

A CRITICAL STUDY OF PRIBILOF FUR SEAL POPULATION ESTIMATES

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ABSTRACT

Previously unresolved problems in the population studies of the Pribilof fur seal are reviewed. The tagging estimates of fur seal pups may have been biased by tag mortality and hence the apparent year class fluctuations after 1952 may be unreal. A set of cumulative estimates are given for the number of pups born in each year since 1950. These cumulative estimates depend on the estimate of the ratio of survival of

females to males from birth to age 3. An estimate of this ratio is given. The implications of this study on the population dynamics model of the fur seal are reviewed: in particular while the exact model is less definite, the suggested optimum population level is almost unchanged from that suggested in earlier studies.

Nagasaki (1961) and Chapman (1961) have published models of the population dynamics of the Pribilof fur seal which, while based on different hypotheses, lead to very similar conclusions. These have been summarized in a report of the North Pacific Fur Seal Commission (PFSC).² Both models are based upon estimates of the pup population from tag recoveries.

Such studies of population dynamics are basic to a proper management of the fur seal herds, both to maximize yield and to evaluate the effect of the herd on other living resources of the sea. Moreover the application of methods to this population which has been extensively studied and for which much data are available, are useful; such applications show up the strength and weakness of theoretical procedures and pave the way for a more intelligent application to other valuable marine resources for which studies are in much earlier stages.

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² North Pacific Fur Seal Commission, 1962. North Pacific Fur Seal Commission Report on Investigations from 1958 to 1961. Manuscript report, Washington, D.C. Frequent reference will be made to this report, hereafter called FSCR.

Both authors also noted that there are two basic unresolved questions:

1. Why did the population estimates increase sharply from 1952 to 1956 and drop suddenly from 1956 to 1957?

2. Why do estimates of male survival to age 3 and the estimates of the female population derived from the tagging estimates lead to the conclusion that the survival rate of females from birth to age 3 is much greater than that of males?

The large fluctuations in the pup population as suggested by the estimates do not seem reasonable when the population of breeding females consists of 10 or more age classes. The survival advantage of human females is well known, and there is some evidence of this in other mammalian populations, but the differences are at most a few percent. In an earlier study, however, I suggested that the survival advantage of females over males is 2 to 1 or more.

This study was undertaken with the aim of attempting to determine (1) if the fluctuations in the pup population estimates could be real, and (2) if the differential survival ratio might be much smaller than 2 to 1 or if the differential existed at

all. Actually it is convenient to treat the problems in the opposite order, looking first at all ways of estimating the female population. The apparent differential survival in favor of females could be explained in two ways: (1) Underestimation of the male survival, and (2) overestimation of the number of females based on the tag estimates and the pregnancy rate.

ESTIMATION OF MALE SURVIVAL

The survival of males to age 3 is estimated by adding to the number of returns as counted in the male kill, the estimated escapement of males from the kill. I need not comment on the first of these two factors, except to note that since the survival being calculated is natural survival the kill of a year class at ages other than age 3 has to be adjusted to this age. Thus, in natural conditions, the animals killed at age 2 would have been part of the 3-year-old returns, except for the mortality from age 2 to 3.

The estimation of the escapement (the number of males that survive to age 3 and are not then or later taken in the male kill) is a more complex problem. Such males form what is known as the breeding reserve; if they survive to sociological maturity (roughly age 7), they will become part of the bull herd.

ESTIMATION OF MALE ESCAPEMENT

The method of estimating male escapement was discussed in Kenyon, Scheffer, and Chapman (1954). The males survive the commercial kill either because they arrive at the islands after killing has ended near the end of July or because they are not of the proper sizes at the time of killing. Formerly, animals estimated by eye to be between 41 inches and 45 $\frac{1}{4}$ inches were those selected for the kill, and after being killed the animals were quickly measured from the tip of the nose to the base of the tail. This measurement served as a check on the selection but obviously did not prevent errors in selection. In some years the desired lengths have been modified slightly, and more recently measurements have been made of a random sample and according to accepted mammalian procedures, with the selection procedures adjusted accordingly.

In general, any male measuring 40 inches or less in one summer and growing to more than 45 inches

by the following summer might well have been spared. If the male survived to age 6 or 7, it would join the herds of harem or idle bulls. The possibilities of this are seen in the analysis of the data on lengths taken from FSCR tables S2 and S3 on pages 167-172. During the spring and early summer both groups grow at about 3.5 cm. per month. The apparent discrepancy between this figure and the small difference in means of the 3's and 4's (8.71 cm.) is easily explained. The commercial kill selects the larger of the 3-year-olds so that the surviving 4's are the smaller members of the year class. Little is known of growth during the other months of the year; undoubtedly it proceeds at a much slower rate in the less favorable months, but a 5-month growth of 17.5 cm. (almost 7 inches) could change a seal from an undersized animal to an oversized one.

Because of the crude methods used in the past for selecting seals and measuring their lengths, estimation of escapement of the males from the kill has been unsatisfactory. The estimation of escapement due to time of arrival has been based upon a fitting of a normal curve to the kill by "rounds" (a round is a 5-day period in which all hauling grounds of an island are visited). The escapement is estimated from the "tail" of this curve. This estimation has been satisfactory in terms of predicting the kill of 4-year-old males from the escapement of 3-year-olds. Nevertheless, several questions remain unanswered in terms of estimates of the final escapement (i.e., the recruitment to the breeding reserve). For example: is the time of return really normally distributed? Do late returners in one year tend to be late returners in the following year? Are there some animals that do not return to the islands at all at ages 3 or 4, but only return when more fully mature at a later age?

