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The Population
Dynamics
of the
Alaska Fur Seal:
What Do We Really Know?

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THE POPULATION DYNAMICS OF THE ALASKA FUR SEAL:
WHAT DO WE REALLY KNOW?

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This report is in fulfillment of a contract to study fur seals from the National Marine Mammal Laboratory to the University of Hawaii. The work was completed in May of 1978. The focus of the study was initially on the possibilities of predicting the effect of changes in the harvest strategy of the Pribilof Island fur seals. Specific changes which were to be considered included reinstating an on-land harvest of females and instituting a harvest of young of the year.

It was not possible to predict the effects of such changes because of a lack of understanding of the population regulatory mechanisms involved. In reviewing the published information on the life history and dynamics of this population in preparation to developing a predictive model, we came to the conclusion that the dynamics are insufficiently understood to adequately describe the history of changes in population size. Prediction of future changes could not be seriously considered until causes of the known changes in population size were understood.

We emphasize that our conclusions are based on the published information available to us, as listed in the literature cited sections. Substantially more information exists in the records of the United States fur seal investigation program in Seattle; this information is in part becoming available in machine readable form and will allow a much more detailed examination of the questions we have explored here. It is to be hoped that a more detailed examination of this information will reveal the causes of change in size of this population.

The present report details our investigations in relationship to this conclusion in four separate appendices, as indicated in the Table of Contents. These sections are more or less independent and present the basis for the detailed conclusions described below. This study has been the joint work of both authors.

In this work we addressed the following general questions:

1. Have there been changes in vital rates of the fur seal populations in the North Pacific associated with changing population size?
2. Can the history of the Pribilof Islands population be explained within the single species density dependent paradigm?
3. What is the nature and magnitude of changes in the life table which are implied, under a density-dependent paradigm, by the observed changes in population growth rates.

Under the first question, we were able to examine information relating to changes in

- a. on-land pup survival,
- b. growth rate of individuals,
- c. pregnancy rates,
- d. age of sexual maturity, and
- e. survival to age 3.

Relative to this last point, survival to age 3, we present a generalization of a method developed by Chapman (1964, 1973) of estimating the number born based on the age structure of the male seal harvest.

In exploring question 2, we developed an age structured single species density-dependent population model. This model is based on Leslie (1945, 1948) and considers only the female component of the population in population "density". This is parameterized very generally in view of our results on question 1 and is used in attempting to simulate the observed history of the Pribilof population from 1912 through 1975.

In exploring question 3, we estimate the parameters of a life table for the Pribilof fur seals under the assumption that the population was stable in the late 1950s. We examine the magnitude in changes in this life table which would be required to allow for the 8% rate of increase in population size observed in the early part of this century.

We had access to existing published data from the reports of the North Pacific Fur Seal Commission, of the U. S. fur seal investigations, and of the Japanese fur seal investigations, along with various more formally published documents through about 1975. We did not have access to the original data, nor to machine readable summaries of that data. In particular, it would be important to examine the data from the pelagic samples by location, and from the on-land samples and harvests, by rookery.

In Smith and Polacheck (1981), originally Appendix IV of this report, we made the comment (page 108) that the Gompertz equation used by Chapman (1964) to smooth the numbers alive at age data, (which we referred to erroneously as 1961), did not fit the data well. Neither the equation given nor the survival values tabled by Chapman fit the data well, as we interpret them. However,

Lander (1981) demonstrated for a larger sample of number of seals by age that a Gompertz equation will in fact fit the data well. Subsequently, we also obtained good fits with a Gompertz equation to the data used by Chapman, although with different parameter estimates. Both our and Lander's (1981) estimated survival rates from age 8 to 20 are consistently higher than those given by Chapman.

This technique of smoothing data of numbers sampled by age by fitting a function, which has been used elsewhere (Seber 1976, p. 405), avoids the variability of survival rates computed directly from such data. Direct estimates from the ratio of numbers at successive ages will not infrequently produce estimates greater than unity (Smith and Polacheck 1981, Polacheck MS). However, in Chapman's approach, one is really estimating a continuous function describing the numbers surviving to each age. The problem remains in the present case of determining annual survival rates. This can be done by dividing values of the fitted function at successive ages, or by evaluations, the instantaneous survival rates obtained by differentiating the function. There are numerous approaches to fitting the smoothing function, including fitting to logarithms of the observed numbers, fitting directly to the observed numbers, and fitting the derivative of the smoothing function to the ratios of the number sampled at successive ages. This latter approach reduces the number of parameters being estimated but involves using dependent variables which are highly correlated pairwise (Smith and Polacheck 1981). One severe limitation of estimating survival rates by smoothing the data with a function is that variances of the estimated survival rates are not available. This whole approach needs additional attention to clarify some of these statistical uncertainties.

CONCLUSIONS

From our investigations we draw the following conclusions.

1. On-land pup survival appears to have changed with population size in the eastern Pacific population (Appendix I).
2. On-land pup survival does not appear to have changed with population size in the western Pacific populations (Appendix I).
3. There does not appear to be a relationship between on-land pup survival and number of idle bulls (Appendix I).
4. Pregnancy rates of older females have not changed in either region (Appendix I).
5. Pregnancy rate of young females may have decreased slightly as population size decreased in the eastern population (Appendix I).
6. Age of sexual maturity of females appears to have changed with population size in the western populations (Appendix I).
7. Pregnancy rates do not appear to be related to harem size (Appendix I).

8. Growth rates of individuals do not appear to change with population size (Appendix I).
9. There are differences in growth rates, reproductive rates and on-land pup survival in the eastern and western populations which probably do not relate to overall population density (Appendix I).
10. The number of seals born in the 1950s must have been at least 350,000 per year in order to account for the male seal harvest, and the increase in adult males (Appendix II). Estimates of the number born using tag and recapture methods are biased (Appendix II), and for the years 1953 to 1960, are unreasonably high (Chapman 1964). Correcting the 1947 to 1952 estimates for bias using the ratio of tag-recapture estimates to shearing-sampling estimates in the 1960's results in an average estimate for that period of 381,000 pups born (Appendix II).
11. The number of male seals escaping the harvest is highly variable, but is affected by regulations on the maximum harvestable length. (Appendix II).
12. Survival to age 3 cannot be estimated reliably during the 1950s (Appendix II).
13. The available data do not suggest changes in the rate of survival to age 3 with population size for numbers of pups born between 143,000 and 237,000 (Appendix II).
14. Small changes in the survival rate to age 3 probably cannot be detected with the available data (Appendix II).
15. There exists confusion on the basis of management of the eastern population, with harvest based on maximum sustained yield being pursued only since the mid-1950's. This harvest appears to have been conducted in a manner inconsistent with the predictions from the then current population models as the harvest of females continued when the estimate of the number of pups born were less than the then current estimates of the number producing maximum sustainable yield (Appendix II).
16. The observed history of the eastern population cannot be explained under the single species density-dependent paradigm, as incorporated in our simulation work, using the information available to us (Appendix III).
17. Changes in the ecosystem as might affect vital rates independent of population size would be sufficient, in conjunction with the density-dependent paradigm, to explain the population history (Appendix III). We did not explore if any such changes are demonstrable.
18. The observed increase in number of pups born in the eastern Pacific fur seal population early in this century, and the estimated survival and fecundity rates from the late 1950's, imply that more than one of three groups of vital rates, juvenile survival, adult survival, and pregnancy, must have changed. Changes in any one group of rates would

either have been inadequate or detectable given available data (Appendix IV).

We conclude that our understanding of the eastern Pacific fur seal population has been overstated. As Bartholomew (1974, p. 296) notes, "... the primary reasons for the successful manipulation of this species (Callorhinus ursinus) are not to be found in remarkable insights by the persons who did the managing ...". Rather as he develops in that paper, success has been due to "uncoupling the harvest from the reproductive capacity of the population" (page 298) through harvest of young males.

This is not to say that the existing information cannot be used to understand the regulation of this population; rather the information which was available to us does not allow explanation of the regulation of the fur seal population.

Additional studies of the existing information which has been collected for the fur seal populations are needed. These studies should include analyses following the single species density dependent paradigm, with much greater resolution, and following an interspecific regulation (ecosystem) paradigm, with much wider scope. Pending the more complete understanding of the regulation of this population which such studies will hopefully provide, great caution must be exercised in making changes in population management as the results cannot be consistently predicted.

Better knowledge of the numbers of pups born and surviving to age three when the eastern Pacific population was near maximum levels is needed to resolve the questions we raise about the natural regulation of this population. The data on the results of the tag and recapture programs from 1947 through the 1960s should be reexamined, with the aim of correcting the biases in the earlier data based on the additional information in the later data. Also, estimates of the number of male seals alive at age three, from the age distribution of the male harvest and the counts of adult males, should be made for all years since 1918. This can be done following extensions of Chapman's (1961) approach (Appendix II), obtaining the age composition of the males killed from the data on lengths and age-length keys.

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TESTING DENSITY DEPENDENCE IN THE REGULATION
OF THE ALASKA FUR SEAL POPULATION

APPENDIX I

INTRODUCTION

The northern fur seal (*Callorhinus ursinus*) was reduced to very low abundances by overharvesting in the early 1900s (Roppel and Davey 1965). Since 1911 this species has been under protection and regulated harvesting as the result of a treaty between Japan, Canada, the U.S.S.R. and the U.S. Under the protection and management afforded by this treaty, the populations of fur seals associated with the major breeding grounds have increased markedly. Also, in conjunction with this treaty, extensive scientific investigations have been conducted to provide a scientific basis for managing these populations. The changes in abundance which have occurred under this treaty have provided an opportunity to observe a number of vital rates over a broad range of population sizes. Based on observation over this time period, a number of papers have suggested and argued that changes in reproductive, growth and survival rates are directly related to population density and that populations of northern fur seals are regulated by these density-dependent changes.

In response, at least in part, to declining harvests of young male seals, a number of analyses were completed through 1960 on several aspects of population regulation of the northern fur seal populations, as will be reviewed below. Based on these analyses, it was concluded that the Pribilof population was above the level giving maximum sustainable yield (MSY), and a herd reduction program was initiated (Roppel and Davey 1965). Much of the initial support for the conclusion that the population was above the MSY level appears to have been based on evidence of changes in on-land pup survival, growth rates of individuals, pregnancy rates and ages of sexual maturity (Kenyon et al. 1954, Baker et al. 1970 York and Hartley 1981). Subsequently, emphasis shifted to density-dependent changes in survival to age three as being the major factor regulating this population and determining MSY levels (Chapman 1961, Nagasaki 1961). As additional data accumulated in the 1960s and 1970s, the hypothesis of density-dependent changes in juvenile survival was re-examined and continued to be the basis for calculating MSY levels (Chapman 1964, 1973).

In this paper, we review the available information to test the hypotheses that on-land pup survival, growth rates, pregnancy rates and age of first reproduction change with population size. In Appendix II, the hypothesis of juvenile survival changing with population size is examined. We conclude from this review that very little data actually supports any of the above hypothesized regulatory mechanisms.

During the summer, fur seals occupy the beaches of their breeding grounds while pupping and mating. Large, mature males establish harems by defending reproductive territories. At present, major breeding grounds are located on the Pribilof Islands in the eastern Pacific, and Robben and Commander Islands in the western Pacific. Immature as well as mature seals tend to return to the breeding grounds each summer, and it is at this time that immature males primarily ages 3 and 4 are harvested.

A strong affinity for breeding near the island of birth results in a segregation of this species into relatively distinct breeding populations based on the geographical separation of the breeding grounds. The population breeding on the Pribilofs is presently the largest and has made the fullest recovery from earlier over-harvesting; on Robben and especially the Commander Islands recovery has apparently been much slower. The population on Commander Islands was estimated to be over 1 million in the 19th century utilizing 25 distinct rookeries (Johnson 1975). The population is now estimated to be about 430,000 and only four rookeries are used (Lander and Kajimura 1976). Because of the differences in present abundance relative to historical abundances, comparison of the vital rates between eastern and western stocks has been used in addition to changes over time to test various hypotheses of density-dependent regulation.

The interpretation of these comparisons is confounded by an intermingling of stocks at sea during the nonbreeding season. This intermingling is asymmetric, with virtually no seals from the western Pacific populations migrating into the eastern Pacific but with an apparently sizable fraction of the eastern stocks migrating into the western Pacific. Thus, the extent to which the realized density during the nonbreeding seasons differs between populations is unclear.

This intermingling also confounds the interpretation of time series data for the western populations. While the western populations have increased by about 50% (see below), it is not clear how large a change in density at sea this represents because of the much larger absolute size of the eastern population and because of declines in abundance in the eastern population. Interpretation of time series data for the eastern (Pribilof) population should not be greatly affected by this intermingling at sea because of the asymmetry in migration and the larger size of the eastern population.

REVIEW OF THE LITERATURE

Major considerations of possible density-dependent mechanism that may regulate the abundance of fur seals began in the late 1940s in response, at least in part, to changes in management requirements. As it became apparent that the yield of males on the Pribilof Islands was not continuing to increase and was possibly decreasing, management concerns shifted from regulating for growth to regulating for maximum sustainable yield (Roppel and Davey 1965), and to the possible impact of the now larger fur seal populations on fisheries.

Kenyon, Scheffer and Chapman (1954) in a general review of the United States' research effort on the fur seals of the Pribilof Islands discuss possible regulatory mechanisms for this population. The primary vital rate for which they present data on changes with abundances is for the survival rates of pups on beaches during their first summer of life. Based on counts of new born pups found dead on beaches and estimates of the number of pups born for 1914-1922, 1924, 1941 and 1949-1951, Kenyon et al. conclude that the on-land mortality had increased markedly, from 1.7 to 3.1% in the earlier period to about 14.6% in the 1949-1951 period, while the number of pups born more than doubled. Chapman (1961) notes that the additional available data through 1955 is consistent with the conclusions of Kenyon et al., but also points out that the on-land mortality constitutes only a small fraction of the total juvenile (i.e. from birth to age 3) mortality. Nagasaki (1961) extended the analysis of on-land mortality through data for the 1956 year class and reviewed data on the causes of death. He concluded that the changes in mortality rates between 1912-1922 and in the 1950s was the result of a density effect and that the available data best fitted a modification of Ricker's spawner-recruit model. It should be noted that the estimate of numbers of pups born during the 1950s which was used as the measure of population abundance in the above papers and other early (i.e. pre-1964) analyses were based on mark-recaptive estimates which were later found to be unreliable and too high (Chapman 1964, Chapman and Johnson 1968). The upward bias of these estimates results in an overestimate of the degree of density-dependent response.

Nagasaki (1961) also compares the on-land mortality rates of Commander and Robben Islands with those of the Pribilof Islands. He notes that for 1959 his estimated rates for Robben are comparable to those for the Pribilof Islands, while the rates on Commander are similar to those observed early in the century on the Pribilof Islands. He points out that the major causes of death of pups while on land in the eastern and western stocks are different. Hookworm infection and emaciation are the major factors on the Pribilofs while traumatic injury caused by fighting bulls is predominant on Robben Island. Parker (1918) considered the mature bulls which are not harem masters to be (p. 173) a "natural maladjustment within the herd," and notes that "they are continually stirring up strife . . . among the breeding bulls and they are accountable for the maiming and death of many seals." This suggests that the mortality of young animals may be related to numbers of idle bulls. No subsequent analysis of the relationship of on-land mortality to population density with data which has accumulated since the 1960s have been published that we are aware of.

The hypothesis that growth rates of fur seals is a function of population density was first explored by Scheffer (1955). He examined the available information on changes in body size of individuals with age as a possible indication of crowding effects. He proposed the mechanisms of 1) decreased food supply to individual females foraging out from the Pribilofs during the summer as the number of females increases, resulting in both increased mortality for the young of the year and a smaller growth rate of individuals, and of 2) a reduced opportunity for breeding. He presents data on the size of male seals at successive ages for the periods 1914 to 1918 and 1943 to 1951 which suggests that the animals are smaller in the latter period, at all ages up to seven. This is consistent with the proposed limitation of food supply.

Nagasaki (1961) and Chapman (1961) both show data suggesting that the seals from the eastern Pacific were smaller in the late 1950s than they were in 1952. Nagasaki also compared the sizes of seals in the eastern and western Pacific and notes that seals collected pelagically in 1959 in the western Pacific were similar in size to those collected in the eastern Pacific in 1952 and thus significantly larger than those collected in the late 1950s. A potential problem with the comparisons of both Nagasaki and Chapman is that they did not take into account the month during which these pelagic samples were taken and young fur seals can grow significantly in a short time period, especially during the spring. See Kajimura et al. (1979) for more recent analyses.

The hypothesis that changes in reproductive success act as a regulatory mechanism has been suggested based primarily on the comparison of the pregnancy rates in pelagic samples from the eastern and western Pacific collected in 1952 and from 1958-1961. These samples indicate a significantly greater average pregnancy rate for the western stock primarily as the result of higher pregnancy rates for younger animals. Analysis of changes in pregnancy over time for the 1950s (Nagasaki 1961, Chapman 1964) showed no changes for either the eastern or western stocks. No subsequent analysis of changes in pregnancy rates over time appears to have been published with the additional data that has become available.

The two hypothesized mechanisms which have been proposed to account for changes in pregnancy rates as a regulatory mechanism are shortages of males (Kenyon 1954, Scheffer 1955), and general effects of crowding presumably through food shortages (Scheffer 1955, North Pacific Fur Seal Commission Report¹ 1975). This second hypothesis as supported by the comparison of pregnancy rates in the eastern and western stocks appears to have been a major consideration in the earliest calculation of a maximum sustainable production level for the Pribilof populations and in the introduction of a female harvest (Baker et al. 1970). Any changes in pregnancy rates could be the results of changes in the age of sexual maturity or the rate of conception among mature females. It has been suggested (NPFSC 1962) that these two aspects of the reproductive process may be affected differently by changes in abundance of males and by changes in relative food supply.

As a point of completeness, Tanner (1966) examined the rates of increase in the Alaska fur seal population as it has changed over time from 1911 to 1930 and concluded that the rate of increase had declined as the population had increased. Unfortunately, he relied on estimates of abundances for the years 1924 to 1930 which were extrapolations from the commercial kill of

¹A great deal of the available data for northern fur seals is contained in reports of the North Pacific Fur Seal Commission (NPFSC), of the Japanese Fur Seal Investigations (JFSI), and of the United States Fur Seal Investigations (USFSI). These will be referenced with the initials as indicated and the year of publication.

males, the counts of harem and idle bulls and the earlier counts of pups born (Chapman and Johnson 1968). Nothing appears to be gained by revising his analysis omitting these extrapolated values as he essentially looked at the same data described better by Kenyon et al. (1954).

MATERIALS

The basic information that we use to test for changes in vital rates of fur seals are taken from previously published papers, and from the reports of the government agencies involved. No new data are presented here. The data used will be described briefly with references to appropriate sources for more complete descriptions. The reader should be cautioned that complete descriptions of the procedures used in collecting some of these data are not available, and that the original data are not generally available in usable forms. We are frequently limited to published summaries, lacking the complete detail which one might desire. Nonetheless, the information as it is available represents what has been observed about the fur seal in the North Pacific and provides the only basis at present to explore the factors controlling the size of this population.

Pelagic collections of fur seals were conducted by the United States in 1952 in both the eastern and western Pacific, by the United States and Canada in the eastern Pacific from 1958 to 1974, and by Japan and the U.S.S.R. in the western Pacific since 1955. Various techniques have been used over the years for capture of the seals over different areas of the Pacific. The data collected by the United States and by Japan are the most complete and are used here. The examination of collected seals included measurements of length and weight, determination of reproductive status of females, and estimation of age. The exact geographic distribution of these sampling cruises is not readily available, and the data summaries used here do not distinguish geographic areas. It has been suggested that geographic segregation by age and possibly reproductive condition occurs, but a detailed analysis of the data on this point has not been made to date. We are assuming in this paper that these data are random samples of all seals within each sex and age category.

Data Relevant to Population Density

The three types of data which measure population density are the counts of adult males, the kill of juvenile males, and estimates of the number of seals born each year. Annual counts are made during the peak of the breeding season of the number of males holding harems and also of the number of idle bulls or mature males not holding harems. This latter count is less accurate because of difficulties in defining when a bull is mature and because an unknown fraction of these idle bulls will be in the water at the time the counts are made. The counts of numbers of adult males on the Pribilof Islands are described in Kenyon, et al. (1954), in Lander and Kajimura (1976) and in the several reports of the North Pacific Fur Seal Commission (Table 1). The counts of males holding harems on Robben Island and on the Commander Islands are described in Lander and Kajimura (1976), in the reports of the North

Table 1. Counts of Harem and Idle Bulls made in mid-July on St. Paul Island (from Lander and Kajimura 1976). A dash indicates no data are available.

Year	Harem	Idle
1911	1,090	258
1912	1,077	93
1913	1,142	77
1914	1,316	159
1915	1,789	546
1916	2,948	2,278
1917	4,116	2,341
1918	4,610	2,245
1919	4,573	2,158
1920	3,542	1,078
1921	3,443	711
1922	3,184	493
1923	3,051	303
1924	3,127	375
1925	3,103	283
1926	3,478	368
1927	3,916	846
1928	5,059	1,208
1929	5,998	1,339
1930	6,823	1,555
1931	7,557	1,519
1932	8,268	1,940
1933	8,334	1,933
1934	8,841	1,860
1935	9,444	2,082
1936	10,055	2,253
1937	10,689	2,516
1938	10,720	1,787
1939	9,122	2,616
1940	9,662	3,968
1941	10,089	5,059
1942	-	-
1943	10,948	3,523
1944	11,080	2,539
1945	10,750	2,539
1946	10,566	3,605
1947	10,160	3,331
1948	10,386	3,400
1949	9,554	2,976
1950	9,442	3,152
1951	9,434	3,581
1952	9,318	4,717
1953	9,848	5,912
1954	9,906	6,847
1955	9,034	8,650
1956	9,384	9,016
1957	9,562	10,060
1958	9,970	9,510
1959	10,003	11,485
1960	10,247	10,407
1961	11,163	11,791
1962	10,332	9,109
1963	9,212	7,650
1964	9,085	7,095
1965	8,553	5,616
1966	7,974	5,839
1967	7,230	4,439
1968	6,176	3,100
1969	5,928	2,535
1970	4,945	1,666
1971	4,200	1,900
1972	3,738	2,384
1973	4,906	2,550
1974	4,563	1,782
1975	5,018	3,535
1976	6,453	2,912
1977	7,256	3,046

Pacific Fur Seal Commission, and in papers referenced therein (Table 2).

Records of the annual kill of juveniles on the Pribilof Islands have been kept since the resumption of the male harvest in 1918. Since 1950, a large sample of the annual kill has been aged by counting rings in the teeth. These samples provide estimates of the kill by year class. The estimates of annual kill and kill by year class used in this paper were taken from Lander and Kajimura (1976) but are not reproduced here.

Data on the annual kills on Robben and Commander Island is not useful for assessing population density (see below). These are available in Lander and Kajimura (1976) and are not reproduced here.

The estimates of the number of seals born in the Pribilof Islands are actual counts made from 1912 to 1924, and mark-recapture estimates made since 1961 (Table 3). The counts of pups on the Pribilof Islands from 1912 to 1924 are described in Kenyon et al. (1954) and in Lander and Kajimura (1976), and the estimates of pups born since 1961 are described in Chapman and Johnson (1968) and in Lander and Kajimura (1976). Estimates of seals born on the Pribilof Islands for the 1950s have been made using a variety of techniques, but are basically unsatisfactory due to their large degree of uncertainty (Chapman 1964).

Estimates of seals born on Robben and Commander Islands are reported in Lander and Kajimura (1976) and are more fully described in the reports of the North Pacific Fur Seal Commission (Table 4). These numbers are not all of equal reliability, and are based variously on complete or partial counts, marked-recovery data, and visual estimates. A complete analysis of the reliability of these estimates has not been done, and they should be interpreted with some caution.

Data Relevant to First Summer Mortality

The numbers of pups found dead on the beaches each summer can be used in comparison to estimates of the numbers of seals born to estimate the magnitude of first summer mortality. Counts of the number of pups which died on land on the Pribilof Islands have been made in scattered years as far back as 1896 on St. Paul, and regular counts have been made since 1950 (Table 3). Counts are usually made after mid-August by which time land mortality is considered nearly complete (Kenyon et al. 1954). Since 1948, a 5% correction factor has been added to the actual counts as an allowance for overlooked animals. A check on the validity of this assumption (NPFSC 1962) indicated that 5.9% of the dead pups had been overlooked in one area.

Counts of numbers of pups which died on land on Robben Island and on the Commander Islands have been made since 1958 as described in the reports of the North Pacific Fur Seal Commission (Table 4). Counts in some years are reported to be underestimated due to problems of organization of the census teams.

Table 2. Estimates of numbers of harem and idle bulls, for Robben and Commander Islands, from 1958 to 1974, from Lander and Kajimura (1976, Table 4).

Year	Robben		Commander	
	Harem	Idle	Harem	Idle
1958	516	500	595	251
1959	666	700	691	399
1960	869	1,146	846	821
1961	935	1,490	933	1,032
1962	1,018	1,612	751	1,078
1963	1,056	1,409	1,215	927
1964	857	1,595	2,495	1,892
1965	741	1,472	1,573	4,670
1966	1,274	1,660	2,330	5,403
1967	1,008	930	1,789	3,853
1968	1,002	1,250	2,390	2,661
1969	754	1,250	2,170	1,661
1970	848	1,120	1,727	1,196
1971	910	954	1,541	813
1972	603	544	1,031	640
1973	356	208	750	858
1974	280	260	280	260

Table 3. Estimates of the number of seals born and of number of pups found dead on the beaches, for St. Paul Island.

Year	Seals born (thousands)	Dead pup counts
1912	70.0	-
1913	79.5	-
1914	79.4	1523
1915	88.1	1607
1916	88.9	2170
1917	108.7	3382
1918	122.6	3779
1919	133.9	4247
1920	143.3	4000
1921	149.9	4000
1922	158.9	2755
1923	-	-
1924	172.5	4488
1941	-	18350
1950	-	53420
1951	-	70663
1953	-	78212
1954	-	96178
1955	-	75554
1956	-	98707
1957	-	61662
1958	-	31187
1959	-	39964
1960	-	62828
1961	337	60760
1962	278	47531
1963	264	34228
1964	285	22651
1965	267	41080
1966	296	22485
1967	284	14780
1968	235	26563
1969	234	13943
1970	230	21610
1971	-	48761
1972	260	23781
1973	305	-
1974	269	-
1975	278	21656
1976	290	24860

Sources: Dead pup counts

1914-16, 22, 61	NPFSC (1962)
1917-19, 24	Total counts for both Pribilof Islands (Kenyon et al., 1954, Table 4), divided by 1.138.
1920-21	Chapman (1961)
1941-60	NPFSC (1962)
1962-63	NPFSC (1971)
1964-66	NPFSC (1969)
1967-76	USFSI (1976)
Seals born	
1912-24	Kenyon et al. (1954)
1961-76	Lander and Kajimura (1976)

Table 4. Estimates or counts of numbers of seals born and of numbers of pups found dead for Robben and Commander Islands.

Year	Robben		Commander	
	Seals born (thousands)	Dead pup counts	Seals born (thousands)	Dead pup counts
1958	32	3,407	38	2,510 ¹
1959	35	5,443	41	1,465
1960	38	3,899	45	4,874
1961	41	5,898	48	4,662
1962	45	6,543	52	4,411
1963	49	8,858	56	7,652 ¹
1964	51	9,200	58	8,029
1965	48	20,286 ³	59	8,307
1966	45	1,493 ²	61	7,395
1967	56	1,354 ²	55	7,580
1968	46	8,740	61	7,369
1969	44	4,100	59	4,771 ¹
1970	32	3,595	62	6,231
1971	41	3,100	66	9,794
1972	44	1,050 ²	61	6,630
1973	35	-	54	-
1974	33	-	69	-

¹Incomplete count.

²Considered underestimates due to known census problems
(NPFSC 1975, p.18)

³Heavy storm induced mortality

Sources: Seals born - Lander and Kajimura (1976)

Dead pups - 1958-61 NPFSC (1962)
1962-64 NPFSC (1971)
1964-66 NPFSC (1969)
1967-72 NPFSC (1975)

Data Relevant to Changes in Growth Rates of Individuals

There are several sources of information on growth rates primarily in the form of length or weight by age. The earliest reliable growth information was collected from recoveries of male seals branded as pups in 1912. A description of this work, and the results in terms of the sizes of branded animals when recovered between the ages of two and seven are described in Scheffer (1955). Summary statistics of the size of male fur seals recovered at each age are given in Table 5 and were taken from Scheffer (1955, Table 1). The actual raw data is recorded in the annual reports published by the U.S. Bureau of Fisheries titled (variously) Alaska Fishery and Fur Seal Industries, from 1912 through 1918.

In 1940, a similar but much larger marking study was initiated, with animals branded (1940, 1941) and metal tagged (1941, 1947, 1948). The length and weight of the animals recovered subsequently on land, but not from the harvest, is given in Table 6 also from Scheffer (1955). It has been suggested that the pups which have been metal tagged are smaller at the end of their first summer than those which have not been metal tagged.

The length of the immature males killed in the annual on-land harvest have been consistently recorded since the resumption of the killing in 1918. Techniques for estimating the age from carcasses were developed in the early 1950s. However, the primary basis of regulating the harvest is based on length limits. Thus, the kill samples may not be representative of all of the animals at each age. While this data is of interest in determining the nature of the killing process, it is not useful in determining size at age as a measure of growth rates.

The pelagic samples should be more representative of the population and provide a basis to compare length and weight of a year class at successive ages. The length and weight of male seals collected pelagically provide the largest samples for this purpose. As the seals are growing rapidly during the spring months when the samples were collected, it is necessary to stratify the data into month groupings. The data used in this paper are for males ages one to seven from the U.S. and the Japanese collections (Tables 7 and 8).

For unknown reasons, pregnant females are on the average longer than nonpregnant females of the same age. This could represent measuring biases, size specific aspects of conception or abortion, or physiological changes during pregnancy (NPFSC 1962). This difference makes it difficult to compare size at age information for females. Females age one to three are rarely pregnant, however, and the size of these seals can usefully be compared over time. The sample sizes from the U.S. samples are inadequate for these ages, but the Japanese data provide a long time series (Table 9).

Table 5. Length and weight of male fur seals born in 1912 killed on hauling grounds at known ages, from Scheffer (1955).

Age	Length (cm)			Weight (kg)		
	Mean	S.D.	N	Mean	S.D.	N
2	102.9	4.73	13	-	-	-
3	110.1	6.81	102	29.5	4.1	102
4	122.1	6.63	74	39.1	5.3	74
5	140.6	6.55	38	53.3	8.3	38
6	154.5	8.20	34	80.5	20.8	34
7	175.8	12.57	24	128.9	43.2	24

Table 6. Length and weight of male seals branded or metal tagged as pups and recovered subsequently on hauling grounds. From Scheffer, 1955, Tables 1 and 2, with data from different years (1941-1951) pooled, and data collected in conjunction with the harvesting omitted.

Age	Length (cm)			Weight (kg)		
	Mean	S.D.	N	Mean	S.D.	N
1	-	-	-	16.8	2.4	12
2	99.9	42.7	138	-	-	-
3	106.7	37.3	2590	28.0	3.1	90
4	114.2	51.0	486	35.5	5.2	26
5	131.6	47.3	26	44.9	7.2	26
6	138.2	68.7	20	60.7	10.3	22
7	153.2	125.2	6	94.5	32.2	6

Table 7. Mean lengths (L, in cm) and weights (W, in kg), with sample sizes (N), of male seals collected pelagically by U.S. researchers, by month-groups and by year, from NPFSC (1962, 1969 and 1971).

