
8	1.07	0.107	−0.0085	−0.49
9	0.98	0.131	−0.0073	−0.46
10	0.73	0.106	−0.0060	−0.52
11	0.87	0.140	−0.0083	−0.53
12	1.07	0.177	−0.0084	−0.48
13	0.88	0.148	−0.0052	−0.52
14	1.02	0.175	−0.0074	−0.47
15	0.81	0.147	−0.0130	−0.41
16	0.44	0.107	−0.0094	−0.60
17	1.04	0.298	−0.0180	−0.37
18	0.40	0.150	−0.0137	−0.54
19	0.70	0.345	−0.0526	−0.36
20	0.29	0.229	—	—

[a]Also given are the estimated standard deviations ($\hat{\sigma}$) for early estimates, and covariances *(C)* and correlation coefficients *(r)* of successive pairs of estimates.

estimates greater than one. The estimates that are greater than one are not limited to those ages where the female kill might have had an effect.

The pairs of estimates of survival rates for successive age classes are negatively correlated, with the correlation coefficient depending only on the actual values of the survival rates for those ages. An expression for the correlation coefficient *(r)* in terms of the two annual survivals (S_x, S_{x+1} for ages x and $x + 1$) can be obtained by simplifying the expression for the correlation coefficient in terms of the covariance and the variances, as given in Seber (1973), obtaining

$$r(S_x, S_{x+1}) = -[(1 + S_x)(1 + S_{x+1}^{-1})]^{-1/2}$$

The magnitude of the second survival rate in a pair has more of an effect on the value of the correlation than does the magnitude of the first, and the correlation cannot exceed 0.7 in absolute value. Also for the survival rates in the neighborhood of those estimated for fur seals, the correlation coefficient will be around −0.5. The covariances and the corresponding correlations between pairs of estimates are given in Table 2.

The average across years of the estimated survival rates in Table 2, weighted inversely by their variances, are given in Table 3 (S), along with Chapman's (1964) estimates of survival rates S_c for these ages, for comparison. Note that the weighted average estimates are generally greater than Chapman's from ages 9 to 15, and lower from ages 16 to 19. These average estimates are shown in Figure 4.

These estimates of the survival rate are probably reliable for ages 12 and older. The estimates for ages 8 to 11 must be used with considerably less confidence owing to possible effects of the female harvest. We have little informa-

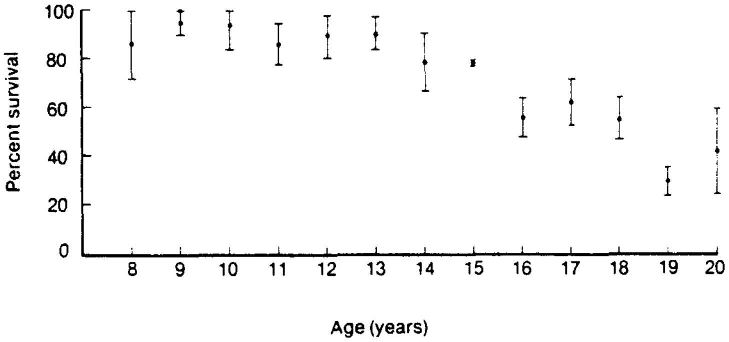

Figure 4 Estimates of annual survival rates by age with associated ranges of plus and minus one standard deviation, from Table 3.

tion on the survival rates for animals younger than 8 because of the apparent nonrepresentativeness of the sampling for these ages. Chapman's (1961) estimates of survival for ages 3 to 7 are very uncertain because of the lack of useful data for these ages and the poor fit of the Gompertz equation he used for extrapolation.

Table 3 Survival Rate Estimates for Female Alaska Fur Seals Pooled Across Years From Table 2 (*S*) and from Chapman (1964)(S_c)[a]

Age	S	S_c
8	0.86 (0.144)	0.91
9	0.95 (0.058)	0.90
10	0.94 (0.099)	0.88
11	0.86 (0.085)	0.86
12	0.90 (0.090)	0.84
13	0.91 (0.066)	0.81
14	0.79 (0.118)	0.77
15	0.80 (0.004)	0.74
16	0.56 (0.080)	0.69
17	0.63 (0.091)	0.64
18	0.56 (0.085)	0.57
19	0.30 (0.063)	0.50
20	0.42 (0.177)	0.41

[a] Standard deviations in parentheses.