To partially resolve this question, we turn to the

TABLE 1.—Mean lengths of pelagically sampled fur seals in the eastern Pacific, 1958-62¹

Age of seals	March	April	May	June	July
Age 3:					
Mean length (cm.).....	98.7	102.4	106.2	109.0	113.4
Number of seals taken.....	16	49	74	43	28
Age 4:					
Mean length (cm.).....	110.0	110.0	115.3	117.8	121.8
Number of seals taken.....	6	20	26	13	11

¹ Data for 1962 from U.S. samples only. Regression lines fitted to this data yield for 3's: $L=106.0+3.56T$ and for 4's: $L=114.7+3.44T$, where in both cases T is measured in months from mid-May.

data on adult males—the harem and idle bulls. These have been counted annually since 1905 except for the war year 1942. The possible errors in the counts of idle bulls noted in Kenyon et al. (1954) are emphasized. To begin with the pelagic samples obtained in recent years are analyzed for mortality rate estimation. The pertinent data are shown in table 2.

Assuming a constant mortality rate \hat{a} , the best estimate of this rate is by the Chapman-Robson (1960) formula

$$\hat{a} = 1 - \frac{x}{1 + x - \frac{1}{\bar{n}}}$$

where \bar{n} = total number of animals taken

\bar{x} = mean age with the ages coded beginning with zero. Here $\hat{a} = 0.36$.

In June and July the breeding animals are on the islands and not as susceptible to pelagic capture; therefore some selection may be involved. For this reason captures in these months have been excluded in the last column of table 2. The estimate of the annual mortality rate based on age composition data from recaptures in months other than June and July is 0.36, identical with the estimate from the whole data. One further check is available on this. In 1960 and 1961 excess bulls were killed on Robben Island by the U.S.S.R. (table 11 of FSCR). Their age classification is shown in table 3.

Since a complete age breakdown is not available, Heincke's estimation procedure is used. This yields:

for 1960 $\hat{a} = 0.37$; for 1961 $\hat{a} = 0.32$;

for the combined data $\hat{a} = 0.34$.

These rates are for a different herd, but their values suggest that the rate given above for the

TABLE 2.—Age distribution of male fur seals taken off Alaska, 1958, 1960, and 1962

Age (in years)	Number taken (all months)	Number taken (excluding June and July)
7.....	35	22
8.....	25	23
9.....	19	11
10.....	12	7
11.....	9	7
12.....	4	2
13.....	4	3
14.....	2	2
15.....		

These data are compiled from FSCR table 30 and from Fiscus, Baines, and Wilke (1964).

TABLE 3.—Age classification of males, age 7 and above, killed on Robben Island, 1960-61

Year	Age (in years)					Total
	7	8	9	10	10+	
1960.....	Number 463	Number 356	Number 166	Number 94	Number 184	Number 1,263
1961.....	354	353	237	67	103	1,114
Total.....	817	709	403	161	287	2,377

Pribilof herd is of the right order of magnitude. As will be shown later this is much higher than the corresponding female rate.

There remains to be estimated the mortality rate of males from ages 3 to 7 and also the number of idle bulls uncounted because they are at sea. On attempt to estimate both of these was based on the historical data. The following equation can be presented:

$$(E_1 + E_2)S = (HM + \Delta H) + k(IM + \Delta I)$$

where E_1 = animals reserved for the breeding stock (a practice in 1923-32)

E_2 = escapement due to size or time of arrival: these animals are also reserved for the breeding stock but no count is made of them.

K = male kill

S = survival rate of males from ages 3 to 7

H = number of harem bulls

M = mortality rate of bulls

ΔH = increase in number of harem bulls

I = number of idle bulls

ΔI = increase in number of idle bulls

k = fraction of idle bulls on land

It is reasonable to assume that E_2 is proportional to $E_1 + K$; hence writing $E_2 = f(E_1 + K)$ the equation is rewritten

$$[E_1 + f(E_1 + K)]S = (HM + \Delta H) + k(IM + \Delta I)$$

This equation holds for any year with the appropriate lag (4 years) between the counts on the left-hand side of the equation and those on the right. While the large variations in annual data preclude my using the equation with such data, I hoped that by averaging over a 5- or 10-year period I might be able to estimate the three unknowns f , S , and k . This presupposes that the fraction escaping the kill remains constant over the several periods involved, that the fraction of idle bulls at sea remains constant, and the seal

counters have had the same definition of an idle bull throughout the period of these data. The method seemed promising because of the large variations in *E* (nearly 10,000 in the 1920's but more recently zero); however, when tried for the periods 1923-27, 1928-37, 1934-38, or for 1923-32, 1933-40, 1946-55, the method gave negative values for *k*. Some of the assumptions made, appear to be invalid.

One other source of information is available—the pelagic catches off Alaska in 1958, 1960, and 1962 (data from same sources as table 2).

TABLE 4.—Comparison of male and female pelagic captures off Alaska, 1958, 1960, and 1962

Month	Number of males age 7 and over taken	Number of females age 4 and over taken	Proportion of males to females
June.....	15	677	0.022
July.....	13	504	.026
Total.....	28	1,181	.024

As will be shown later, the herd of females 4 years old or older has in these years averaged about 600,000. Assuming that 80 percent of the females are in the water at any time (based on observations of Bartholomew and Hoel, 1953), this suggests that not more than 12,000 males are in the water. This figure is consistent with the male total (25,000) if these animals spend half their time in the water. More reasonable is the suggestion that harem bulls spend about one quarter of these 2 months at sea, while idle bulls spend half their time on land and half at sea. This suggests that the idle bull count should be increased by about 50 percent to give the correct total. I believe this to be a maximum figure.

Data to estimate the mortality rate from ages 3 to 7 are even more tenuous. A mortality rate of 50 percent in the first year and 20 percent per year thereafter from ages 1 to 3 would be in accord with the observed returns. The mortality rate probably will be lower for these ages than for the mature animals competing for harems, so I use a figure of 0.20 (annual rate) here.

From 1950 to 1959 the bulls recruited through escapement from years of uniform killing averaged about 25,000 (with the idle bull count multiplied by 1.5). The annual mortality of this number at a 0.36 rate is 9,000. The growth of the herd averaged about 1,000 per year so that the recruit-

ment must have been 10,000. To produce this recruitment at age 7 required (if mortality is 0.20 at ages 3 to 7) an escapement of $\frac{10,000}{(0.80)^4}$ or about 25,000.

