POTENTIAL IMPACT OF ENTANGLEMENT IN MARINE DEBRIS ON THE POPULATION DYNAMICS OF THE NORTHERN FUR SEAL, *CALLORHINUS URSINUS*

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ABSTRACT

A model of the population dynamics of the Pribilof Island population of the northern fur seal, *Callorhinus ursinus*, was developed using field estimates of age- and sex-specific mortality and reproductive rates. In the model, mortality rates of pups and juveniles are density dependent, while rates for older seals are constants for each age and by sex. Model-predicted pup production is compared to pup counts made in the field.

If initialized at 1912 numbers, the model population increases at the rate observed between 1912 and 1940, then oscillates around the population level of the 1940's and 1950's, thought to be the carrying capacity of the Pribilof Islands. When the female harvest (including pelagic collections) of 1956-74 is added to the simulation at the annually specified rates, the predicted pup production decreases until 1965, but recovers to preharvest levels by 1975.

Entanglement rate and resulting mortality are assumed to be proportional to the rate of entanglement of subadult males in the harvest, specified by year. When both female harvest and mortality resulting from entanglement in plastic debris are added to the simulation, the model population declines at observed rates, suggesting that entanglement mortality can account for the recent decline in the fur seal population. The model indicates that the population will continue to decline at 1% per year if mortality remains at current levels. This rate of decline is slower than the 4-8% decrease per year of the 1970's because of higher pup and juvenile survival rates at lower population density. The model indicates that a reduction in entanglement mortality rates by 20% would be enough to stop the current population decline and maintain the population at current levels.

In R. S. Shomura and M. L. Godfrey (editors), Proceedings of the Second International Conference on Marine Debris, 2-7 April 1989, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFSC-154. 1990.

INTRODUCTION

In the early 1900's, the population of the northern fur seal, *Callorhinus ursinus*, breeding on the Pribilof Islands in the Bering Sea had been reduced by harvesting to about 300,000 total individuals and fewer than 100,000 pups born per year. A ban on harvesting in 1911 by international agreement allowed the population to recover, such that a population level estimated at about 2 million total individuals was reached by the 1940's and continued through the 1950's. (See reviews by York and Hartley 1981; Lander and Kajimura 1982; Scheffer et al. 1984; Fowler 1985a.) In 1956, harvest of females was begun in an effort to reduce the population size to a level at which the then-predicted maximum sustainable yield in pup production could be obtained. The harvest of females was continued until 1968, and pelagic collections of females for research purposes were made between 1958 and 1974 (York and Hartley 1981). When the female harvest was ended, it was expected that the population would increase and return to the 1950's population level. However, the population has continued to decline at 4-8% per year since the late 1970's (Briggs and Fowler 1984). Evidence indicates that this decline may be the result of lethal entanglement in fishing debris and plastic packing bands (Fowler 1985a, 1985b).

In order to evaluate quantitatively the effect of the female harvest and entanglement on the Pribilof Island fur seals, we have developed a population dynamics model and have compared resulting predicted pup production against estimates made in the field. The population model consists of annual age classes of males and females with mortality and reproductive rates which are dependent on age and sex. Mortality of pups on land and of juveniles during their first 20 months at sea is density dependent, while mortality rates of older seals and pregnancy rates of females are density-independent, age-specific constants using best available estimates. Harvest mortality is considered separate from natural mortality and, when applicable, occurs only during the summer harvest season. Entanglement mortality rates are added to natural mortality when simulating the population dynamics of the last two decades.

MODEL ASSUMPTIONS

The age-specific pregnancy rates calculated by York (1979), using data from the pelagic collections conducted by the United States and Canadian Governments between 1958 and 1974, are assumed as birth rates (Table 1 and Fig. 1). Therefore, reproductive rates in the model are dependent solely on the number of adult females, assuming that enough adult males are present to impregnate those females at all population densities. The sex ratio at birth is assumed 1:1.

Natural mortality of seals age 2 or more years is assumed to be constant by age class and sex. In the model, natural mortality does not include mortality due to commercial harvest (or pelagic collection for research purposes) or recent mortality believed to be due to entanglement in fishing gear. Natural mortality rate estimates by age and sex are available from several sources (Chapman 1964; Lander 1979, 1980a, 1981; Eberhardt 1981; Smith and Polacheck 1984). Those of Lander (1980a, 1981;

Table 1.--Pregnancy rates (York 1979), age-specific natural mortality rates (Lander 1980a, 1981), and harvest rates on immature males (Lander 1980a) used in the population dynamics model. (Asterisks indicate rates which are density dependent and therefore not constants.)

Age	Percent of females pregnant	Natural survival rate (per year)		Male harvest rate (per year)
		Female	Male	
1	0	*	*	0
2	0	0.840	0.78	0.028
3	0	0.920	0.77	0.403
4	4	0.940	0.76	0.573
5	37	0.940	0.74	0.147
6	70	0.945	0.72	0
7	80	0.950	0.72	0
8	85	0.950	0.72	0
9	87	0.938	0.70	0
10	88	0.924	0.65	0
11	88	0.906	0.63	0
12	88	0.884	0.60	0
13	87	0.858	0.55	0
14	84	0.876	0.50	0
15	81	0.789	0.43	0
16	77	0.743	0.30	0
17	71	0.692	0.20	0
18	63	0.630	0.10	0
19	56	0.564	0	0
20	47	0.490		
21	37	0.411		
22	26	0.330		
23	11	0.300		
24	0	0.250		
25	0	0.200		
26	0	0.150		
27	0	0.100		
28	0	0.050		
29	0	0		

Table 1 and Fig. 2) are assumed in the present model, after correction for subadult male harvest rate was made.

The use of constant mortality rates assumes that mortality is independent of population density. While there is no evidence to date that mortality of older fur seals is density dependent, there is evidence of density dependence for the mortality of pups on land and for juveniles <2 years old (Fowler 1984, 1985a; Smith and Polacheck 1984). Thus, density-dependent relationships for these age groups are included in the model.