YEAR	1952			1958			1960			1961					
MONTH	Feb-July			Apr-May			Apr-May			June-Aug			Mar-Apr		
AGE	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N
1	82	-	7	81.5	10.2	6	77.2	10.3	6	80.5	10.5	2	77.2	9.1	19
2	105	-	21	-	-	-	96.2	17.9	10	99.1	17.8	20	93.9	13.5	16
3	117	-	61	106.4	22.8	41	107.9	23.5	16	110.9	25.3	34	102.6	18.6	20
4	125	-	14	115.7	28.5	18	118.0	32.6	5	122.9	32.9	7	110.0	22.2	9
5	151	-	1	128.5	41.3	2	130.7	41.7	3	127.8	38.3	6	119.0	29.5	2
6	158	-	1	147.5	56.9	4	0	0	0	144.4	55.8	8	-	-	-
7	-	-	0	150.2	69.4	16	0	0	0	154.0	74.7	6	-	-	-

YEAR	1962			1963			1968			1971		
MONTH	Jun-Aug			July-Aug			Jun-Aug			Mar-May		
AGE	L	W	N	L	W	N	L	W	N	L	W	N
1	90.0	15.8	2	98.7	18.7	3	-	-	0	80.9	10.7	20
2	101.9	19.4	17	104.4	21.0	32	104.4	20.9	12	95.7	15.9	17
3	110.3	26.5	33	113.0	27.9	25	114.7	27.6	28	104.2	21.7	6
4	119.0	32.4	18	119.6	32.6	14	123.0	36.1	6	116.7	26.6	10
5	132.0	44.8	4	136.9	49.7	15	134.0	46.5	4	-	-	0
6	148.8	66.0	4	147.0	62.0	2	-	-	0	-	-	0
7	156.5	78.4	8	166.6	94.0	5	166.3	85.7	3	-	-	0

Table 8. Mean lengths (L, in cm) and weights (W, in kg), with sample sizes (N), for male seals sampled pelagically in April and May by Japanese researchers, by month groups and by year, from NPFSC (1962, 1969 and 1971).

YEAR	1958			1959			1960			1961			1962		
AGE	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N
1	87.2	13.5	48	88.4	13.0	74	88.9	12.7	19	84.6	12.1	24	85	13.3	27
2	100.9	19.3	334	102.4	18.4	261	101.1	18.5	178	100.1	18.8	111	101	19.3	126
3	111.3	24.5	503	112.9	25.3	229	112.1	25.2	173	110.6	25.2	226	111	24.6	241
4	121.9	32.7	102	125.7	35.6	218	124.3	34.0	49	122.7	34.4	81	121	33.1	132
5	134.4	43.3	30	136.6	45.8	37	139.0	49.3	23	134.2	48.1	20	140	50.9	37
6	150.0	62.9	16	155.3	76.7	12		72.0	5	153.9	68.5	13	153	63.6	19
7	160.6	114.0	13	158.4	83.2	5		108.0	1	159.0	89.5	7	174	101.7	6

YEAR	1963			1964			1965			1966			1967		
AGE	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N
1	86.0	13.0	44	85.0	12.6	38	84.5	11.1	26	86.5	12.2	4	86.4	12.9	1
2	102.6	19.2	150	103.0	19.6	108	101.0	18.9	44	102.1	18.8	37	101.3	19.3	2
3	112.7	24.3	148	113.0	26.4	104	112.4	25.4	101	113.7	24.9	51	111.6	25.2	4
4	121.6	34.4	108	124.8	35.2	51	124.7	34.9	38	126.6	34.8	21	123.0	33.2	2
5	138.3	50.5	43	139.2	48.0	27	141.8	53.1	8	149.0	56.7	3	131.5	40.8	
6	153.4	74.2	28	153.4	70.2	18	151.3	75.2	6	150.0	62.0	1	145.0	55.0	
7	170.5	101.2	10	166.3	88.4	9	154.0	80.4	6	-	96.5	2	163.0	88.5	

Table 9. Mean length (L, in cm) and weight (W, in kg) of female seals aged one to three, collected in April and May from Japanese pelagic samples, from NPFSC (1962, 1969, 1971 and 1975).

YEAR AGE	1958			1959			1960		
	L	W	N	L	W	N	L	W	N
1	87.1	11.4	19	80.0	10.0	35	84.6	12.1	9
2	95.2	15.8	179	100.8	14.8	185	95.7	12.4	127
3	104.6	19.7	410	104.2	19.0	275	104.8	19.3	148

YEAR AGE	1961			1962			1963		
	L	W	N	L	W	N	L	W	N
1	82.6	11.2	5	81.0	10.7	16	80.8	10.6	13
2	93.5	15.2	111	94.1	15.2	122	93.4	15.0	72
3	103.1	18.9	156	103.3	19.6	151	103.9	20.0	94

YEAR AGE	1964			1965			1966		
	L	W	N	L	W	N	L	W	N
1	80.0	10.8	22	74.6	9.2	7	83.0	10.0	1
2	96.0	15.1	55	93.0	14.1	22	96.0	15.6	25
3	105.0	20.1	96	102.8	19.6	46	106.9	19.7	48

YEAR AGE	1967		
	L	W	N
1	87.6	10.4	4
2	94.4	15.1	22
3	106.4	19.5	51

Data Relevant to Changes in Reproductive Rates

The seals collected pelagically, as described above, were examined for reproductive condition. The levels of resolution in this examination varied between the U.S. and the Japanese collections, and to a lesser extent, between years. The determination of pregnancy was always made. In the Japanese collections, it was frequently determined if nonpregnant seals had ovulated previously (i.e. were sexually mature) and had been pregnant one or more times previously. The available data by age and by year of collection are given here in Tables 10 and 11 for the U.S. and the Japanese samples respectively. The number examined and the proportion of those which were pregnant, with the corresponding estimated standard deviation of the proportion (assuming a binomial distribution) are given for both the U.S. and the Japanese samples. In addition, for the Japanese samples in the years with more resolution (1959 to 1963 and 1968 to 1973), the number classified as immature, mature and pregnant, and mature but not pregnant are given. For these latter years, besides the proportion pregnant, the proportions sexually mature and their standard deviations are estimated.

RESULTS

Changes in Population Size

The observations on the numbers of male seals killed in the commercial harvest since 1918 (Figure 1) imply that the Pribilof Island population has increased in size during this century and that the rate of increase was initially approximately 8%. The rate of increase was declining by the mid-1930s and the annual kills would suggest that the population had reached an equilibrium around 1940. However, since harvest regulations (i.e., size limits and length of the killing season) were constant during this period (Roppel and Davy 1965), the stability of the annual kills during the 1940s may merely reflect the constancy of the harvesting process. The more recent observations of the kill by year class suggest that the population began decreasing in the mid-1950s (Figure 1). Interpreting these figures is complicated by harvests of females which were conducted from 1956 to 1968 and changes in the harvesting size limits for males starting in the mid-1950s as the annual harvest started to decline.

To the extent that changes in harvesting regulations increased the kill rate for a year class, the observed decline in the yield from a year class is an underestimate of the decline in populations that apparently took place during this period. Moreover, based on our effort to simulate the history of this population (Appendix III), it appears unlikely that the magnitude of the female harvest was sufficient to entirely account for the decline in annual kills (see also York and Hartley, 1981).

The observations on numbers of male seals holding harems each year on the Pribilof Islands (Figure 2) suggest the same general pattern of population change with a sharp decline in population size beginning around 1960. Since the number of adult male seals available to occupy harems depends on the

Table 10. Proportion of female seals pregnant (P) in U.S. samples, from 1958 to 1974, with sample sizes (N) and standard deviations (SD, assuming binomial proportions). Data from reports of the USFSI.

YEAR AGE	P	1958 N	SD	P	1959 N	SD	P	1960 N	SD
3	0.026	39	0.0255	0.0	43	0.0	0.0	18	0.0
4	0.024	42	0.0236	0.064	93	0.0254	0.028	36	0.0275
5	0.457	70	0.0595	0.561	114	0.0465	0.491	55	0.0674
6	0.808	99	0.0396	0.771	118	0.0387	0.800	45	0.0596
7	0.893	103	0.0305	0.762	143	0.0356	0.788	66	0.0503
8	0.892	102	0.0307	0.866	164	0.0266	0.857	105	0.0342
9	0.963	81	0.0210	0.889	108	0.0302	0.924	144	0.0221
>10	0.806	750	0.0144	0.842	651	0.0270	0.855	601	0.0143

YEAR AGE	P	1961 N	SD	P	1962 N	SD	P	1963 N	SD
3	0.0	84	0.0	0.011	93	0.0103	0.0	53	0.0
4	0.010	96	0.0102	0.029	140	0.0142	0.071	113	0.0242
5	0.206	68	0.0490	0.260	123	0.0396	0.438	162	0.0390
6	0.758	62	0.0544	0.542	72	0.0587	0.744	90	0.0460
7	0.758	92	0.0447	0.849	93	0.0371	0.883	77	0.0366
8	0.794	107	0.0391	0.898	98	0.0306	0.977	87	0.0161
9	0.939	114	0.0224	0.836	73	0.0374	0.850	60	0.0461
>10	0.855	601	0.0144	0.852	616	0.0143	0.852	510	0.0157

YEAR AGE	P	1964 N	SD	P	1965 N	SD	P	1966 N	SD
3	0.0	74	0.0	0.0	51	0.0	0.0	30	0.0
4	0.016	62	0.0159	0.0	73	0.0	0.015	68	0.0147
5	0.357	84	0.0523	0.261	23	0.0916	0.273	66	0.0548
6	0.753	81	0.0479	0.568	37	0.0814	0.714	35	0.0764
7	0.773	44	0.0632	0.792	24	0.0828	0.783	46	0.0609
8	0.848	46	0.0529	0.848	33	0.0625	0.791	43	0.0620
9	0.833	30	0.0681	0.706	17	0.1105	1.000	20	0.0
>10	0.758	335	0.0234	0.748	111	0.0412	0.833	108	0.0359

Table 10. Continued

YEAR AGE	P	1967 N	SD	P	1968 N	SD	P	1969 N	SD
3	0.0	10	0.0	0.0	35	0.0	0.0	19	0.0
4	0.0	9	0.0	0.053	95	0.0230	0.031	32	0.0306
5	0.444	9	0.1656	0.378	37	0.0797	0.348	23	0.0993
6	0.600	20	0.1095	0.766	47	0.0618	0.565	23	0.1034
7	0.714	7	0.1708	0.725	69	0.0538	0.634	27	0.0927
8	0.857	7	0.1323	0.789	38	0.0662	0.727	22	0.0950
9	1.0	12	0.0	0.825	40	0.0601	1.0	5	0.0
>10	0.749	35	0.0733	0.804	281	0.0237	0.721	111	0.0426

YEAR AGE	P	1970 N	SD	P	1971 N	SD	P	1972 N	SD
3	0.0	62	0.0	0.0	39	0.0	0.0	15	0.0
4	0.0	66	0.0	0.0	56	0.0	0.0	17	0.0
5	0.351	37	0.0785	0.250	24	0.0884	0.139	36	0.0577
6	0.634	41	0.0752	0.654	26	0.0905	0.500	26	0.0981
7	0.842	19	0.0837	0.870	23	0.0701	0.550	20	0.1112
8	0.826	23	0.0790	0.800	15	0.1033	0.800	20	0.0894
9	0.773	22	0.0893	0.545	11	0.1501	0.615	13	0.1350
>10	0.653	72	0.0561	0.750	72	0.0508	0.773	66	0.0511

YEAR AGE	P	1973 N	SD	P	1974 N	SD
3	0.0	36	0.0	0.0	13	0.0
4	0.150	40	0.0565	0.391	33	0.0849
5	0.591	44	0.0741	0.536	28	0.0942
6	0.806	67	0.0483	0.808	26	0.0772
7	0.878	66	0.0403	0.881	42	0.0500
8	0.961	51	0.0271	0.950	40	0.0345
9	0.895	57	0.0406	0.939	33	0.0417
>10	0.926	229	0.0173	0.798	98	0.0406

Table 11. Reproductive condition of seals collected pelagically by Japanese researchers, by age and by year. Sexual maturity data unavailable for samples in 1958 and 1962 to 1964. The proportion pregnant (P) and the proportion sexually mature (M) is estimated for each age class, along with the corresponding standard deviations of the proportion. A dash (-) indicates data not available or calculation not possible as no animals observed in that age class. Data from JFSI reports. Some totals in the 1959 table are not consistent.

Age	# Examined	# Immature	1958		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	11	11	0	0	0.0	0.0	0.0	0.0
2	124	124	0	0	0.0	0.0	0.0	0.0
3	339	319	16	4	0.012	0.059	0.059	0.022
4	174	59	31	84	0.483	0.0329	0.661	0.036
5	142	3	16	123	0.866	0.0256	0.979	0.012
6	82	2	14	66	0.805	0.0438	0.976	0.017
7	41	0	3	38	0.927	0.0407	1.0	0.0
>8	123	0	21	102	0.829	0.0339	1.0	0.0

Age	# Examined	# Immature	1959		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	55	54	1	0	0.0	0.0	0.018	0.0180
2	246	222	23	0	0.0	0.0	0.094	0.0186
3	357	34	319	3	0.008	0.0048	0.902	0.0157
4	278	1	112	164	0.590	0.0295	0.996	0.0036
5	161	0	19	138	0.857	0.0276	1.0	0.0
6	107	0	10	94	0.879	0.0316	1.0	0.0
7	60	0	4	54	0.900	0.0387	1.0	0.0
8	43	0	4	39	0.907	0.0443	1.0	0.0
9	23	0	1	22	0.957	0.0425	1.0	0.0
>10	140	0	30	110	0.786	0.0347	1.0	0.0

Age	# Examined	# Immature	1960		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	9	9	0	0	0.0	0.0	0.0	
2	131	102	29	0	0.0	0.0	0.221	0.0363
3	155	9	145	1	0.007	0.0064	0.942	0.0188
4	144	1	64	79	0.549	0.0415	0.993	0.0069
5	136	0	20	116	0.853	0.0304	1.0	0.0
6	83	0	7	76	0.916	0.0305	1.0	0.0
7	57	0	1	56	0.983	0.0174	1.0	0.0
8	31	0	0	31	1.000	0.0	1.0	0.0
9	17	0	1	16	0.941	0.0571	1.0	0.0
<10	51	0	0	51	1.000	0.0	1.0	0.0

Table 11. Continued

1961										
Age	# Examined	# Immature	# Mature		P	SD	M	SD		
			Not preg	Preg						
1	5	5	0	0	0.0	0.0	0.0	0.0		
2	112	93	19	0	0.0	0.0	0.170	0.0355		
3	167	29	136	2	0.012	0.0084	0.826	0.0293		
4	148	5	66	77	0.520	0.0411	0.966	0.0149		
5	108	1	18	89	0.824	0.0366	0.991	0.0092		
6	104	1	10	93	0.894	0.0302	0.990	0.0096		
7	60	2	8	50	0.833	0.0481	0.967	0.0232		
8	27	0	2	25	0.926	0.0504	1.0	0.0		
9	21	0	1	20	0.952	0.0465	1.0	0.0		
>10	92	0	14	78	0.848	0.0374	1.0	0.0		

1962										
Age	# Examined	# Immature	# Mature		P	SD	M	SD		
			Not preg	Preg						
1	17	13	4	0	0.0	0.0	0.235	0.1029		
2	99	77	22	0	0.0	0.0	0.222	0.0782		
3	139	6	130	3	0.022	0.0123	0.957	0.0172		
4	115	1	53	61	0.530	0.0465	0.991	0.0087		
5	62	0	11	51	0.823	0.0485	1.0	0.0		
6	58	0	9	49	0.845	0.0475	1.0	0.0		
7	52	0	7	45	0.865	0.0473	1.0	0.0		
8	30	0	3	27	0.900	0.0548	1.0	0.0		
9	19	0	3	16	0.842	0.0837	1.0	0.0		
>10	45	0	1	44	0.978	0.0220	1.0	0.0		

1963										
Age	# Examined	# Immature	# Mature		P	SD	M	SD	Prop preg if mature	SD
			Not preg	Preg						
1	17	15	2	0	0.0	0.0	0.118	0.0781	0.0	0.0
2	107	52	55	0	0.0	0.0	0.514	0.0483	0.0	0.0
3	171	8	163	0	0.0	0.0	0.953	0.0161	0.0	0.0
4	151	1	85	65	0.431	0.0403	0.993	0.0066	0.433	0.0405
5	140	0	48	92	0.657	0.0401	1.0	0.0	0.657	0.0401
6	82	0	13	69	0.842	0.0403	1.0	0.0	0.842	0.0403
7	38	0	6	32	0.842	0.0592	1.0	0.0	0.842	0.0592
8	55	0	8	47	0.855	0.0475	1.0	0.0	0.855	0.0475
9	35	0	1	34	0.971	0.0282	1.0	0.0	0.971	0.0282
<10	49	0	9	40	0.816	0.0553	1.0	0.0	0.816	0.0553

1964										
Age	# Examined	# Immature	# Mature		P	SD	M	SD		
			Not preg	Preg						
1	21	-	-	0	0.0	0.0	-	-		
2	80	-	-	0	0.0	0.0	-	-		
3	134	-	-	0	0.0	0.0	-	-		
4	123	-	-	65	0.529	0.0450	-	-		
5	120	-	-	101	0.842	0.0333	-	-		
6	81	-	-	68	0.840	0.0408	-	-		
7	48	-	-	48	1.0	0.0	-	-		
8	47	-	-	44	0.936	0.0369	-	-		
9	44	-	-	41	0.932	0.0380	-	-		
>10	120	-	-	92	0.767	0.0386	-	-		

Table 11. Continued

Age	# Examined	# Immature	1965		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	13	-	-	0	0.0	0.0	-	-
2	48	-	-	0	0.0	0.0	-	-
3	100	-	-	0	0.0	0.0	-	-
4	102	-	-	39	0.382	0.0481	-	-
5	80	-	-	52	0.650	0.0533	-	-
6	73	-	-	59	0.808	0.0461	-	-
7	83	-	-	73	0.880	0.0357	-	-
8	44	-	-	34	0.773	0.0632	-	-
9	42	-	-	36	0.857	0.0540	-	-
>10	98	-	-	84	0.857	0.0353	-	-

Age	# Examined	# Immature	1966		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	1	-	-	0	0.0	0.0	-	-
2	37	-	-	0	0.0	0.0	-	-
3	86	-	-	0	0.0	0.0	-	-
4	88	-	-	28	0.318	0.0497	-	-
5	91	-	-	73	0.802	0.0418	-	-
6	55	-	-	42	0.764	0.0573	-	-
7	46	-	-	37	0.804	0.0585	-	-
8	39	-	-	32	0.821	0.0615	-	-
9	25	-	-	24	0.960	0.0392	-	-
>10	70	-	-	55	0.786	0.0490	-	-

Age	# Examined	# Immature	1967		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	9	-	-	0	0.0	0.0	-	-
2	28	-	-	0	0.0	0.0	-	-
3	84	-	-	3	0.036	0.0202	-	-
4	73	-	-	28	0.384	0.0569	-	-
5	94	-	-	77	0.819	0.0397	-	-
6	68	-	-	60	0.882	0.0391	-	-
7	69	-	-	56	0.812	0.0471	-	-
8	67	-	-	61	0.910	0.0349	-	-
9	49	-	-	43	0.878	0.0468	-	-
<10	195	-	-	164	0.841		-	-

Age	# Examined	# Immature	1968		P	SD	M	SD
			# Mature					
			Not preg	Preg				
1	0	-	-	-	-	-	-	-
2	3	3	0	0	0.0	0.0	0.0	0.0
3	3	3	0	0	0.0	0.0	0.0	0.0
4	10	8	1	1	0.100	0.0949	0.200	0.1265
5	22	5	5	12	0.546	0.1062	0.773	0.0893
6	18	1	1	16	0.889	0.0741	0.944	0.0540
7	24	0	2	22	0.917	0.0564	1.0	0.0
8	43	0	4	39	0.907	0.0443	1.0	0.0
9	26	0	3	23	0.885	0.0627	1.0	0.0
>10	86	0	11	75	0.872	0.0360	1.0	0.0

Table 11. Continued

Age	# Examined	# Immature	1969 # Mature		P	SD	M	SD
			Not preg	Preg				

1	1	1	0	0	0.0	0.0	0.0	0.0
2	9	9	0	0	0.0	0.0	0.0	0.0
3	27	26	1	0	0.0	0.0	0.037	0.0363
4	14	9	4	1	0.071	0.0688	0.357	0.1281
5	25	2	4	19	0.760	0.0854	0.920	0.0543
6	20	0	4	16	0.800	0.0894	1.0	0.0
7	30	0	1	29	0.967	0.0328	1.0	0.0
8	31	0	2	29	0.936	0.0441	1.0	0.0
9	18	0	1	17	0.944	0.0540	1.0	0.0
>10	88	0	14	74	0.841	0.0390	1.0	0.0

Age	# Examined	# Immature	1970 # Mature		P	SD	M	SD
			Not preg	Preg				

1	2	2	0	0	0.0	0.0	0.0	0.0
2	7	7	0	0	0.0	0.0	0.0	0.0
3	26	26	0	0	0.0	0.0	0.0	0.0
4	30	23	2	5	0.167	0.0680	0.233	0.0772
5	22	2	6	10	0.455	0.1062	0.727	0.0950
6	48	0	13	35	0.729	0.0641	1.0	0.0
7	49	0	15	34	0.694	0.0658	1.0	0.0
8	43	0	8	35	0.814	0.0593	1.0	0.0
9	53	0	6	47	0.887	0.0435	1.0	0.0
>10	261	0	37	224	0.858	0.0216	1.0	0.0

Age	# Examined	# Immature	1971 # Mature		P	SD	M	SD
			Not preg	Preg				

1	2	2	0	0	0.0	0.0	0.0	0.0
2	27	27	0	0	0.0	0.0	0.0	0.0
3	67	67	0	0	0.0	0.0	0.0	0.0
4	76	54	8	14	0.184	0.0445	0.290	0.0520
5	54	10	10	34	0.630	0.0657	0.815	0.0529
6	20	1	6	13	0.650	0.1067	0.950	0.0487
7	15	0	4	11	0.733	0.1142	1.0	0.0
8	17	0	5	12	0.706	0.1105	1.0	0.0
9	13	0	2	11	0.846	0.1001	1.0	0.0
<10	91	0	14	77	0.846	0.0378	1.0	0.0

Age	# Examined	# Immature	1972 # Mature		P	SD	M	SD
			Not preg	Preg				

1	0	-	-	-	-	-	-	-
2	14	14	0	0	0.0	0.0	0.0	0.0
3	36	36	0	0	0.0	0.0	0.0	0.0
4	56	42	3	11	0.196	0.0531	0.250	0.0579
5	71	9	22	40	0.563	0.0589	0.873	0.0395
6	34	3	9	22	0.647	0.0820	0.912	0.0486
7	21	0	3	18	0.857	0.0764	1.0	0.0
8	31	1	8	22	0.716	0.0267	0.968	0.0317
9	27	0	4	23	0.852	0.0684	1.0	0.0
>10	209	0	55	154	0.737	0.0305	1.0	0.0

Table 11. Continued

Age	# Examined	# Immature	1973 # Mature		P	SD	M	SD
			Not preg	Preg				
1	6	6	0	0	0.0	0.0	0.0	0.0
2	23	23	0	0	0.0	0.0	0.0	0.0
3	45	45	0	0	0.0	0.0	0.0	0.0
4	40	28	7	5	0.125	0.0523	0.300	0.0725
5	16	2	7	7	0.438	0.1240	0.875	0.0827
6	19	0	9	10	0.526	0.1145	1.0	0.0
7	20	0	9	11	0.550	0.1112	1.0	0.0
8	9	0	3	6	0.667	0.1571	1.0	0.0
9	18	0	2	16	0.889	0.0741	1.0	0.0
>10	92	0	37	55	0.598	0.0511	1.0	0.0

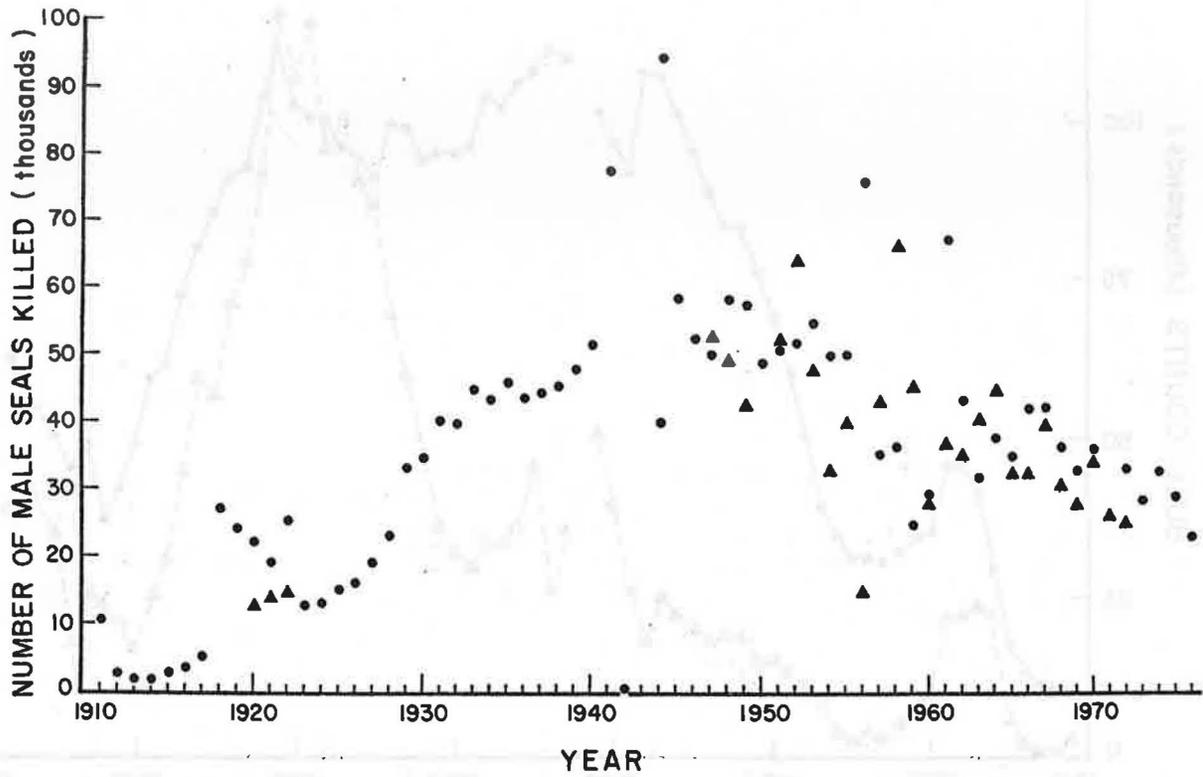


Figure 1. Numbers of male seals killed on St. Paul Island in the annual harvests, by year (circle) and by year class (triangle), from NPFSC (1961, 1964, 1971, 1975) and NMFS (1978).

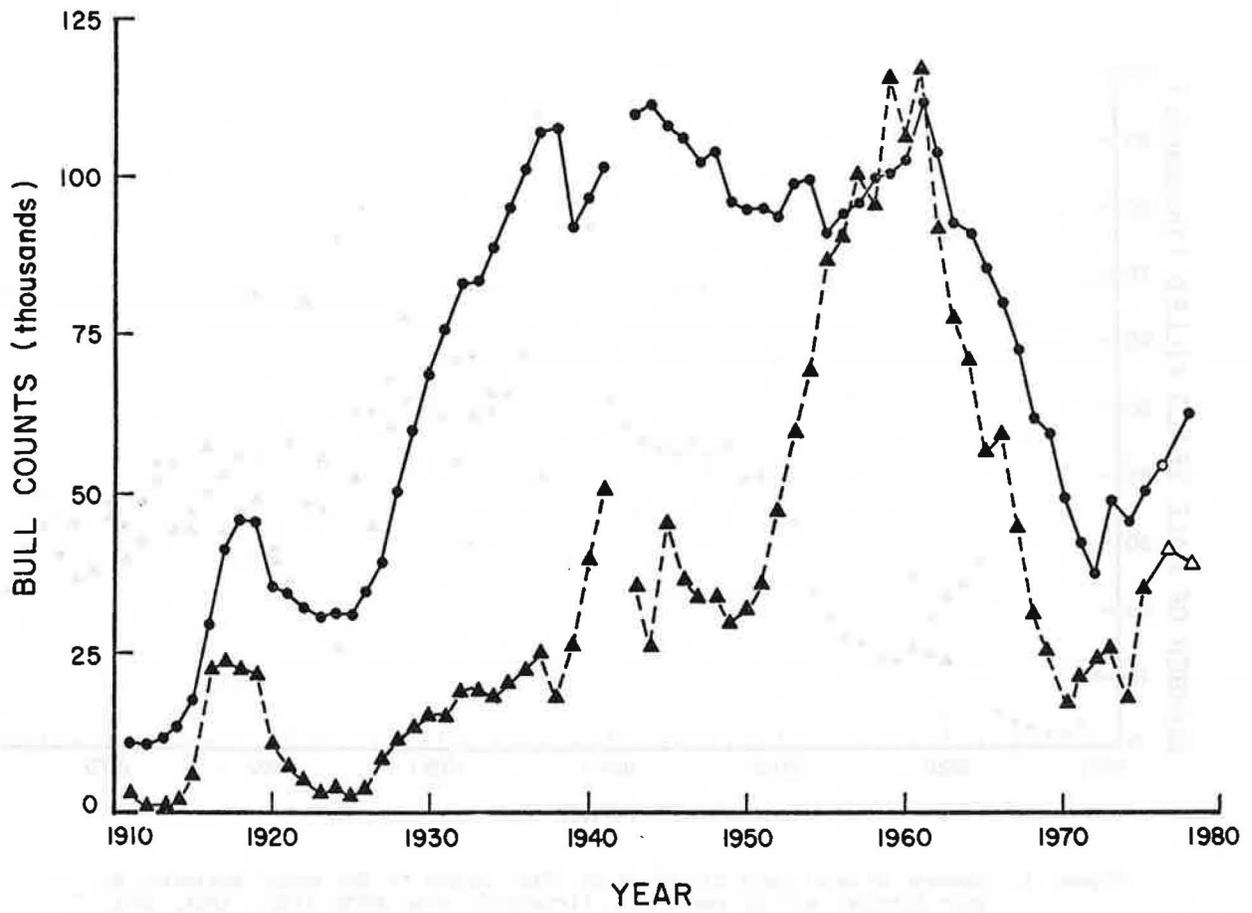


Figure 2. Counts of harem (circles) and idle (triangles) bulls on St. Paul Island, from Lander and Kajimura (1976).

commercial harvest of males in the years 2 to 5 years earlier, the timing of this decline is consistent with the decline in male harvest beginning in the mid-1950s. To the extent that the changes in harvesting regulations during the 1950s decreased the overall escapement rate (but again see Appendix II), this observed decline in the number of harem bulls is an overestimate of the actual decline.

The counts of idle bulls (Figure 2) did not reach an equilibrium during the 1940s but continue to increase until 1960 when they also began a rapid decline. These counts may be an indication that the population did not reach an equilibrium during the 1940s but continued to increase. However, a constant escapement from the harvest in excess of the number of males needed to replace dying adult males could also result in increasing number of idle bulls during this period. It should also be noted that there are questions about the consistency of the counting procedure for idle bulls during these years (A. Johnson, pers. comm.).

The estimates of the numbers of pups born provide a more direct measure of population size, but useful estimates are not available from 1925 to 1960. The available estimates (Figure 3) suggest that the population was increasing from 1911 to 1924, and that the population has been relatively constant in size since 1960. The statistical significance of the changes which are apparent since 1960 is not clear as the variance of these estimates, while straight forward to compute (Chapman and Johnson, 1968), are not available.

Other estimates of numbers of pups born which were made based on tag and recapture data during the 1950s, suggest that the population achieved a maximum size in the 1950s. However, these estimates are considered biased and unusable (Chapman, 1964). Estimates made by Chapman (1964) based on the age structure of the males in the commercial harvest suggest that the population was higher in the 1950s than in the 1960s. However, these are fundamentally based on the kill of males from each year class, and as such, offer no additional insight into the history of the population beyond that contained in the kill of males by year class itself (Appendix II). While there appears to be no satisfactory method to estimate the number of pups born during the 1950s, given the substantial kill of mature females, the decline in the kill by year class and observations by workers on the rookeries, pup production must have been substantially higher in the 1950s than the 1960s. In Appendix II, we develop a model for estimating the number of male 3-year-olds which survive from a year class based on the age structure of the kill and counts of adult males. Based on this model and assuming juvenile survival rates were no lower in the 1950s than in the 1960s, a minimum estimate of the average number of pups born during the 1950s would have been around 350,000.

Taken together, these various lines of evidence suggest that the population initially increased following protection in 1911, possibly leveled off during the 1940s, and subsequently declined in abundance. The current abundance appears approximately constant, with the average annual number of pups born since 1961 about four times the number born in 1912.