During 1946-55 the annual male kill averaged 64,350 (25,000 represents a 40-percent escapement). This absolute total and percentage are both much higher than the estimates obtained by methods used formerly. It is clear now from the above analysis that these methods underestimated escapement. Even without allowing for idle bulls at sea and using a mortality rate from ages 3 to 7 of 0.15 the needed escapement for this period was 16,000. This escapement estimate of 25,000, which will be used hereafter as the best figure for the 1946-55 period, applies to both islands. A corresponding estimate for St. Paul only is 80 percent of this, i.e., 20,000.

ESTIMATION OF THE NUMBER OF FEMALES

PREGNANCY RATES

Estimation of the number of females has been based upon the pregnancy rate and the estimated number of pups born. The pregnancy rate is well estimated from pelagic samples for each age class, but to get an average for the whole adult female population, the size of each age class must be known. The age-specific pregnancy rates have been in good agreement from year to year (table 5 and Chapman, 1961, p. 365).

The broad picture for the Pribilof fur seals seems to be that few females give birth at age 4, about 50 percent at age 5, 80 percent at age 6, and 80-90 percent at ages 7 to 10. Thereafter the pregnancy rate declines slowly with age. Before obtaining a best estimate of the pregnancy rate for the whole female herd it is necessary to estimate the age composition.

A serious problem in studying the fur seal has been obtaining representative samples of the whole herd or of major components of it. There is segregation by sex and age at sea and on land. On land the segregation is in part a result of the differential behavior of pregnant females, which tend to come ashore on rookeries, and nonpregnant females, which come ashore on hauling grounds and at the edges of rookeries. This behavior is not without exceptions, and the two kinds inter-

TABLE 5.—Pregnancy rates of northern fur seals¹

Age	North American		Asian	
	1952 sample	1958-61 samples combined	1952 sample	1958-61 samples combined
4.....	0.01 (80)	0.04 (375)	0.37 (288)	0.43 (1133)
5.....	.43 (28)	.45 (403)	.80 (211)	.83 (837)
6.....	.82 (49)	.76 (445)	.89 (120)	.86 (571)
7.....	.72 (39)	.80 (545)	.85 (99)	.89 (340)
8.....	.77 (55)	.85 (609)	.91 (80)	.89 (199)
9.....	.89 (35)	.90 (555)	.88 (58)	.90 (123)
10.....	.74 (31)	.89 (513)	.88 (72)	.89 (72)
10+.....	.75 (187)	.82 (2641)	.84 (124)	.75 (340)

¹ Figures in parentheses represent number of females in the sample. The rates for 1952 are taken from table G, page 82, of Taylor, Fujinaga, and Wilke (1955). The 1958-61 data are given in FSCR table 20, page 94.

mix. In particular, some animals that have given birth are killed with other females on hauling grounds. The pelagic samples show immediately that the youngest age groups are underrepresented. Table 6 shows the combined female catches of the U.S. pelagic research expeditions of 1958-61 off the Pacific Coast of North America. In discussing age-specific pregnancy rates I need to mention mortality rates, since the age composition of the female class is partly reconstructed on the basis of estimated mortality rates. The method of estimating mortality rates (table 6) is given below.

Sampling below age 8 is unrepresentative, but if it is assumed that sampling is representative for age 8 and up, then mortality or survival rates can be estimated from these data. After study, I decided that the most satisfactory fit is obtained with a Gompertz curve, a form used for actuarial studies. The fitted curve is:

$$Y = 6.9143 - (0.5109)(1.1714)^{-X}$$

where Y represents ln (number) and X is age.

The rather low mortality rates during ages 3-10 are in close agreement with those used in

TABLE 6.—Age composition of female seals taken by U.S. research vessels, 1958-61 combined, and estimated mortality rates

Age	Females taken	Mortality rate ¹	Age	Females taken	Mortality rate
Years	Number	Percent	Years	Number	Percent
1.....			14.....	336	0.226
2.....			15.....	293	.265
3.....		0.040	16.....	233	.311
4.....	267	.046	17.....	142	.364
5.....	307	.054	18.....	97	.425
6.....	324	.064	19.....	59	.499
7.....	407	.075	20.....	21	.585
8.....	478	.088	21.....	16	.685
9.....	447	.103	22.....	6	.803
10.....	434	.120	23.....	3	.940
11.....	429	.141	24.....	3	
12.....	387	.165	25.....		
13.....	362	.193	26.....	1	

¹ Percent of each age class dying during the year.

Kenyon et al. (1954, p. 39), based on fewer data and estimated more crudely.

This composite sample (table 6) can also be compared with the 1952 pelagic sample (Taylor et al., 1955, p. 49). Since, in the 1952 sample, ages above 10 were not identified, it is possible only to use a Heincke-type estimate, i.e., the relation of the age 10 group to the 10-year and older animals. For 1952 the average mortality by this method for the 10+ group of females is estimated as 0.142, while from the composite sample (table 6) it is estimated as 0.154. The two estimates are in reasonable agreement.

The rates estimated here are somewhat lower than those given by Chapman (1961, p. 365), based upon the assumption of a constant mortality rate above age 9. More careful scrutiny of the data suggests that mortality increases with age. The average for the female population given in the 1961 paper was 0.14, here it is 0.11. The latter rate is used in the present study but, where pertinent, the implications of the higher rate will be considered.

What are the annual fluctuations in the pregnancy rate? Using the same age distribution and applying the age-specific pregnancy rates obtained in pelagic samples for 1952 (table 5) and for 1958-62 (Fiscus, Baines, and Wilke, 1964, p. 36) the following weighted averages are obtained: 1952, 0.595; 1958, 0.629; 1959, 0.629; 1960, 0.625; 1961, 0.588; and 1962, 0.578. The standard deviation of the six rates is 0.023, which is about 3.8 percent of the average.

A stable herd with these age-specific mortality rates and the age-specific pregnancy rates of the 1958-61 combined samples (table 5) would have an overall pregnancy rate of 0.62. With the somewhat higher mortality rates used by Chapman (1961, p. 366), the estimated pregnancy rate was 0.58. Both rates apply to the female population of ages 3 and older. It is clear that the estimate of 0.6 used for pregnancy rate in Chapman (1961) may be adopted as the most reasonable.