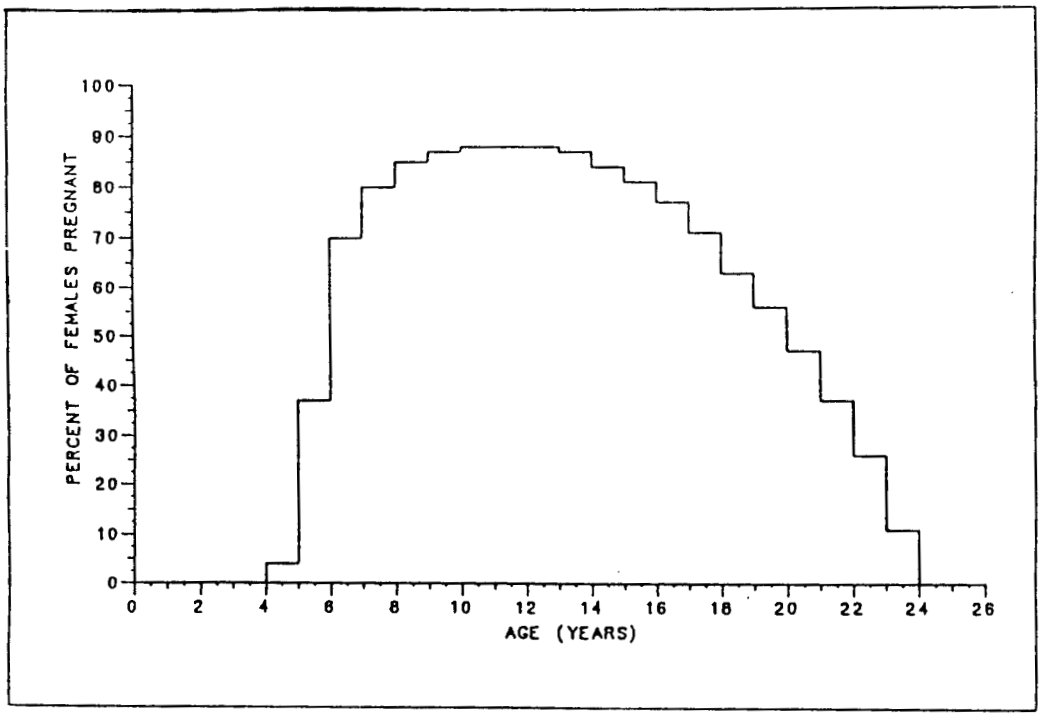

Figure 1.--Pregnancy rate as a function of age.

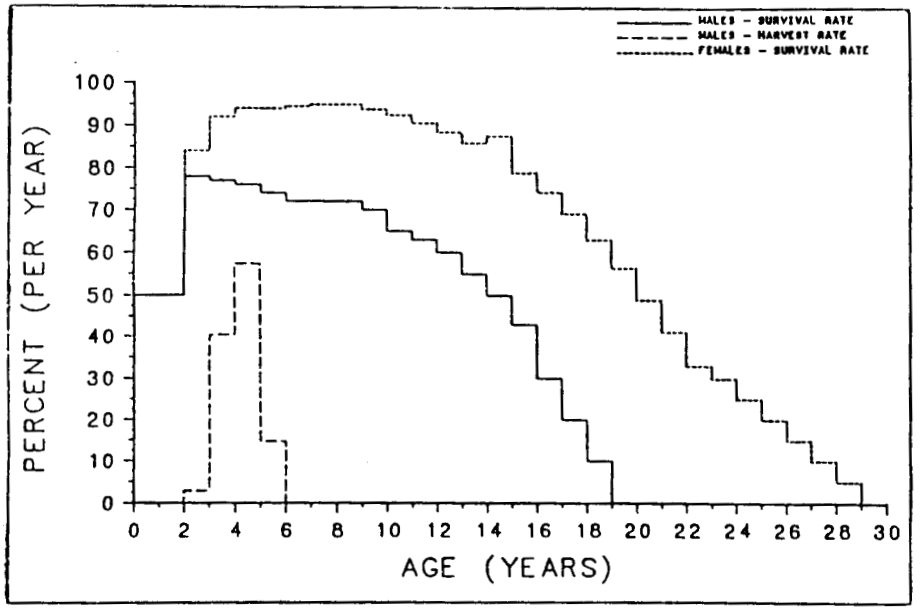

Figure 2.--Natural survival and harvest rates as functions of age and sex (after Lander 1980a, 1981).

The mortality of pups on land appears to increase with increasing number of pups counted on the rookeries (Lander 1979; Swartzman 1984). the model, natural mortality rate of pups on land is a function of the In number of pups born, assuming the functional relationship drawn by Swartzman (1984) between pups born on St. Paul Island and their estimated mortality (line SL in Fig. 3). Pups born on St. Paul are assumed to represent 80% of the total for the two islands, St. Paul and St. George (Briggs and Fowler 1984; Smith and Polacheck 1984). Pups are assumed to remain on land for 128 days (based on data of Gentry and Holt 1986) and on-land mortality is applied over that time period. Male and female pups suffer the same rate of mortality while on land.

Survival during the first 20 months at sea also appears to be related to the number of pups born (Chapman 1961; Lander 1979; Eberhardt 1981; Fowler 1985a, 1985b). Using data for the 1950 to 1970 year classes (Fig. 4, line PA), Lander (1979) found that survival of males during their first 20 months at sea is linearly related to pup survival on land. As pointed out by Fowler (1985b), when data for the years after 1970 are included, the relationship no longer holds. Fowler presented evidence that this difference in juvenile mortality is related to the increase of entanglement in fishing debris and other plastic materials, which he believed to become significant after 1965. Therefore, a linear regression for the data of 1950-65, excluding 1956, is used in the present model, as suggested by Fowler (1985b, line PB in Fig. 4).

Survival rates of female juveniles appear to be higher than those of males of the same age (Chapman 1961, 1964; York 1987). However, the magnitude and density dependence of female juvenile survival is unknown. Using a variety of techniques, Chapman (1961, 1964) estimated the ratio of female to male survival to age 3. From a simple population model using weighted-average pregnancy rates and mortality rates of females older than 3 years, Chapman (1961) calculated that this ratio should be about 2.0. In a similar analysis, Chapman (1964) calculated a ratio of 1.72 using 1920's population estimates and 1.27 using 1950's data. Based on tagging returns, Chapman (1964) estimated the ratio of female to male survival to age 3 for 10 year classes (1951-60), finding an average value of 1.64. However, he pointed out that these estimates are probably biased such that the ratio should be higher. Two of the ten tagging estimates were about 1.27, and the other eight (later) estimates averaged 1.74. Thus, two values for the ratio of female to male survival to age 3 were tried in the present model, 1.27 and 1.74. Since mortality of pups on land is assumed the same for both sexes and mortality from age 2 to 3 is 1.077 times as high for females as males (Table 1), the ratio of female to male survival during the first 20 months at sea is assumed 1.18 or 1.62.

Because the number of males over the age of 2 years has no influence on female survival rate, reproductive rate, or future population size in the model, the mortality rate of males older than 2 influences only the number of males in the population. Thus, harvest rate of subadult males is assumed to be zero in all simulations reported here, except as indicated where the 1970's harvest rates in Table 1 and Figure 3 are used.

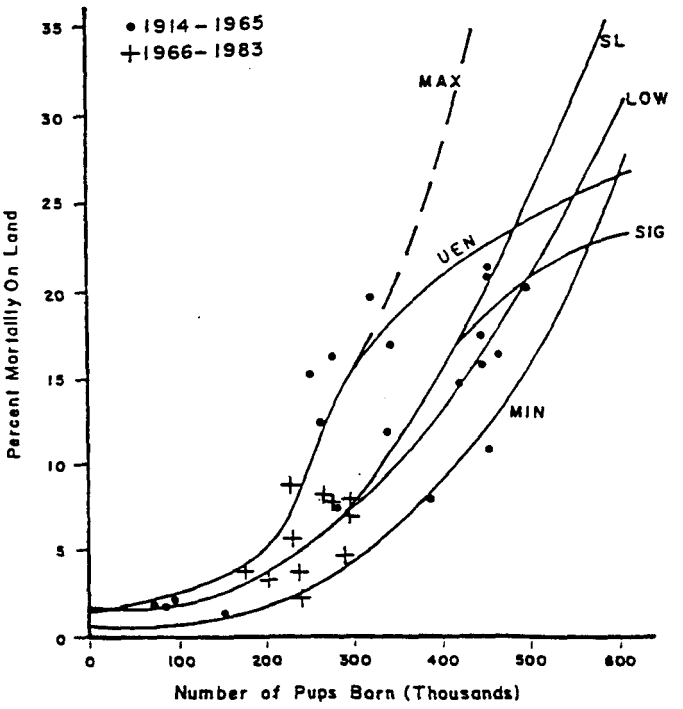

Figure 3.--Alternate density-dependent pup mortality curves. Data are from Lander (1980b); SL is the curve drawn by Swartzman (1984) through the data; MAX and MIN are the maximum and minimum curves tested here; UEN is a sigmoid alternative to MAX; SIG is a sigmoid alternative to SL; and LOW is a lower version of SL.