REPRODUCTIVE RATES

Previous Estimates

The pelagic samples of female seals (1958-1974) provide the basic data for estimating reproductive rates. The seals reproduce annually on the breeding islands, mate immediately after parturition, and have delayed implantation of the ovum. The females collected pelagically are classified as pregnant or nonpregnant on the basis of a detailed examination of the reproductive tract.

Chapman (1961) examined the proportion pregnant for the 1958, 1959, and 1960 samples. Utilizing his estimates of the age-specific mortality rates as discussed above, Chapman estimated the average pregnancy rate for seals 3 years of age and older at 0.60 (i.e., for a population with a stable age distribution, 60% of the females aged 3 and older are estimated to give birth each year). Nagasaki (1961) analyzed a mixture of pelagic and land-based samples for pregnancy rates. He concluded that there were differences in the pregnancy rate between the Japanese and U.S. pelagic samples for the younger ages, and that the land-based samples suffered consistent biases in the representativeness of reproductive condition. (Nagasaki's precise estimates are not tabulated, but are shown in his Figure 8.) Chapman (1964) further analyzed the pelagic samples from 1952, and 1958 to 1961 combined, for both U.S. and Japanese researchers. He also noted the difference between the U.S. and Japanese samples and concluded that his previous estimate of 0.60 for the Pribilof seals is the most reasonable.

Revised Reproductive Rate Estimates

The published analyses of pregnancy rates do not exhibit all the age-specific values (except perhaps Nagasaki's untabulated values). Also, the variability associated with these estimates is not given. We have calculated the values by year with their standard deviations (Table 4). The standard deviations are obtained by assuming binomial sampling within an age class (i.e., $\hat{\sigma}(P) = (p(1 - p)/n)^{1/2}$, where p denotes the estimated proportion pregnant and n denotes the number samples of that age). Combined age-specific pregnancy rates over the four years are also given as the average of the annual estimates weighted inversely with their variances. The averaged pregnancy rates from Table 4 are shown in Figure 5. Useful samples for pregnancy rates are available for years beyond 1961. These are not included in order to be consistent with the data from which survival rates were estimated above, but they do not affect the general conclusions of this chapter. These samples are discussed further in Smith and Polacheck (1981).

The problems of bias apparent in estimating survival from the pelagic samples are not as important in estimating pregnancy rates. For unbiased estimates in this regard females of any particular age must be equally likely to be in the sample, regardless of reproductive condition. The estimates of pregnancy rate by age are consistent over the four years shown in Table 4 and are similarly consistent for the data from 1962 to 1970 for females older than 5 years of age. There is some evidence of a declining pregnancy rate for ages 3, 4, and 5, between 1962 and 1970, but the changes are neither large nor consistent and may represent sampling variability and sampling area differences (A. Johnson, personal communication).

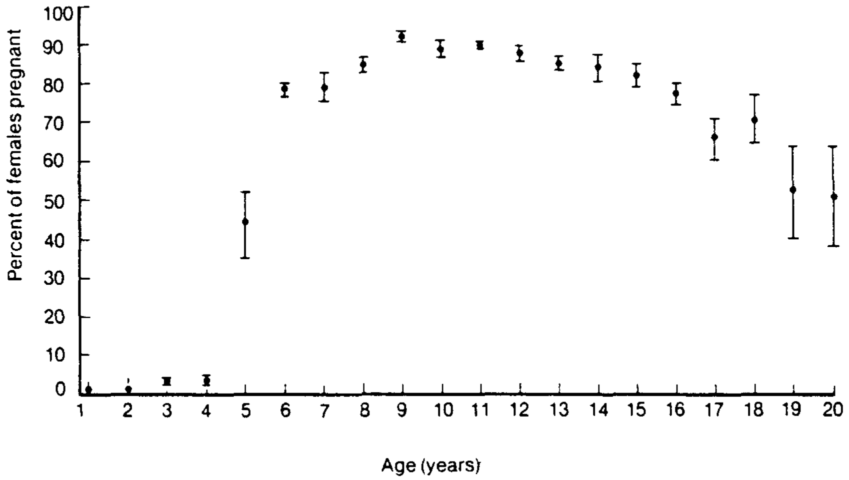

Figure 5 Estimates of annual reproductive rates as percent pregnant, by age, with associated intervals of plus and minus one standard deviation from Table 4.