CUMULATIVE ESTIMATES OF THE NUMBER OF FEMALES

The estimates made of mortality and pregnancy rates could be used to estimate the total number of females in any year, if the female recruitments at age 3 for several years past were known. But

all that is known is the male kill by ages for year classes since 1947 and by size groups only for earlier years, together with the escapement estimates derived earlier. From 1940 to 1949 the average male kill was 53,840 per year. The escapement during this period may be estimated at 40 percent of this or 21,536, hence a reasonable estimate of the male survival to age 3 for these years is about 75,000. An estimate of 75,000 may be slightly high for the year classes prior to 1937, but by 1956 such year classes constituted a negligible part of the population or either males or females.

The estimated male natural survival to age 3 (if no 2-year-olds were killed) for the year classes 1947-59 is shown in table 7. This has been calculated using the 40 percent escapement figure for year classes for which killing terminated by July 31. For year classes that experienced an August kill, I have assumed that one third of the August 3-year-male kill and all the August 4-year-male kill represents animals that would have formerly been part of the escapement. Hence, the 40 percent escapement estimate is applied to the balance of the kill from the year class. Raw data for table 7 are found in FSCR table 6.

To estimate the female recruitment I need to know λ (lambda), the ratio of female survival rate to age 3 to the corresponding male survival rate. Because λ is not known, several values are tried, viz, $\lambda=1.0, 1.25, 1.5, 2.0$.

The basic procedure is illustrated with the 1956 estimate of the female population and with $\lambda=1.0$.

The cumulative estimate of the 3-year and older female population in 1956 is:

1953 year class survival to age 3 $\times 1.000 = 62,000$ (1.000)
 +1952 year class survival to age 3 $\times 0.960 =$
 +93,000 (0.960)
 +1951 year class survival to age 3 $\times 0.915 =$
 +83,000 (0.915)
 +1950 year class survival to age 3 $\times 0.866 =$
 +84,000 (0.866)
 +1949 year class survival to age 3 $\times 0.810 =$
 +62,000 (0.810)
 +1948 year class survival to age 3 $\times 0.749 =$
 +70,000 (0.749)
 +1947 year class survival to age 3 $\times 0.683 =$
 +83,000 (0.683)
 +1946 and earlier survival to age 3 $\times 3.013 =$
 +75,000 (3.013)
 Total = 685,000

TABLE 7.—Estimated natural survival of males to age 3, St. Paul Island, 1947-59 year classes

Year class	Total	Year class	Total
1947.....	83,000	1953.....	62,000
1948.....	70,000	1954.....	44,000
1949.....	62,000	1955.....	55,000
1950.....	84,000	1956.....	21,000
1951.....	83,000	1957.....	56,000
1952.....	98,000	1958.....	79,000
		1959.....	60,000

The mortality factors are obtained from those shown in table 6 by successive multiplication.

The foregoing procedure is applied to other years, with other values of λ (table 8). The earliest estimates in the table are biased upward by an overestimate of the contribution of the pre-1940 year classes. There is also some upward bias of the earlier estimates from tagging. In 1960 and subsequently, a more intensive search for tag-lost animals was undertaken, and it was demonstrated that there had been some oversight earlier. (A tag-lost animal is a seal that had been tagged and had lost the tag before recapture; it is identified as an animal that had been tagged by the checkmark that is also placed on the flipper at the time of tagging.) The largest estimate from tagging, however, is of the 1956 year class; the 1960 kill from this class was searched carefully for tags and tag-lost animals.

The last column of table 8 shows 10 different estimates of λ , which are valid only if the tagging estimates are valid.

If the annual mortality rates used here are too low, i.e., if the true rates are similar to the rates

TABLE 8.—Cumulative estimate of 3-year and older female population, St. Paul Island, 1950-62

Year	Postulated differential survival rate of females to males to age 3 (λ)				Best estimate of number of females from tagging estimate of pups ¹	Estimate of λ from tagging estimate of pups
	1.00	1.25	1.50	2.00		
1950.....	683	854	1,024	1,368	No estimate	-----
1951.....	677	846	1,016	1,354	813,000	1.20
1952.....	664	830	996	1,328	² 828,000	1.25
1953.....	674	842	1,011	1,348	1,140,000	1.69
1954.....	682	852	1,023	1,364	1,208,000	1.76
1955.....	699	874	1,048	1,398	1,240,000	1.77
1956.....	685	861	1,034	1,378	1,337,000	1.94
1957.....	635	798	961	1,288	955,000	1.49
1958.....	583	738	892	1,201	967,000	1.62
1959.....	514	648	782	1,050	1,040,000	1.98
1960.....	483	610	736	989	³ 828,000	1.68
1961.....	499	625	750	1,001	(⁴)	-----
1962.....	468	593	719	970	(⁴)	-----
Average.....						1.64

¹ Number of pups as estimated from male tag recoveries in commercial kill divided by best estimate of average pregnancy rate viz 0.6.

² Dead pup count estimated from counts of two areas to be 45,000. Note that a slightly different estimate was used in table 2 of Chapman (1961, p. 359).

³ Estimate based on returns of 3-year males only.

⁴ Estimate not yet available.

given in Chapman (1961), then the present cumulative estimates are too high. This would yield even higher estimates of λ . If the tagging estimates are correct then the differential survival advantage of females at ages 0 to 3 is indeed large. The tagging estimates possess, however, internal inconsistencies, and the possible explanations for these are now considered.

FLUCTUATIONS IN THE APPARENT NUMBER OF PUPS BORN

Another unresolved question is: How could the estimated number of pups born, about 500,000 in 1947-49 and 1952, increase to 584,000 in 1953 in 722,000 in 1954, 744,000 in 1955, and 802,000 in 1956; then drop to 573,000-580,000 in 1957 and 1958? What are the possible explanations of the fluctuation? If there is no bias in the estimates from tagging, there are three explanations: (1) Sampling variations, (2) variations in the pregnancy rate and, (3) variations in the number of adult females.