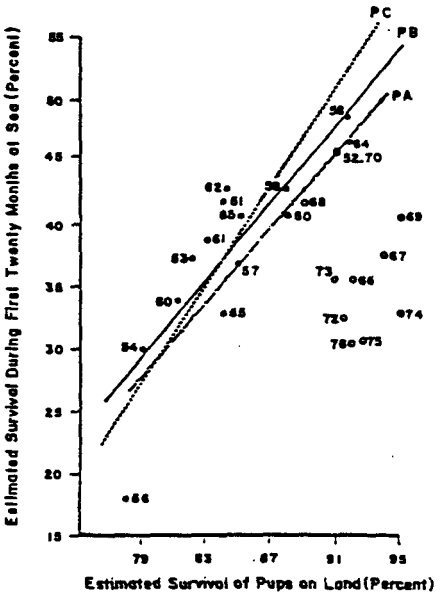

Figure 4.--Alternate linear regressions of juvenile mortality rate as a function of pup survival. PA is from Lander (1979), regressed on the data for 1950-70; PC is the same, but for 1950-65 (before significant entanglement is thought to have occurred); and PB is for 1950-65, excluding 1956.

Harvest rate of females is assumed to be zero, except when specifically simulating the years 1956 to 1974. For those years, the numbers of females by age harvested or collected pelagically (as reported in York and Hartley 1981) are subtracted from the model population at the time of harvest during the specific year. As assumed by York and Hartley, the age distribution of females in the harvest where age was not determined is assumed to be the same as that for harvested females of known age. The age distribution of females grouped as older than a specified age (e.g., 10 years) is assumed to be equivalent to the age distribution in the model population for that year.

Entanglement mortality rates are the least known of the model parameters which must be estimated. Fowler (1985a, 1985b) has shown that, while there is a linear relationship between male juvenile survival the first 20 months at sea and pup survival on land using data up to 1965, following 1965 the model no longer fits the observations. The discrepancy between the model and observed juvenile mortality for the years after 1965 is linearly correlated with the rate of entanglement observed in the subadult male harvest. This suggests the discrepancy is due to entanglement mortality. The discrepancy (as percent mortality) is added to natural mortality of juveniles up to 2 years of age in the model when entanglement is added to the simulation. Because the average percent entanglement in the harvest has stabilized at 0.4% since the late 1970's, the corresponding discrepancy of 15% mortality is assumed for both male and female juveniles as a starting point in model simulations. The discrepancy has ranged from 7 to 25% since 1966 as rates of entanglement have varied (Fowler 1985b).

Mortality rate for entangled males between 2 and 3 years of age was estimated by Fowler (1985b) from the relative frequency of entangled males in the 2- and 3-year-old age classes in the harvest. His estimate is that 5.5% of 2- to 3-year-old males become entangled each year and that 90.3% of entangled males die. Thus, 5% mortality due to entanglement is used in model simulations for male seals between 2 and 3 years of age. Females of this age are assumed to suffer the same or higher rates of entanglement mortality, due to their smaller size (see Discussion).

Entanglement mortality rates of older seals are not available. Fowler (1985b) suggests that entanglement mortality of seals over 3 years of age is assumed to be between 0 and 5% per year. Different values were tried in various simulations. Both males and females are assumed to suffer the same entanglement mortality once past the age of 3.

For all simulations, the populations were initialized at 1 January sizes and ages. A daily time step was used. Mortalities and births were calculated on appropriate dates in the yearly cycle.

RESULTS

Simulation of the Population at Carrying Capacity

Assuming the above-described pregnancy rates, constant natural mortality rates for seals over age 2, no harvest on either males or females, and

no entanglement mortality, the density-dependent pup mortality relationship SL in Figure 3, and the male juvenile survival relationship PB in Figure 4, population equilibria were found for each of the two assumed values of the ratio of female to male survival up to the age of 3, 1.27 and 1.74. Assuming this ratio is 1.27, the population reaches 1.73 million total individuals (censused on 1 January), 1.15 million total females, and 442,000 pups born per year. If the female to male survival ratio is assumed to be 1.74, the total population reaches 1.95 million seals, 1.39 million females, and 540,000 pups born each year.

In the 1940's and 1950's, the fur seal population on the Pribilofs was relatively stable, with 525,000-576,000 pups born each year in the 1950's. This population is thought to have been at carrying capacity for the Pribilof Islands (Fowler 1985a). The model population, assuming a female-to-male survival ratio to age 3 of 1.74, is consistent with observations, while the lower ratio of 1.27 causes the model population to fall short of the observed levels.

If the model is initialized at 15% of the equilibrium population size, a level where pup production matches that of 1912, the model population and number of pups born increase at the same rate as observed pup counts in the 1910's and 1920's, 7.4% per year (Fig. 5). The model population overshoots the equilibrium size in the early 1940's, and afterwards oscillates around the equilibrium of 540,000 pups born per year, with the oscillation damping out over time. The agreement between the model and the observed rate of increase in the 1910's and 1920's suggests that the assumed pregnancy and mortality rates are realistic. Furthermore, a ratio of female to male survival to age 3 on the order of 1.74 is consistent with available data. This ratio was suggested by Chapman's results (1961, 1964), even though he and others have been more comfortable with a much lower ratio. When this same simulation is run with the female-to-male juvenile mortality ratio at 1.27, the projected population increase from the 1912 level is less than the observed rate of increase (Fig. 6).

To determine how sensitive the simulated carrying capacity population is to the various pregnancy and mortality rates assumed, these rates were varied individually within the range of possibilities observed to determine resulting population size. Alternate pregnancy rates by age (up to age 11) were taken from Chapman (1964) and from estimates reported in Smith and Polacheck (1984, table 11), which were based on Japanese collections of females between 1958 and 1960. The Japanese estimates represent the highest reported values for pregnancy rates of younger females. These high rates increase pup production to 583,000 per year (+8%) and decrease the total number of females by 9% (Table 2). Chapman's pregnancy rate estimates increase pup production by only 2% and have almost no effect on the total number of females in the population.

The density-dependent relationship between pups born and pup mortality on land is associated with a large amount of variation, and a number of alternate curves through the observed data were tried (Fig. 3). The resulting carrying capacity population varies from 23% higher to 25% lower than the model result using the standard assumptions (Table 2). Thus, the model is fairly sensitive to this assumed relationship.