SURVIVAL DURING THE FIRST SUMMER

The annual counts of dead pups can be compared to the estimates of numbers of pups born to get estimates of survival to the time the pups leave the islands at the end of summer. These data, up to 1951, have been analyzed by Kenyon et al. (1954), where it is noted that the estimated mortality rates had increased substantially just prior to 1951 and that this increase was associated with an apparent large increase in population size. Nagasaki (1961) presented an analysis of much the same data and also concludes that a density-dependent relationship was involved. However, the estimates of the number of pups born since 1924 used in both papers have subsequently been considered unreliable (see above and Chapman, 1964).

The same type of analysis has been extended up to 1976 using estimates of numbers of pups born from shearing and recapture estimates (Smith and Polacheck, 1981). In that analysis, the survival of pups to the end of the summer exhibits a decline with increased population size. This decline is apparent in the estimates of first summer survival in Table 5, which are calculated from data in Smith and Polacheck (1981, Table 3 of Appendix I in that reference).

Table 4 Proportion of Pregnant Female Seals by Age and Year of Sample ($\hat{p}$) and Weighted Average Proportion of Pregnant Over All Years ($\bar{p}$)[a]

	1958		1959		1960		1961		Average	
Age	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	p	$\hat{\sigma}(\bar{p})$
3	0.03	0.025	0	0	0	0	0	0	0.03	0.008
4	0.02	0.024	0.06	0.025	0.03	0.027	0.01	0.010	0.03	0.009
5	0.46	0.060	0.56	0.046	0.49	0.067	0.21	0.049	0.44	0.084
6	0.81	0.040	0.77	0.039	0.80	0.060	0.76	0.054	0.79	0.012
7	0.89	0.030	0.76	0.036	0.79	0.050	0.76	0.044	0.79	0.035
8	0.89	0.031	0.87	0.027	0.86	0.034	0.79	0.039	0.85	0.019
9	0.96	0.021	0.89	0.030	0.92	0.022	0.94	0.023	0.92	0.014
10	0.88	0.033	0.85	0.036	0.92	0.025	0.94	0.023	0.89	0.019
11	0.92	0.026	0.90	0.031	0.91	0.024	0.89	0.035	0.90	0.006
12	0.82	0.033	0.88	0.037	0.91	0.028	0.43	0.030	0.88	0.024
13	0.83	0.036	0.89	0.041	0.88	0.030	0.83	0.043	0.86	0.015
14	0.82	0.040	0.84	0.043	0.80	0.038	0.93	0.032	0.84	0.032
15	0.79	0.048	0.89	0.034	0.84	0.045	0.79	0.049	0.82	0.025
16	0.79	0.055	0.75	0.052	0.72	0.062	0.86	0.047	0.78	0.031
17	0.57	0.083	0.81	0.066	0.67	0.069	0.63	0.099	0.66	0.053
18	0.59	0.105	0.85	0.068	0.83	0.079	0.64	0.096	0.71	0.062
19	0.29	0.121	0.81	0.097	0.58	0.113	0.50	0.158	0.53	0.115
20	0.40	0.219	0.59	0.119	0.33	0.136	0.89	0.105	0.51	0.131

[a] $\hat{\sigma}(\bar{p})$ indicates standard deviations.

SURVIVAL TO AGE 3

Several estimates of the survival of younger seals are given in the literature (Chapman, 1961, 1964, 1973). This has been an area of great interest and research, since the primary hypothesis for the natural regulation of fur seal populations has been that the survival of younger animals varies with population size. Unfortunately, most of the data available to estimate juvenile survival rates are not easy to interpret. Certain key observations are missing in some critical years, and vital rates that would permit estimation of the missing information from other information are poorly known.

The basic technique used to estimate the survival rate for this period is to divide the number of male seals born into the sum of the male seals harvested and escaping harvest. The number escaping has not been reliably estimated. These estimates are discussed in Smith and Polacheck (1981), where it is concluded that reliable estimates of survival rates for these ages are not available.