SAMPLING VARIATIONS

The magnitude of sampling variations is discussed elsewhere (Chapman 1963).³ I showed that the standard deviation of the 1952 or 1956 estimates is less than 20,000, so sampling variation can reasonably explain less than 60,000 of the 300,000 difference. Moreover, there are also the 1953 and 1954 estimates to explain.

VARIATIONS IN THE PREGNANCY RATE

Turning to variations in the pregnancy rate, it is unfortunate that there was no pelagic sample in 1956 nor, in fact, in the years of highest estimates from tagging. However, the samples taken in six different seasons have shown very similar rates, with the variation from highest to lowest of the mean annual rates being only 8.4 percent of the 6-season mean. Furthermore, such variations are inadequate to explain the apparent change in number of pups born, a 60 percent increase from 1952 to 1956. In fact, if the observed 1952 pregnancy rate and the 1952 pup estimate (497,000) were both true, the number of females in 1952 would have been 835,000. If this many females

had 802,000 pups in 1956, the pregnancy rate was 0.96, a rate that is inconsistent with any data available.

VARIATIONS IN THE NUMBER OF ADULT FEMALES

Finally, was there a substantial increase in the number of females between 1952 and 1956? The cumulative estimates suggest, with $\lambda \leq 2$ that the change was 50,000 or less, accounting for a possible increase of about 30,000 pups.

No single cause explains the 1952-56 change; perhaps there was a combination of causes. Consider the 1952 pup estimate $+2$ standard deviations, i.e., 537,000. With λ pregnancy rate $P=0.595$ this means 903,000 females. Suppose that from 1952 to 1956 there was an increase to 968,000 females. Assume that in 1956 P was 0.653 ($P+2$ standard deviations). This suggests a 1956 pup crop of 69,000. Allowing for the sampling error in the 1956 estimate (2 standard deviations is less than 40,000), the unaccounted discrepancy is still 133,000. That all three factors (nonrepresentative sampling, variation in pregnancy rate, and variation in number of adult females) should act in the same direction in any given year is improbable. Even so, there remains a large unexplained discrepancy in the estimated number of pups born.

BIAS IN ESTIMATES FROM TAGGING

Some of the estimates of pups born from tagging must be biased, and the most likely cause is excess mortality caused by the tag or tagging operation. In general, the years with the poorest survival had highest estimates. An upward biased estimate would result from an increased tendency for tagged pups to die during the fall and winter. The tagging need not bring immediate mortality, though a 1962 experiment indicated that this may occur. Roppel et al. (1963) showed that the mortality on land of tagged pups counted during September was 2.7 times that of untagged pups (33 dead tagged pups expected, 84 dead tagged pups observed), however, such mortality in general appeared to be less than 6 percent of the mortality that occurred prior to the tagging period so that even this differential mortality does not explain the excess mortality postulated to account for the excessive tagging estimates. Consequently, this is a hypothesis rather than a firm fact.

Tagging mortality may be greater in years when

³ Douglas G. Chapman. 1963. Problems in the analysis of tagging experiments with particular reference to Alaska fur seal data. To be published.

survival is poor, but this does not explain why survival has varied so greatly over the past several years. A population at or near its ceiling is expected to fluctuate more widely than one that is actively growing, and, moreover, the range of fluctuation will tend to increase with time through purely random causes. The largest fluctuations in the fur seal herd will be brought about by random fluctuations in survival of the youngest animals, though fluctuations in the pregnancy rate may also contribute some variability.

A possible explanation also may be found in external factors. Abegglen, Roppel, Johnson, and Wilke (1961)⁴ speculated about the relationship between the average temperature for the preceding year and the dead pup counts. They reported the correlation between these variables to be -0.853 , which is significant at the 1 percent level. The correlation between average temperature and total male survival for the year classes 1950-59 is 0.924 , which is also highly significant and even higher numerically than the correlation between dead pup counts and temperature. Data are not yet available for survival from subsequent year classes. The temperatures considered are for the St. Paul Island weather station. It would be more useful to have water temperature for the Bering Sea. Without such data it is only possible to speculate that water temperatures are rather closely related to land temperatures with, however, some lag. A lower water temperature might have a direct effect on the young seals or it might reduce their food supply. Either could result in increased mortality on land during the summer and at sea during the fall and winter. A model I proposed (1961) was based on food at sea as the limiting factor on growth of the pup. Clearly, temperature dependence would be more important if the population were pressing on its food supply than if it were not.

In summary, the tagging estimates show fluctuations that are not explicable in terms of the structure of the herd and known values of other parameters and which therefore suggest some bias is inherent in the estimates. It is, therefore, important to turn to other methods of estimating λ or the female herd size.

⁴ Carl E. Abegglen, Alton Y. Roppel, Ancel M. Johnson, and Ford Wilke. 1961. Fur seal investigations, Pribilof Islands, Alaska, Report of field activities, June-November 1961. Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, Wash.

Another method of population estimation is based upon differential kill of the sexes (Chapman, 1955). This method appears to be ideal for the fur seal where in excess of 70 percent of the males are killed at ages 3 or 4, but only a small proportion of the females is removed. However, the method also requires estimates of the sex ratio before and after the differential kill. While these are available from large pelagic samples in 1958-61, the segregation of the sexes at sea creates difficulties. If the segregation pattern remains constant from year to year, these difficulties might be overcome. The following model was considered:

Let N_1, N_2 be the number of males and females, respectively, at the beginning of any summer season. Define $N = N_1 + N_2$. Assume that a proportion ϕ_i of the N_i are to be found in any area at sea in any season. Then the proportion of males at sea in this area and season will be

$$p' = \frac{\phi_1 N_1}{\phi_1 N_1 + \phi_2 N_2} = \frac{N_1}{N_1 + \phi N_2} \quad (1)$$

where

$$\phi = \frac{\phi_2}{\phi_1}$$

Let R_i be the kill of the N_i in the summer season and s_i the rate of natural survival during the following winter. Then the proportion of males at sea in the same area next spring will be

$$p'' = \frac{N_1 - R_1}{(N_1 - R_1) + \phi s (N_2 - R_2)} \quad (2)$$

where

$$s = \frac{s_2}{s_1}$$

and where all that needs to be assumed is that ϕ , the ratio of ϕ_2 to ϕ_1 , remains constant between years.