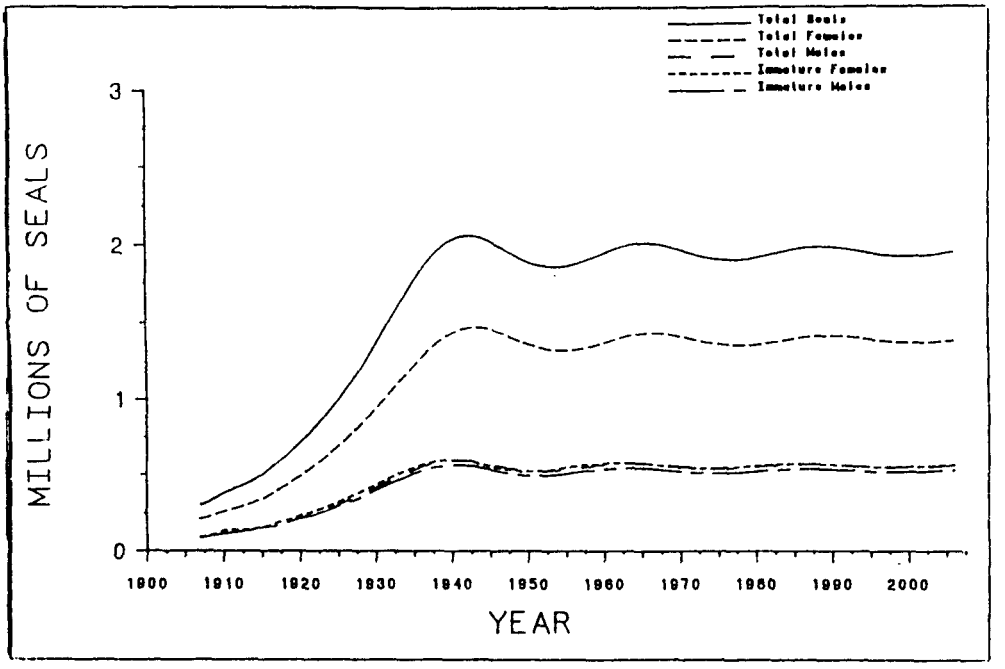

Figure 5a.

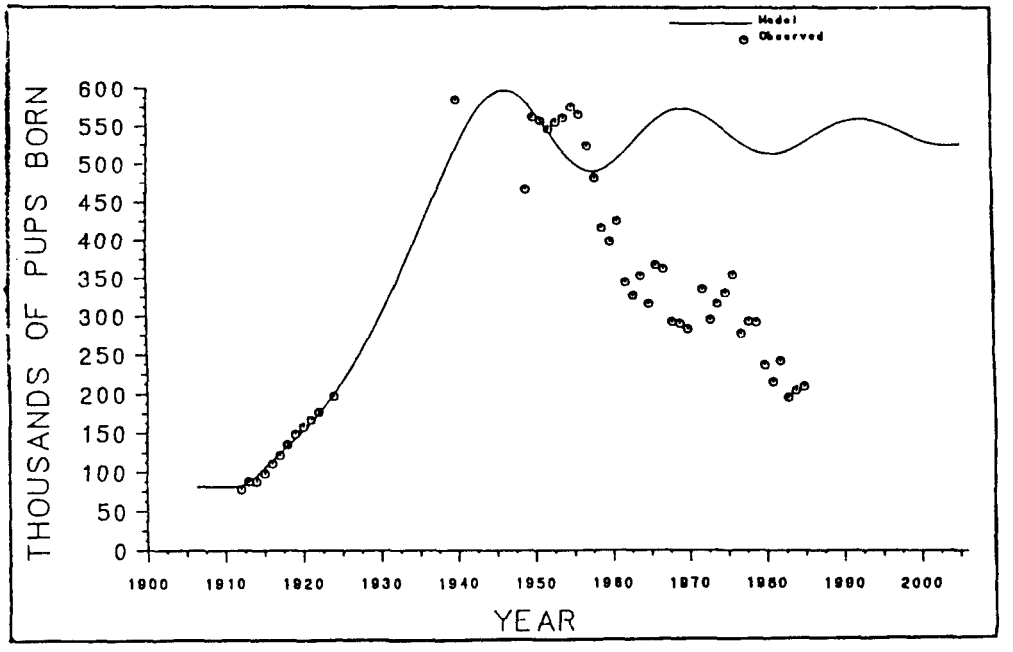

Figure 5b.

Figure 5.--Simulated increase in (a) population level (on 1 January) and (b) number of pups born each year from the depleted population of 1912 to carrying capacity reached by the 1940's. The ratio of female to male survival to age 3 is 1.74. Harvest and entanglement-induced mortality are assumed zero in the simulation.

Table 2.--Resulting equilibrium population levels (on 1 January) and number of pups born each year (in millions of seals) when reproductive rates or mortality rates of certain age groups are varied (see text for specific rate variations) from the standard run producing the best fit to the 1950's carrying capacity population (pregnancy as in Table 1; pup mortality as curve SL in Figure 3; male juvenile survival as line PB in Figure 4; ratio of female to male survival to age 3 = 1.74; no harvest; and mortality over age 2 as in Table 1).

Reproductive or mortality rate(s) varied	Total seals	Total females	Pups born
Standard run (equilibrium of Fig. 5)	1.95	1.39	0.540
Pregnancy rates:			
As in Chapman (1964)	1.93	1.38	0.553
As in Japanese collections, 1958-60	1.79	1.27	0.583
Pup mortality curve (from Fig. 3):			
MIN	2.37	1.71	0.647
LOW	2.23	1.59	0.622
SIG	2.20	1.57	0.611
UEN	1.62	1.16	0.450
MAX	1.46	1.04	0.407
Male juvenile survival line (from Fig. 4):			
PA	1.92	1.37	0.533
PC	1.91	1.36	0.527
Ratio of female to male survival to age 3:			
2.0	2.00	1.46	0.570
1.64	1.92	1.36	0.529
1.37	1.81	1.23	0.473
1.27	1.73	1.15	0.442
1.08	1.54	0.99	0.376
Subadult male harvest rates:			
As in Table 1	1.92	1.39	0.540
Adult female mortality rates:			
As in Chapman (1964)	1.96	1.39	0.509
As in Smith and Polacheck (1984)	1.90	1.31	0.454

Male juvenile survival as a function of pup survival on land was varied to be as line PA in Figure 4, i.e., the relationship in Lander (1979), and as line PC in Figure 4, i.e., including all data from 1950 to 1965 in the regression. The resulting population size differed from the standard run using line PB (Fig. 4) by at most 2%. Thus, the results are insensitive to this amount of variation of the relationship.

The ratio of female to male survival to age 3 has been estimated by Chapman (1961, 1964) as between 1.25 and 2.0. The resulting model population sizes range from 18% less than to 5% greater than the standard population model run where the ratio is 1.74 (Table 2). Thus, the model is fairly sensitive to the assumed ratio within the range of estimates which have been made. If the ratio is assumed to be 1.0, the population reaches an equilibrium 30% lower than the standard model equilibrium (Table 2), a level well below the 1950's population size.