In the absence of estimates of the actual survival rates, the ratio of the male kills from each year class and the estimates of pups born provide a lower bound to the actual survival rates. The available data are shown in Table 5, with the corresponding estimated lower bounds. Values are not presented for the 1950s because of the problems associated with the estimates of numbers of pups born during this period. Also included in Table 5 are estimated lower bounds for their survival from 1920 to 1922. These estimates are also based on the ratio of the actual kill of males from each year class to the estimated number of pups born. However, in this case, the actual kill from each year class was estimated from the size-frequency distribution of the male kill and may contain larger biases.

The average of these estimates of lower bounds for the survival rates for the years 1920 to 1922 (0.21) is significantly different from the average for the years 1961 to 1970 (0.26), but the difference is not in the expected direction. However, it is not clear that these lower bounds are comparable, since the number of males surviving the harvest at age 4, which is the primary factor causing these numbers to be less than the true survival rates, has presumable changed significantly with changing harvesting procedures (Roppel and Davey, 1965).

These lower bounds for the survival from birth to age 3 can be adjusted to the period from the end of the first summer to age 3 by dividing by the estimated first summer's survival rates indicated in Table 5. This adjustment serves to increase the difference between the two periods, although the latter period (when populations were higher), continues to have higher estimated lower bounds of survival rates.

We have explored in detail the general problem of estimating the survival rate of male seals from the annual kills and the annual counts of harem and idle bulls in Smith and Polacheck (1981). Calculations in that report suggest that the available information is consistent with a wide range of values of juvenile survival, but that a maximum value may be about 72%. This may be considered a minimal upper bound for the juvenile survival rate.

EQUILIBRIUM RATES

If available estimates of survival and pregnancy rates are asssumed to be for a period of time when the population was not markedly changing in size, the net rate of change should have been approximately zero. Making this assumption and ignoring any possible bias that would result from nonrandom sampling, we have estimates of pregnancy rates for all age classes, of survival rates for females ages 12 and older, and of survival rates for both sexes during the first summer of life. In addition, we have some estimates of lower bounds for survival of males from birth to age 3. We have no direct estimates of survival from ages 3 to 8, and some possibly biased estimates of survival from ages 8 to 12. The existing estimates can be used to calculate estimates for those values of survival rates for which we have little or no information and which are consistent with a population growth rate of zero.

Using standard life-table calculations, we computed the rate of survival of females between birth and age 3 that would result in a zero net rate of increase. This was done for a range of values of survival rates from ages 3 to 23 and for ranges of estimates of pregnancy rates and survival rates of older females consistent with the variances of the above estimates. The results are shown in Table 6.

Table 5 Estimated Number of Pups Born and Subsequent Harvest of Males from that Year Class on St. Paul Island, and Estimated Survival over the First Summer

	Pups Born[a] × 1000	Kill of Males[b]	Survival to Age 3[c]	First Summer's Survival Rate[d]
1920	143	14,751	0.206	0.972
1921	150	15,375	0.205	0.973
1922	159	17,050	0.215	0.983
1961	337	36,882	0.219	0.820
1962	278	34,991	0.252	0.829
1963	264	40,126	0.304	0.870
1964	285	44,882	0.315	0.920
1965	267	32,202	0.241	0.846
1966	296	32,285	0.219	0.924
1967	284	39,504	0.278	0.948
1968	235	30,266	0.258	0.887
1969	234	27,778	0.237	0.940
1970	230	34,188	0.297	0.906

[a] 1920 to 1922 from Chapman (1961, his Table 2); 1961-1970 from Lander and Kajimura (1976, their Table 2).

[b] 1920 to 1922 from Chapman (1961, his Table 3) as the sum of commercial and native kills; 1961-1970 from Lander and Kajimura (1976, their Table 6); 1970 from Marine Mammal Division (1977).

[c] Lower bound, assuming all kill was at age 3.

[d] Calculated from Smith and Polacheck (1981, Table 3 of Appendix I), for those years where the kill of males is known.