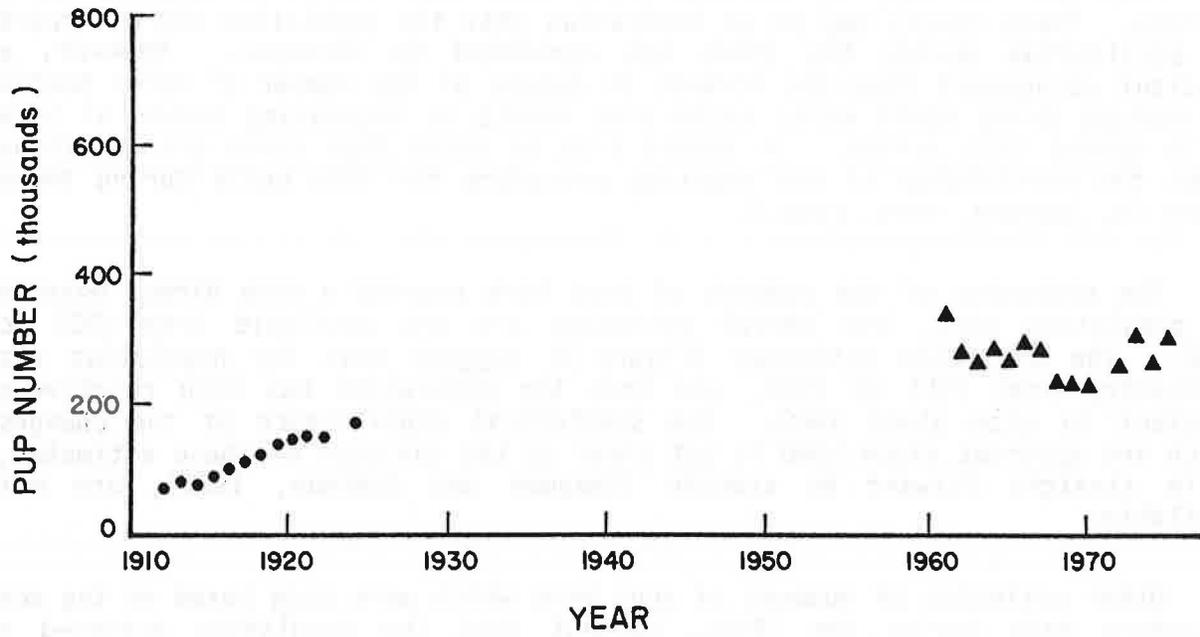


Figure 3. Counts (circles) and estimates (triangles) of numbers of pups born on St. Paul Island, from Lander and Kajimura (1976).

The western Pacific populations have had a more complicated and less well documented history in this century. Recovery has apparently been much slower; a significant harvest of male seals has occurred on both islands in this century (Chapman pers. comm.), which has been continuous and well documented only since 1958. Intensive investigations also began in 1958. The estimates of the number of pups born provide the most information of the available data on changes in population size since 1958 (Figure 4). These estimates suggest that these populations were increasing in 1963 and continued to increase but at a declining rate until around 1967. The numbers from Robben Island suggest a subsequent decline, starting in 1967, to levels similar to those observed in 1958 and 1959. The numbers on the Commander Islands show, after a short decline, a continuing but slower general increase. Taken together, the total number of seals breeding in the western Pacific appears to have been approximately steady from the early 1960s, with perhaps a slight downward trend.

The counts of harem and idle bulls in the western Pacific (Figure 5) also suggest that these populations were increasing in 1958. These counts became roughly constant during the 1960s but with large year-to-year variation, especially on the Commander Islands, and started declining rapidly in the 1970s. Taking into account the time lag between when a seal is vulnerable to the harvest and when it becomes a bull, the initiation of the male harvest in 1958 confounds the interpretation of these counts past about 1963-1964. The rapid decline in both bull counts in the 1970s probably reflects the fact that the number of males harvested increased at a much faster rate than the number of pups born. The harem and idle counts on Robben Island are further complicated by variable harvests of older males in an effort to reduce the number of bulls.

Little information is available on the actual harvesting regulations employed on Robben and the Commander Islands, but the harvesting of males has apparently not been under a single consistent set of regulations. As such, the actual yield from these populations provides little or no information on changes in abundance.

Although not as clearly as for the Pribilof Islands population, the available data suggest that the western Pacific populations increased, and then leveled off, at least in the aggregate, with the annual average number of pups born since 1964 being about 1.5 times larger than the number born in 1958. One must be careful when interpreting any changes in vital rates because of the apparent decline in the Robben Island population, especially for vital rates which may be effected by the on-land phase. Treatment in the aggregate is necessary, however, as most of the information on possible changes in vital rates comes from the pelagic samples where individuals cannot be separated by island of origin.

Change in Mortality Rates During the First Summer

The numbers of seals born on the Pribilof Islands and the numbers of pups found dead on the beaches during systematic searches (Table 3) can be used to estimate the mortality rate of seals during their first summer for those years

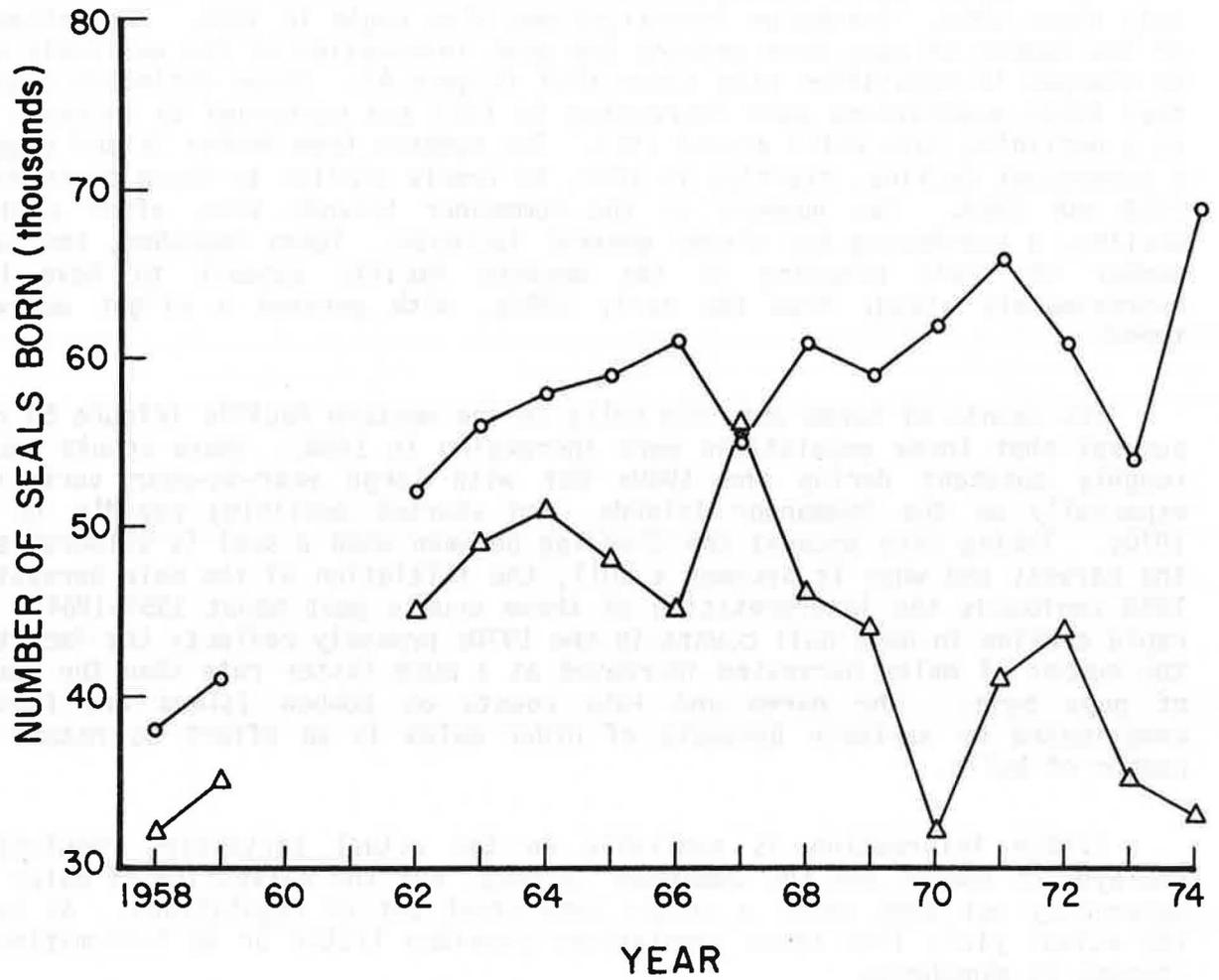


Figure 4. Estimated numbers of seals born by year on Robben (triangles) and the Commander Islands (circles), from Lander and Kajimura (1976), for the period 1958 to 1974.

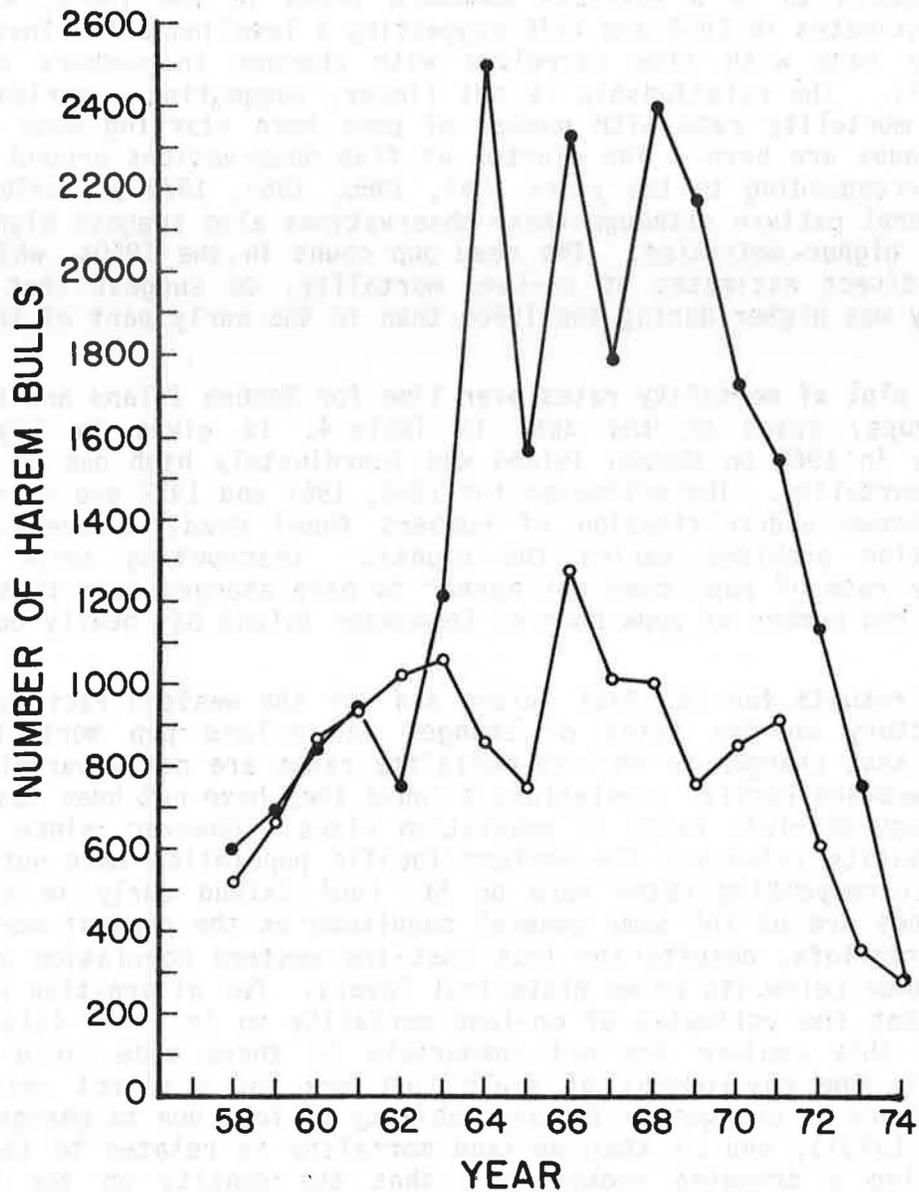


Figure 5. Estimates of male seals holding harems on Robben Island (closed circles) and on the Commander Islands (open circles) for the period 1958 to 1974, from Lander and Kajimura (1976).

in which estimates of both quantities are available. The estimated mortality rates are much higher since 1960 than in the period 1914-1924 (Figure 6). There appears to be a possible downward trend in the 1960s, with the most recent estimates in 1975 and 1976 suggesting a leveling off. These changes in mortality rate with time correlate with changes in numbers of pups born (Figure 7). The relationship is not linear, suggesting a variable but rapid rise in mortality rate with number of pups born starting when greater than 200,000 pups are born. The cluster of five observations around 280,000 pups born (corresponding to the years 1964, 1966, 1967, 1975 and 1976) do not fit this general pattern although these observations also suggest higher mortality rates at higher densities. The dead pup count in the 1950s, while unable to provide direct estimates of on-land mortality, do suggest that the on-land mortality was higher during the 1950s than in the early part of the century.

The plot of mortality rates over time for Robben Island and the Commander Island pups, based on the data in Table 4, is given in Figure 8. The mortality in 1965 on Robben Island was inordinately high due to heavy storm-induced mortality. The estimates for 1966, 1967 and 1972 are inordinately low due to known underestimation of numbers found dead, apparently caused by organization problems during the counts. Discounting these points, the mortality rate of pups does not appear to have changed over this time period although the number of pups born on Commander Island has nearly doubled.

The results for St. Paul Island and for the western Pacific Islands are contradictory on the point of changes in on-land pup mortality. It is possible that changes in on-land mortality rates are not apparent in the data for the western Pacific populations because they have not been observed over a wide enough absolute range in population sizes. However, since 1958 the on-land mortality rates for the western Pacific population have not been as low as the corresponding rates were on St. Paul Island early in this century. Rather they are of the same general magnitude as the present mortality rates on the Pribilofs, despite the fact that the western population appears to be much farther below its known historical levels. Two alternative possibilities are 1) that the estimates of on-land mortality on St. Paul Island rates for early in this century are not comparable to those made since 1960 due to changes in the environment of seals that are not a direct result of their density (such as changes in the availability of food due to changes in fishing (Chapman 1973)), and 2) that on-land mortality is related to the density of seals using a breeding rookery and that the density on the few breeding rookeries presently being used on Commander Island may be relatively high despite their low total numbers.

The available data can be used to get an indication of whether the on-land mortality of pups is a function of the density of idle bulls as first suggested by Parker (1918). Using the ratio of the counts of idle bulls to the number of pups born as an index of the relative density of idle bulls, there appears to be no relationship between the observed on-land mortality rate and the density of idle bulls despite the fact that in all cases the density of idle bulls has varied considerably without any changes in the number of pups born (see Tables 1, 2, 3 and 4).

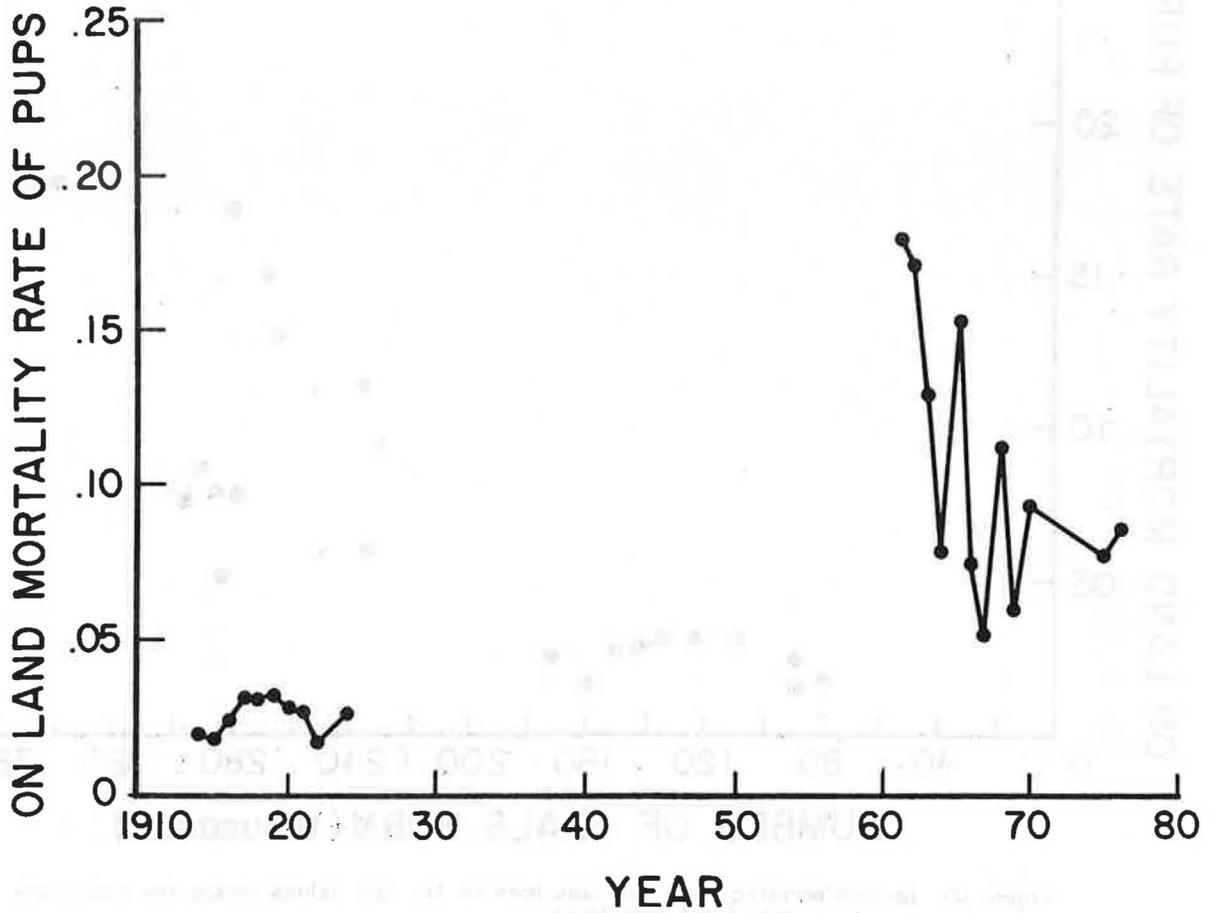


Figure 6. On-land mortality rate for seals born on St. Paul Island for the years 1910 to 1976, from Table 3.

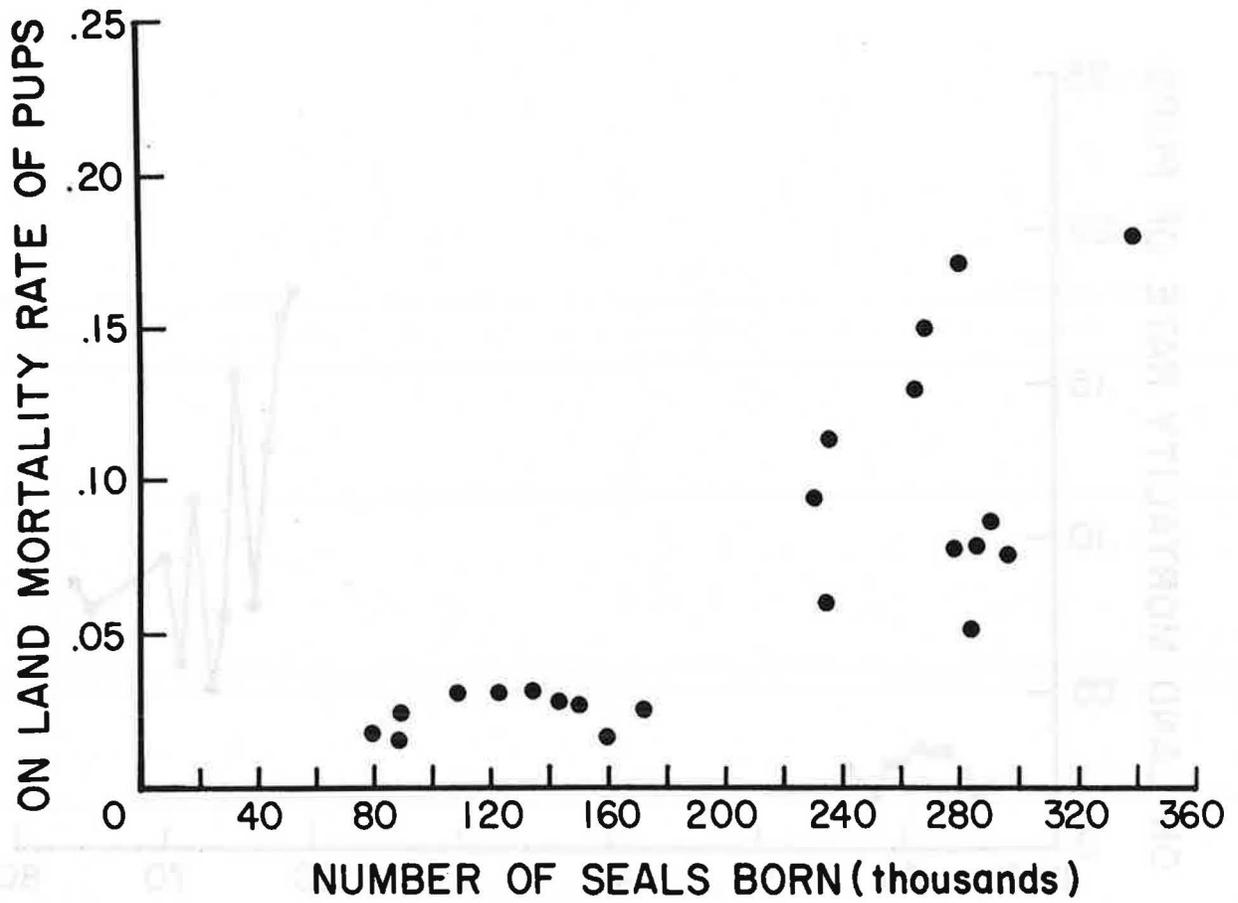


Figure 7. On-land mortality rate for pups born on St. Paul Island versus the number of pups born, calculated from Table 3.

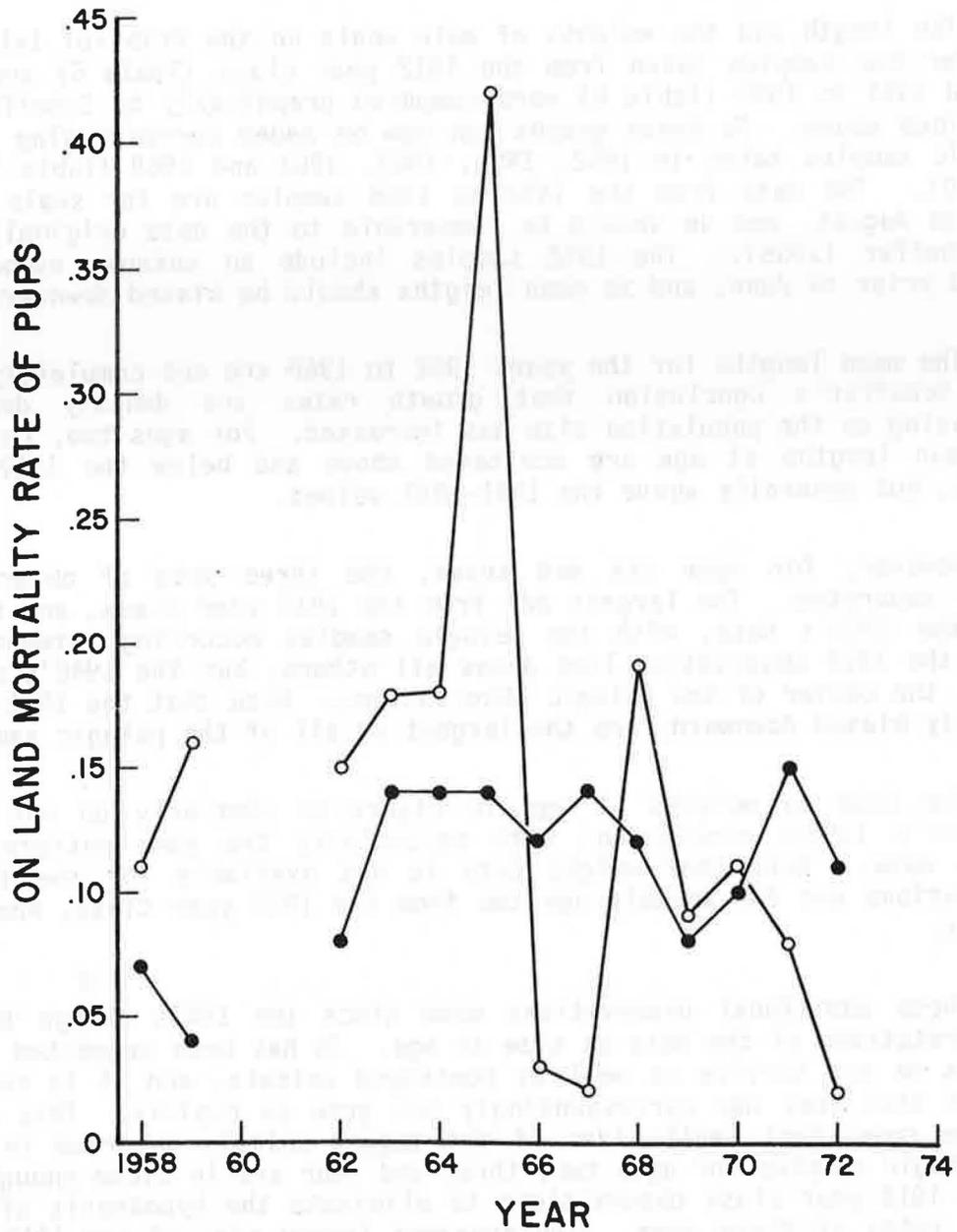


Figure 8. On-land mortality rate for seals born on Robben Island (open circles) from Table 4 and on the Commander Islands (closed circles) for the years 1958-1972.

Changes in Growth Rates

The length and the weights of male seals on the Pribilof Islands at each age for the samples taken from the 1912 year class (Table 5) and during the period 1941 to 1950 (Table 6) were compared graphically by Scheffer (1955) as described above. To these graphs can now be added corresponding data for the pelagic samples taken in 1952, 1960, 1962, 1963 and 1968 (Table 7, Figures 9 and 10). The data from the 1962 to 1968 samples are for seals killed from June to August, and so should be comparable to the data originally presented by Scheffer (1955). The 1952 samples include an unknown number of seals killed prior to June, and so mean lengths should be biased downwards.

The mean lengths for the years 1952 to 1968 are not completely consistent with Scheffer's conclusion that growth rates are density dependent and decreasing as the population size has increased. For ages two, three and four the mean lengths at age are scattered above and below the 1912 year class values, but generally above the 1941-1951 values.

However, for ages six and seven, the three sets of observations are rather separated. The largest are from the 1912 year class, and the smallest from the 1940's data, with the pelagic samples occurring between. For age five, the 1912 observation lies above all others, but the 1940's observations lie in the center of the pelagic observations. Note that the 1952 data, while possibly biased downward, are the largest of all of the pelagic samples.

The data on weights at age in Figure 10 similarly do not agree with Scheffer's (1955) conclusion, with essentially the same pattern as in the length data. Note that weight data is not available for the 1952 pelagic observations and for animals age two from the 1912 year class, whereas length data is.

These additional observations made since the 1940s change the possible interpretations of the data on size at age. It has been suggested that tagged animals do not survive as well as nontagged animals, and it is reasonable to suspect that they may correspondingly not grow as rapidly. This may account for the consistent small sizes of the tagged animals observed in the 1940s. The pelagic samples for ages two, three and four are in close enough agreement to the 1912 year class observations to eliminate the hypothesis of changes in growth rates at these ages. The apparent larger size of the 1912 year class at ages five, six and seven is consistent and possibly statistically significant. Variability is not available from the summary tables of the pelagic samples, but 95% confidence intervals for the 1912 estimates of length for ages five, six seven would not include any of the more recent pelagic means. These differences could be the result of one or more of the following factors: 1) density related differences in growth rates at older ages, 2) size selective harvesting of males at ages two to five of all year class since 1918 allowing differential survival of smaller animals, or 3) changes in the secondary growth phase of males over time as the result of changes in the onset of sexual maturity, 4) possible differences in measurement techniques by Japanese and United States scientists, and 5) possible differences in measurements between pelagic and land-caught animals. Little evidence is

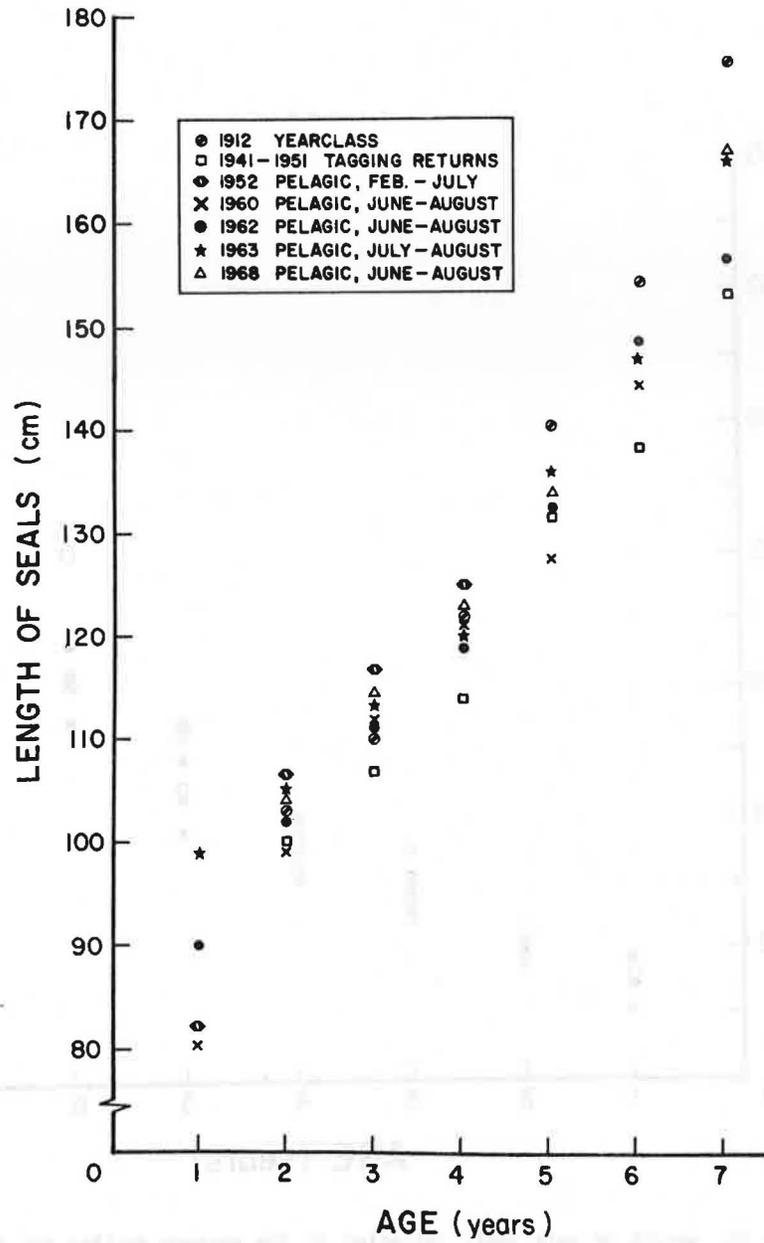


Figure 9. Length of male seals in the eastern Pacific during different periods, from Tables 5, 6 and 7.