As mortality of males over the age of 2 has no influence on female or pup population size in the model, the model population is insensitive to variation in subadult male harvest rates or variation in natural mortality of males over the age of 2. A subadult male harvest rate equivalent to that in the 1970's (Lander 1980a) reduces the total male population by 5% (Table 2).

Mortality rates of females over the age of 3 as given by Chapman (1964) result in the same number of total females in the population as the standard model assumptions (Lander 1981), but the age distribution is such that only 509,000 pups are born per year (-6%, Table 2). The lower estimated survival rates of Smith and Polacheck (1984) reduce the female population by 6% and pup production at equilibrium by 16%. However, the estimates of Lander (1981) are based on considerably more data than the other two sets of estimates, and the error of the standard model run associated with error in adult female mortality rates is probably somewhat less than these results.

Simulation of the Pribilof Population Decline Since 1958

When the female harvest and pelagic collection of 1956-74 is removed from the simulated carrying capacity population during those years, the predicted number of pups born decreases until 1965 and subsequently recovers to the preharvest level by 1975 (Fig. 7). While the female harvest may account for some of the decline after 1958, it is clearly a minor perturbation from which the population should have rapidly recovered, assuming the carrying capacity remained unchanged from the 1950's level.

The population decline after the female harvest ceased has been a subject of much discussion in recent years, with the prevailing opinion being that lethal entanglement is the most likely causative factor (Fowler 1985a, 1985b). Assuming that entanglement became significant in 1966 (as suggested by Fowler), that an additional 15% of males and females die from entanglement by age 2, and that 5% mortality of all seals age 2 and older is due to entanglement, the resulting pup production is as in Figure 8. Under these assumptions, the model population does not decline as fast as the observed pup production indicates it should. This suggests that entanglement mortality may have been significant before 1966, or that there is some other cause of the additional mortality after 1958. If the same assumed mortality rates are initiated in 1960, the model decline fits the observed more closely (Fig. 9).

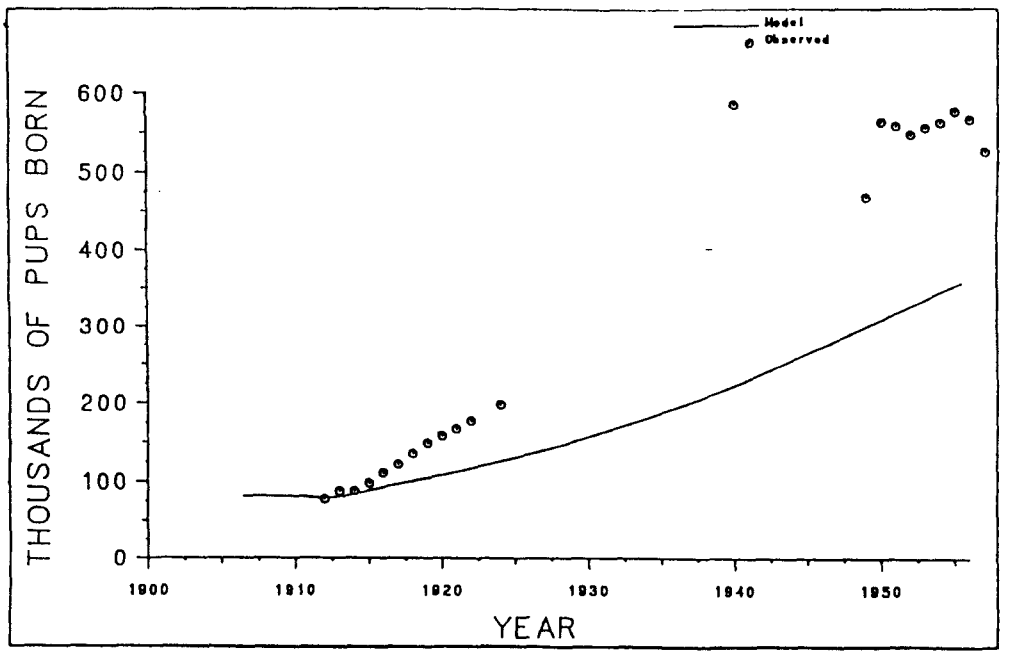

Figure 6.--Number of pups born in model population assuming the same rates as in Figure 5, except the ratio of female to male survival to age 3 is assumed to be 1.27.

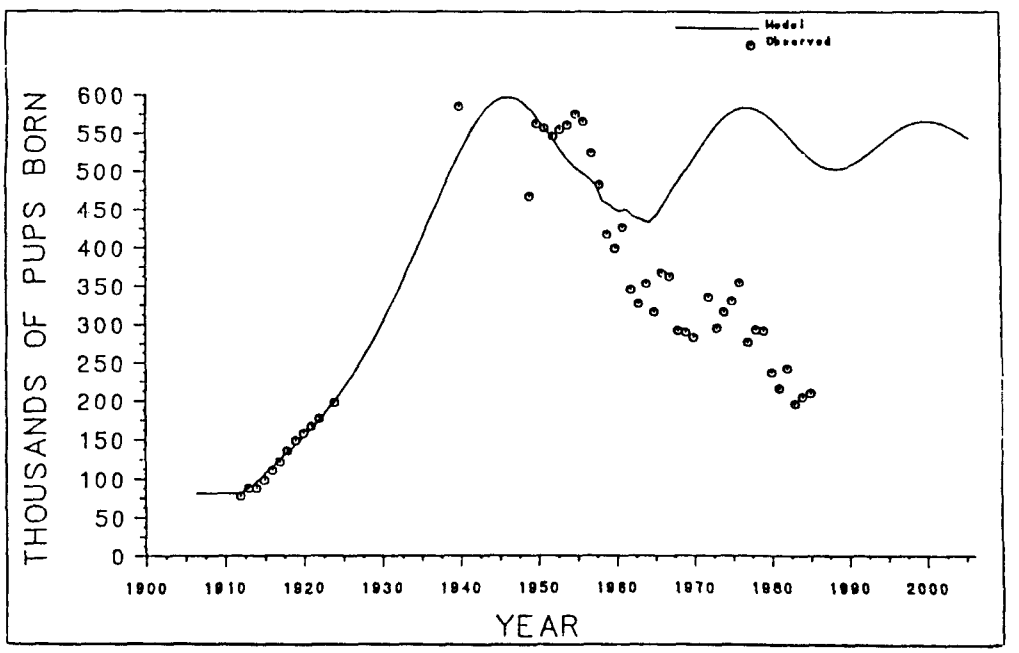

Figure 7.--Number of pups born to modeled and observed populations over time, including simulation of female harvest between 1958 and 1974 but assuming no mortality due to entanglement.