Table 6 The Calculated Survival Rates from Birth to Age 3 that Result in a Net Rate of Increase of Zero, Using Combinations of Ranges of Other Survival Rates and Pregnancy Rates

		Pregnancy Rates		
Survival Rates for Older Animals	$S_{3,4}$[a]	Low	Central	High
Low	0.80	0.90	0.85	0.81
	0.85	0.71	0.68	0.65
	0.90	0.57	0.55	0.52
	0.95	0.46	0.44	0.42
Central	0.80	0.71	0.68	0.65
	0.85	0.56	0.54	0.51
	0.90	0.45	0.43	0.41
	0.95	0.36	0.34	0.33
High	0.80	0.54	0.51	0.49
	0.85	0.42	0.40	0.39
	0.90	0.33	0.32	0.31
	0.95	0.27	0.25	0.24

[a] $S_{3,4}$ is the survival from ages 3 to 4.

rates would have had to have been when the population was increasing. The counts of pups made from 1912 to 1924 provide our best estimate of how fast the population is capable of increasing. This was about 8%/year (see Eberhardt, Chapter 10). This rate is also supported by the increases in the annual kills of males from around 1924 to 1931 (Figure 1).

The dominant feature of the survival and reproductive rates as estimated for fur seals for a rate of increase of zero is that they are rather close to biologically reasonable or even logically possible maximum values. Thus, there is little scope for changes in these rates in a density-dependent response to changes in population size that would result in a rate of increase of 8%. To explore the implications of this limited range on the density-dependent mechanisms that are possible or reasonable for this population, we have calculated the percentage changes in each of several rates that would be necessary were an 8% rate of increase to prevail. We have considered the changes in each rate as a percent of the difference between the maximum value and the rate corresponding to a zero rate of increase for the population, as illustrated in Figure 7.

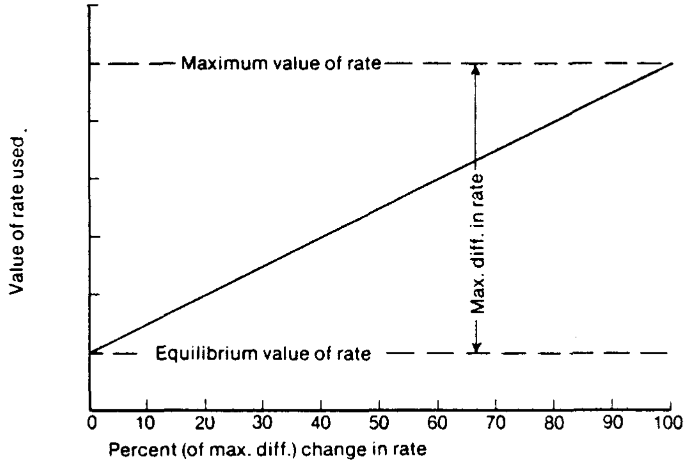

Figure 7 Diagram of the method of specifying changes in vital rates, as a percent of the difference between the biologically maximal value and the value at equilibrium. Values on the ordinate depend on the variable involved.

For survival the absolute maximum is obviously unity. We have little biological information to specify any values less than unity for this maximum. Estimated rates for ages 12 and 13 are around 0.94, suggesting that very high rates of survival are possible. Maximum values or survival rates may vary with age, as is observed for the estimated values. In particular, survival from birth through the first year probably has a lower maximum value than for any other age class, except perhaps for very old animals. Again, little information for a value below unity is available. However, it is not reasonable that the animals are

The survival rates used between ages 3 and 12 were constructed by linear interpolation between the estimated value at age 12 and a range of values at age 3, as shown in Figure 6. The ranges of values for the pregnancy rate and the survival rate of older animals used in the computations in Table 6 were constructed as the weighted average estimates given in Tables 3 and 4 and these estimates plus (high) and minus (low) one standard error. These ranges of survival and pregnancy rates are not meant to represent confidence intervals, as discussed above, but rather to serve as a basis for considering the ranges of values of survival from birth to age 3 consistent with a zero rate of increase of the population.

It can be seen from Table 6 that within the range of uncertainty of the parameter estimates, allowable values of survival from birth to age 3 are generally higher than the lower bounds for this rate given in Table 5. To get values as low as the average estimated lower bounds from 1961 to 1970 (0.26) one must have rather high survival rates for all ages. Moreover, the lowest estimates of the adult survival rates tend to give biologically unreasonable estimates of the survival rates from birth to age 3. It can also be seen that within the sampling variability of the estimates of pregnancy and survival rates the calculations are rather more sensitive to changes in survival rates than to changes in pregnancy rates.