If N_1 refers to the number of males at age 3, this can be assumed known, and if information is available as to s , then observations of p', p'' from pelagic data can be used to estimate ϕ and N_2 . In particular, it is reasonable to assume that s equals 1, approximately, since both s_1 and s_2 are close to 1.

Writing $N_2 = \lambda N_1$ and setting $s = 1$ equations (1) (2) may be rewritten

$$\frac{1}{p'} = 1 + \phi\lambda; \frac{1}{p''} = 1 + \phi \left(\frac{\lambda N_1 - R_2}{N_1 - R_1} \right)$$

or

$$\phi = \frac{1 - p'}{\lambda p'}$$

Substituting this last equation in $\frac{1}{p''}$ yields

$$\frac{1 - p''}{p''} = \frac{1}{\lambda} \left(\frac{1 - p'}{p'} \right) \frac{\lambda N_1 - R_2 / \lambda}{N_1 - R}$$

Put

$$\frac{(1 - p'')p'}{p''(1 - p')} = Q$$

Then

$$Q = \frac{N_1 - R_2 / \lambda}{N_1 - R}$$

or

$$(N_1 - R)Q - N_1 = -R_2 / \lambda$$

Changing signs and taking reciprocals produces an equation for λ :

$$\lambda = \frac{R_2}{N_1 - Q(N_1 - R_1)} \quad (3)$$

The following estimates of λ were obtained from the indicated pelagic samples (from which estimates of p' , p'' were obtained). The year in the second column refers to the first year of the paired samples and the year for which the N_1 estimate is determined.

The tagging results and other data suggest that λ should be 1 or greater. The estimates of λ from table 9 are quite unreasonable. This may be due to failure of the basic assumption that the proportion of males to females in any one area and season remains constant from year to year. The estimates of λ by the dichotomy method depend primarily on the size of R_2 . In the standard

application of the dichotomy method, the greater the difference between R_1 and R_2 , the better the estimation of population size; however, with these data this is not so. Perhaps the R_2 values are too small. Also, the small size of the pelagic samples—when only one age-sex class is considered—makes correspondingly great variability in p' , p'' . I attempted to combine data from different years to eliminate or reduce the variability, but the results proved equally unsatisfactory and are not shown here.

POPULATION DYNAMICS OF THE FUR SEAL HERD AND ESTIMATION OF THE NUMBER OF FEMALES

Recent data do not permit resolving the question: What is the value of λ , the ratio of female to male survival from birth to age 3? There are also the data of the early 1920's when counts were made of the number of pups born. Both sets of data are considered below.

We have the obvious fundamental relationship (equation 4):

$$\frac{PS}{2} = (a + g)(1 + g)^2 \quad (4)$$

where

P = proportion of females age 3 and older that are pregnant in any one year

S = survival rate of pups (female) from birth to age 3

a = annual mortality rate (average) of female population

g = annual growth rate of female population

The factor one-half on the left-hand side arises from the assumption that half of the pups born are females, which is consistent with all available information. The factor $(1 + g)^2$ on the right-hand side follows because of the time lapse from

TABLE 9.—Estimate of λ , ratio of differential survival of females to males, by dichotomy method

Area	Year	Age group	p'	p''	R_1	R_2	N_1	λ
Washington	1958	3	0.0	0.06	35,109	11,393	68,000	0.17
Do	1959	3	.33	.25	12,922	2,016	25,000	.29
Do	1960	3	.27	.15	29,381	281	66,000	-.02
Do	1960	4	.25	.07	4,149	562	10,000	-.04
British Columbia	1959	3	.33	.10	12,922	2,016	25,000	-.05
Do	1960	3	.33	.20	29,381	281	66,000	-.01
Do	1961	3	.40	.17	57,871	4,534	96,000	-.14
Do	1961	4	.20	.08	19,836	6,776	31,000	-15.5
California	1958	3	.03	.06	35,109	11,393	68,000	.23
Alaska	1958 (June)	3	.80	.33	35,109	11,393	68,000	-.06
Do	1958 (before June)	3	.35	.28	48,489	18,560	68,000	-.09

¹ 1958 and 1960 pelagic samples are combined so that R_1 , R_2 represent the combined kill of 3s in 1958 and 4s in 1959 for this calculation.

birth to recruitment. It can best be shown by the following diagram:

Year	0	1	2	3
Number of females.....	N	$N(1+g)$	$N(1+g)^2$	$N(1+g)^3$
Increase.....			$N(1+g)^2g$	
Mortality.....			$N(1+g)^2a$	
Number of female pups.....	$\frac{NP}{2}$			
Survivors.....			$\frac{NPS}{2}$	

The recruitment (survivors) must account for growth and mortality losses, whence we have equation (4) above. This equation, of course, is trivial. What is significant is how P , S , and a change as the population changes from a growing one to a stable one.

For later purposes it is convenient to rewrite (4) as (equation 5):

$$\frac{PS'\lambda}{2} = (a+g)(1+g)^2 \quad (5)$$

where S' = survival rate of male pups from birth to age 3 and as before

λ = differential survival of females to males (from birth to age 3)

From data of the early 1920's (Chapman, 1961) the St. Paul kill from the 1920-22 year classes averaged 13,590 (size groups 2, 3, 4). In addition, 22,666 were reserved for the breeding stock in these 3 years (average, 7,555 per year). Adding these two and also adding an estimated 40 percent escapement yields an average male survival of 30,000. Since the average pup count was 150,000 (half male and half female) the estimate of S' is 0.40.