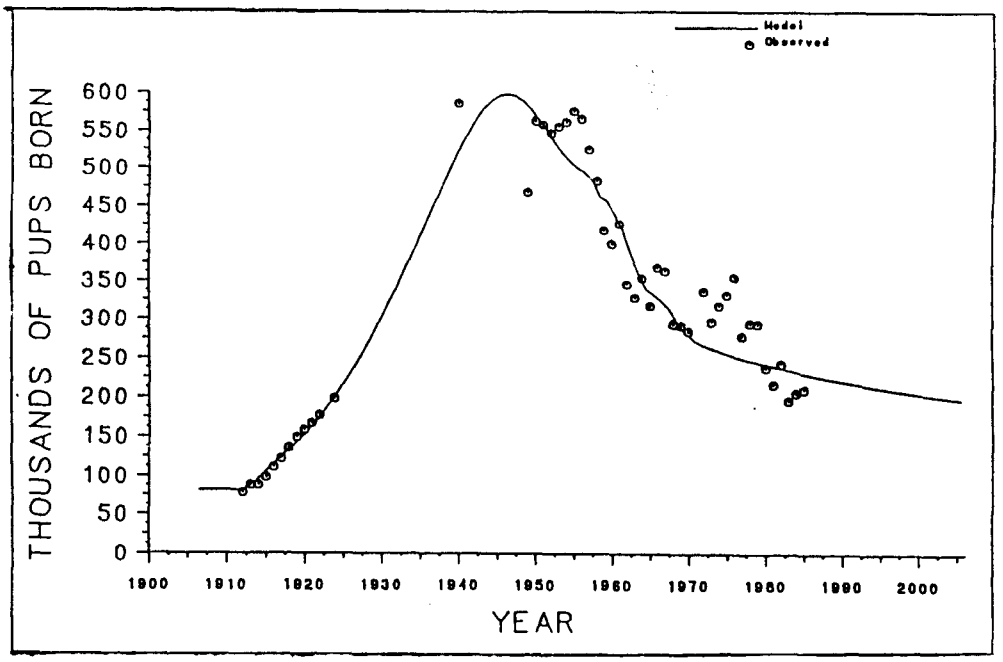

Figure 8.--Number of pups born to modeled and observed populations over time, including simulation of female harvest (1958-79) and constant entanglement mortality of 15% before and 5% after 2 years of age beginning in 1966.

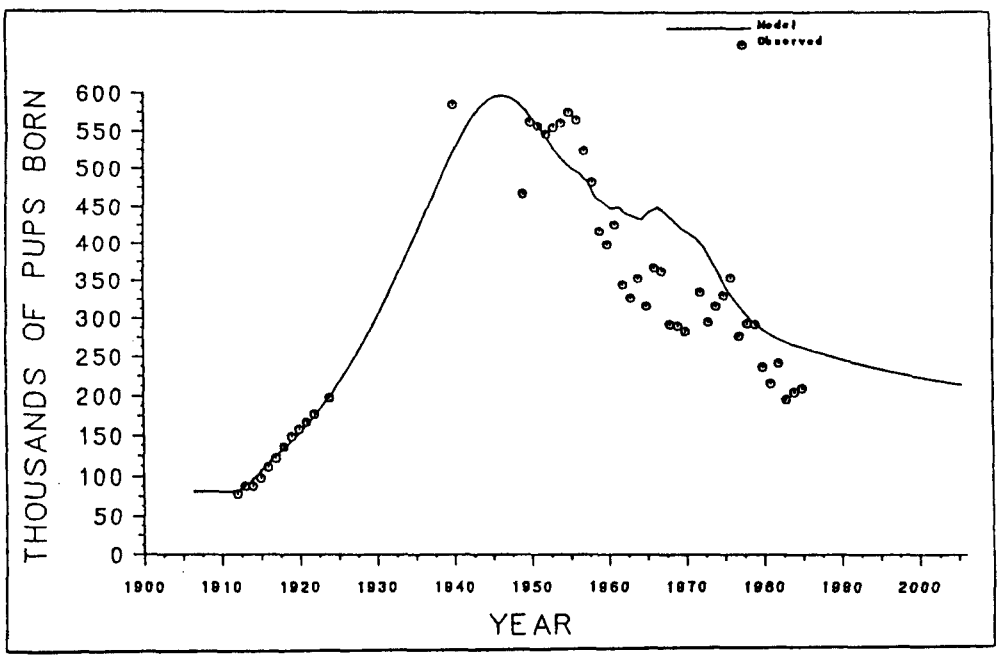

Figure 9.--Number of pups born to modeled and observed populations over time, including simulation of female harvest (1958-79) and constant entanglement mortality of 15% before and 5% after 2 years of age beginning in 1960.

In the model runs shown in Figures 8 and 9, all seals over age 2 are assumed to suffer 5% mortality per year due to entanglement. If seals over age 3 are assumed to suffer insignificant (zero) mortality due to entanglement, as suggested by Fowler (1985b), the model population declines to only 1.06 million total females with 401,000 pups born per year, a level much higher than observations for the last two decades (Fig. 10). Thus, adult females must be suffering mortality over and above Lander's (1981) estimated rates, whether due to entanglement or some other cause.

The rate of entanglement in the subadult male harvest was not constant between 1967 (the first year of observation) and the present. Before 1970, entanglement rate was below 0.4%. From 1973 to 1975 it increased to about 0.7% and subsequently stabilized at about 0.4% (Fowler 1985b). Before 1970, male juvenile survival was closer to 10%, rather than 15%, below the expected rate from line PB in Figure 4. Between 1973 and 1975 the discrepancy between observed and expected (line PB) was about 20%.

Assuming that entanglement varied proportionately for all age classes of seals, all entanglement mortality rates in the model were reduced by one-third over 20 months (one-fifth per year) before 1970 and increased by the same amount for 1973 to 1975. Thus, an additional 10 to 20% of juveniles are assumed to die from entanglement by age 2. Entanglement mortality of all seals over 2 years is assumed to vary between 4 and 6% per year. The resulting pup production is compared to the observed in Figure 11. The fit to the observed is improved by this inclusion of variable entanglement rate in the model (compare Figs. 9 and 11).

If the same assumptions used for the simulation of Figure 11 are made, only with 2- to 3-year-olds suffering 8 to 12% mortality per year (an annual rate equivalent to the additional 15% lost over 20 months as juveniles $\pm$20% of that value) while rates for seals over 3 remain at 4 to 6% per year, the resulting decline is as in Figure 12. This latter simulation brings the model population level down to the same level as the current pup counts on St. Paul Island indicate. Figure 13 shows associated total population numbers.