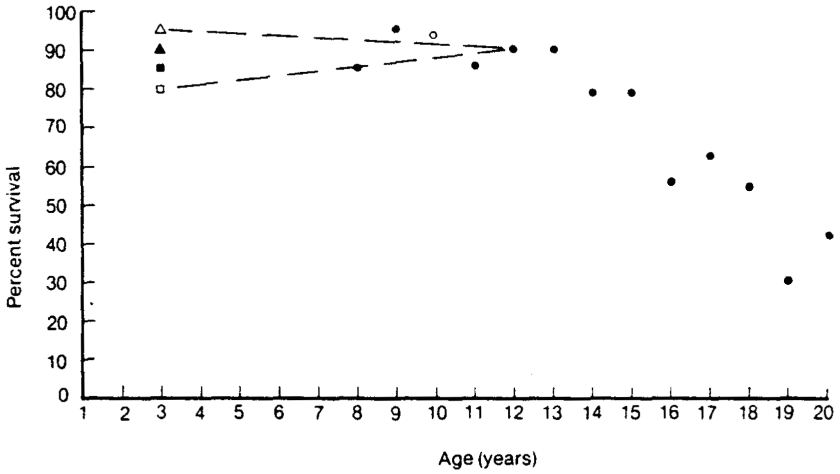

Figure 6 Survival estimates used in life-table calculations, and the method of interpolating values (dashed lines) between age 3 and 12. See text for details.

MAXIMUM POPULATION GROWTH RATES

While it is apparent that there are many uncertainties in our understanding of the reproductive and survival rates for Alaska fur seals when the population was at equilibrium, it is still possible to usefully address the question of what these capable of experiencing no natural mortality over any significant portion of their life span. In the present calculations maximum values in the range 0.96 to 1.0 were used for all ages above 3.

Maximum rates of survival from birth to age 3 are difficult to determine, as the animals are weaning, learning to feed in a new environment, and experiencing intensive growth during this period. Unlike pregnancy rates and adult survival rates, however, there is some information from the 1920s when the survival should have been higher if dependent on density. Chapman (1961, 1973) calculates the juvenile survival for this period as either approximately 31 or 36%, on the basis of estimates of the number of pups born, the number harvested from a year class (Table 5) and estimates of the possible number escaping kill. These values may represent maximal levels for this survival rate, but Chapman's calculations involve a number of assumptions that are not completely documented. We have further explored estimates of juvenile survival for this period with results which suggest that a rate of 54% may be a more reasonable upper bound (Smith and Polacheck, 1981).

Maximum values for reproductive rates are probably one pup per year for sexually mature females. Very little twinning has ever been observed (even in the period when the population was rapidly expanding). The sex ratio at birth is apparently even. This results in a maximum production of one-half daughter per sexually mature female per year. The proportion of the females that are sexually mature increases from age 3 up to age 6. The proportions may themselves be subject to changes as population size changes. For instance, it is observed that females collected in the western Pacific, primarily from Asian rookeries, show reproductive activity as much as one year earlier than those from the eastern Pacific. Thus for the younger ages the same maximum of one-half seems appropriate. The maximum reproductive rate for ages 1 and 2 is apparently zero as none have been observed to be sexually mature.

Using these maximum values for survival and reproductive rates, the life-table calculations suggest that if only reproductive rates are changed it is not possible to obtain a net rate of increase of 8% for any of the combinations rates considered in Table 6. The maximum rates of increase that can be obtained are at most a few percent. This is due to the estimated reproductive rates which are already high. The maximum rate of increase that can be obtained, for example, for the combination of rates labeled in Table 6 as "high" for survival rates and "central" for reproductive rates is 4.6 to 5.4%, depending on the value of survival from ages 3 to 4 used in determining the estimates for survival between age 3 and 12.

If only adult survival rates are changed, it is possible to obtain an 8% rate of increase for some of the combinations considered in Table 6. In particular, when the adult survival rates are low and when pregnancy rates are high, and given that the maximum survival rate possible is very close to 1.0, rates of increase of 8 to 10% are possible. It is necessary, in these cases, that the difference between the survival rates for a zero rate of increase and the maximum survival rates be large. This also requires that the pregnancy rates and the survival rates from birth to age 3 be high. Even so, the survival rates that are required to obtain 8% rates of increase are unreasonably high. Further, the percentage changes in adult survival rates that result in 8% rates of increase are on the order of 5 to 10%, changes that would be almost impossible to detect given the sampling variability apparent in Table 2.