Early pup counts (Kenyon et al., 1954, p. 20) show that the 1916-22 annual rate of increase was 0.08 on St. Paul Island. The St. George rate of increase, however, was 0.07, and the 1920-24 St. Paul annual rate of increase was 0.07. The latter is based on partial counts, but it is likely that the growth rate would begin to decrease about this time, so g is taken to be 0.07. At present the growth of the Asian herds as measured by the pup counts is 8-9 percent annually.

Unfortunately, the values of P and a are not known for 1916-22. It is possible, however, to calculate λ for a range of reasonable values of P and a , assuming that P was no smaller than at

TABLE 10.—Values of λ (differential survival of females to males) corresponding to various possible values of P , pregnancy rate, and a , annual mortality rate (1920's data)

Values of P	Values of a				
	0.11	0.10	0.09	0.08	0.07
0.6.....	1.72	1.62	1.53	1.43	1.34
0.7.....	1.47	1.39	1.31	1.22	1.14
0.8.....	1.29	1.22	1.14	1.07	1.00

present and a no larger. Values for λ are shown in table 10.

Such a table does not provide a close estimate of λ but it does suggest that it was then larger than 1. Concerning the value of P (the pregnancy rate) and a (the annual mortality rate), the following comments are pertinent. If the observed age-specific pregnancy rates from western Pacific samples (1958-61) shown in table 5 are applied to the eastern Pacific age distribution, the resulting pregnancy rate for the whole population would be 0.70. The pregnancy rate of the females on the Asian islands must be slightly higher than this since there is some intermixture of Pribilof seals in these western Pacific samples. To allow for this, average intermixture rates have been calculated from table 43 of FSCR (p. 120). For ages 3 to 6 these averages are 0.18, 0.22, 0.42, and 0.70 (when the dashes are correctly interpreted as zeros). This yields adjusted intermixture rates for those ages of 0.12, 0.60, 1, and 1, respectively.

The equation to determine these adjusted rates is:

$$\pi_p P_p + \pi_A P_A = P_w$$

or

$$P_A = \frac{P_w - \pi_p P_p}{\pi_A}$$

where

π_p = proportion of Pribilof seals in western Pacific samples

π_A = proportion of Asian seals in western Pacific samples

P_p = pregnancy rate of Pribilof seals

P_A = pregnancy rate of Asian seals

P_w = observed pregnancy rate of western Pacific samples

For 4-year-olds the equation becomes

$$(0.04) + (0.78)P_A = 0.48 \text{ or } P_A = 0.60 \quad (22)$$

Since the estimates for ages 5 and 6 are impossible, we have used the maximum observed rate, or 0.90, for these ages and for ages 7 and 8 where no intermingling estimates are available. The resulting adjusted pregnancy rates (Asian females) are as follows: Age 3, 0.13; age 4, 0.60; ages 5-9, 0.90; age 10, 0.89; age 10+, 0.75; weighted mean, 0.74.

It seems, therefore, that 0.80 is a reasonable upper limit for the pregnancy rate of the early Pribilof herd.

There is little direct information available as to the annual mortality rate in the early 1920's. The present age distribution of the western Pacific samples suggests higher mortality rates than for the eastern Pacific samples. I do not know whether this is due to nonrepresentative sampling or to a variable intermixture of Pribilof seals. With a growing population the proportion of younger animals would be greater. According to the model given earlier (pages 21 and 22) younger seals have lower mortality rates, so that the average rate for the whole herd would be reduced. The reduction due to this cause would be slight.

Turning to the present data we have $a=0.11$, $g=0$, $P=0.6$ so that equation (5) yields:

$$s'\lambda=0.37$$

Since it is reasonable to suppose s' is less now than in a growing herd $s' \leq 0.40$, whence $\lambda \geq 0.925$. If the 1947-49 and 1952 tagging estimates are accepted (Chapman, 1961, tables 2 and 3) $s'=0.294$ so that $\lambda=1.27$. These agree very closely with the estimates of λ from 1951 and 1952 in table 3. The latter were based on a comparison of cumulative and tagging estimates of the female population. Too much importance must not be attached to this agreement, since essentially the same supporting data are involved.

BEST ESTIMATE OF λ

At the present time there seems to be no best estimate of λ . The data indicate a range of values and suggest that λ is probably slightly greater than 1. A reasonable value for λ from the 1920's data is approximately 1.25, which is also consistent with the 1947-49 and 1952 tagging data. This value is adopted here as best. Higher values of λ are possibly consistent with the available data but seem biologically less reasonable.

IMPLICATIONS FOR THE POPULATION DYNAMICS OF THE FUR SEAL HERD

The population models of both Nagasaki (1961) and Chapman (1961), utilized the high estimates from tag recoveries of the 1952-56 period. If such estimates are discounted, then the right-hand limb of the parent-progeny relationship (e.g., Chapman, 1961, fig. 1, p. 361) and hence the probable optimum population level is much less well defined.

Nevertheless, the models fitted in my earlier paper may still be fitted either to data from tagging estimates through 1952 or to the cumulative estimates. The results in either case are similar and differ very little from the equations given in the earlier paper. For example, using the cumulative estimates (with $\lambda=1.25$) for the period 1950-59 the average female population was 814,300 which with a pregnancy rate of 0.6 produced an annual pup crop of 489,000. The male survival to age 3 from three-year classes averaged 64,000. Combining this with the 1920's data yields:

$$N_m=0.0293 E^{3/2}-0.00106 E^2 \text{ (Chapman model)}$$

or

$$N_m=0.2306 E-0.000204 E^2 \text{ (parabolic model)}$$

where

N_m =male survival to age 3 (in thousands)

E =number of pups born (both sexes, in thousands)

From these equations the maximum sustainable yield (with $\lambda=1.25$, $P=0.6$, and an average mortality rate of the females 3 and older equal to 0.11) is attained when

$$E^x=351 \text{ (Chapman model)}$$

or

$$E^{xx}=366 \text{ (parabolic model)}$$

The estimated male return at these levels would be 64,000 or 57,000 according to the two different models. Of these, about 71 percent or perhaps somewhat more would be available for the commercial harvest. The sustainable female yield according to these equations is 14,000 (Chapman model) or 7,000 (parabolic model).