Model Predictions of Future Population Numbers

The model simulation of Figure 13 (and Figs. 8, 9, 11, and 12 as well) indicates that, while the current rate of decline is much slower than the 4 to 8% decline of the 1970's, the Pribilof fur seal population would continue to decline at about 1% per year for the next 50 years or more if mortality rates remain at current levels. If entanglement mortality were eliminated (and assuming pre-1960 survival rates still hold), the population could recover to the 1950's carrying capacity level after about 15 years, as evidenced by the increase from the late 1920's to the 1940's (Fig. 5). If current entanglement mortality rates (as assumed in Figs. 8 and 9) were halved for all age groups, the population could recover in about 50 years to a total of 1.61 million seals, 1.13 million total females, and 400,000 pups born, where the model population stabilizes (Fig. 14). This is a size equivalent to the observed population in 1960. If entanglement mortality rates were held at the levels assumed for the 1960's

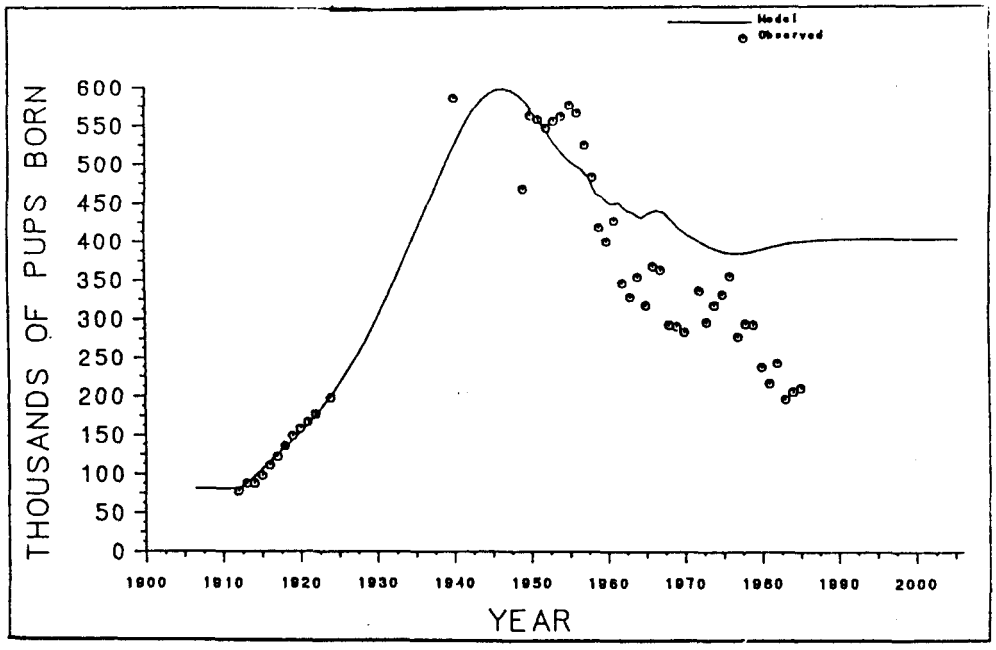

Figure 10.--Number of pups born to modeled and observed populations over time, including simulation of female harvest (1958-74) and, beginning in 1966, constant entanglement mortality of 15% before age 2, 5% from age 2 to 3, and no entanglement mortality over the age of 3 years.

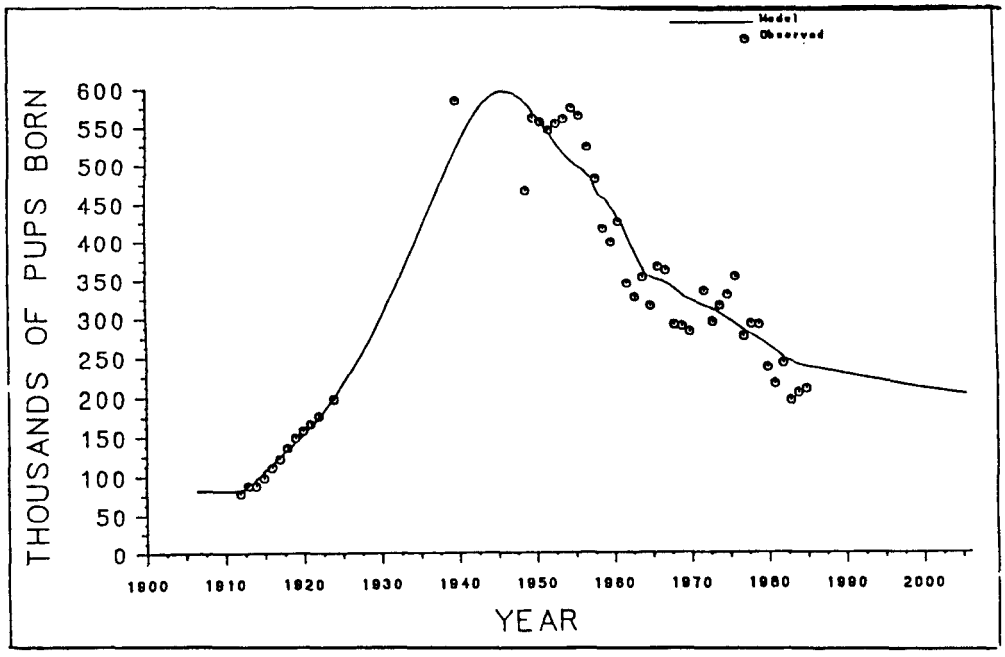

Figure 11.--Number of pups born to modeled and observed populations over time, including simulation of female harvest (1958-74) and variable entanglement mortality rates (10-20% before and 4-6% after age 2 years) beginning in 1960.

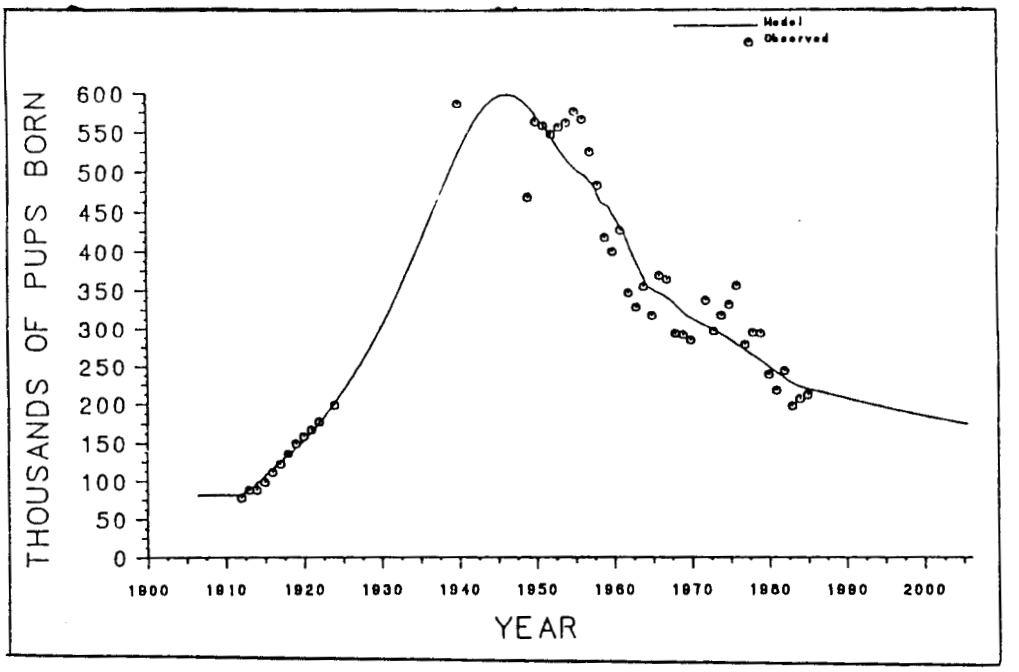

Figure 12.--Number of pups born to modeled and observed populations over time, including simulation of female harvest (1958-74) and variable entanglement mortality rates (10-20% before age 2, 8-12% between 2 and 3 years, and 4-6% after age 3 years) beginning in 1960.