If only juvenile survival rates are allowed to change, it is possible to obtain 8% rates of increase for many of the combinations in Table 6 with higher adult survival rates and pregnancy rates. These combinations result in smaller values of survival from birth to age 3 at equilibrium, and hence more range for possible changes in this rate. For example, for the combination of rates labeled "high" for survival rate and "central" for pregnancy rates in Table 6, the survival rate from birth to age 3 required to give an 8% rate of increase range from 61 to 79% for a corresponding range of survival from age 3 to 4 of 0.80 to 0.95. This range of three year rates correspond to unreasonably large annual rates of 85 to 93% if the rates were constant over the three years, and suggest that increases in juvenile survival of approximately 130% are required to obtain an 8% rate of increase of the population. Changes of this magnitude should have been relatively easy to detect, and are not suggested by the differences in the estimates of the survival rates in the 1920s and the 1960s, under any current interpretation of the data.

The general conclusion from considering the effect of changing one factor at a time is that the changes that must have occurred in the vital rates to account for the history of this population are not likely to involve only one of the three types of rates considered.

It is possible to consider changes in pairs of factors that could result in an 8% rate of increase. However, the number of possibilities and combinations becomes overwhelming quite quickly. Examination of some of these combinations gives an indication of the tradeoffs between changes in the different factors being considered can be obtained. Generally when two factors are being considered, only moderate changes in each are needed to obtain an 8% rate of increase. This is particularly worrisome, as the possibilities for detecting any such changes are related to the magnitudes of the changes. Thus as the numbers of factors changing increases, the possibilities for detecting the changes and hence determining which vital rates are involved, decrease.

DISCUSSION AND CONCLUSIONS

The Alaskan fur seal population has been considered as the one marine mammal population for which we have a good understanding of a population that has recovered from very reduced numbers while supporting a considerable harvest. In spite of this, the data and analyses presented here suggest that there are large gaps in our understanding of the dynamics of this population, both in the vital rates when the population was thought to have a rate of increase near zero and in the changes in the vital rates regulating the size of this population.

The major gaps in our understanding of the vital rates during a period of apparent zero population growth include estimates for the survival rates from ages 3 to 12, and for the survival rate from birth to age 3. While several analyses have been conducted to estimate values for some of these rates, such analyses are based on unsupported assumptions about several parameter values, and the sensitivities of the resulting estimates to these assumptions have generally not been considered.

Our analyses suggest that the survival of female seals from birth to age 3 must be substantially higher when the population is at equilibrium than the estimated lower bounds for this rate for juvenile males. Moreover, past estimates of survival rates for juvenile males (e.g., Chapman, 1961, 1964) when applied to females would require either or both adult survival and pregnancy rates near the upper range of the estimates presented in this chapter (e.g., Table 6) in order to be consistent with a net rate of increase that is nonnegative. This inconsistency between the estimates of the survival rates of juvenile males and the estimates of fecundity and survival rates of adult females has been reconciled in earlier papers by assuming that survival of juvenile females exceeds that of males by a constant factor (see Chapman, 1961, 1964, 1973).

However, given the lack of evidence for a differential rate of survival between males and females and the large uncertainties in all the estimated survival rates, there appears little reason to favor the assumption of differential rates of juvenile survival between the sexes in order to reconcile inconsistencies in estimates of the vital rates near equilibrium. Thus, within the ranges of the adult female survival and pregnancy rates presented here and what might be considered a reasonable range for estimates of the survival rate of juveniles near equilibrium based on estimates derived from the male kill, there are a large number of combinations of estimates that are consistent with a non-negative rate of growth without involving a differential survival rate.

The analyses of the changes in rates needed to obtain the observed high rates of increase in the 1920s indicate that there is not sufficient range in any one of the three major components of the life table (i.e., reproductive rates, survival rates from birth to age 3, and adult survival rates) for changes in one of these components to account for the observed dynamics of this population. These analyses strongly suggest that this population must be regulated by changes in at least two and possibly all three of these major components of its life table. If two or more of these components do vary with density, our calculations indicate that only small to moderate changes are needed in any single component to achieve a rate of growth of 8%. This fact may be responsible for the failure of the available data to provide convincing evidence for density-dependent changes and implies that an understanding of the mechanism regulating this population may be difficult to obtain.