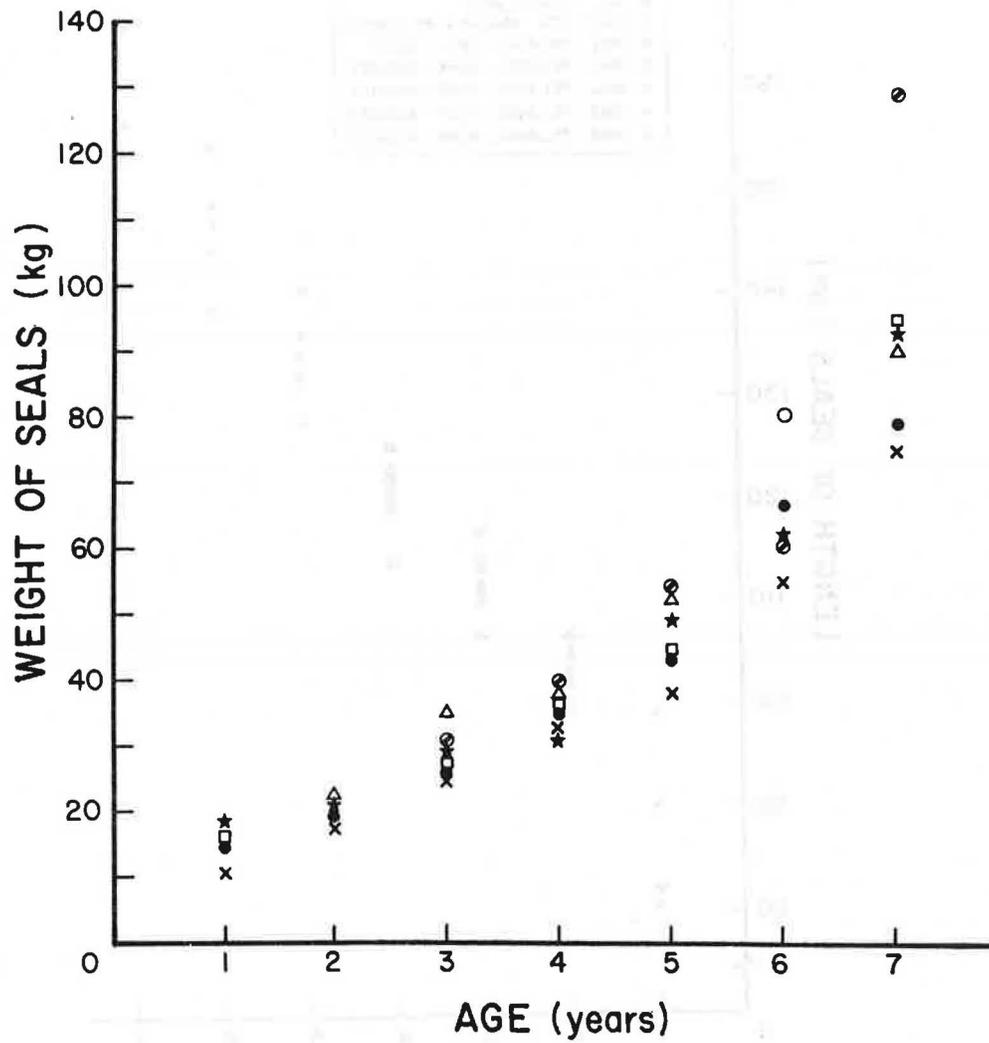


Figure 10. Weight of male seals collected in the eastern Pacific for different periods. Symbols and sources are the same as in Figure 9.

available to support any of these possibilities. However, it seems unlikely population crowding would only have effect past age four, especially since older males tend to be segregated at sea during the nonbreeding (growing) periods of the year and their numbers have been kept "unnaturally" low by the harvest of juvenile males. Alternatively, changes in the onset of sexual maturity is a possibility since the number of harem bulls has varied with low numbers in the early years and since the 1960s (Figure 2). If the size of males at ages five to seven were increasing in recent years, it would be supportive of the possibility of changes in the age of onset of sexual maturity in males. The differences in the size at age between the 1960 to 1968 samples do not show a consistent trend here, but the sample sizes may be too small in the latter years to detect a trend. While we cannot explain the differences in size at these older ages, it does not seem likely to us that they are related to changes in growth rate due to a general density induced shortages of food as Scheffer (1955) concluded based on the earlier data alone.

The length and weight observations on male seals in the Japanese pelagic samples can similarly be examined for changes in size at age over time. Because of the long series of data available (Table 8), the size at age of individual year classes can be compared. The graph of length at successive ages of seals born in the years 1957 to 1964 is given in Figure 11. Following the symbols across the graph for seals of the same age, no trend is apparent. A similar examination of changes in weight at age for these samples reveals no changes. The length and weight observations on young female seals from the Japanese pelagic samples (Table 9) similarly show no evidence for a change in size at age over the years 1958 to 1967, for ages one, two and three. As discussed above, the observations for older females are not considered due to the unexplained size difference between pregnant and nonpregnant seals.

Taken together, the above lack of evidence for change in size at age in seals collected in the western Pacific over the time period when the size of the populations on Robben Island and Commander Islands increased by 50% in size suggests that density-dependent changes in growth rates are not occurring in those populations. However, since a significant proportion of the eastern Pacific stocks may feed during the nonbreeding seasons in the western Pacific, a lack of change is not necessarily inconsistent with a density-dependent response as the Pribilof Islands populations has apparently not changed appreciably in the time period where data are available.

A comparison of the size between male seals taken in the eastern and western Pacific indicates that seals taken in the western Pacific are larger. This is true for a comparison of the length or weight of seals taken during the same period of any year (Tables 5 and 6) or for the mean length or weight obtained from pooling data for the same months for all years (Table 12).

Since this analysis was completed, additional studies of fur seal growth rates have been published by Kajimura et al. (1979).

Table 12. Comparison of mean length of male fur seals in the eastern and western Pacific collected during the same month. The data for western Pacific combines all the data in Table 8 while the data for the eastern Pacific combines the spring data for 1958, 1960, and 1971 in Table 7.

Age	Length		Weight		Sample Size ¹	
	Eastern	Western	Eastern	Western	Eastern	Western
1	80.3	86.5	10.5	12.8	32	320
2	95.9	101.6	16.6	19.0	27	1372
3	106.6	111.8	22.9	24.9	63	1822
4	116.4	123.4	28.5	34.3	33	820
5	129.8	137.7	41.5	48.2	5	234
6	147.5	152.9	56.9	69.7	4	114(119)
7	150.2	163.6	69.4	96.9	16	57(60)

¹Sample sizes in parenthesis are for weights when sample size differs.

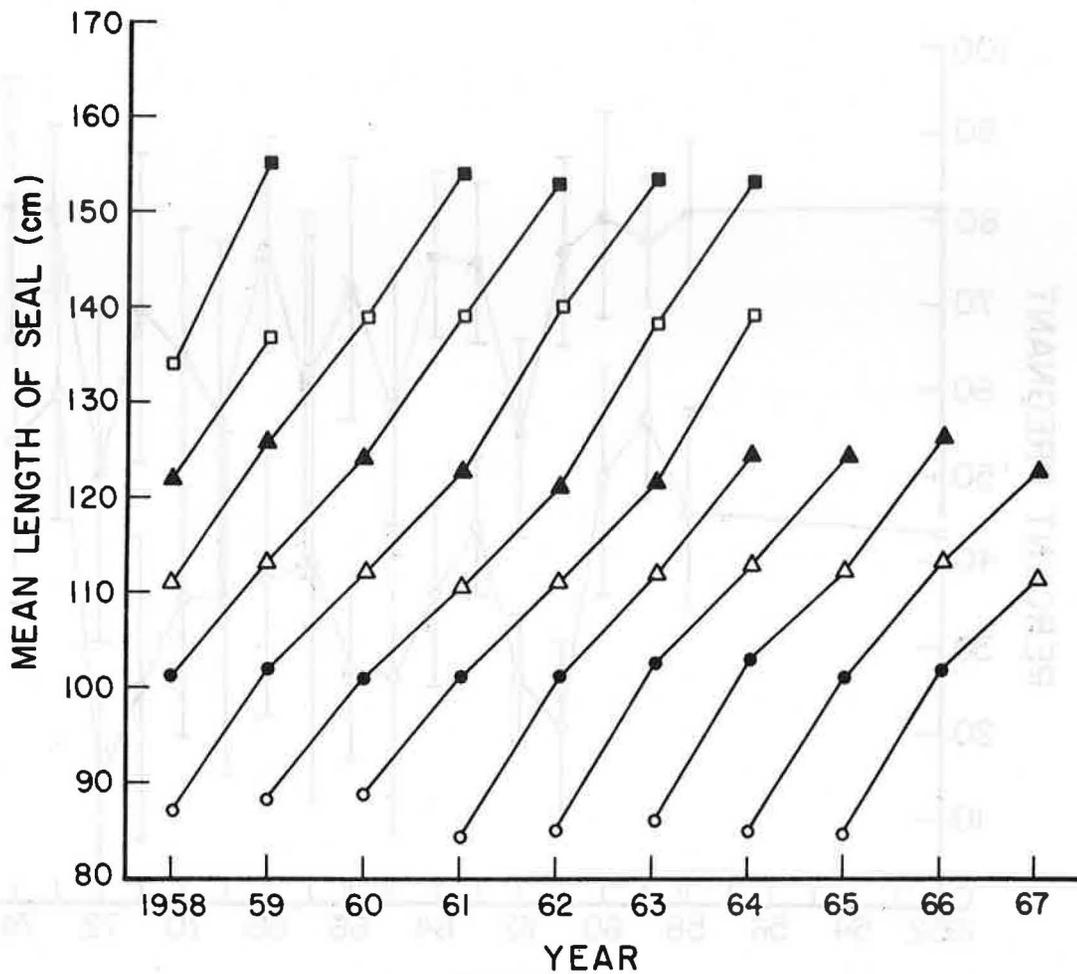


Figure 11. Mean length of male seals in each cohort, from the 1957 year class to the 1964 year class, over the years 1958 to 1967 in Japanese pelagic collections. The lines show the movement of seals of each class through time, with ages 1 to 6 denoted by open and closed circles, triangles and squares, respectively. Samples of less than 10 seals omitted.

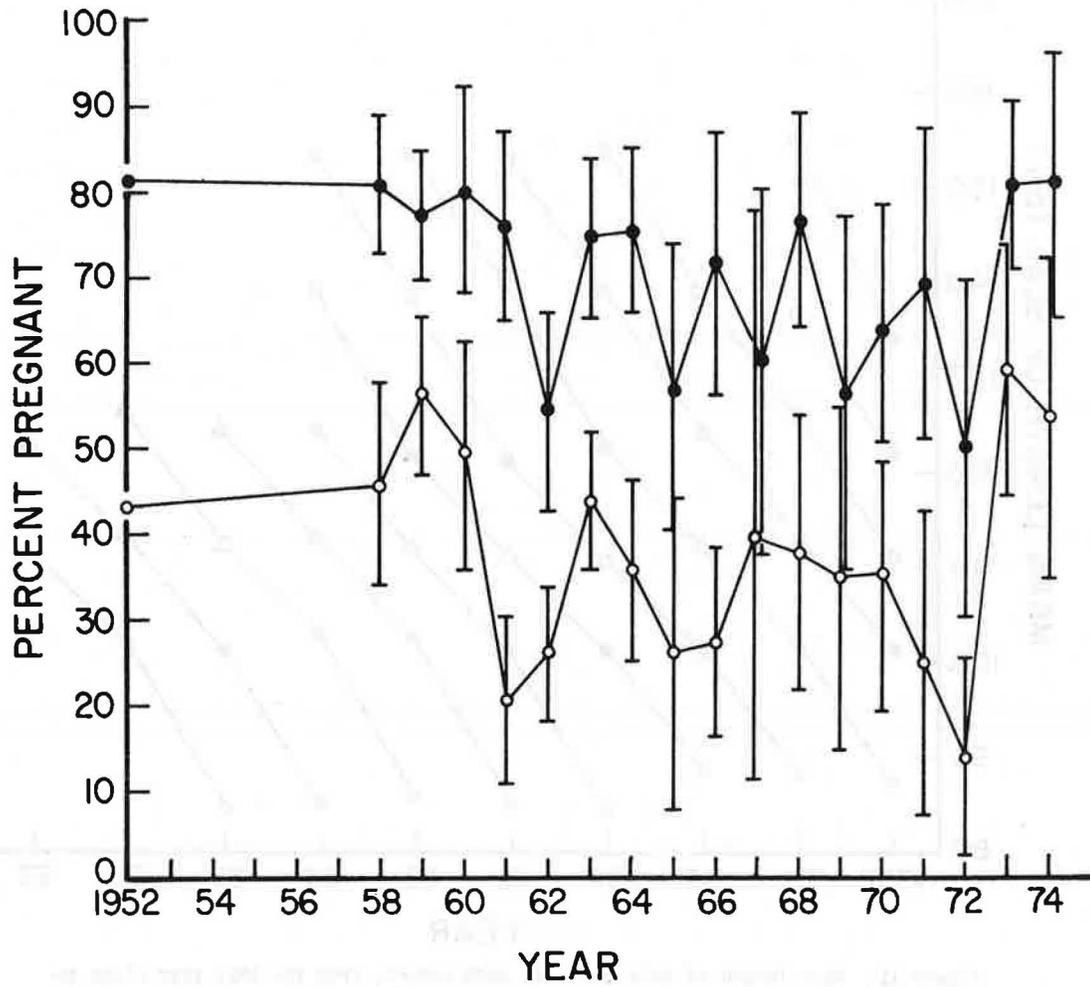


Figure 12. Proportion of female seals in the U. S. pelagic samples which were pregnant for ages 5 (open circles) and 6 (closed circles), from 1958 to 1974. Bars denote approximate 95% confidence intervals, assuming a binomial model (Table 10).

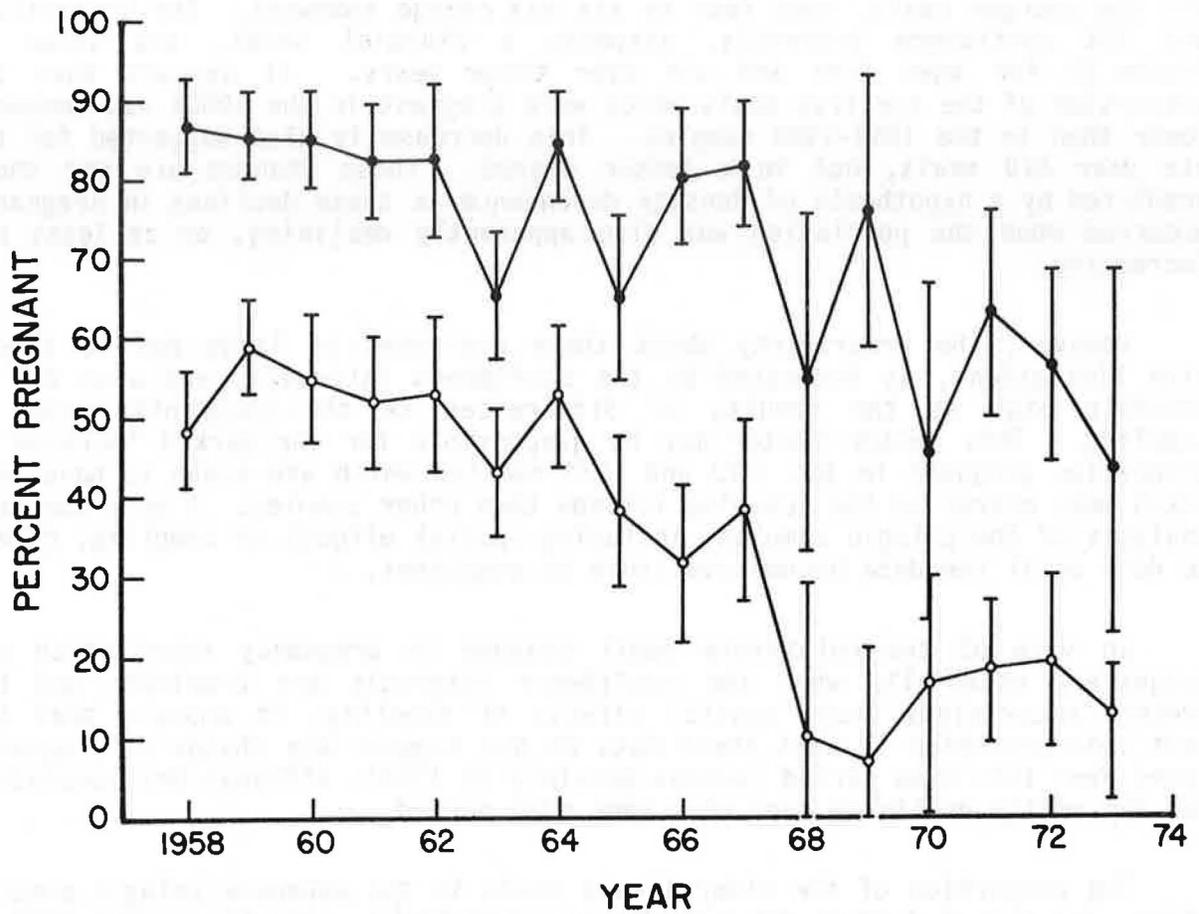


Figure 13. Proportion of female seals in Japanese pelagic samples which were pregnant, for ages 4 (open circles) and 5 (closed circles), from 1958 to 1973. Bars denote approximate 95% confidence intervals, assuming a binomial model (Table 11).

Changes in Reproductive Rates

The proportion of the female seals older than age 7 collected in the U.S. pelagic sampling program which were pregnant did not change appreciably over the years 1958 to 1974, as can be seen in Table 10. The estimated proportions for the younger seals, ages four to six did change somewhat. The proportions and 95% confidence intervals, assuming a binomial model, are shown in Figure 12 for ages five and six over these years. It appears that the proportion of the age five seals which were pregnant in the 1960s was somewhat lower than in the 1958-1960 samples. This decrease is also suggested for the six year old seals, but to a lesser degree. These changes are not those predicted by a hypothesis of density dependence as these declines in pregnancy occurred when the population was also apparently declining, or at least not increasing.

However, the uncertainty about these estimates is large due to sample size limitations, as indicated by the confidence intervals, and also due to possible bias as the results of differences in the geographic area of sampling. This latter factor may be responsible for the marked increase in proportion pregnant in the 1973 and 1974 samples which are known to have been taken much nearer to the breeding islands than other samples. A more complete analysis of the pelagic samples, including spatial effects of sampling, cannot be done until the data become available on computers.

In view of the relatively small changes in pregnancy rates which are suggested, especially when the confidence intervals are examined, and the present uncertainty about spatial effects of sampling, it appears that the best interpretation is that these data do not suggest any change in pregnancy rates over this time period (except possibly in 1973), although the population was apparently declining over this same time period.

The proportion of the older female seals in the Japanese pelagic samples which were pregnant also did not change appreciably, over the period 1958 to 1973. The estimated proportion pregnant for the younger seals, ages 3, 4 and 5, did change, however. The proportions and 95% confidence intervals for ages four and five are shown for these years in Figure 13. It appears that substantial changes did occur in both of these ages from approximately 0.55 to 0.15 for age four seals, and from 0.85 to 0.55 for age five seals.

These changes in proportion pregnant occurred while the number of pups born in both the Robben Island and the Commander Islands population increased by approximately 50%. It is interesting that in both the U.S. and the Japanese samples, the only suggestion that pregnancy rates have changed is for younger animals.

Any changes in the proportion pregnant which might be occurring could be due to changes in either or both the age of sexual maturity and the birth rates for sexually mature females. The Japanese observations on the numbers of the nonpregnant seals which were not sexually mature allow estimation of the proportion sexually mature with age (Table 11). It is clear that all

seals are sexually mature by age seven. The proportions sexually mature at ages two to five, however, has varied over the years (Figure 14). It appears that the 10 to 50% of the 2-year-olds were sexually mature in the 1958 to 1963 period, while none were sexually mature in the samples since 1968. Similarly while more than 80% of the 3-year-olds were sexually mature in the early period, only in the 1969 sample were any sexually mature in the later period. It appears, in general, that the age of onset of sexual maturity is approximately 2 years later in the period after 1968, with the proportion sexually mature at age five similar to that at age three in the earlier period.

Examining only the females which were sexually mature, the proportion pregnant at ages four and five are shown plotted over time in Figure 15. The sample sizes are substantially less in this data, but the same marked shift seen in proportion sexually mature does not appear.

From the above, we can conclude that the cause of change of the proportion pregnant is most likely a change in the proportion sexually mature with age and not in the reproductive rates of sexually mature seals. As the changes observed in the western Pacific change occurred while the population increased by one and one half times, it is possible that this represents a density-dependent change in reproductive rates.

Comparison of rates between samples collected in the eastern and western Pacific suggest that pregnancy rates for females age eight and older are similar. This is shown in Table 13 where pregnancy rates for age seven and older have been calculated pooling all data from 1958-1974 since for these ages, there is no indication that pregnancy rates have changed over this time period. For animals age seven, the pregnancy rates are about 10% lower in the eastern Pacific samples. This difference is significant using a chi-squared test. For older animals, the differences are smaller and are not significant, with the eastern Pacific rate being greater for ages 10 and older. For ages younger than seven, pregnancy rates in the western samples have been consistently higher, although the magnitude of the discrepancy decreases through the 1960s as the pregnancy rates in both sets of samples declined. In the 1973 estimates, this discrepancy entirely disappears with the U.S. pelagic samples being only slightly higher than the Japanese.

The U.S. samples in 1973-1974 were taken near the Pribilofs near the time of pupping and are likely to be biased upward compared to the other samples, raising the question of the reality of these differences given the possibility of geographical biases. While geographical biases might account for the discrepancy in the latter years, the magnitude of the differences in the 1958-1964 samples appear too large. Moreover, in the female harvest conducted on land on the Pribilof Islands for ages 3 and 4, virtually no sexually mature females were found in 1961 (the only year for which data are available on reproductive condition) and only 51% of the age 5 females were sexually mature (NPFSC 1962). Considering that pregnancy rates from the on-land female harvest are probably biased upward (Nagasaki 1961), these figures suggest that substantial differences did exist between the eastern and western stocks.

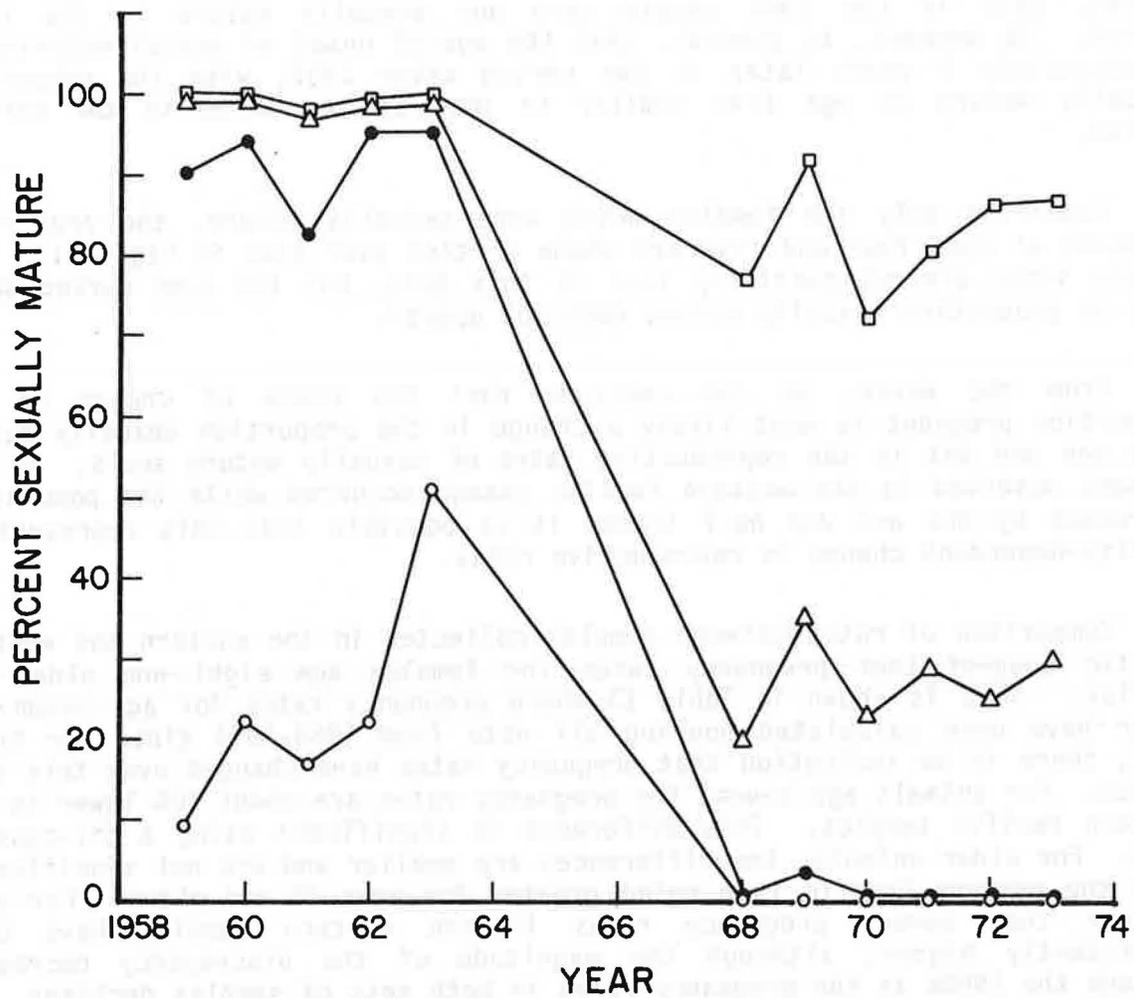


Figure 14. Proportion of female seals in the Japanese pelagic samples which were sexually mature, for age 2 to 5 (open and closed circles, triangles and squares, respectively), from 1959 to 1973 where data available.

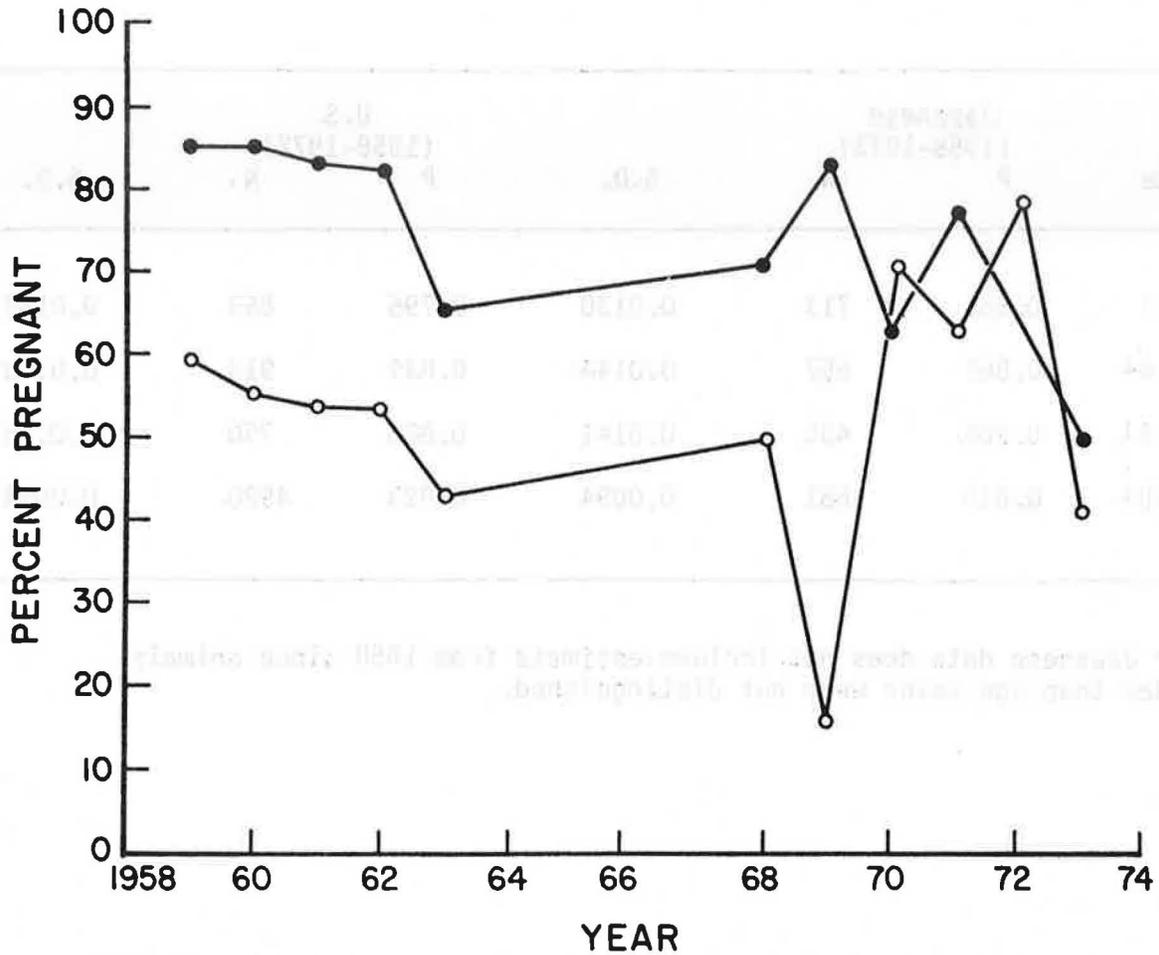


Figure 15. Proportion of the sexually mature female seals in the Japanese pelagic samples which were also pregnant, for ages 4 (open circles) and 5 (closed circles), from 1959 to 1973 where available.

Table 13. Comparison of the pregnancy rate (P) between U.S. and Japanese samples for females age seven and older pooling over samples indicated with standard deviations (S.D.).

Age	Japanese (1958-1973)			U.S. (1958-1972)		
	P	N	S.D.	P	N	S.D.
7	0.861	713	0.0130	0.795	853	0.0142
8 ¹	0.867	557	0.0144	0.849	910	0.0119
9 ¹	0.905	430	0.0141	0.886	750	0.0116
+10 ¹	0.819	1681	0.0094	0.823	4920	0.0054

¹For Japanese data does not include estimate from 1958 since animals older than age seven were not distinguished.

Kenyon et al. (1954) hypothesized that the shortage of harem bulls could be an important factor regulating pregnancy rates. The ratio of the number of pups born to the number of harem bulls can be used as a rough measure of average harem size and of the availability of harem bulls. While this measure of availability may be complicated by age structure shift in adult males (e.g., recently mature males may be less fertile), and the fact that harem size may not change at the same rate as the availability of harem bulls for both eastern and western populations, there is no apparent relationship between harem size and pregnancy rates. Thus, the average harem size has varied by over a factor of two between 1958 and 1973 for all populations (Figure 16), yet there was no change in the pregnancy rates of older animals during this same time span. The decline in pregnancy rates of younger females in the eastern Pacific that was observed during the 1960s in general does not correlate with an increase in average harem size except that the lowest observed pregnancy rate for these ages occurred in 1972 when the average harem sizes took a dramatic increase (Figure 17). The other observed pregnancy rates for these ages with similarly high harem size (i.e. in 1973 and 1974) are the highest that have been observed but unfortunately are probably biased upward due to geographic location of the sampling. More generally other factors besides the suggested harem size could affect pregnancy rates. This might be analyzed using multiple regression techniques.

It is not clear how to combine the average harem size on Commander and Robben Islands to examine their possible effect on the changes that have been observed in the pregnancy rate of younger females. Yet, it does not appear that the changes in harem size which have occurred can account for these changes in pregnancy rates. Thus, in 1958 and 1959 average harem size and pregnancy rates were both high. Subsequently, average harem size on both islands tends to be lower through 1971 and yet pregnancy rates declined. The dramatic increase in average harem size in 1973 and 1974 came after pregnancy rates had already declined, and there is no subsequent decline reflecting these large increases in harem size. Moreover, the fact that the observed changes in pregnancy rates resulted from a shift in the age of sexual maturity and not in the pregnancy rate of mature females suggests that a shortage of harem masters is not likely the factor responsible for these changes.

DISCUSSION AND CONCLUSIONS

Comparison of Eastern and Western Stocks

The data and analyses presented above suggest there have been consistent differences in the vital rates for the eastern and western stocks. Males captured in the western Pacific appear to grow faster, and younger females have higher pregnancy rates. There also appear to be differences in the cause of on-land mortality although the overall rates have been similar in recent years for all islands. These differences could be the result of one or more of the following causes:

- 1) genetic differences between the populations,

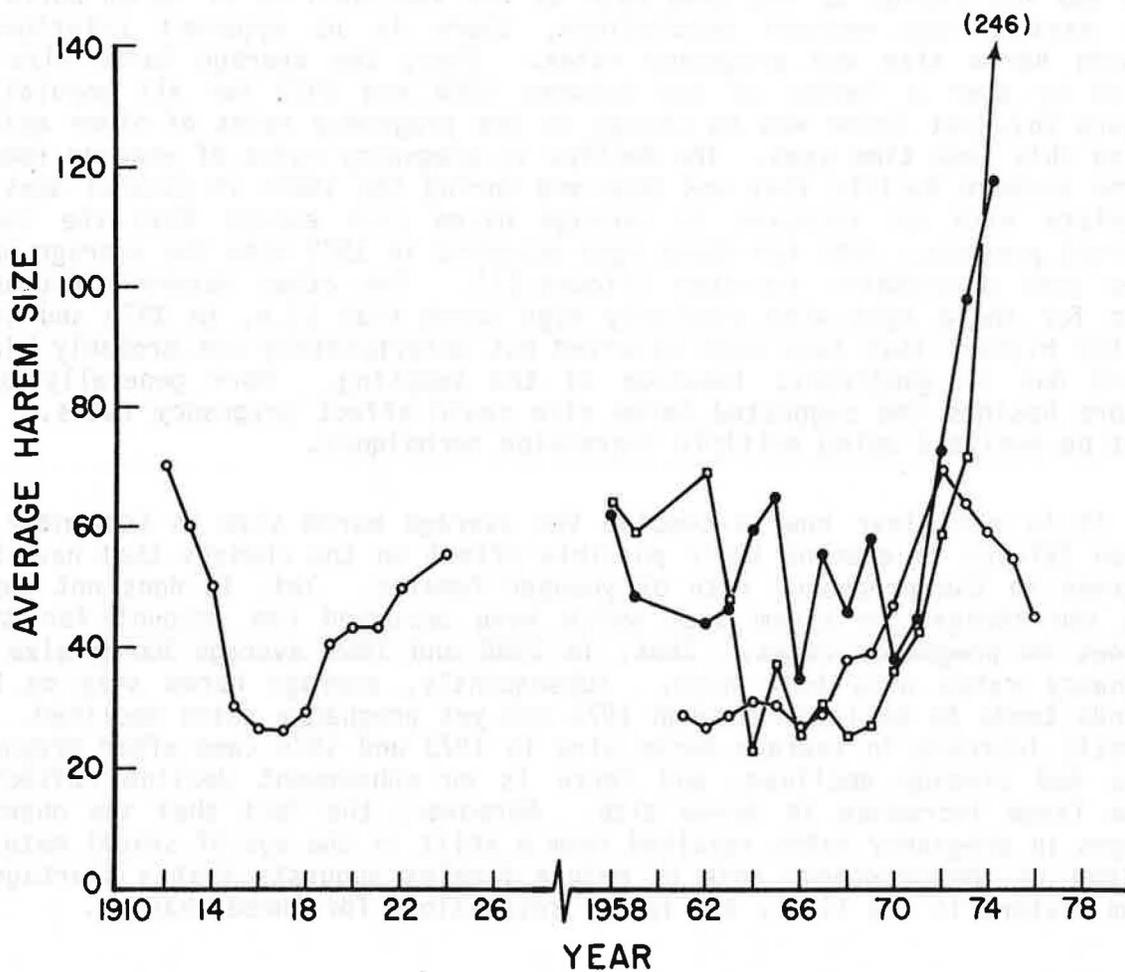


Figure 16. Average harem size for the years where available for St. Paul Island (open circles), Robben Island (closed circles) and the Commander Islands (squares).