If the female mortality rates are underestimated, the E^* E^{**} values given here are slightly high and so are the levels of sustainable kill. On the other hand if the pregnancy rate should increase as the female herd is reduced, the effect would be an opposite one. Such an increase in P may occur only with some time lag.

If we accept the hypothesis that the estimates from tagging since 1953 have been inflated, possibly by tagging-induced mortality, immediate or delayed, and that the best estimate of λ , the ratio of female to male survival from birth to age 3 is about 1.25, then the best estimate of the average 3-year and older female population for 1960-62 is about 609,000. If P , the pregnancy rate, is about 0.6 this implies the average number of pups born in these years was 365,000, very close to the current best estimate of the optimum.

In conclusion, the figures on population sizes, harvests, etc. apply to St. Paul Island. The figures for the Pribilof herd as a whole can be obtained by the usual extrapolation.

In recent years a method of fall sampling has been developed to estimate the number of pups in the year of birth. While this procedure also has biases that are not yet fully resolved, preliminary results indicate strongly that the actual year classes are much less than have been indicated by tagging estimates. Some of the preliminary results are shown in Roppel et al. (1964); additional results of the improved 1963 experiment are to be found in the unpublished annual report of fur seal investigations for 1963.⁵

SUMMARY

1. This study was undertaken to review critically the unresolved questions about Pribilof fur seal population estimates—the apparent large fluctuations in the number of pups born and the apparent differential survival of males and females from birth to age 3.

2. The adult male annual mortality rate is estimated from pelagic samples to be 0.36; the age distribution of the much larger samples from the adult females taken pelagically are fitted by a Gompertz-Makeham curve. The average annual mortality rate for these adult females is estimated to be 0.11.

⁵ Alton Y. Roppel, Ancel M. Johnson, Douglas G. Chapman. 1964. Fur seal investigations, Pribilof Islands, Alaska, 1963. Marine Mammal Biological Laboratory, Seattle, Wash.

3. From counts made in the 1920's, and tagging estimates of 1947-49 and 1952, the best estimate of the ratio of female to male survival from birth to age 3 appears to be about 1.25.

4. This estimate of the differential survival ratio of 1.25 is used in computing a cumulative estimate of the female population 3 years old and older. The best cumulative estimate of the St. Paul Island adult female population is 854 thousand in 1950 fluctuating slightly to 861 thousand in 1956 and decreasing thereafter to 593 thousand in 1962.

5. Possible explanations for the fluctuations in the tagging estimates for post-1952 year classes are reviewed, and it is shown that these are inadequate to explain the magnitude of the changes. The tagging estimates have been biased by tag mortality, and such tag mortality is heaviest in year classes that have poor overall survival. Variations in overall survival may be due to temperature changes that are important at a high population level.

6. An unsuccessful attempt is made to estimate the female herd by a dichotomy method to resolve the contradiction between cumulative and tagging estimates.

7. Equations relating male survival to the original pup population on St. Paul Island are recalculated using the new data and from these the optimum pup population levels determined. These are estimated to be 351-366 thousand pups which corresponds at present pregnancy rates to approximately six hundred thousand adult females.

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APPENDIX

COMPARISON OF U.S.S.R. COUNTS AND TAGGING ESTIMATES

Because it has been possible to count the pups on the Asian islands we hoped that these counts would shed light on the validity of the tagging

estimates there, and by implication, on the Pribilof estimates. Unfortunately, the comparison of counts and estimates on the different areas are contradictory. On Robben Island, where the counting is easy and is believed to be reliable, the counts and estimates (allowing for tag loss of the same order of magnitude as occurs with Pribilof tags) agree (appendix table 1). On the Commander Islands, where counting is difficult and less reliable, the estimates from tagging and the actual counts disagree markedly (appendix table 2).

The estimates from tagging are high because of tag loss, and to a very slight degree because some seals in the kill came from other islands. If the latter factor is ignored, the Robben Island data of appendix table 1 can be used to estimate the tag-lost/tagged ratio. To make N agree with the counted total, s should have been 1,236 for the 1958 year class and 938 for the 1959.

APPENDIX TABLE 1.—Robben Island estimates from tagging¹

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (s)	$N = \frac{(n+1)(t+1)}{s+1}$	Pups counted
1958	1961-62	Number 4,932	Number 7,225	Number 911	Number 38,077	Number 28,813
1959	1962	3,080	9,015	587	47,242	29,598

¹ Data from FSCR.

APPENDIX TABLE 2.—Commander Islands estimates from tagging¹

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (s)	Adjusted ²	$N = \frac{(n+1)(t+1)}{s+1}$	Pups ³ counted
1958	1961-62	Number 4,593	Number 4,887	Number 277	Number 377	Number 59,408	Number 38,100
1959	1962	3,570	7,971	248	397	71,528	41,200

¹ Data from FSCR.

² $s^1 = 1.36s$ for 1958 year class and $s^1 = 1.60s$ for 1959 year class.

³ The 1958 count was marked as incomplete. In FSCR an attempt was made to correct for this. Revised figures are here taken from Report on U.S.S.R. Fur Seal Investigations in 1963, V. A. Arseniev, 1963, p. 34. These are based on counts in subsequent years.

Hence we have

Tag-lost/tagged ratio

$$= \frac{1236 - 911}{911} = 0.36 \text{ (1958 year class)}$$

$$= \frac{938 - 587}{587} = 0.60 \text{ (1959 year class)}$$

The estimate for the 1958 year class is very similar to the tag-lost estimates for the Pribilofs; the

larger 1959 value is not higher than the highest observed on the Pribilofs.

These tag-lost estimates have been applied to the Commander Islands recovery data (appendix table 7).

Even allowing for tag loss, the estimates greatly exceed the counts. The estimates may be about 10 percent too high because of the presence of Pribilof animals in the kill. The bulk of the discrepancy is unexplained; whether due to tag mortality or some other cause is unknown. The discrepancy can be used to support the contention that the Pribilof tagging estimates are also in error.

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