While changes in more than a single major component of the life tables are biologically reasonable, the implications of this conclusion for managing this population are basically unexplored. The management for this population has been based on two concepts. The first concept, elaborated by Parker (1918), is that there are large numbers of male seals born that are not required to maintain the population. This has been shown to be true, at least in time frames of decades, as the populations continued to increase in the face of removal of large numbers of males. The second concept, introduced initially by Scheffer (1955), elaborated by Chapman (1961), and further developed (Chapman, 1964, 1973; Nagasaki, 1961; Bulgakova, 1971), is that changes in survival rates of young animals are responsible for the regulation of the population. The implication that the total yield from the population would be higher if both males and females were harvested has been drawn from this concept (Chapman, 1961, 1964). This deduction was tested by changing management policies from 1956 to 1966 to include a harvest of females. An increase in total yield did not result under this experimental harvesting regime. From the analysis put forward here it appears that this second concept on which management has been based, even if true, is insufficient in itself to account adequately for the dynamics of the population, and suggests the need to consider more complex models.

While our conclusions apply directly only to the Alaskan fur seal population breeding on the Pribilof Islands, the hypothesis that population regulation involves more than a single component of the life table should be considered for other large mammals which appear to have similar life tables at equilibrium with vital rates near their biological maximum (see Chapter 7). Mechanisms of regulation will likely be difficult to determine, since only small to moderate changes in vital rates may be occurring.

LITERATURE CITED

Anas, R. E. 1970. Accuracy in assigning ages to fur seals. J. Wildl. Manage. 34:844-852.

Bulgakova, T. Y. 1971. The estimation of the optimum sustainable kill from the Robben Island fur seal herd. VNIRO. Unpublished manuscript.

Chapman, D. G. 1961. Population dynamics of the Alaska fur seal herd. Trans. N. Am. Wildl. Nat. Resour. Conf. 26:356-369.

Chapman, D. G. 1964. A critical study of Pribilof fur seal population estimates. U.S. Fish Wildl. Serv. Fish. Bull. 63:657-669.

Chapman, D. G. 1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Rapp. P. V. Reun. Cons. Int. Explor. Mer 164:325-332.

Chapman, D. G., and A. M. Johnson. 1968. Estimation of fur seal pup populations by randomized sampling. Trans. Am. Fish. Soc. 97:264-270.

Ichihara, T. 1972. Maximum sustainable yield from the Robbin Island fur seal herd. Bull. Far Seas Fish. Res. Lab. 6:77-94.

Kenyon, K. W., V. B. Scheffer and D. G. Chapman. 1954. A population study of the Alaska fur seal herd. U.S. Fish Wildl. Serv. Spec. Sci. Rep. 12, 77 pp.

Lander, R. H., and H. Kajimura. 1976. Status of northern fur seals. Scientific Consultation on Marine Mammals, FAO, Bergen, Norway, 50 pp.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Marine Mammal Division. 1977. Fur Seal Investigations, 1976. U.S. Dept. Commer., Natl. Mar. Fish. Serv., Northwest Fish Center, Seattle, Wash., 92 pp. (Processed).

Mertz, D. B. 1971. Life history phenomena in increasing and decreasing populations. Pp. 361-399 *in:* G. P. Patil, E. C. Pielov and W. E. Waters (eds.). Statistical Ecology Vol. 2: Sampling and Modeling Biological Populations and Population Dynamics. Pennsylvania State University Press, University Park, Pennsylvania.

Nagasaki, F. 1961. Population study on the fur seal herd. Spec. Publ. Tokai Fish. Lab. No. 365, 60 pp.

Parker, G. H. 1918. The growth of the Alaskan fur seal herd between 1912 and 1917. Proc. Natl. Acad. Sci. 4:168-174.

Roppel, A. Y., and S. P. Davey. 1965. Evolution of fur seal management of the Pribilof Islands. J. Wildl. Manage. 20:448-463.

Scheffer, V. B. 1955. Body size with relation to population density in mammals. J. Mammal. 36:493-515.

Seber, G. A. F. 1973. The Estimation of Animal Abundance and Related Parameters. Griffin, London.

Smith, T., and T. Polacheck. 1980. The population dynamics of the Alaska fur seal: What do we really know? Report to the National Marine Mammal Laboratory, Seattle, Washington.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical Methods. Iowa State University Press, Ames.