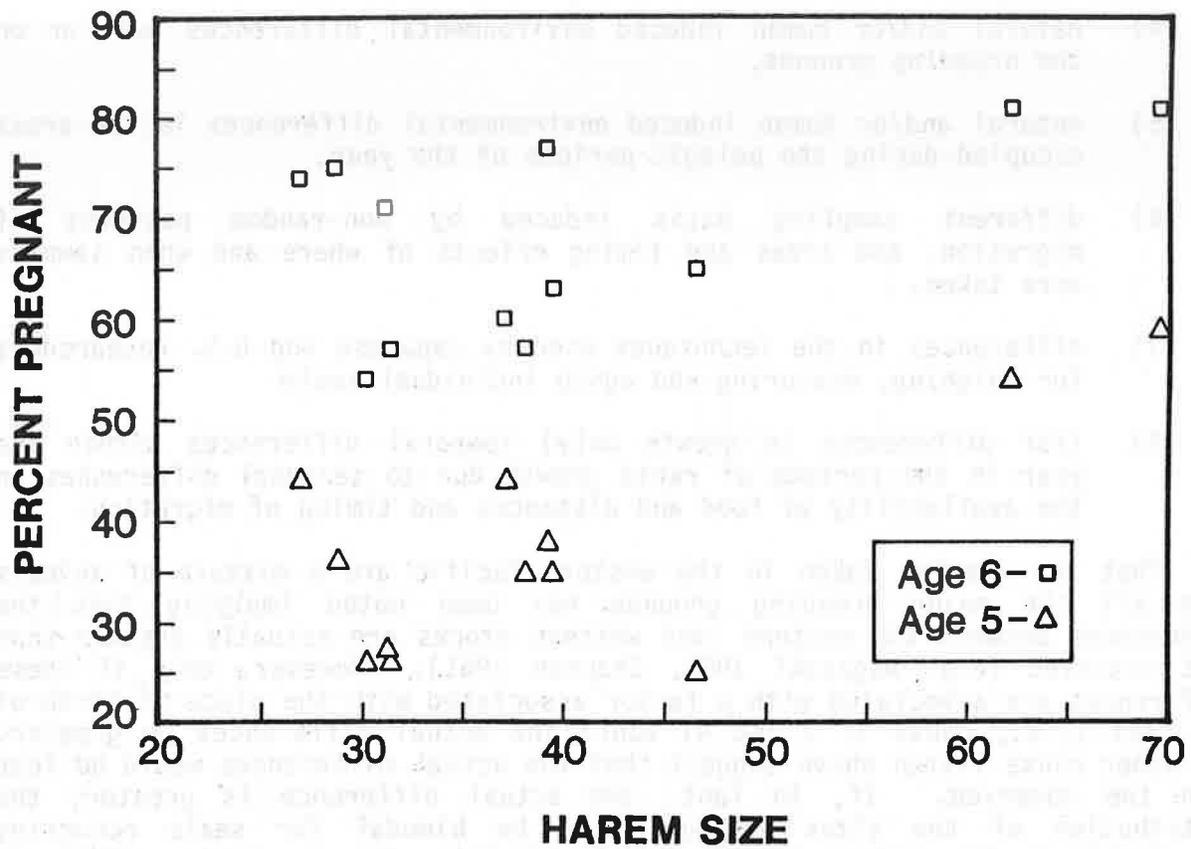


Figure 17. Pregnancy rate versus harem size for females ages 5 and 6, from the eastern Pacific pelagic collections, from Table 1 and Table 10.

- 2) environmental differences induced by differences in relative density on or near the breeding grounds,
- 3) environmental differences induced by the relative density of seals during the pelagic, nonbreeding periods of the year,
- 4) natural and/or human induced environmental differences near or on the breeding grounds,
- 5) natural and/or human induced environmental differences in the areas occupied during the pelagic periods of the year,
- 6) different sampling basis induced by non-random patterns of migration, and areas and timing effects of where and when samples were taken,
- 7) differences in the techniques used by Japanese and U.S. researchers for weighing, measuring and aging individual seals
- 8) (for differences in growth only) temporal differences within the year in the periods of rapid growth due to seasonal differences in the availability of food and distances and timing of migration.

That the samples taken in the western Pacific are a mixture of animals from all the major breeding grounds has been noted implying that the differences between the eastern and western stocks are actually greater than that observed (e.g. Nagasaki 1961, Chapman 1961). However, only if these differences are associated with a factor associated with the place of birth of the seal (i.e., cause 1, 2 and 4) would the actual differences be greater. The other cause listed above suggest that the actual differences would be less than the observed. If, in fact, the actual difference is greater, the distribution of the sizes at age would be bimodal for seals occurring pelagically in the western Pacific. Unfortunately, the raw data available to examine these distributions are not presently available.

Differences in the observed eastern and western populations have been cited as evidence for density-dependent changes in these rates. While these differences are consistent with density-dependent changes in these vital rates, they are also consistent with a number of non-density-dependent hypotheses. At present, there appears to be no reason to favor any of the above listed possible causes for the observed differences. We are especially reticent to draw any general conclusions based on these observed differences until the possibility that these differences may be an artifact of the data (i.e., causes 6 and 7) is explored more fully than is possible with the data in its present form.

Mechanisms of Regulation

The purpose of this paper is to review the evidence relative to the hypothesis of density-dependent changes in vital rates as might pertain to population regulation. The above analyses suggest that 1) the on-land mortality rates for pups in the Pribilofs during their first summer has changed over a 40-year period, 2) the age of sexual maturity of female seals in the western Pacific has changed over a 10-year period, and 3) the pregnancy rate of young females in the eastern Pacific may have changed slightly over a 10-year period. The data do not show changes over time in 4) the on-land mortality in the western Pacific populations, 5) the pregnancy rates of older females in the eastern Pacific samples, 6) the pregnancy rate of mature females in the western Pacific samples, 7) the growth rate of male seals on the Pribilof Islands over a 50-year period, and 8) the growth rate of male and of female seals over a 15-year period in the western Pacific.

Additionally, it does not appear from our analyses that changes in pregnancy rates are related to the availability of harem bulls or that the relative density of idle bulls is related to the on-land survival of new born pups.

The changes that have occurred over time correspond to fourfold increases in population size in the Pribilof Islands, and to a 50% increase in the number of pups born in the western Pacific populations. There is no evidence which would causally associate the observed changes in vital rates with changes in availability of some resource which may be in short supply due to increased abundance. The only evidence for any density-dependent effects are the rough correlation between population size items 1, 2 and 3 above. The magnitude of the density-dependent effects suggested by these correlations is insufficient to account for the decline in the growth rate of pups of the Pribilof population from the 8% observed in 1912-1924 (Appendix IV). One possible factor contributing to our present inability to detect mechanisms that are regulating changes in abundance is that the magnitude of the changes in any single vital rate may be below our precision in measuring these rates. In Appendix IV, we argue that given the rates of survival and fecundity estimated from data available from the 1960s, it is unlikely that the 8% rate of increase observed in the early part of this century could have been the result of a difference in only a single component of the life table (i.e., adult survival, juvenile survival or fecundity). Moreover, if more than a single component changes, only small to moderate changes could be expected to occur for any single component. In this context, the failure to detect such changes is not surprising given the limitations of the data and techniques for measuring these rates.

In addition to the possibility that only small to moderate changes in rates may be occurring, it is possible that major changes unrelated to the density of fur seals have occurred in the North Pacific ecosystem since 1950. Such changes, if they have occurred, further increase the difficulty in detecting and interpreting differences in vital rates. In density-dependent theory jargon, the failure to detect any increase in growth and fecundity rates in the Pribilofs from 1952 to 1974, although the population apparently decreased appreciably, may reflect a shift in the "carrying capacity" of the

system rather than a lack of a density dependent response. There is no evidence at present to distinguish between these two hypotheses.

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DENSITY DEPENDENT CHANGES IN THE SURVIVAL RATE OF
JUVENILE FUR SEALS (CALLORHINUS URSINUS)
APPENDIX II

INTRODUCTION

The harvesting of the Alaska fur seal (Callorhinus ursinus) population breeding on the Pribilof Islands has been considered as one example of successful management of a marine mammal population (Bartholomew 1974; Holt and Talbot 1978). The population has recovered from very low abundances in the early part of this century, and has been subject to a sustained harvest since 1918 (Lander and Kajimura 1976; Roppel and Davey 1965). The management was initially based on the hypothesis that a high proportion of the males born are unnecessary for the reproductive process, and hence harvestable as "surplus males." This procedure has worked well since 1918 with the population increasing from its low level.

More recently the management has also been based on the hypothesis that the survival of seals during their early years depends on the numbers of seals born (Kenyon et al. 1954); Chapman 1961, 1964, 1973a, 1973b). This hypothesis was developed when it became apparent that the population had increased to a fairly steady level, and that the harvest of males was lower than the estimated numbers of pups born would suggest based on the experience in the earlier part of the century. Females were harvested from 1956 to 1965, in addition to the ongoing harvest of young males, based to a large extent on this hypothesis.

Kenyon et al. (1954) first suggested that juvenile survival of fur seals changes with population size, and supported this hypothesis with evidence of changes in the survival of pups during their first summer as the population increased. No data were presented on changes in the survival rate following the first summer of life.

Chapman (1961) presented a theoretical analysis of the possibility that juvenile survival depends on the foraging success of nursing adult females in the summer around the Pribilof Islands. From this analysis Chapman derived a functional relationship predicting from the number of pups born the subsequent survival to age three. Nagasaki (1961) also derived a functional relationship for density dependent juvenile survival based on a different analysis. The functional relationships derived by Chapman and Nagasaki have similar behavior and both authors evaluated their predicted relationship by comparing estimates of the numbers of pups born in a given year and estimates of the number of male seals from that yearclass that were alive at age three. The available data fit the predicted relationships, and thus were consistent with the hypothesis of density dependent juvenile survival. This did not prove the hypothesis, of course, and as Chapman (1961, p. 366-367) pointed out: "It is simply a model that seems to fit the data presently available and hence is worthwhile exploring."

Unfortunately, some of the data then available had serious problems, and subsequent analysis suggested that the estimates of numbers of pups born in the 1950s were too high (Chapman, 1964). As he noted in that paper (p. 667), without those particular estimates "the right-hand limb of the parent-progeny relationship. . . is much less well defined." He concluded, nonetheless, that the remaining data were still consistent with his hypothesized relationship between pups born and survival to age three.

Substantial additional information on numbers of pups born accumulated during the 1960s as a new procedure for estimation (Chapman and Johnson, 1968) was developed. Using these estimates of pups born (converted to estimates of numbers of females), and estimates of numbers alive at age three, Chapman (1973) again examined the hypothesis of density dependent juvenile survival. In this analysis he used a general spawner and recruit model and suggested a method of estimating maximum sustainable yield which does not rely on a specific parametric equation. He concluded that the data still support the general hypothesis that juvenile survival is density dependent, and that it is a major factor in regulating the abundance of this population. He noted that the biological mechanisms underlying these changes in juvenile survival are unknown.

The data that have been used in the examination of the survival of seals to age 3 are estimates of number of pups born and estimates of number of male seals surviving to age 3. In this paper we present a generalization of the methods presented in Chapman (1961, 1973) for estimating the number of male seals surviving to age 3 based on the age structure of the harvest of males. We also examine the estimates of numbers of pups born from 1950 to 1960 presented in Chapman (1964, 1973), and suggest an alternative interpretation of the available information. Finally, we use this information to estimate survival rates of seals to age 3 and test for changes associated with population density.

There are two islands comprising the Pribilof Islands, St. Paul and St. George. The rookeries on St. Paul are better studied, and the data are more extensive. Where data are available for St. George, similar and parallel trends are usually apparent. Following Chapman (1964, 1973), in this paper we only present the data for St. Paul Island.

Available Data

The data available to examine the hypothesis of density dependent changes in the survival rate of young fur seals are 1) the annual kills of males by year and by yearclass, 2) the annual counts of harem and idle bulls, and 3) the counts and estimates of the numbers of pups born.

1) The annual harvest of males is described in Roppel and Davey (1965), Lander and Kajimura (1976), Kenyon et al. (1954), and Chapman (1961, 1973). The age structure of the harvest has been estimated since 1950, based on counts of ridges and layers from the teeth (Scheffer, 1955). From these estimates, the number of male seals from each yearclass which are subsequently

killed at each age can be obtained. This data is available for the yearclasses from 1947 to 1974 (Table 1).

Prior to 1950 ages of the males harvested were not determined, although lengths were recorded. Length has been used to estimate the age structure of the kill for the 1920 to 1922 yearclasses (Chapman 1961) using an age-length key (Table 1). The age-length key used in this estimation was developed from recapture of tagged males from the 1912 yearclass, and appears to be biased in under-representing the numbers of 4 year olds (Kenyon et al. 1954).

2) Since 1911, regular counts of the adult male herd have been made (Table 2). The adult males are distinguished as harem bulls, guarding one or more females on the breeding ground, and idle bulls, adult males not holding a breeding territory. Idle bulls can be (Kenyon et al., 1954) young adults which are neither strong enough nor experienced enough to gain a territory on the breeding grounds, older "senile" bulls, or exhausted former harem bulls. Traditionally males are termed bulls when they become 7 years of age. However, in practice, the distinction between idle bulls and large, "sub-adult" males is a matter of personal opinion (Kenyon et al. 1954) and no information is available on what proportion of the number of 6, 7, and 8 year olds are actually included in the counts of idle bulls. The counts of harem bulls should be relatively accurate since harem bulls stand out clearly over smaller females and do not periodically leave their territories. Kenyon et al. estimate that the counts of harem bulls are accurate within 5% although no data is available to confirm accuracy of these counts. The idle bull counts are more uncertain because of the difficulty in clearly defining an idle bull and also because an unknown fraction of the idle bulls are at sea at any given time.

3) Published estimates of the number of pups born on the Pribilof Islands span the years from 1912 to 1924 and from 1947 to the present (Table 3). Four procedures have been used to arrive at these estimates: counts on rookeries, tagging, shearing, and extrapolation from the age composition of the male harvest. All of the estimates except those based on yearclass strength (Chapman 1964, 1973) are of the number of pups alive in the fall after the breeding season. For all of these estimates the number of pups which died on the rookeries have been added to arrive at the estimate of the number of pups born.

During the period 1912 to 1924 actual counts of the total number of pups occurring on a rookery were made, the first method of determining the number of pups. Counts were made in late August or early September after all pups were born. In the years 1912 to 1916 and in 1922 pup counts were conducted on all rookeries, while in the years 1917 to 1921 and in 1924 counts were made on selected rookeries with the total number of pups born on all rookeries being estimated by extrapolations based on the proportion of pups born on the different rookeries in years for which complete counts were made. There exists no analysis of the accuracy of this counting procedure. However, Parker (1918) states "it is perfectly clear to anyone who has counted pups on the rookeries of the Pribilofs that even the most accurate count is bound to fall short of the real number," while noting in particular that the count for 1913 appears too high. No subsequent publication has questioned the accuracy

Table 1. Kill by age and yearclass on St. Paul Island.

Year class	Age when killed				Total
	2	3	4	5	
1920 ^{1,2}	527	11,725	232	---	12,484
1921 ^{1,2}	697	12,726	396	---	13,819
1922 ^{1,2}	346	13,630	491	---	14,467
1947	---	30,100	23,697	854	54,661
1948	486	25,714	19,995	103	46,298
1949	---	29,697	12,326	249	42,272
1950	855	40,656	15,365	371	57,247
1951	1,384	32,350	18,107	3,057	54,898
1952	1,735	30,661	3,410	675	64,481
1953	838	38,312	8,885	54	48,089
1954	2,918	23,473	5,599	554	32,544
1955	1,015	27,863	10,555	115	39,548
1956	885	10,671	2,762	532	14,850
1957	2,590	24,283	15,344	773	42,990
1958	1,977	48,458	14,149	1,587	66,171
1959	2,820	26,456	14,184	1,764	45,224
1960	1,619	14,310	10,533	1,240	27,702
1961	1,098	22,468	12,046	1,270	36,882
1962	2,539	19,009	12,156	1,287	34,991
1963	1,264	25,535	11,785	1,542	40,126
1964	3,143	26,991	13,279	1,469	44,882
1965	2,200	18,706	10,565	731	32,202
1966	1,673	17,826	11,548	1,338	32,385
1967	2,640	22,176	12,503	2,185	39,504
1968	1,725	12,888	14,932	721	30,266
1969	323	15,024	10,800	1,631	27,778
1970	916	16,337	15,533	1,402	34,188
1971	557	14,652	10,768	722	26,199
1972	1,025	15,186	8,050	707	24,968
1973	1,642	13,397	9,421	598	25,058
1974	893	16,476	8,955	470	26,794
1975	1,783	13,752	7,918	651	24,104

¹ Estimated from length distributions of the kill.

² For these yearclasses, between 6 and 8 thousand animals were specifically excluded from the harvest to form a breeding reserve.

Sources: 1920-1922 from Chapman (1961).

1947-1953 from NPFSC (1962).

1954-1961 from Lander and Kajimura (1976).

1961-1975 from USFSI (1975, 1976) and Engel, et al. 1980.

Table 2. Counts of harem and idle bulls made in Mid-July on St. Paul Island (from Lander and Kajimura 1976). A dash indicates no data are available.

Year	Harem	Idle
1911	1,090	258
1912	1,077	93
1913	1,142	77
1914	1,316	159
1915	1,789	546
1916	2,948	2,278
1917	4,116	2,341
1918	4,610	2,245
1919	4,573	2,158
1920	3,542	1,078
1921	3,443	711
1922	3,184	493
1923	3,051	303
1924	3,127	375
1925	3,103	283
1926	3,478	368
1927	3,916	846
1928	5,059	1,208
1929	5,998	1,339
1930	6,823	1,555
1931	7,557	1,519
1932	8,268	1,940
1933	8,334	1,933
1934	8,841	1,860
1935	9,444	2,082
1936	10,055	2,253
1937	10,689	2,516
1938	10,720	1,787
1939	9,122	2,616
1940	9,662	3,968
1941	10,089	5,059
1942	-	-
1943	10,948	3,523
1944	11,080	2,539
1945	10,750	4,055
1946	10,566	3,605
1947	10,160	3,331
1948	10,386	3,400
1949	9,554	2,976
1950	9,442	3,152
1951	9,434	3,581
1952	9,318	4,717
1953	9,848	5,912

Table 2. (cont.)

Year	Harem	Idle
1954	9,906	6,847
1955	9,034	8,650
1956	9,384	9,016
1957	9,562	10,060
1958	9,970	9,510
1959	10,003	11,485
1960	10,247	10,407
1961	11,163	11,791
1962	10,332	9,109
1963	9,212	7,650
1964	9,085	7,095
1965	8,553	5,616
1966	7,974	5,839
1967	7,230	4,439
1968	6,176	3,100
1969	5,928	2,535
1970	4,945	1,666
1971	4,200	1,900
1972	3,738	2,384
1973	4,906	2,550
1974	4,563	1,782
1975	5,018	3,535
1976	5,324	4,041
1977	6,457	3,845
1978	6,496	3,908
1979	6,242	4,457
1980	5,490	4,248
1981	5,120	4,003

Table 3. Estimates of the number of pups born in thousands on St. Paul Island.

Year	Counts	Tagging ⁴	Yearclass	Shearing ⁴
1912	70.0 (c)			
1913	79.5 (c)			
1914	79.4 (c)			
1915	88.1 (c)			
1916	98.9 (c)			
1917	108.7 (P)			
1918	122.6 (P)			
1919	133.9 (P)			
1920	143.3 (P)			
1921	149.9 (P)			
1922	158.9 (c)			
1923	-			
1924	172.5 (P)			
1947		426 ¹		
1948		459 ¹		
1949		470 ¹		
1950			451	
1951		451	447	
1952		452	438	
1953		601	445	
1954		621	450	
1955		665	461	
1956		786	453	
1957		564	420	
1958		578	387	
1959		616	335	
1960		509	320	
1961		442		337
1962		282		278
1963		352		264
1964		332		285
1965		314		267
1966		364		296
1967		352		284
1968		435 ²		235
1969		266 ²		234
1970		560 ²		230
1971				-
1972				260
1973				305 ³
1974				269 ³
1975				278 ³
1976				290 ³

¹Estimated number of pups dying on land estimated by 1950 count of dead pups.

²Based on partial returns.

³Based on estimates on selected rookeries on St. Paul Island extrapolated to the whole island.

⁴Published estimates vary slightly.

Notes: c = complete counts.

P = partial counts on selected rookeries extrapolated by preparations in complete counts.

Source:

Counts - Kenyon et al. (1954).

Tagging - 1947-1949 and 1952-1955 from

Chapman (1961). Other estimates based on

the average proportion of .79 for the years

in which published estimates exist for all

of the Pribilofs and St. Paul alone.

Yearclass - Chapman (1964, 1973).

Shearing - Landers and Kajimura (1976).

of these counts, with the implied assumption that the uncertainty in these counts is small compared to that for estimates in the number of pups in other years.

In 1947 a program of tagging young pups, the second method, was initiated. The proportion of tagged seals recaptured in the kill in subsequent years was used to estimate the number of pups that were alive at the time of tagging. Published estimates of the number born using this procedure are available for the years 1947 to 1970 (Table 3). Chapman (1964) has strongly questioned the reliability of these estimates, particularly for the years since 1952. He concludes that they are biased upwards, and are internally inconsistent and highly variable. These estimates indicate a general and substantial increase in the number of pups born from 1953 to 1956, with a sharp decline in 1957 and a generally declining trend through most of the 1960s. As Chapman (1964) points out, the yearly ranges of fluctuations as well as the implied rate of growth through 1956 appear to be outside the ranges that could be expected, either because of sampling error, or because of variations in pregnancy rates or growth of the herd. The reason this estimation procedure fails to yield satisfactory results is unknown. Chapman (1964) suggests as possible reasons that tagged animals may sustain higher mortality rates, and that such tag induced mortality may be heaviest in the yearclasses that have poor overall survival. Also, variation in overall juvenile survival rates may be related to temperature at higher population density.

These possible explanations of why the estimates of number of pups born from 1953 to 1960 are too high are not completely satisfactory. First, if the bias in the tagging estimates is due to differential mortality rates for tagged seals, then the bias should be related to the number of animals tagged. However, the large increase in the estimated number of pups born for the 1953 and 1954 yearclasses occurred when the number of tags being applied was decreasing. Second, if the effect of tagging on the survival of animals is more severe for yearclasses which have poor overall survival, then higher estimates of numbers of pups born might be expected for yearclasses which had lower numbers of male seals harvested. However, high estimates were obtained for 1953, 1957, 1958, and 1959, all years with larger harvest than 1948 and 1949; these later years had much lower estimates of the number of pups born.

Chapman (1964) does not reject the 1947 to 1952 tagging estimates, noting (pers. comm.) that alternative estimates were given in Kenyon et al (1954) which suggest that the tagging estimates are in the correct range. Three estimates are given in that source, two for the 1949 yearclass and one for the 1951 yearclass. The 1949 estimates were based on complete counts of the pups on one rookery; numbers of harem masters and area of rookeries determined from aerial photographs were used to extrapolate these counts, yielding estimates of 470,000 and 580,000, respectively. The tagging estimate for 1949 was also 470,000. The 1951 estimate was based on a rapid counting technique which was calibrated against complete counts on one rookery. The estimate was 359,000, compared to the tagging estimate of 451,000. The range of these alternate estimates is large compared to the consistency of the 1947 to 1952 tagging estimates, and only the extrapolation based on the numbers of harem masters gives confirmation to the tagging estimates. The validity of this procedure

might be checked further.

The effect of handling and tagging on the subsequent survival of pups could be responsible for the variability of the estimates of numbers of pups born. Experiments in 1966 confirmed that handled pups weigh less at the end of the summer (USFSI 1969), and experiments in 1963 and 1964 confirmed that pups tagged later in the summer subsequently survive better (USFSI 1970). These latter experiments compared pups tagged in the middle of August to those tagged in the latter half of September.

From data provided by Fowler (per. comm.), tags were applied late in September in 1947, and progressively earlier in 1948 and 1949, late again in 1952 and progressively earlier from 1953 through 1965. In response to the 1963 and 1964 experiments, the tags were applied in late September following 1965. Thus the tags were applied increasingly earlier over the period when the tagging estimates were at first too high (1953 to 1960), and then more reasonable (since 1961). This is contrary to the hypothesis that biases due to the time of application of tags were the primary problem in the 1950s, and leaves unresolved the problem of the 1950s estimates.

Chapman and Johnson (1968) present the third method of estimating the number of pups born, based on the recapture of marked pups during their first summer (Table 3). These pups were marked by shearing a small patch of fur. Estimates are available from 1961 to 1976, and are thought to be reliable.

The parallel series of estimate of numbers of pups born in the 1960s from Chapman and Johnson's new shearing procedure and the ongoing tagging procedure (Table 3) can be used to correct the tagging based estimates for 1947 to 1952, which Chapman (1964) does not reject, for bias due to increased mortality of tagged seals. For example, the average ratio of the estimates of the numbers of pups born using the shearing and tagging procedures from 1962 to 1967 is 0.84. The 1961 shearing estimate is thought to be less reliable as the procedure was still being developed, and the tagging estimates after 1967 are based on incomplete returns, so these years are not used in this calculation. The 1947 to 1952 tagging estimates could be corrected by this amount, yielding an average estimate of the number of pups born for that period of 381,000. However, lacking an explanation of why the tagging procedure failed to yield reasonable estimates from 1953 to 1960, any interpretation of the earlier period tagging estimates must be suspect.

Finally, Chapman (1964, 1973) presents the fourth method of number of pups born for the years 1950 to 1960, based on the harvest of males by yearclass (Table 3). The method used to obtain these numbers is quite complex, and involves a number of assumptions about the recent history of the population, about the killing process, and about the difference between the survival rate of male and female seals from birth to age three. Little information is available on any of these assumptions. These yearclass estimates have become widely accepted and are currently used rather uncritically (Lander and Kajimura 1976). We review these estimates below and suggest an alternative interpretation of the available data.

METHODS

We estimate survival rates from birth to age 3 using the procedure shown in Figure 1. The notation indicated there is:

$N_0(t)$ = the number of male pups born in the t^{th} year

$N_i(t)$ = the number of males from the t^{th} yearclass that survive to beginning of the i^{th} year of age

S_i = the survival rate during the i^{th} year

$S_{0,3}$ = $S_1S_2S_3$

$K_i(t)$ = the number of male seals from the t^{th} yearclass killed at age i

$E_i(t)$ = the number of seals from the t^{th} yearclass escaping the harvest at age i

$N'_i(t)$ = the number of the t^{th} yearclass that would have been alive at the beginning of the i^{th} year of life if no kill had occurred at younger ages

S_a = average survival rate of adult males

m = the average age at which males enter the adult male population

$H(t)$ = the counted number of harem masters in year t

$I(t)$ = the counted number of idle bulls in year t

α = the inverse of the proportion of the idle bulls actually counted.

Estimates of the number of seals which would have survived to age 3 in the absence of any harvest at age 2 ($N'_3(t)$) can be expressed as the sum of number of male seals actually alive and the number killed at age two which would have survived natural mortality to become age three, or

$$N'_3(t) = S_2K_2(t) + N_3(t).$$

The number which would have been alive at age three ($N'_3(t)$) can be re-expressed as the sum of the number of 3 year olds killed in the commercial harvest that year and the number of 3 year olds escaping the harvest, or

$$N'_3(t) = S_2K_2(t) + K_3(t) + E_3(t).$$

In a similar fashion, the following expressions can be obtained.

$$N'_3(t) = S_2K_2(t) + K_3(t) + K_4(t)/S_3 + E_4(t)/S_3$$

$$N'_3(t) = S_2 K_2(t) + K_3(t) + K_4(t)/S_3 + K_5(t)/S_3 S_4 + E_5(t)/S_3 S_4. \quad (1)$$

Equation one can be used to estimate $N'_3(t)$ if the escapement at age five ($E_5(t)$) and the survivals between age two and five are known. The calculations in equation (1) correspond to combining blocks 3 and 4 to obtain 5 in Figure 1.

The escapement at age five ($E_5(t)$) can be estimated from the counts of harem and idle bulls by determining how many bulls must have been recruited from a yearclass at the age (m) at which they become part of these counts ($N_m(t)$). This quantity can be expressed as the difference between the number alive in the mature group in one year and the number which survived from those alive in this group the preceding year, or

$$N_m(t) = (H(t+m) + \alpha I(t+m)) - S_a (H(t+m-1) + \alpha I(t+m-1)). \quad (2)$$

Equation 2 corresponds to obtaining block 2 from block 1 in Figure 1. The number which must have been alive at each age prior to age m can be obtained by dividing this value of $N_m(t)$ by the survival which prevailed in the previous year. Thus the number which must have been alive on their sixth birthday must be

$$N_6(t) = N_m(t) / \prod_{i=6}^m S_i$$

The number of 5 year olds alive at the end of the harvesting in their fifth year is

$$E_5(t) = N_6(t) / S_5 = N_m(t) \prod_{i=5}^m S_i \quad (3)$$

This corresponds to obtaining block 3 from block 2 in Figure 1. Equation (3) can be substituted directly into Equation (1) for an expression for the number of seals from the t^{th} yearclass which would have been alive on their third birthday in the absence of the commercial harvest at age two, $N'_3(t)$.

Using equations 1 and 3 to estimate $N'_3(t)$, the survival to age 3 can be estimated as

$$S_{0,3} = N'_3(t) / N_0(t) \quad (4)$$

This corresponds to obtaining block 7 in Figure 1 from blocks 5 and 6.

To utilize equation 4 estimates are needed of the average age at which males enter the adult population (m), of the fraction of the idle bulls which are actually counted (α^{-1}), of the survival rate of adult males (S_a), and of the annual survival of males from age 2 to age m (S_i , $i = 2, \dots, m$).

Chapman (1964) presents an estimate of the average survival rate of males ages 7 and older of 0.64 per year. These seals are mostly sexually mature and suffer increased mortality due to the stress of defending harems. Johnson (1968) gives an estimate of 0.62 per year for the survival rate of territorial males past age 10. The survival

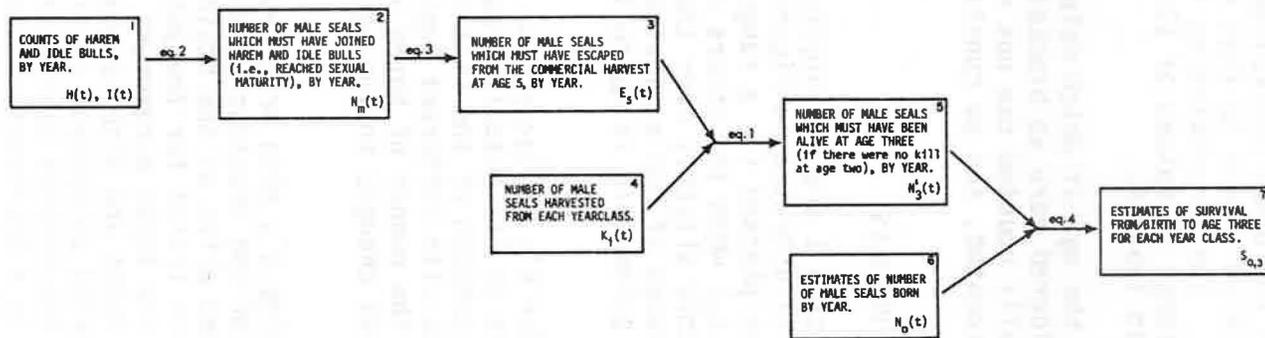


Figure 1. Diagram of the use of data on counts of Alaska fur seals on the rookeries and in the harvest to estimate natural survival rates to age 3. Equations from the text and notation are indicated.

rates of females are around 0.90 and decline with age (Chapman 1961, 1964, 1973), suggesting that the survival rates of immature males may be higher than for mature males.

Based on this information Chapman (1964) suggested values for survival rates as shown in the middle column of Table 4. Given the meager amount of information, we consider his values and other bracketing values. For example the survival of immature males could be closer to that of mature males (0.7) or closer to that of females (0.9). The uncertainties in Chapman's estimate of mature male survival suggest a range of values of 10 percentage points greater and smaller, as indicated in Table 4.

Chapman (1964) suggested 7 as the age at which males become sexually mature. Values of 6 to 8 are considered here as bracketing Chapman's value years. The fraction of the idle bulls counted can not exceed unity. We assume that at least one half are counted, and so consider a range for from 1.0 to 2.0.

RESULTS

The estimates of N'_3 from equation 1 are not highly sensitive to any of the estimated parameters. This is illustrated in Figure 2 in which the estimates of N'_3 over time have been plotted for a range of values for each of the unknown parameters (m , α , S_i , S_a) when the others are held constant. While the magnitude of N'_3 varies only slightly over the range of any single parameter considered, the maximum range of the estimates of N'_3 based on all combinations for the ranges of the parameters is quite large (Figure 3, Table 5).

While the range of magnitude for N'_3 is large, the relative pattern of N'_3 over time is much less sensitive to the actual values of the parameters and reflects to a large extent the pattern of the kill by yearclass. The difference in the patterns over time with different input parameter values are primarily the result of changes in the number of harem and idle bulls relative to the harvest and to a lesser extent changes in the age structure of the kill.

The procedure used for estimating N'_3 also provides estimates of the escapement. In Table 6, estimates of the fraction of the males of ages 3, 4 and 5 that are estimated to have been alive at the beginning of the harvest that escaped being killed (E_i/N_i) are listed for the year in which the harvest occurred for the central values of the input parameters (Table 2). The relative pattern of the escapement rates are also basically independent of the actual parameter values. The estimated escapement at age 3 show no consistent trend over time. The reduction in the minimum harvestable size which occurred in 1969 (Table 7) is not reflected in a decreased escapement for the 3 year old animals. However, the increase in the maximum harvestable length and its subsequent reduction appear to be reflected in the escapement rates of four and five year olds. Thus, between 1951 and 1961, the average of estimates escapement rate was 0.568 (s.e. = 0.041) for four year olds and 0.956 (s.e. = 0.017) for five year olds compared to 0.380 (s.e. = 0.025) and 0.753 (s.e. = 0.040) for the period from 1964 to 1973 (1962 and 1963 were transitional years

Table 4. Values used for the various parameters to explore the estimates of N'_3 derived by using equations 5, 6 and 8. The underlined, central estimates are from Chapman (1964).

Parameter	Values Explored		
Mature Age (m)	6.0	<u>7.0</u>	8.0
Inverse of the proportion of idle bulls counted (α)	1.0	<u>1.5</u>	2.0
Survival Rate from age 2 to m ($S_2 \rightarrow S_m$)	0.7	<u>0.8</u>	0.9
Average Adult Male Survival Rate (S_a)	0.54	<u>0.64</u>	0.74

Table 5: Estimates of N'_3 for 3 sets of parameter estimates. The column labeled central is for the underlined values in Table 4, the one labeled maximum is for the combination of values in Table 4 yielding the largest estimates (i.e., $m = 8$, $\alpha = 2.0$, $s_i = 0.70$ for $i = 2$ to 8 , $S_a = 0.54$) and the one labeled minimum is for the combination yielding the smallest (i.e., $m = 6$, $\alpha = 1.0$, $S_i = 0.90$ for $i = 2$ to 8 , $S_i = 0.54$).

Yearclass	Central	Maximum	Minimum
1920	18,798	38,883	14,296
1921	22,452	41,384	16,421
1922	23,332	45,798	18,250
1947	81,071	146,555	64,856
1948	73,465	133,341	55,478
1949	67,032	136,333	50,952
1950	85,518	141,083	66,245
1951	81,516	168,468	65,727
1952	<u>100,980</u>	156,994	74,759
1953	70,754	158,634	58,707
1954	63,703	92,881	39,524
1955	55,554	98,001	51,168
1956	28,675	76,050	18,561
1957	62,582	92,531	48,013
1958	80,829	126,653	72,996
1959	63,523	84,993	49,944
1960	38,472	54,903	33,566
1961	45,118	68,711	40,394
1962	45,087	54,690	37,269
1963	46,657	67,408	43,864
1964	53,980	76,065	46,866
1965	41,655	69,036	34,984
1966	45,778	54,431	36,020
1967	47,355	92,155	45,155
1968	47,950	77,825	33,057
1969	43,002	75,108	34,620
1970	50,732	81,731	40,315
1971	40,772	76,105	32,652
1972	39,425	63,366	29,740
1973	36,182	62,388	30,196
1974	37,744		30,308
1975			27,679

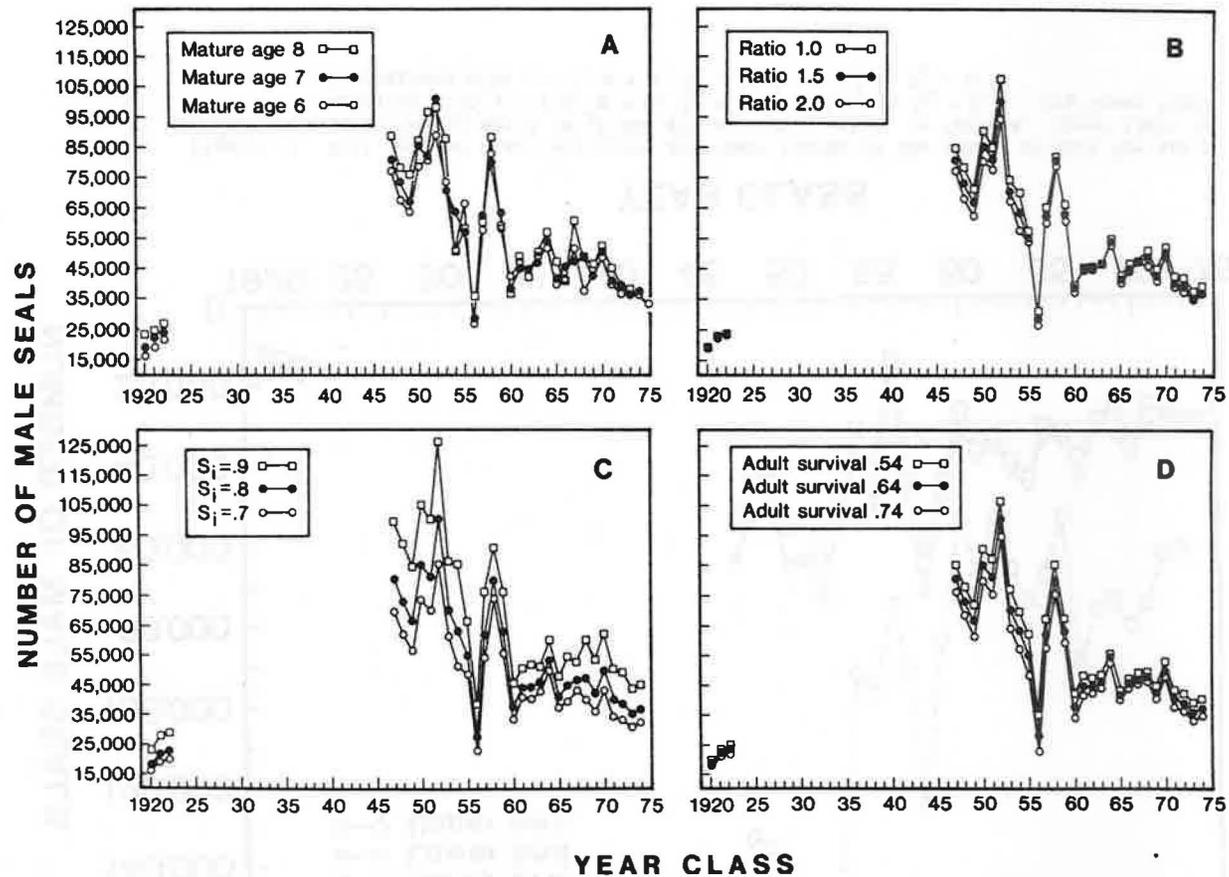


Figure 2. Estimates of number of male fur seals which would have survived to age 3 in the absence of a harvest at age 2 (N'_3), for the time period 1920 to 1922 and 1947 to 1971. Calculations in all frames use parameter values from the central column of Table 4 (solid circles), except as indicated.

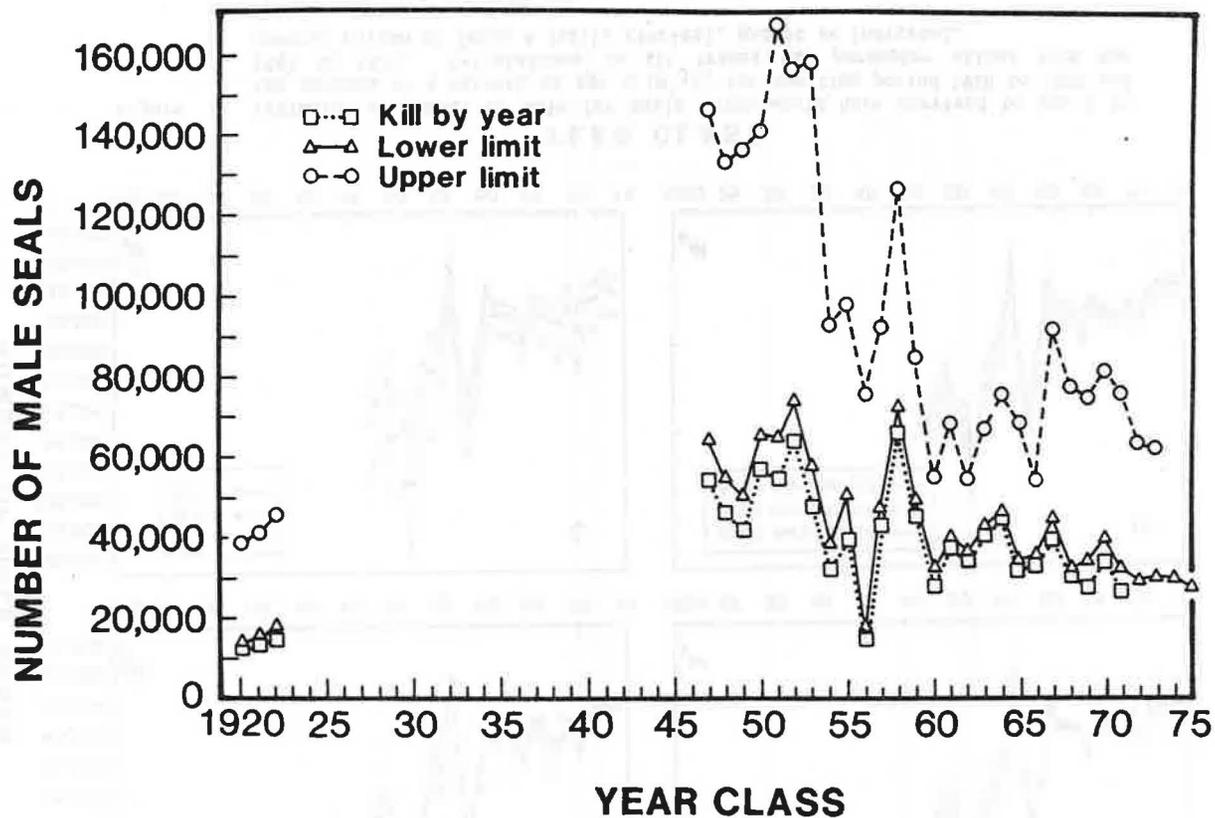


Figure 3. Kill by year class and upper and lower bounds of the number of male fur seals surviving to age 3 (N'_3) for all parameter values in Table 4. Upper limit is obtained with $\alpha = 2.0$, $m = 8$, $S_a = 0.54$ and S_2 to $S_m = 0.7$. The lower limit is obtained with $\alpha = 1$, $m = 6$, $S_a = 0.74$ and S_2 to $S_m = 0.9$.

Table 6: Estimates of the escapement rate for the animals at risk (E_j/N_j) using the central parameter estimates of Table 4.

Year killed	E_3/N_3	E_4/N_4	E_5/N_5
1923	0.362	0.000	0.000
1924	0.419	0.956	0.000
1925	0.409	0.946	1.000
1926	0.000	0.935	1.000
1927	0.000	0.000	1.000
1950	0.629	0.000	0.000
1951	0.648	0.419	0.000
1952	0.557	0.472	0.937
1953	0.521	0.587	0.993
1954	0.598	0.565	0.982
1955	0.692	0.529	0.977
1956	0.453	0.430	0.812
1957	0.618	0.650	0.964
1958	0.491	0.815	0.996
1959	0.618	0.509	0.972
1960	0.599	0.800	0.987
1961	0.389	0.471	0.940
1962	0.568	0.426	0.929
1963	0.615	0.491	0.811
1964	0.492	0.424	0.839
1965	0.558	0.308	0.800
1966	0.441	0.368	0.704
1967	0.476	0.267	0.773
1968	0.531	0.322	0.552
1969	0.597	0.377	0.709
1970	0.510	0.453	0.857
1971	0.723	0.322	0.825
1972	0.649	0.446	0.541
1973	0.673	0.513	0.925
1974	0.637	0.423	0.821
1975	0.607	0.475	0.846
1976	0.616	0.570	0.908
1977	0.555	0.452	0.917
1978	0.000	0.455	0.904
1979	0.000	0.000	0.922

Table 7. History of the harvesting process 1950-1975, Pribilof Islands.

Year	Date of beginning of	Date of end of season	Length of season (days)	Minimum size ⁶ (inches)	Maximum size ⁶ (inches)
1950	6/17	7/21	41	41	45.00
1951	6/24 ¹	7/29	38 ¹	41	46.75
1952	6/22	7/27	36	41	45.75
1953	6/22	7/29	38	41	45.75
1954	6/22	7/27	36	41	45.75
1955	6/27	7/31	35	41	45.75
1956	6/27	8/15	50	41	45.75
1957	6/27	8/10	45	41	45.75
1958	6/27	7/31	35	41	46.75
1959	6/27	7/31	35	41	46.75
1960	6/27	8/07	42	41	46.75
1961	6/27	8/10	42	41	45.75
1962	7/02	8/05	35	42	47.75
1963	7/02	8/05 ²	35	42	Mane ³
1964	7/01	8/05 ²	36	42 ⁴	Mane
1965	7/07	8/09	36	42 ⁴	Mane
1966	7/07	8/05	32	42	Mane
1967	6/27	8/05	40	42	Mane
1968	6/26	8/02	37	40	Mane
1969	6/25	8/01	38	None	54.00
1970	6/24	7/31	38	None	Mane
1971 ⁵	6/23	7/31	39	None	Mane
1972	6/26	7/29	35	None	Mane
1973	6/25	7/28	35	None	Mane
1974	6/24	7/27	34	None	49.00
1975	6/30	8/02	34	None	46.00
1976	6/28	7/31	34	None	46.00
1977	6/27	7/29	33	None	47.00
1978	6/26	7/31	36	None	47/49 ⁷
1979	6/26	7/31	36	None	47.00

¹Pre-season kills on 6/20 and 6/22.

²Plus 1,140 males killed between 8/17 and 8/28.

³During early part of season 48-3/4" limit used.

⁴None during the period 7/22-7/26.

⁵Seals on inaccessible hauling grounds were not disturbed in 1971 but were in earlier years in an effort to make them haul out on accessible hauling grounds.

⁶Until 1961, measurements were made from tip of the nose to base of the tail. After 1961, length was measured from the tip of the nose to the tip of the tail.

⁷47 until July 10, 49 thereafter.

Source: Engle, et al., 1980.

and are not included in these averages. The maximum size was decreased again beginning in 1974. The average escapement rates rose but not quite to the pre-1962 levels. Thus, from 1975 to 1979 the average escapement rate is estimated to be 0.488 (s.e. = 0.028) for four year olds and 0.899 (s.e. = 0.014) for five.

The overall escapement rates for a yearclass (i.e., the fraction of the males which would have survived to age 3 in the absence of a harvest at age two which subsequently escaped the harvest at age i (E_i/N'_3)) also roughly reflect these changes in the harvesting regulations (Table 8). However, even during periods when the harvesting regulations were relatively constant, there is high variability in the estimated rate, particularly for the 1958 to 1969 yearclasses. The 1960 to 1964 plus the 1967 yearclasses have particularly low estimated escapement rates, which raises the possibility that survival rates either for sub-adult or adult males were particularly poor in these years.

Using the pup estimates from the 1920-1922 and post 1922 yearclasses, there is little evidence for changes in survival rates through age 3 (Figure 4). When the central values for the input parameters are used, the average survival for the 1920-1922 yearclasses is lower than the average rate for the post 1960 ones (0.285 versus 0.337) while the estimated annual number of pups born during 1920-1922 is approximately 40% lower. Only for combinations of values for the input parameters which yield nearly maximum values for the estimates of N'_3 does the average survival estimate for the 1920-1922 yearclasses slightly exceed the average for the post 1960 ones. For this to occur for the set of parameter values in Table 2, the age of maturity must equal 8, the survival rate from age to maturity must equal 0.70 and the value of one of the other two parameters must also equal the value which yields the maximum estimates of N'_3 (i.e. $S_a = 0.54$ or $\alpha = 2.0$).

However, for those combinations of the input parameter which yield survival estimates for the 1920's exceeding the estimates post 1960, the estimate of the annual rate from 0 to age 3 (i.e. the cube root of $S_{0,3}$ of equation 4) exceeds the value for the input parameter for the survival rate from age 2 to maturity. This seems highly unlikely and the assumption has generally been made that survival rates for juveniles are lowest during the first year or two of life (Lander 1975). As such, those combinations of parameter values which yield higher survival rate estimates for the 1920-1922 yearclasses than for the post 1960 ones can be considered as unrealistic.

This criterion that the average survival rate from birth to age 3 be less than the value for input parameter for the survival rate from age 2 to maturity can be used to limit the set of reasonable input parameters. Thus, it is unlikely that the survival rate from age 2 to maturity is as low as 0.70 since for all combinations of the values for the other input parameters in Table 2 this criterion is not met for the survival estimates for most yearclasses. Similar statements can not be made about the values of the other parameters that were considered, although other combinations of parameter values fail to meet this criterion. This criterion can also be used to provide an estimate of the upper bound for the survival estimates from birth to age 3 (see also Lander 1975). Given α , m and s_a and using equation 4, the value

Table 8: Estimates of the overall escapement rate for a yearclass (E_i/N_3) a using the central parameter estimates of Table 4.

Yearclass	E_3/N'_3	E_4/N'_3	E_5/N'_3
1920	0.354	0.271	0.217
1921	0.408	0.309	0.247
1922	0.404	0.302	0.242
1947	0.629	0.211	0.158
1948	0.645	0.244	0.193
1949	0.557	0.262	0.206
1950	0.517	0.234	0.183
1951	0.590	0.250	0.162
1952	0.683	0.235	0.181
1953	0.449	0.234	0.186
1954	0.595	0.388	0.302
1955	0.484	0.197	0.156
1956	0.603	0.386	0.290
1957	0.579	0.218	0.162
1958	0.381	0.130	0.084
1959	0.548	0.215	0.144
1960	0.594	0.202	0.129
1961	0.483	0.119	0.067
1962	0.533	0.157	0.097
1963	0.431	0.092	0.041
1964	0.453	0.117	0.066
1965	0.509	0.153	0.105
1966	0.580	0.210	0.139
1967	0.487	0.126	0.054
1968	0.702	0.251	0.185
1969	0.645	0.265	0.174
1970	0.664	0.225	0.152
1971	0.629	0.239	0.174
1972	0.594	0.271	0.199
1973	0.593	0.241	0.155
1974	0.545	0.198	0.146

of S_i for $i = 2$ to m can be found such that the estimate of average annual survival rate from birth to age 3 (i.e., the cube root of $S_{0,3}$) equals this value of S_i . When this is done for the central values of α , m and S_a , the upper bound average is 0.72 for the post 1960 yearclasses. Considering the entire range of values for the parameters α , m and S_a in Table 2, the upper bound is 0.76.

Considering only the set of post 1960 survival estimates, there is little evidence for any relationship between survival rates and the number of pups born. For the central values for the parameter estimates, the 1961 yearclass, which is estimated to be largest, had the lowest estimated survival rate of any post 1960 yearclass (Figure 4). However, this is not true for other combinations of values for the input parameters and the estimate of the number of pups born for this yearclass is the most uncertain.

As discussed above, the estimates of the kill by yearclass used in estimating N'_3 in the 1920s are based on the size frequency distribution of the kill, which probably underestimates the number of 4 year olds actually killed. This means that estimates of N'_3 (and thus estimates of juvenile survival) in the 1920s are actually too low. However, even if the total annual kill during the twenties is assumed to be composed entirely of 4 year olds, average estimated juvenile survival rates for the 1920-1922 yearclass just equal estimated rates post 1960 for the central values for the input parameters.

The estimates of N'_3 are based on the assumption that the parameters α , m , S_a , and S_2 to S_m have remained constant over time. However, only if immature (S_i) or adult survival rates were lower in the twenties than in the sixties, or if the age at which bachelors entered the adult herd (m) or the proportion of idle males actually counted (α) were higher, could the violation of the assumption of constant values for the parameters decrease the difference between estimated juvenile survival rates in the 1920s and 1960s. For S_i or S_a to be lower or m to be higher would mean that either or both male survival and growth after age three increase with density, which is an untenable hypothesis to invoke in order to support an hypothesis of density dependent survival until age three. The possibility exists that α could be lower in the sixties than in the twenties as the result of differences in the definition of an idle bull.

The age structure of the adult male herd is ignored in these estimates of N'_3 . If the adult male herd contained proportionately more older individuals in the twenties than in the sixties and seventies and if adult male mortality rates increase with age, then the annual recruitment to the male herd, and thus juvenile survival rates, would have been relatively greater in the twenties than those estimated above. While the possibility does exist that the resumption in 1918 of the male harvest after a ban of 7 years could have induced an age structure effect, it seems unlikely that the juvenile survival rates in the twenties could be greatly underestimated because of this factor. Thus, even if the average adult male mortality rates were at the opposite extreme values considered in Table 4 due to an age structure effect (i.e., a difference of 0.20), the average juvenile mortality rate for the 1920-1922 yearclasses (0.30) would still be less than the estimated average for 1961-1969 (0.32) for the central values for the other input parameters.

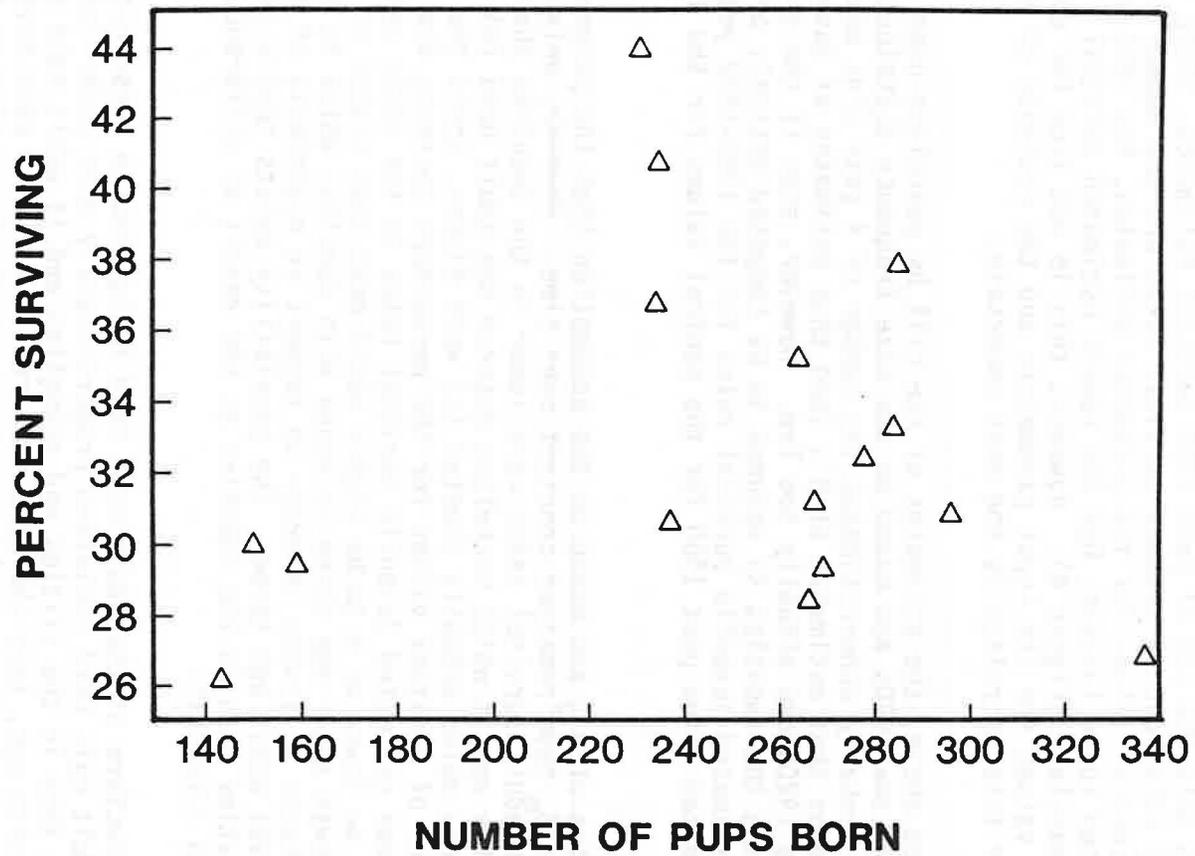


Figure 4. Estimates of the percent of the male pups surviving to age 3 plotted against numbers of pups born showing an apparent lack of relationship, contrary to that hypothesized under negative density dependence.

The estimates of N'_3 for the 1947 to 1960 yearclass can be used to estimate a lower bound for the average annual number of pups born during this period by assuming that on the average the survival rate during this period did not exceed the average rate for the post 1960 yearclasses. In Table 9, estimates of this lower bound are presented for the central values of the input parameters and for the values yielding the maximum and minimum estimates for N'_3 . These lower bounds were calculated by taking the average estimate of N'_3 for the yearclasses from 1947 to 1960 and finding the number of pups which needed to have been born to yield the same survival rate as the average rate for the post 1960 yearclasses. Estimates of the lower bound are also presented considering only the 1947 to 1952 yearclasses and the 1947 to 1956 yearclasses. The estimates of the lower bound is greater for those values for the input parameter yielding the larger estimates of N'_3 and range from 393 to 545 thousand pups. These estimates can be compared with the average of the estimates from Chapman (1964) for the same period (Table 9). This comparison suggests that if Chapman's estimates of the number of pups born are correct, than the survival rates in the 1950s would be at most slightly less than the rates post 1960.

DISCUSSION

Our results suggest that there is no evidence for the survival of male seals to age 3 being negatively related to the number of pups born. Additionally, our results suggest that while the overall fraction of the male seals which escape the harvest is highly variable, changes in the maximum harvestable length do affect the escapement of four and five year old seals.

We have not considered the statistical properties of our estimates of N'_3 or escapement and survival rates since the input parameters are not based on statistical estimates. If procedures were available for obtaining statistical estimates for the input parameters, it would be worthwhile exploring the statistical properties of the estimates in this paper.

The estimates of N'_3 are based only on data from St. Paul Island. The effect of possible movement between islands of juvenile, sub-adult, and adult males has not been considered but may be important. Thus, the fraction of the total harem and idle count from St. Paul and the fraction of the total kill of a yearclass from St. Paul has varied over time. In addition, these two fractions do not vary in synchrony.

Our results differ from Chapman's conclusions (1961, 1964, 1973) because we have used a more realistic method of estimating number surviving to age 3 (N'_3) and because we have not utilized his yearclass estimates of the numbers of pups born from 1950 to 1960.

Our equation 1 is a generalization of Chapman's (1964) method. The primary difference is that Chapman did not allow the numbers escaping the kill ($E_i(t)$) to vary with time. Instead he estimates the average value for the annual number of males which must have been alive at age 3 to produce the recruitment to the adult males or equivalently to produce the escapement at age 5 (i.e. E_5/S_4S_5). Chapman refers to this number as the "escapement." We will refer to it as the "recruitment escapement" to distinguish it from the E_i

Table 9: Estimates of the average number of pups born (in thousands) for the 1947 to 1960 yearclasses such that the average survival rate estimate for this period would equal the average rate for the post 1960 yearclasses. Estimates are given for three combinations of parameter estimates. Column headings are the same as for Table 5.

Time Frame (yearclasses)	Central Estimates of N'_3	Maximum Estimates of N'_3	Minimum Estimate of N'_3	Chapman's 1964 Pup γ Estimates
1947-1960	405	447	393	419
1947-1956	420	491	400	449
1947-1952	461	545	445	445

(1) beginning with the 1950 yearclass.

of this paper. Based on the 1950 to 1959 harem and idle counts, corresponding to the 1943 to 1952 yearclasses, he estimates the average recruitment escapement to be 25,000. This was done using the approach in our equations 1 to 3, with $S_a = 0.64$, S_2 to $S_m = 0.80$, $\alpha = 1.5$ and $m = 7$. This corresponds to an annual male kill for the period 1946 to 1955 (when these seals would have been age three) of 64,350, suggesting that recruitment escapement was approximately 40% of the total annual kill.

Chapman (1964) used this average ratio of 40% to estimate the number alive at age three from the observed kill of males from each yearclass from 1947 to 1959. In 1973, Chapman presents further estimates of the numbers of seals surviving to age three (his Table 112) for the 1950 to 1965 yearclasses. The estimates of numbers surviving to age three for the 1950 to 1965 yearclasses include an adjustment for a possible decreasing escapement from the harvest for the years following 1956, but the amount by which the escapement was decreased below the 40% figure is not given.

Chapman estimated the number of male seals which would have been alive at age 3 in the absence of a harvest at age 2 for the 1920 to 1922 yearclasses in his 1961 and 1973 papers. In both papers he summed the estimated number killed at ages 2, 3, and 4 from each yearclass and an estimate of the number escaping the harvest (1961, Table 3). He increased the number of seals killed at age 4 by 10% to account for those dying naturally. In 1961 he estimated the number escaping the harvest as the sum of the seals spared for a breeding reserve and the seals killed by the local population (native kill), thus obtaining estimates of 23,190, 22,241, and 24,523 for 1920 to 1922, respectively. In 1973 he estimated the number escaping as the sum of the seals spared for a breeding reserve and 40% of the seals killed from each yearclass at ages 2, 3, and 4, thus obtaining 25,800, 26,200, and 27,700 (1973, Table 112).

Using the method developed here for estimating Chapman's "recruitment escapement" (i.e. the last column of Table 8 divided by S_4S_5) suggests that it varies considerably among year (i.e. by a factor of 2). This suggests that Chapman's simplifying assumption may not be warranted. Based on our method a comparable estimate to Chapman's ratio of 40% for the 1950 to 1956 yearclasses is 48% using the central parameter values in Table 2 (i.e. the same values Chapman used to derive his 40% estimate). Considering the parameter values yielding the extreme estimates for N'_3 Table 2 results in a range for this ratio from 17 to 173%.

We did not use Chapman's yearclass estimates of the number of pups born from 1950 to 1959 in our calculation of survival rates (Figure 4). The procedure he used is based on the same data on number of males killed by yearclass (block 4, Figure 1) as is used for estimates of number surviving to age 3 (N'_3), and is shown diagrammatically in Figure 5. One type of information he uses are estimates of the number of male seals which would have survived to age 3 in the absence of a harvest at age 2 ($N'_3(t)$), as in block 5 in Figure 1 and in block 1 in Figure 5. Another input is the number of females which were harvested at each age from each yearclass (block 3). Denote this by $K'_j(t)$.

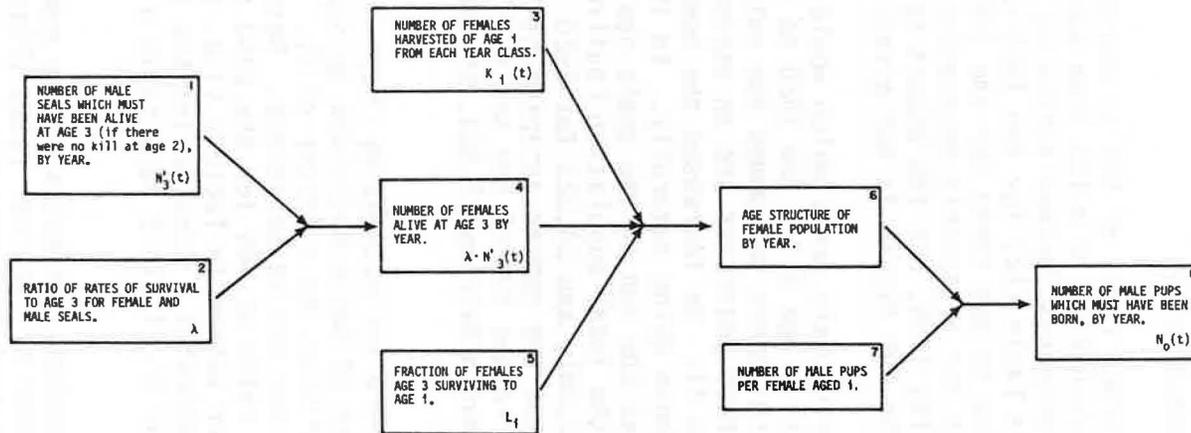


Figure 5. Diagram of Chapman's year class method of estimating numbers of male pups born for 1950 to 1959.

From these two quantities and estimates of age specific survival (block 5) and fecundity (block 7) rates for females and an estimate of the ratio of the survival rates of females and males, λ , (block 2), Chapman estimates the number of male pups (block 8). The number of females which must have been alive at age 3 is estimated as the product $\lambda N'_3$. Let L_i denote the probability of a female aged three surviving to age i , and P_i denote the number of male pups produced by a female of age i . The total number of pups produced in year t can be estimated as

$$N_0(t) = \sum_{i=3}^{\infty} \left(\lambda N'_3(t+3-i) L_i - K'_i(t+3-i) \right) P_i \quad (5)$$

where the term in parentheses represents the age structure of the female population by year (block 6, Figure 5).

The estimates of male pups born from equation 5 depend on a number of estimated and assumed values. These will be discussed in approximate order of the sensitivity of the estimate to each. First is the estimates of numbers of males which would have been alive at age three in the absence of a harvest of 2 year olds (block 1). The actual value of these numbers for the years 1947 and on has been shown earlier in this paper to depend on the several unknown parameter values in equations 1 to 3. Chapman (1964) used his earlier estimate of 40% escapement to adjust the kills by yearclass for this period to estimates of numbers surviving to age three. Our estimates of N'_3 for the 1947 to 1959 yearclasses averaged 7% higher than estimates in Chapman (1964) based on the central parameter values. The largest discrepancy is for the 1954 yearclass for which our estimate exceeds Chapman's by 32%.

Data on the age structure of the male kill are not available for the years 1922 to 1947. In this period Chapman assumes that the number of males which must have been alive at age three was constant. This assumes that the population had been at an equilibrium abundance by the early 1930s. To the extent the population was increasing in size over this period the resulting estimates of number of pups born will be too high. Chapman (1964) estimated this constant value to be 75,000, based on increasing the average annual kill by 40%. This value dominates the sum in equation 5 in the early 1950s, accounting for 88% of the total of N'_3 in 1950, decreasing approximately linearly to account for 28% by 1957.

Thirdly, the difference in survival rates between males and females (block 2) enters as a direct multiplier to the estimates from equation 5. Chapman (1964, 1973) assumes that the female survival rate is 10% higher than that for the males. The basis for this figure is indirect and quite complex, but relates to the survival to age three which must hold if the age specific reproductive and survival rates estimated from pelagic samples taken from 1958 to 1962 represent a population at equilibrium. The calculated value of this survival rate depends on the age specific reproductive and survival rates of older animals. The uncertainties in this value are large.

Lastly, the actual estimates of age specific female survival and reproductive rates which are used affect the ultimate calculation of numbers of females which must have been alive. In Appendix IV we review these estimates and noted that Chapman's estimates of survival rates for the younger

yearclasses are biased upward due to the particular functional form he used for smoothing the data. The effect of uncertainty in the survival and reproductive rate estimates on the ultimate estimates of numbers of pups born from equation 5 is significant, with the overestimation of survival rates biasing the pup estimates upward.

These four sources of uncertainty in the assumptions and parameters used in equation 5 make the reliability of the estimates of the number of male pups born questionable, in our opinion. The lack of direct information of differential survival rates to age 3 for males and females, the sensitivity of the estimates to the assumed constant number of males surviving to age 3 prior to 1950, and the above demonstrated uncertainties in the estimates of N'_3 from the kill of males by yearclass data cause us to place little reliability in these numbers.

Chapman (1973a) argued from the comparison of estimates of numbers of males surviving to age three and of numbers born that the survival of males had declined at higher abundances. In light of the above discussion of the uncertainty of his estimates of pups born in the 1950s, it is interesting to re-examine his implicit estimates of survival rates. Chapman's data as presented in his Table 112 are re-expressed in Figure 6, where the survivals to age three implied by his estimates of male seals surviving to age three and pups born are plotted against pups born. Note that his pups born figures included both sexes. Using the same grouping of data points by years which Chapman used, the three mean values of survival rates are shown. Also shown are approximate 90% confidence intervals about these means, derived from the standard deviation of the estimated survivals within each group of data points. These intervals are approximately correct (except probably for the left most group of size three) if one assumes that the survival during each of the three time periods was constant, and invokes the central limit theorem for the averages. If the survival was not actually constant within each period these intervals are overestimates.

The confidence intervals about the group means overlap completely, suggesting that the apparent trend noted by Chapman may not be real even using his estimates. If the estimates of the numbers of pups born in the 1950s are as uncertain as we suggest above, any evidence for change, or indeed for lack of change at high abundances, is lost. Given the uncertainty in the estimates of the number of pups born in the 1950s, the right most group of points is very uncertain. Without those points the evidence for changes in survival rates, even using Chapman's analysis, is lacking.

While we believe that the present data indicates that there is no density dependence in juvenile survival over the range of pup population sizes of 143 to 237 thousand, these data contains enough uncertainty (e.g., the comparability of the two methods used to estimate the number of pups born and the reliability of the harem and idle counts) that if small changes in juvenile survival had occurred over this range of population sizes, they may have been undetectable.

In this respect, it is worth noting that estimates of on-land mortality for pups during their first summer of life does indicate a slight density

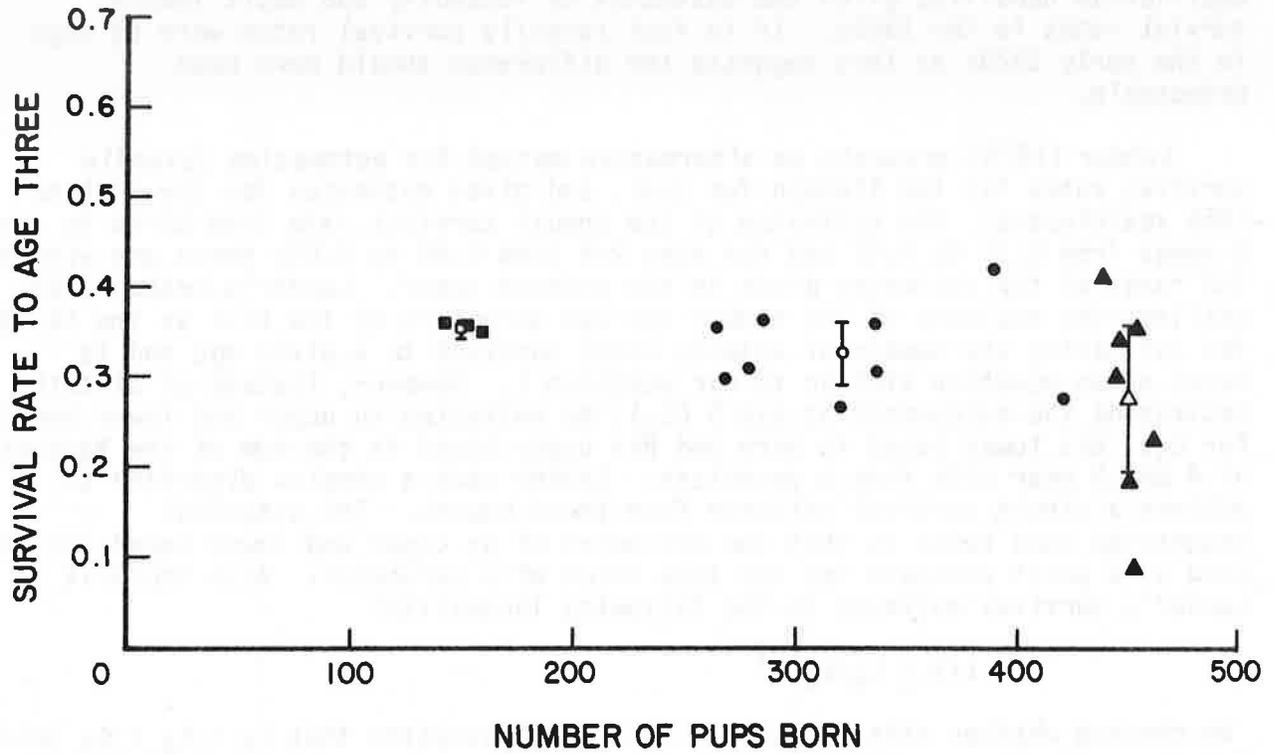


Figure 6. Survival to age three for male Alaska fur seals versus numbers of pups born. Means of the three groups of data points are shown as the open symbol of the same type, with approximate 90% confidence intervals.

dependent relationship over these same population sizes (Appendix I). However, the failure to detect higher survival rates in the early 1920s when the population was apparently growing rapidly (approximately 7 to 8% a year) than during the 1960s when the population was essentially not changing in size suggests that juvenile survival rates are not the sole density dependent factor regulating this population. As noted in Appendix IV, in order to achieve a growth rate of approximately 7 to 8% per year if juvenile survival rates are the only density dependent vital rates, juvenile survival rates need to be approximately 1.5 to 2.4 times as great at low densities than at equilibrium densities given the estimates of fecundity and adult female survival rates in the 1960s. If in fact juvenile survival rates were as high in the early 1920s as this suggests the difference should have been detectable.

Lander (1975) presents an alternative method for estimating juvenile survival rates for the Alaskan fur seal, and gives estimates for the 1961 to 1966 yearclasses. His estimates of the annual survival rate from birth to age 2 range from 0.31 to 0.41 and for ages 2-5 from 0.84 to 0.89; these are within the range of the estimates given in the present paper. Lander's method also utilizes the estimate of the number and age structure of the kill as the basis for estimating the number of animals which survived to a given age and is based on an equation similar to our equation 1. However, instead of directly estimating the escapement at age 5 (E_5), he estimates an upper and lower bound for E_5 . His lower bound is zero and his upper bound is the sum of the harvest of 4 and 5 year olds from a yearclass. Lander uses a complex algorithm to achieve a single survival estimate from these bounds. The essential assumption used twice is that the mid-point of an upper and lower bound can be used as a point estimate for the true value of a parameter. Also implicit in Lander's survival estimate is the following inequality:

$$1/3 \leq E_4/N_4 \quad (1)$$

We checked whether this inequality plus the assumption that $E_5 < K_4 + K_5$ held for the estimates generated by the method developed here and found that both conditions are not satisfied for all yearclasses for the set of values for the parameter that was used (Table 10).

There is some confusion in the literature on the basis for the success of the management of Alaskan fur seals. Holt and Talbot (1978) in discussing the concept of maximum sustained yield say (p.8, caption to Figure 1), ". . . the Pribilof fur seals were long regarded as the classic example of the success of single species management according to the concept of maximum sustainable yield." They continue with the suggestion that the recent declines in

¹Expression 5 can be derived by noting that Lander's R_4 is 1/2 the numerator of his equation 13. Our E_4 is equivalent to Lander's R_4 minus K_4 . Subtracting K_4 from Lander's estimate of R_4 and simplifying using the inequalities that $S < 1$ and $K_5 < 0$ yields the result that $E_4 \geq K_4/2$ which is equivalent to expression 5.

Table 10. Percent of the yearclasses in which estimates of $K_4 + K_5 > E_5$ and $1/3 < E_4/N_4$ for three combinations of parameter estimates. Maximum, minimum and central are as defined in Table 5.

Set of parameter estimates	Yearclasses	% of the Yearclasses in which	
		$1/3 < E_4/N_4$	$K_4 + K_5 > E_5$
central	1920-1922	100	0
	1947-1960	100	71
	1961-1974	79	100
Maximum Estimates for N'_3	1920-1922	100	0
	1947-1960	100	7
	1961-1973	100	38
Minimum Estimates N'_3	1920-1922	100	0
	1947-1960	50	100
	1961-1975	13	100

productivity of the herd are due to factors separate from the population itself, such as possible changes in food availability, which are not included in the scope of the management concepts to date. There are two important points here. First, while the management during the recovery of the population since 1918 was primarily based on single species considerations, it was based on the concept of surplus males, not maximum sustainable yield. This latter concept was putatively operational since the mid-1950s, and the management policies carried out under it were not successful (Chapman, 1973b).

The second point is that the actual history of the harvest of females does not in reality appear to have been consistent with the policy of maximum sustained yield. The estimates of the numbers of pups born necessary to obtain the maximum sustained yield have decreased as the models have been revised, from 480,000 in Chapman (1961), to between 351,000 and 360,000 in Chapman (1964) to 283,000 in Chapman (1973a). The estimates of the numbers of pups born were below the 1964 estimate of the maximum sustained yield when the first shearing based pup estimates were made in 1961, and the pup estimates averaged 279,000 from 1962 to 1967. This level was 72,000 to 87,000 pups below the then prevailing estimates of the number of pups yielding maximum sustained yield. It is puzzling as to why the harvest of females, supposedly instituted to achieve maximum sustained yield, continued at levels predicted under maximum sustained yield then, when fewer pups were being born than were predicted.

It has since become apparent that the total harvest did not increase as expected under this policy and actually decreased. However, the decreases in the total harvest and pup production are not easily explained solely in terms of the female harvest (Appendix III). The analysis in this paper suggests that the actual scientific basis for the maximum sustained yield management policy does not appear strong, and hence that the failure of the harvest to increase does not appear surprising, at least in retrospect.

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SIMULATION OF THE DYNAMICS OF THE ALASKA FUR
SEAL (CALLORHINUS URSINUS) POPULATION

APPENDIX III

The population of Alaskan fur seals (Callorhinus ursinus) breeding on the Pribilof Islands has been harvested extensively since the late 18th century. As the result of indiscriminate harvesting, this population has twice been reduced to a small fraction of its original size, once during the 19th century and again in the early part of the 20th century (Roppel and Davey 1965). In response to the second reduction, which almost resulted in the extermination of the herd, a four nation agreement (the North Pacific Fur Seal Convention) was established in 1911 as a basis for managing the herd. The underlying concept in the management of this population since 1918 has been that a large proportion of the males born each year are not required (and may even be harmful) for the growth and maintenance of the population because of the harem structure of the breeding system (Parker 1915; Kenyon et al. 1954; Roppel and Davey 1965).

More recently, the concept that the survival of juveniles is density dependent has been suggested, with the implication that the total yield from this population might be higher if the size of the population were reduced and if a sustained harvest of females as well as males occurred each year (Chapman 1961, 1964, 1973a; Nagasaki 1961). From 1956 to 1968 a herd reduction and sustained female harvesting program were carried out, putatively to test this hypothesis (Roppel and Davey 1965, p. 460), but see York and Hartley (1981) for a contrary viewpoint. This program of harvesting females did not result in the expected increase in total yield, and the number of pups born each year declined below expected levels. Since the cessation of the female harvest in 1968, neither the yield of males nor the number of pups born have returned to apparent earlier levels.

Several explanations have been offered for the failure of the female harvesting program to result in increased yield, and for the failure of the numbers of pups born to increase following cessation of the female harvest. Chapman (1973b) suggests that this failure could be the result of not accounting for either the age structure of the herd in the models used for predicting increased yield, or changes in the North Pacific ecosystem which may have adversely affected survival of fur seals. In Appendix IV, we argue that changes only in juvenile survival cannot account for the observed growth rate of the fur seal herd from 1912 to 1924, and that this population may be regulated by more than a single density dependent factor. Thus, the failure to accurately predict the result of the female harvesting program may have been the result of not adequately accounting for the regulatory mechanism in this population.

To investigate the effects of age structure and density dependence on the results of harvesting females, we constructed an age structured population model with density dependent reproductive and survival rates. We have used this model to test the hypothesis that the changes in abundance of the Pribilof fur seal population between 1911 and the present can be explained by density-dependent population regulation mechanisms.

Population Changes

The three sources of data on changes in abundance of Alaska fur seal population are (1) estimates of the number of pups born for some years, (2) estimates of number of adult males on the rookeries, and (3) records of the number of males harvested each year.

Reliable estimates of the number of pups born are available for the years 1912 to 1924 and 1961 to 1975 (Table 1). The estimates made in the earlier years were based on complete counts of some or all of the several rookeries. The estimates in the latter years are based on mark and recovery procedures (Chapman and Johnson 1968). The estimates of the number of pups born from 1912 to 1924 indicate that pup production was increasing throughout this period at a rate of approximately 8% per year, from 70,000 in 1912 to 173,000 in 1924. The estimates of pups born from 1961 to 1975 show a decline up to 1971, followed by a general increasing tendency up to 1975, the last year of data available to us. These estimates of pups born are the most direct and unambiguous measure that is available for estimating the abundance and changes in abundance of this population.

Less reliable estimates of the number of pups born in the period 1950 to 1960 have been made by Chapman (1961, 1964) based on tag and recapture data. These estimates are much higher than the estimates for the 1960s but are thought to be unreliable and biased upward substantially for unknown reasons (Chapman 1964). It appears, however, that the number of pups born per year in the 1950s must have been significantly greater than in the 1960s because the annual harvest of males in the 1960s was smaller than in the 1950s (Figure 1), and because a large number of females were removed from the population between 1956 and 1968. Additionally, general observations of conditions on the rookeries in the 1950s and the 1960s suggest that there was more crowding in the earlier years (A. Johnson, pers. comm.).

We reviewed the available estimates of numbers of pups born from 1947 to 1960 in Appendix II, concluding that the failure of the tagging estimates of numbers of pups born from 1953 to 1960 has not been explained. Thus, tagging estimates for 1947 to 1952 and since 1960 cannot be reliably interpreted. We note, however, that if the estimates from these two periods have the same biases, then an approximate average number of pups born from 1947 to 1952 of 381,000 can be obtained based on the ratio of the estimates of number of pups in the 1960s from the shearing and the tagging procedures.

Chapman (1964, 1973a) estimated the number of pups born in the 1950s from data on the number of males killed from each year class and an estimated

Table 1. Estimates of the number of pups born on St. Paul Island, from Table 3, Appendix 2.

Year	Number of Pups (thousands)
1912	70
1913	80
1914	79
1915	88
1916	99
1917	109
1918	123
1919	134
1920	143
1921	150
1922	159
1923	---
1924	173
1961	337
1962	278
1963	264
1964	285
1965	267
1966	296
1967	284
1968	235
1969	234
1970	230
1971	---
1972	260
1973	305
1974	269
1975	278

fraction of the males escaping the harvest. His estimates are shown in Table 1. We have generalized this estimation technique to be more realistic in accounting for the males escaping and estimate a lower bound for the number of pups born per year in the 1950s of 350,000 (Appendix II). While Chapman's estimates for this period are greater than our lower bound, we feel that any specific point estimates are arbitrary given the uncertainty in the numbers of males escaping the harvest and the survival rates of male fur seals. This lower bound is consistent with the 381,000 value obtained by adjusting the 1947 to 1952 tagging estimates.

The number of pups born during the 1950s are thought to be near maximal or equilibrium levels; these levels are thought to have been achieved by the early 1940s (Roppel and Davey 1965; Scheffer 1955; Kenyon et al. 1954). This hypothesis has been primarily based on leveling off of the annual harvest of males by 1942 (Figure 1). However, the relative constancy of the annual yield during these years could merely be a reflection of the constant size limits and the constant length of the harvesting season used during most of this period, and not a reflection of constant numbers of pups born (Roppel and Davey 1965). The annual estimates of the number of harem bulls (Figure 2) also suggests that the rate of growth of the population leveled off by the 1940s. However, the counts of idle bulls (Figure 2) continued to increase until 1960 and could be an indication of either increasing numbers of pups being born or of the escapement from the harvest in excess of the number of males needed to replace dying adult males. In this latter case, the number of pups could have been constant or could have been increasing. Also, the counting procedure for idle bulls may not have been consistent during these years (A. Johnson, pers. comm.). There appears to be no satisfactory way to determine if the pup production reached an equilibrium before the initiation of the female kill in 1956.

In summary, the number of pups born is our best measure of changes in the Alaska fur seal population. The numbers are known to have increased at about 8% between 1912 and 1924, and to have been relatively constant since 1960. The numbers of pups born may have reached an equilibrium level in the early 1940s, and the numbers of pups born in the 1950s was at least 350,000. The reasons for the lower number born in the 1960s and 1970s are not fully known (York and Hartley, 1981). This understanding of the changes in the number of pups born will be compared to the results of an age structure density-dependent population model to test hypotheses about the natural regulation of the Alaska fur seal population. We primarily emphasize the data from 1912 to 1924 and since 1960 and use our lower bound estimate for the 1950s. Chapman's estimates for the 1950s shown in Table 1 are included in our presentation of results only for reference, as they are widely quoted.

The two islands composing the Pribilof Islands both have rookery areas used by fur seals. The rookeries on St. Paul Island have been much better studied than those on St. George, and the available data on numbers of pups born are, therefore, more reliable for St. Paul Island rookeries. We will use only St. Paul Island data here. Where sufficient data are available, similar trends for the two islands are usually apparent.

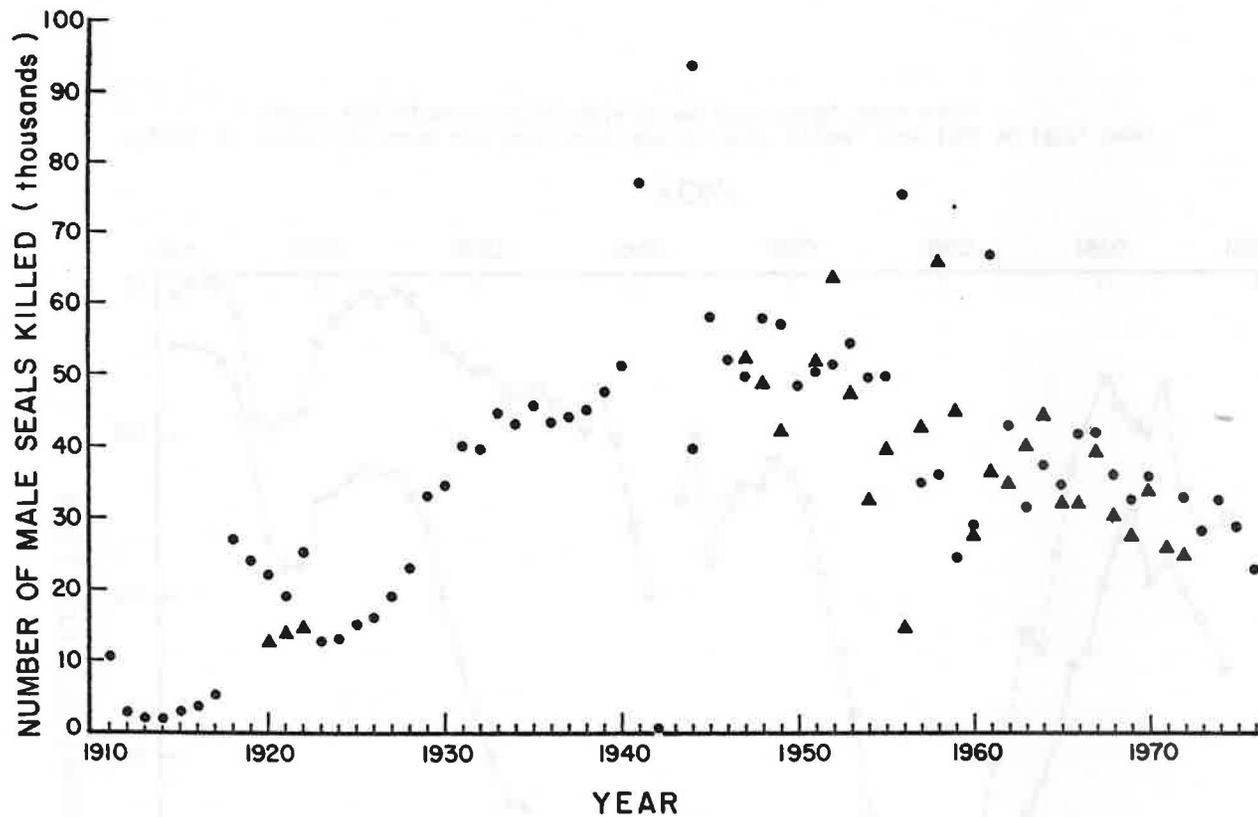


Figure 1. Numbers of male seals killed on St. Paul Island in the annual harvests, by year (circle) and by year class (triangle), from NPFSC (1961, 1964, 1971, 1975) and NMFS (1978).

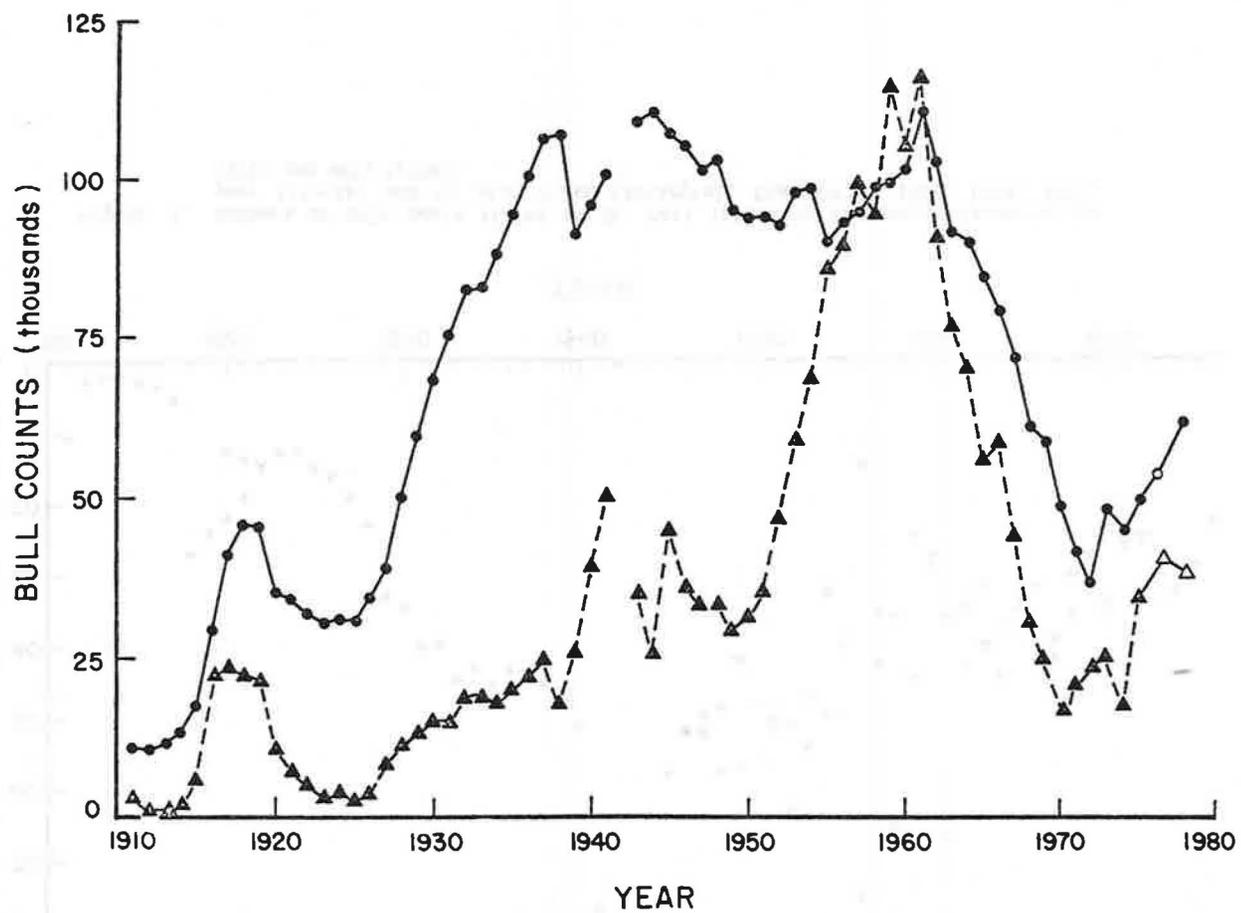


Figure 2. Counts of harem and idle bulls for St. Paul Island, from 1911 to 1977, from Lander and Kajimura (1976, Table 3) and NMFS (1978, Table A-8).

The Model

The model we constructed to simulate the Alaskan fur seal population is based on work by Leslie (1945, 1948). The approach considers each age class separately, and the parameters of the model are age-specific annual reproduction and mortality rates. Leslie defined the matrix equation.

$$N_{t+1} = M N_t \quad (1)$$

where M denotes the square matrix composed of the age-specific reproduction and mortality rates, and N_t denotes the vector of the number of individuals in each age class at time t .

The age specific reproductive rates used in this model appear in the top row of M , and defined as the number of daughters which are produced by a female of each age which survive to their first birthday. The age specific survival rates appear on the first subdiagonal of M and are defined as the fraction of females of each age which survive to the next age. All other elements of M are zero.

Leslie (1948) reformulated this model, with the elements of the projection matrix functions of total population size. This generalization allows density-dependent changes in the parameters to be described. More generally, the elements of M can be arbitrary functions. The corresponding matrix equation in this case is

$$N_{t+1} = M(\bullet) N_t$$

where $M(\bullet)$ denotes the matrix of reproductive and survival rates as arbitrary functions. In general, equation 2 is intractable to analysis but with proper definitions of the elements of $M(\bullet)$ and an initial age distribution, it can be used to simulate the age distribution of the population over time.

Only the female component of a population is described by this model. This is reasonable for simulating numbers of fur seal pups born because the number of males does not appear to affect the pregnancy rate of females over the ranges which have been observed (Appendix I) and because adult males form only a small proportion of the total population.

The female harvest from 1956 to 1968 is incorporated into the model by subtracting the number of females killed (K_t) in each year by age from the right hand side of equation 2. Equation 2 becomes

$$N_{t+1} = M(\cdot)N_t - K_t \quad (3)$$

Equation 3 allows females to reproduce before they are killed, which corresponds to the actual killing procedures. The possible bias in the killing process towards nonpregnant females and that pups whose mothers are killed have a higher probability of dying on land during their first summer of life, are not taken into account.

Changes in the survival and reproductive rates are considered to be primarily determined by population size. In addition, in some simulations, arbitrary changes in the population parameters occurring in the 1960s were considered reflecting a possible shift in food resources or other aspects of the ecosystem exogenous to the population.

A review of the available data on the Pribilof fur seal population provides little evidence that any of the population parameters are density-dependent (Appendices I and II). The only exception appears to be small changes in on-land mortality of pups. Analysis of available estimates of the population parameters suggests that small to moderate changes in at least two, and perhaps three, of the groups of parameters, adult survival rates, juvenile survival rates and fecundity rates, must have occurred to account for the 8% growth rate of the population from 1911 to 1924 (Appendix IV). This possibility may account for the lack of evidence for density dependency in the existing data. In lieu of any observed density dependent changes in vital rates, we have adopted for the purposes of this paper a general function relating vital rates to population density. Letting X_i stand for either the fecundity rate or survival rate of an individual which is i years old, we postulate that

$$X_i(P) = X_i^* + (X_i' - X_i^*) (1 - P/p^*)^{Z_i} \quad (4)$$

where X_i^* = the value of X_i when the population is stationary,
 X_i' = the maximum value for the parameter X_i
 P = the number of pups born,
 p^* = the number of pups born when the population is stationary,
and Z_i = a positive constant.

Equation 4 allows for a variety of density dependent relationships depending on the value of the parameter Z . If $Z = 1$, the relationship between density and the parameter X_j is linear; for values of Z greater than 1, the relationship is concave downward, and for values less than 1, the relationship is concave upward. Similar formulations have been used by Allen (1975) for large whales, where he argues essentially intuitively that for such a model the parameter Z would be greater than or equal to one for large mammals. Fowler (1981) argues both on theoretical and empirical grounds that this would be the case.

Chapman (1961, 1964) proposed a possible functional relationship between the number of pups born and the number surviving to age three. In his parabolic model, juvenile survival alone is density dependent and is a linear function of the number of pups born. This is equivalent to using equation 4 to describe the survival from birth to age three with $Z = 1$, and assuming all other survivals and all fecundities are unchanging ($Z = 0$ in equation 4). Chapman's other model, which he derived based on simple assumptions about foraging behavior, is not directly transferrable in equation 4. However, over the population densities considered here, juvenile survival is a convex function of the number of pups born in this model, and its general behavior is encompassed by equation 4 with $Z > 1$.

Equation 4 considers density dependent changes in various vital rates as they might correlate with the current level of density of the population. It is reasonable to hypothesize that vital rates may be more closely related to nutritional levels in the first few years of life, in which case changes in vital rates would correlate most closely to population size within a few years of birth of each animal. It is known that for population models, such time lags in density dependent responses tend to result in oscillations in predicted population sizes, and that the longer the period of delay, the more radical the oscillations (May 1973).

However, without some concrete information on such delays in response the number of possibilities which could be considered is almost infinite. We explored equations 2 and 4 when the vital rates are made to change according to the density various years earlier (i.e. when P in equation 4 is replaced by the same quantity at some earlier time). We do not report any systematic examination of all such possibilities, but rather the general effect of such mechanisms on the attempt to simulate the time history of the number of pups born is discussed.

Parameter Estimates

We have used estimates of survival rates for ages 12 and older and of fecundity rates following the approach of Smith and Polacheck (1981) (Table 2). The values we use differ slightly from those in that paper, however, because different methods of averaging the 4 year's data were used. The survival rates for ages 4 through 11 are obtained by interpolating linearly between the estimated value for age 12 and an assumed value of 0.90 for age 3. The survival rate from birth to age 3 at equilibrium (S^*_j) was

Table 2. Estimates of age specific survival and fecundity rates used as the parameter estimates for S_a^* and F^* .

Age	Survival	Fecundity
3	0.900	0.005
4	0.898	0.015
5	0.897	0.215
6	0.896	0.380
7	0.895	0.400
8	0.894	0.425
9	0.893	0.465
10	0.892	0.450
11	0.891	0.455
12	0.890	0.445
13	0.900	0.430
14	0.850	0.425
15	0.800	0.415
16	0.620	0.390
17	0.720	0.335
18	0.620	0.365
19	0.390	0.275
20	0.660	0.240

obtained as that rate necessary to give a net rate of population growth equal to zero for given values S^*_a and F^* . For the estimated pregnancy and adult survival rates in Table 2, the equilibrium juvenile survival is 0.426. Since female fur seals do not begin to reproduce until age 3, the determination of the relative survival rates during each of the first 3 years of life is immaterial to the simulation model. In the actual calculations, we arbitrarily set the survival from age 1 to 2 and age 2 to 3, equal to one and assigned all juvenile mortality to the first year of life.

We examined a range of maximum values for the survival (S'_a) and fecundity (F') parameters. Maximum values were specified as the equilibrium rate plus a fraction of the difference between the equilibrium rate and the biological upper bound for that rate - 1.0 for survival rates and 0.5 for fecundity rates. One half is a maximum for fur seals since twinning is extremely rare (Scheffer and Todd 1967). Fecundity rates for females younger than 3 were assumed to be zero at all densities since even for populations in the western Pacific which reproduce at younger ages only a very small fraction of the 2 year olds are ever sexually mature. To reduce the number of possible combinations of parameter values to a manageable number, the maximum value for all adult survivals and for all fecundities were specified by the same proportional increase above the equilibrium levels.

$$S'_i = M_a(1 - S^*_i) + S^*_i \quad (5)$$

$$F'_i = M_f(0.5 - F^*_i) + F^*_i \quad (6)$$

$$S'_j = M_j(1 - S^*_j) + S^*_j \quad (7)$$

M_a , M_f and M_j are the proportion of the difference that the maximum adult survival rates, fecundity rates and juvenile survival rates are set above their equilibrium value.

All elements of the adult survival vector and the fecundity vector are given the same value of Z_i in equation 4, designated as Z_a and Z_f , respectively. The exponent for the juvenile rate is designated as Z_j . The range of values for the parameter Z that we investigated was 0.5 to 5.0.

We explored a range of values for the equilibrium number of pups born (P^*) from 350,000 to 500,000 in increments of 25,000.

The number of females killed in the years 1956 to 1968 are known by age (Table 3). Ages were not generally determined beyond age 10, and for some years not beyond age 8. The animals aged 10 and older were prorated to age classes 11 to 24 using the proportions shown in Table 4, based on a sample of the 1960 kill which was aged completely. In 1963 to 1967 animals were prorated to ages up to 11 by the observed proportions in the 1968 kill.

Table 3. Kill of female fur seals on St. Paul Island by age from 1956 to 1968[†]

Year	1	2	3	4	5	Age 6	7	8	9	10	>10
1956	0	0	1,601	4,795	3,111	1,921	1,448	1,126	685	443	3,303
1957	0	0	953	4,551	9,373	4,747	3,201	2,880	2,599	1,389	7,816
1958	0	477	9,762	6,736	2,719	2,387	649	293	292	430	213
1959	0	215	1,769	6,379	3,098	2,414	2,847	1,495	913	849	4,230
1960	0	19	253	466	760	478	296	271	222	135	394
1961	0	352	3,599	5,468	3,545	3,853	2,302	2,196	2,435	1,601	9,736
1962	0	318	3,421	6,401	4,926	2,675	2,304	2,255	1,840	1,321	9,364
1963	0	499	2,077	5,910	6,950	3,150	1,406	14,883*	-	-	-
1964	0	266	2,239	2,387	2,462	1,446	432	1,519*	-	-	-
1965	0	147	966	1,719	603	200	148	108*	-	-	-
1966	0	0	0	0	0	0	0	0	0	0	0
1967	0	18	588	1,083	1,176	933	3,559**	-	-	-	-
1968	0	32	620	2,143	1,457	1,211	765	494	567	464	2,791

[†]Data taken from North Pacific Fur Seal Commission Reports for the time periods 1958-1961, 1962-1963, 1964-1966 and 1967-1972.

*Includes all females age 8 and older killed

**Includes all females age 7 and older killed

Table 4. The proportion of the age eleven and older females killed in 1968 in each age class. (From unpublished data supplied by R. Lander, National Marine Mammal Laboratory, Seattle, WN.)

Age	Proportion
11	.154
12	.103
13	.113
14	.110
15	.121
16	.118
17	.086
18	.068
19	.063
20	.032
21	.024
22	.005
23	.001
24	.003

To examine the hypothesis that changes in the North Pacific Ocean may be responsible for the observed history of the population, we examined the model with the parameter estimates specified as in the general density-dependent model except that, following 1959, the values for the equilibrium parameters for the adult survival rates vector, the fecundity rates, or the juvenile survival rate were decreased separately and in combination by a specified proportion ranging from 0 to 40%.

The model was analyzed over the period 1912 to 1975. The initial age structure in 1912 was determined by calculating the stable age distribution (dominant eigenvector) for a population with fixed survival and fecundity rates equal to those specified by the particular set of density-dependent relations being used assuming the number of pups born was equal the number estimated to be born in 1912, 70,000. The stable age distribution was then scaled to a female population size which would have produced 70,000 pups. The sensitivity of the simulation model to this method of determining an initial age distribution is examined.

Results

The predicted number of pups born over time can be compared to the estimated numbers actually born (Table 1). The three specific aspects of such comparison which are most useful are the 8% rate of increase in the years 1912 to 1924, the decline in pups born following initiating the harvest of females in 1956 with a possible slight increase in the 1970s, and the possibility of an equilibrium number of pups having been achieved in the 1940s or 1950s. The estimate of 381,000 pups born annually, on average, which we derived from the tagging data, is used in our comparisons to denote this latter possibility.

There exists a large set of parameter values which allows the simulated population to achieve a growth rate of 8% from 1912 to 1924. For most values of P^* and Z_j an 8% rate of growth could be achieved if adult survival rates or juvenile survival rates were the only density-dependent response. This is not true if changes in fecundity rates were the only density-dependent response. However, to achieve an 8% rate of growth with only adult survival rates requires that adult survival rates be close to their absolute biological maximum of 100% per year for most of the life span of an animal. For changes in the juvenile survival rate which result in a growth rate of 8%, large changes with density (i.e. $M_j = 0.8$ to 1.0) are required. Such changes should have been detectable if they had been occurring (Appendix IV).

If more than a single factor is density dependent, a large number of combinations of parameter values will allow the simulated population to grow at approximately 8% from 1912 to 1924, while the magnitude of the change in any single factor in response to density is moderate. Figure 3 shows this for high and low values of P^* with moderate changes in survival and reproduction rates. These results about the changes needed to achieve an 8% rate of growth in 1912 are similar to the results of Appendix IV from an examination of the eigenvalues of the projection matrix, and suggest that changes in more than a single factor are responsible for the regulation of this population. The overall behavior of the simulation model is generally insensitive to the

choice of the combinations of density dependent factors used to achieve an 8% rate of growth. Therefore, the behavior of the model provides no basis to favor any particular set of density-dependent mechanisms as best describing the regulation of this population.

For the strictly density-dependent model, any set of parameters which provides for an approximately 8% rate of increase in 1912 will result in only a small and short-lived decline in pup production following the beginning of the harvesting of females in 1956 (Figure 3).

The relatively small decline in the number of pups born beginning in 1956 and the rapid increase with the cessation of the female kill are features of the model which are persistent in all our attempts to simulate the history of this population using only density-dependent mechanisms. The best fit of the strictly density-dependent model to the observed number of pups born since 1961 occurs when the equilibrium number of pups (P^*) is low. However, even when $P^* = 350,000$, the decline in the number of pups born usually does not reach the low level of the late 1960s, and with the cessation of the female kill the number of pups born always begins to climb steadily towards P^* (Figure 3).

A high value for the Z parameters in equation 4 can result in the population greatly overshooting its equilibrium, followed by a subsequent decline and oscillations. The values of Z which results in a large overshoot and oscillation depends on the combination of density-dependent mechanisms that are used in the model. If juvenile survival is the only factor which changes with density and if the changes in juvenile survival are of a sufficient magnitude to obtain an 8% rate of growth, then values of Z_j greater than 2.5 result in large oscillations. If juvenile survival rates, adult survival rates, and fecundity rates are all density dependent and $M_j = M_a = M_f$, then a value of Z_j as high as 5 does not result in large oscillations.

We examined the possibility that the number of pups born through the 1960s could be the result of an overshoot in the 1950s and a subsequent decline that happened to coincide with the timing of the female harvest. While it is possible to magnify the effect of the female kill by having the kill coincide with a declining population following an overshoot, the period of the induced oscillation from the high values of the Z parameters is relatively short and the simulated population always climbs rapidly to another overshoot of its equilibrium size. Moreover, for values of P^* greater than 400,000, if the values of Z are large enough so that the size of oscillations are great enough to reduce pup production to the lowest levels observed in the 1960s, then pup production usually goes through a large oscillation prior to the initiation of the female harvesting in the 1950s (Figure 4).

When the simulated population approaches a steady state is determined by the parameters Z and P^* , given the criterion for an initial growth rate of approximately 8% from 1912 to 1924. If the relationship between density and survival is linear ($Z = 1$) then the model does not approach an equilibrium by the early 1940s, even with $P^* = 350,000$ (e.g. Figure 3). For nonlinear

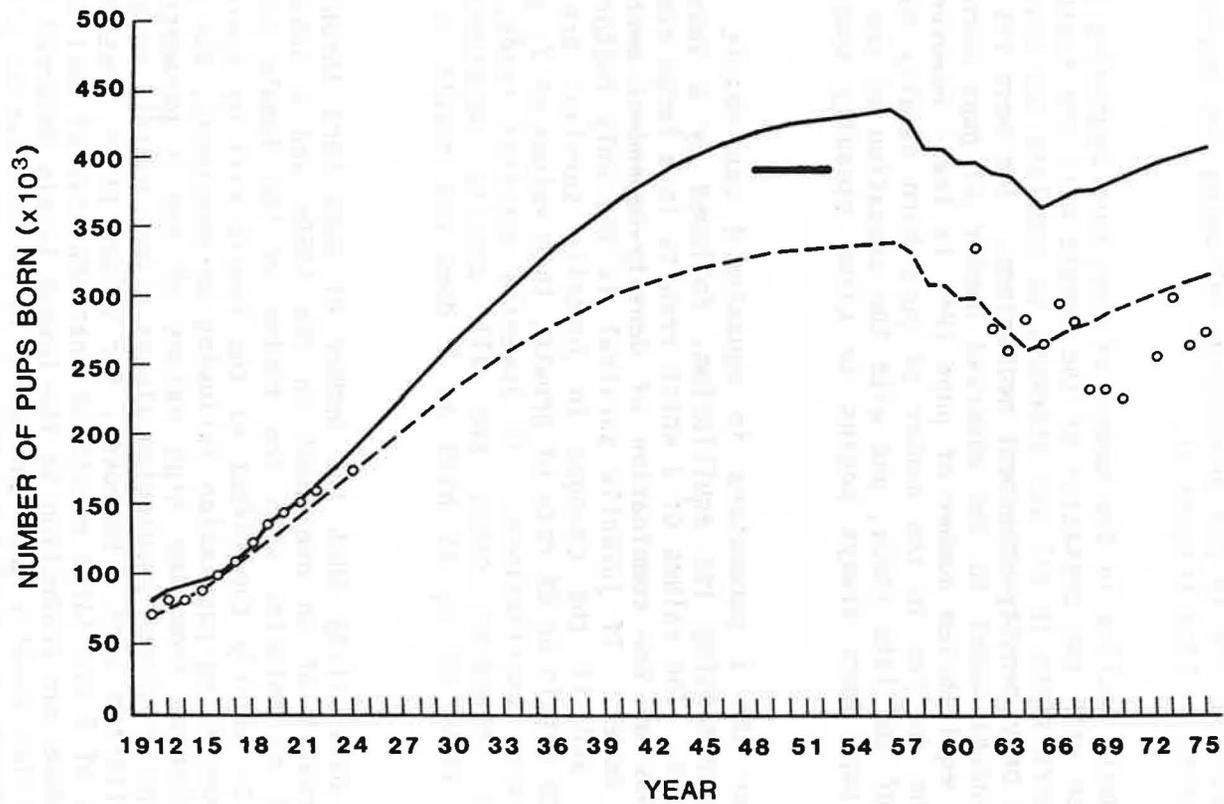


Figure 3. Simulated numbers of pups born from equation 3 over time for equilibrium levels of 450,000 (solid line) and 350,000 (dashed line). Estimated numbers of pups born are shown as open circles, and as a bold line from 1947 to 1952.

relationships with $Z > 1$, an equilibrium can be approached by 1940 (Figure 5). The higher the equilibrium level (P^*) is set, the larger the value of Z_s needed to achieve an early equilibrium. This places some constraints on the combinations of P^* and density-dependent mechanisms which are consistent with the hypothesis that pup production leveled off in the early 1940s. For example, if $P^* = 450,000$ and only the juvenile survival rate is density dependent, then a value of Z_j that allows the pup production to approach P^* by 1940 results in large oscillations (Figure 4). Thus if the population had reached a steady state in the 1940s, changes in juvenile survival rates cannot be the only mechanisms regulating this population. The constraints arising from the hypothesis of an early equilibrium appear not to be sufficient to favor any value of P^* or any combination of density-dependent mechanisms. However, if the equilibrium hypothesis is true, the higher values of the Z parameters which are required for high values of P^* result in a smaller effect of the female kill on pup production (Figure 5). In this case there would be a greater need to find an alternate explanation for the decline in pup production in the 1960s.

While the history of this population cannot be explained on strictly density-dependent bases, one can produce simulated values of pup production which are similar to those actually observed by introducing exogenous changes in the life history parameters. Small to moderate changes in any of the sets of rates of juvenile survival, adult survival and fecundity at equilibrium (S_j^* , S_a^* and F^*) starting in 1960 are sufficient to achieve a close fit of observed and predicted numbers of pups born. Examples of this are shown in Figure 6 for high and low values of the equilibrium population density P^* . Close fits can be achieved essentially for any set of parameters which gives adequate initial growth and for which the values of Z_j are not so large as to induce large oscillations into the population size over time. The magnitude of the change in the equilibrium parameter level depends on the value of P^* . Thus, in Figure 6 with $P^* = 450,000$, a decrease in S_a^* of approximately 10% is required, while with $P^* = 350,000$, a decrease of only approximately 4% is required.

The model is most sensitive to percentage change in S_a^* and least sensitive to percentage changes in S_j^* . To achieve model behavior similar to that in Figure 6 with $P^* = 350,000$ from a decrease in fecundity would require an approximately 15% change and from a decrease in S_j , an approximately 30% change. Changing the values of the equilibrium rates of either or both survivals and fecundities means that the growth rate of the population will become zero at a different population size than P^* . Thus similar results can be obtained by merely changing in 1960 the value of P^* in equation 4. In both cases the behavior of the model in the 1960s is essentially a readjustment to a new equilibrium level. In this situation, the female harvest happened to coincide with the change in the equilibrium level and the main effect of the female harvest is to increase the rate of adjustment to the new equilibrium which would have taken place without it.

The above conclusions are not altered by considering alternate age distributions in 1912, the beginning of the simulation. By beginning with an initial age structure which is skewed towards younger animals, an 8% rate of increase can be achieved with weaker density-dependent effects than for the

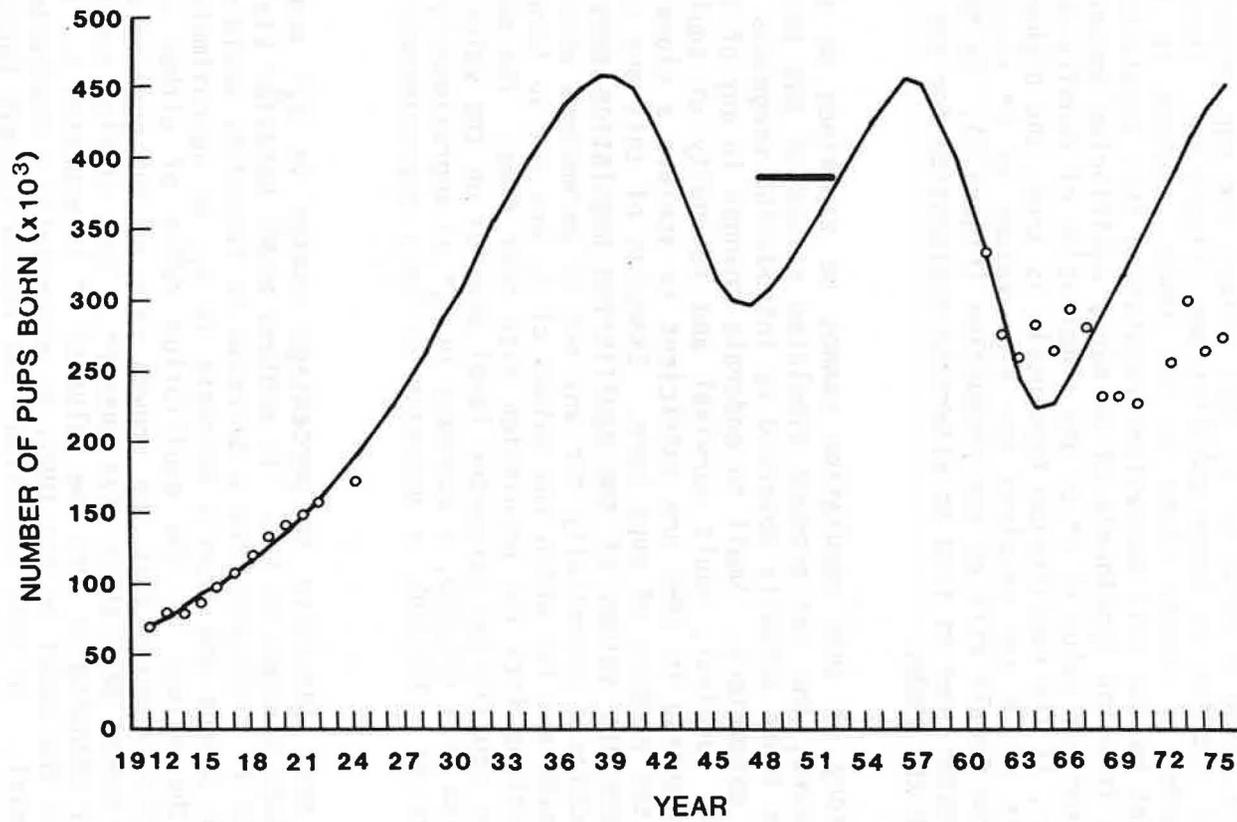


Figure 4. Simulated numbers of pups born from equation 3 over time, for an equilibrium level of 450,000 and a Z value of 3.0. Estimated numbers of pups born are shown as open circles, and as a bold line from 1947 to 1952.

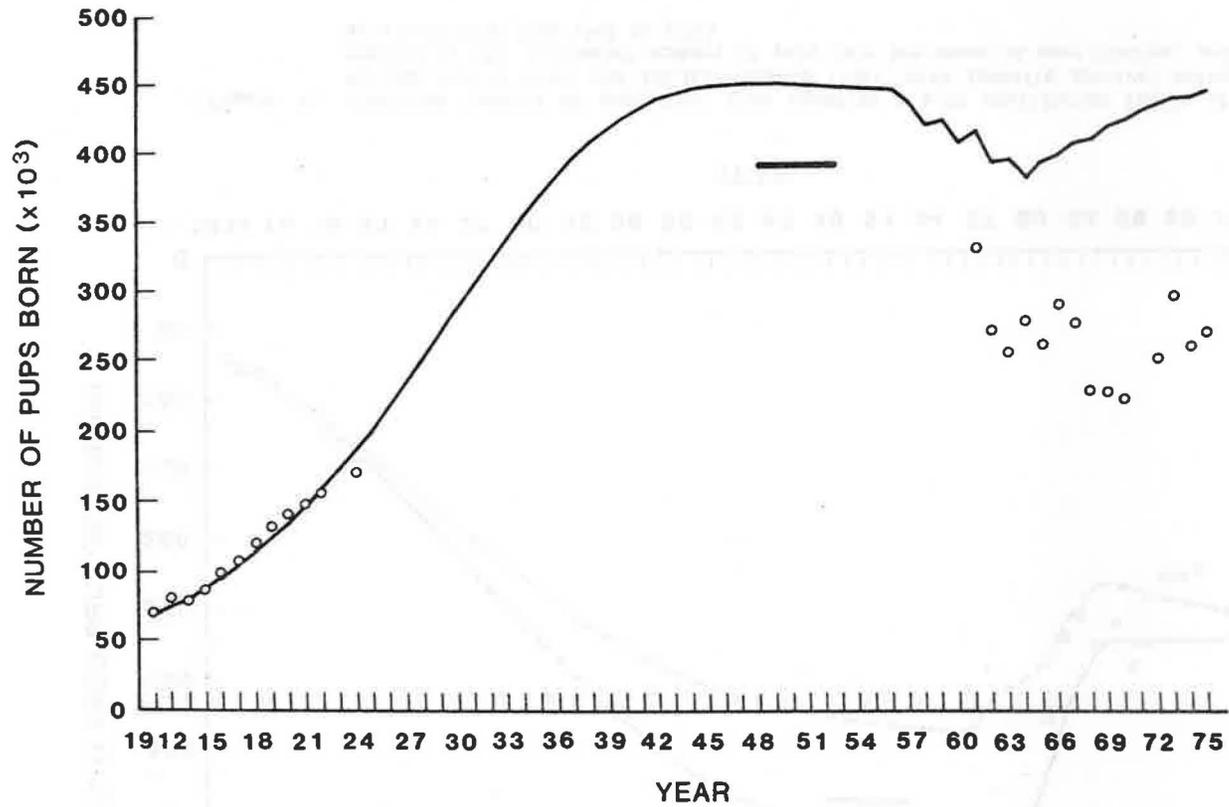


Figure 5. Simulated numbers of pups born from equation 3 over time, for an equilibrium level of 450,000 and a Z value of 3.0. Estimated numbers of pups born are shown as open circles, and as a bold line from 1947 to 1952.

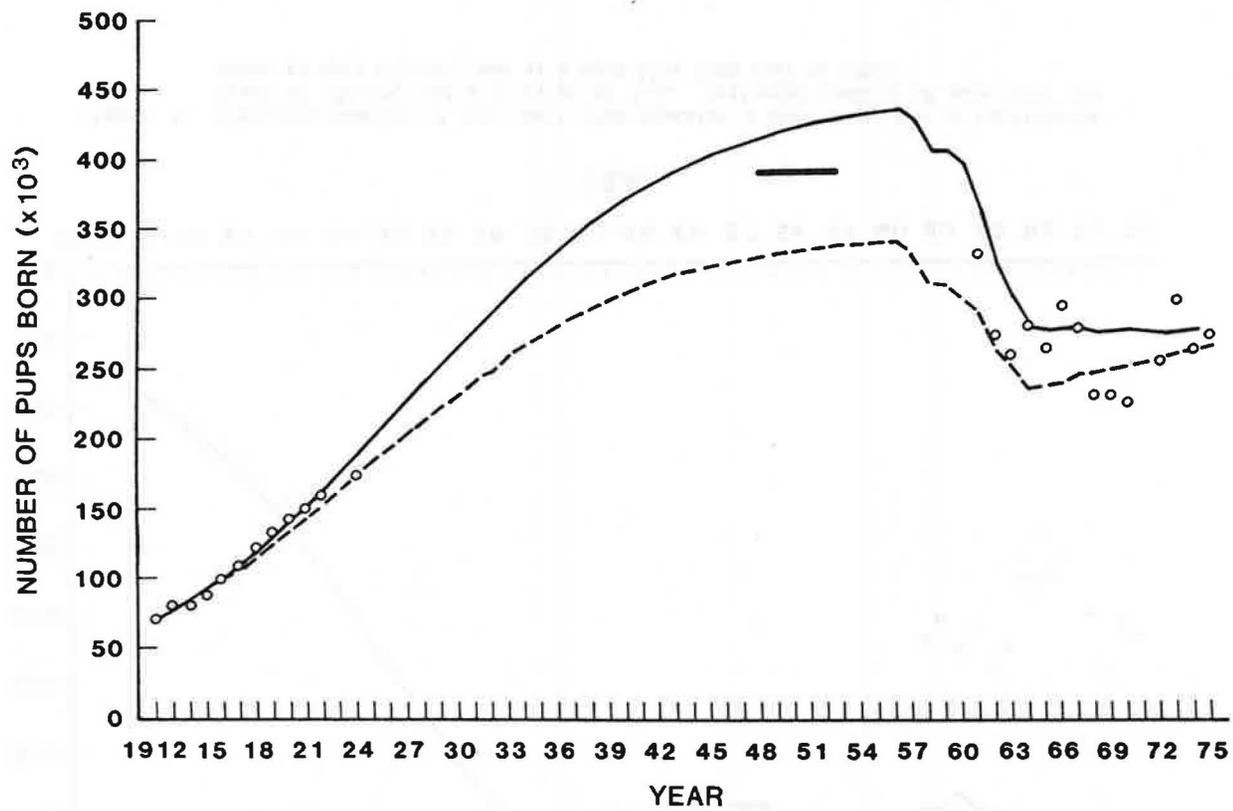


Figure 6. Simulated numbers of pups born from equation 3 with equilibrium levels of 450,000 (solid line) and 350,000 (dashed line), with juvenile survival being reduced by 4%. Estimated numbers of pups born are shown as open circles, and as a bold line from 1947 to 1952.

stable age distribution used in the above simulations. A weaker density-dependent response has the potential to increase the drop in pup production resulting from the female kill and can slow the recovery after the cessation of the female kill, providing a better fit to the observed data. The limit that such an initial age structure effect could have on the behavior of the model in the 1960s can be seen by examining the effect the female harvest would have had if there were no density-dependent changes in the survival and fecundity rates. If one assumes a stationary age structure at the initiation of the female kill, then with no density-dependent responses our model predicts that the drop in pup production resulting from the female kill should have been about 120,000. This should represent an approximate limit of the effect that the initial age structure could have on the behavior of the model. Therefore, if the pup production in the 1950s was greater than 120,000 more than the levels of production in the 1960s, then the initial age structure could not account for the failure of the density-dependent models to simulate the number of pups born. This point was also explored by York and Hartley (1981).

We have also examined a number of skewed initial age distribution by truncating the stable age distribution above a certain age for $P^* = 350,000$ but have not been able to find a combination of an age structure and a set of density-dependent functions that simulates the history of the population. In these simulations if the increase in pup production for 1912 to 1924 is obtained primarily as a consequence of the initial age structure with only a small contribution from density-dependent effects, then the increase in pup production between 1924 and the beginning of the female harvest is insufficient to account for the estimated pup production in the 1960s.

In our exploratory examinations on the effects of time lags on the model presented in this paper, we have not been able to achieve a model which approximates the observed number of pups born. The difficulties in obtaining an adequate fit stem from the fact that any time lag which is of sufficient duration to allow for an almost stationary pup production from 1962 to 1975 induces large oscillations into the population, and the timing of the first downward cycle of these oscillations has to coincide with the timing of the female kill. The length of time that the pup production has remained low (15 years) is approaching the maximum that could be expected as the result of a time lag since the maximum life span of a female fur seal is approximately 20 years. It seems unlikely to us that a time-lag can be responsible for this period of stationary pup production. However, if a time-lag is responsible, then pup production should begin to increase in the near future and the rate of increase should be relatively rapid given the length of the time delay.

Discussion

The results of this simulation work suggest that the observed history of the number of pups born on the Pribilof Islands cannot be explained in terms of a simple model of self regulation. The strictly density-dependent simulation models predict that the effect of the female harvest should have been relatively small and that the number of pups born should have begun to grow with the cessation of the female kill. For a self-regulating population,

the rapid rate of growth observed from 1912 to 1924 and the presumed continued growth of the population to a size with an annual pup production of at least 350,000 appears to be irreconcilable with the levels of pup production that have been observed since 1962.

The difficulty in finding any simple density-dependent model which can adequately explain the stationary level of pup production that has been observed in the 1960s, combined with the ease in which only small to moderate changes in the population parameters around 1960 can result in a reasonable fit to the data, suggests that disturbances may have occurred within the habitat of the Alaska fur seal which have resulted in decreased survival or fecundities. Increased competition for food as the result of increases in commercial fishing, higher mortality rates caused by seals becoming entangled in discarded netting and binding materials, physiological impacts from heavy metals and pesticides and changes in the social structure on the rookeries have been suggested as factors which would be decreasing survival and reproduction rates in recent years (Chapman 1973b; Holt and Talbot 1978). There is no information to evaluate how important these factors are in regulating the abundance of fur seals. The most parsimonious conclusion based on the results of our simulation work is that one or more of these external disturbances are responsible for the reduced pup production since the early 1960s.

However, it should be noted that our present model uses simple density-dependent relationships. It may be possible that changes in survival and fecundity are related to changes in densities of various components of the herd and a more complex set of interactions could be responsible for the observed pup production. This factor combined with our present lack of understanding of the mechanisms important in regulating this population prevents us from adopting the conclusion that disturbances are solely responsible for the present pup production without more information.

If, in fact, changes in the habitat of fur seals are responsible for the decrease yield and pup production compared to the 1950s, the magnitude of the decline is important in evaluating how serious these changes have been. The estimates of the number of pups in the 1950s given by Chapman (1964, 1973a) which have been widely used (Lander and Kajimura 1976) would suggest a decline of 33 to 45%. However, as discussed in Appendix 11, these estimates contain a large amount of uncertainty and at present there appears to be no satisfactory way to estimate what the actual number of pups born was during the 1950s. The results of the simulation model described have provided little insight into what the actual number of pups born during the 1950s must have been. Given the possibility that this population has suffered a marked decline as the result of disturbance from man's activity, close monitoring of pup production is important in order to know if further declines are occurring.

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