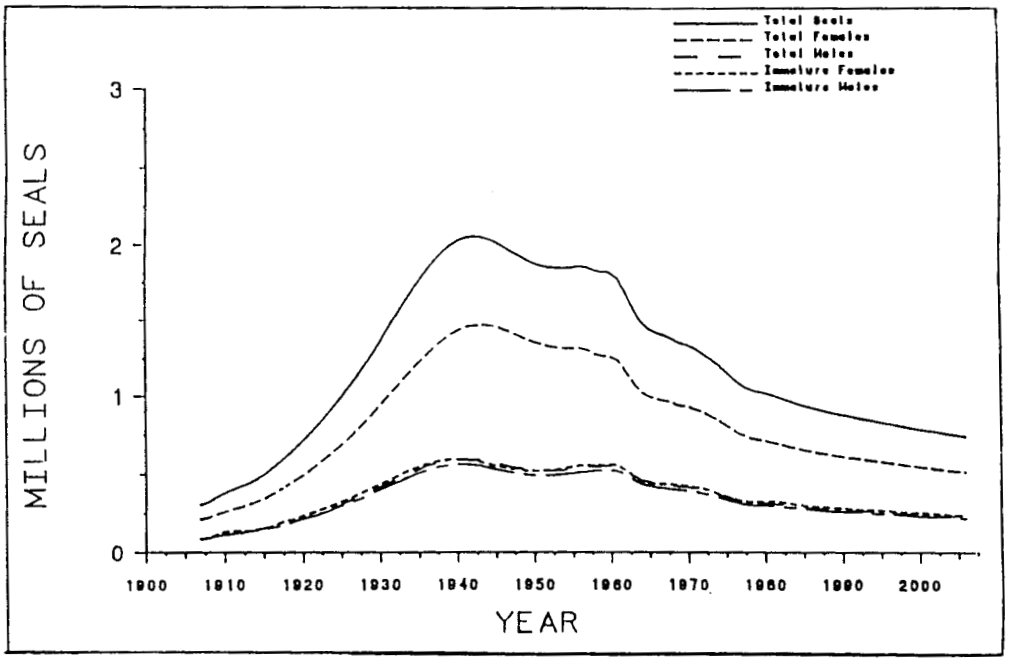

Figure 13.--Simulated population numbers (on 1 January) for the simulation of Figure 12.

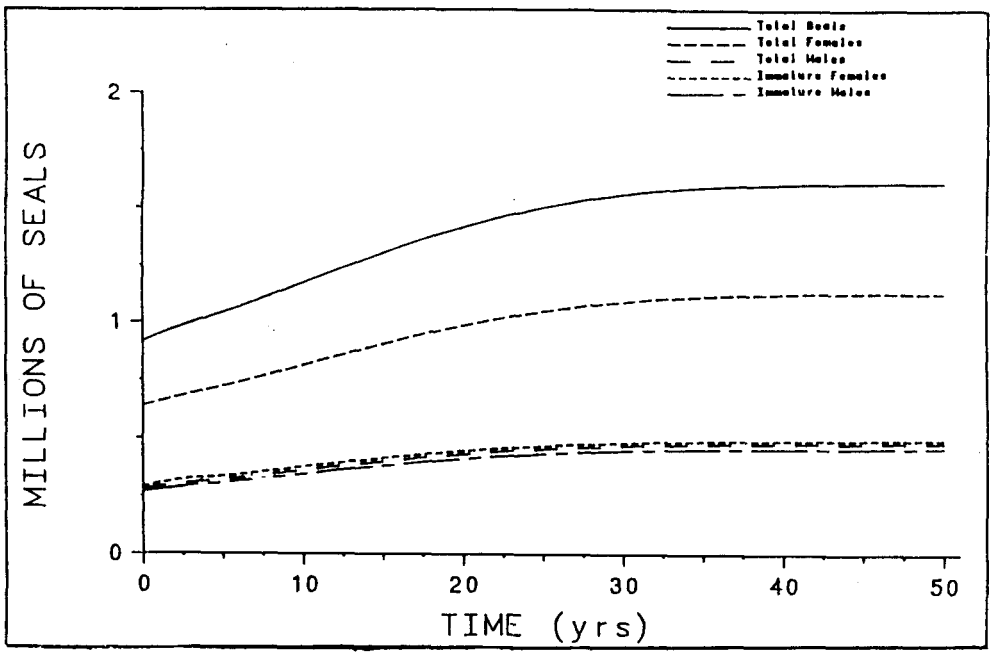

Figure 14.--Simulated population numbers (on 1 January) assuming that current entanglement rates are halved and after initializing with the estimated population size in 1987.

in the model run of Figure 12 (an additional 10% of juveniles die before age 2, 8% per year from age 2 to 3, and 4% per year over age 3), the population would increase slowly from present levels (917,000 total seals, 637,000 females, and 214,000 pups born in the 1987 simulated population) to 1.29 million seals, 896,000 females, and 301,000 pups born per year after 50 years and would stabilize at 1.34 million seals, 932,000 females, and 315,000 pups after 90 years.

DISCUSSION

The model results show that current estimates of pregnancy and natural mortality rates as outlined above are consistent with observational data from 1912 to 1958 if the ratio of female to male survival to age 3 is assumed to be 1.74. The model simulates the population increase from 1912 to the 1940's and predicts the appropriate carrying capacity level thought to have prevailed in the 1940's and 1950's. Lower estimates of the female-to-male juvenile survival ratio yield much lower equilibria and rates of population increase than have been observed on the Pribilofs. Clearly, the model is sensitive to female juvenile survival rate. However, this vital statistic is the least well known and least studied of all the vital rates involved. Tagging or other studies on female juveniles would greatly facilitate the estimation of their current survival rates.

Model sensitivity analysis shows that model results are also highly dependent upon the choice of the density-dependent relationship between pup mortality and number of pups born. The considerable variability associated with this functional relationship (Fig. 3) is undoubtedly due to the dependence of pup mortality on other factors besides total number of pups born. Actual pup density on the rookeries, climatic conditions, and competition with other species for food are other possible factors (which are not necessarily independent) which could be considered in developing more predictive functional relationships.

The model is relatively insensitive to changes in pregnancy rates and adult female natural mortality rates within the range of estimates available in the literature. Therefore, these vital statistics appear to be well enough known for modeling purposes.

The carrying capacity of the Pribilof Islands population appears to be regulated by the density of pups born on the rookeries. Subsequent survival as juveniles appears to be causally related to survival rate on land (Lander 1979, Fig. 4). This suggests that lower survival rate at higher population density is primarily due to reduced fitness of pups, whether by increased spread of disease, slower weight gain due to competition for food or space among lactating females, or other effects of crowding. The model is consistent with the view that there is no significant density-dependent control of mortality over the age of 2 years.

Owing to the weak density-dependent control of the fur seal population, the maximum pup production is at carrying capacity, not at a lower population size. This is in agreement with observations in the field during and after the period of female harvest in the late 1950's and 1960's.

The population decline after 1958 has been a subject of intense interest in recent years (e.g., Eberhardt 1981; Fowler 1984, 1985a, 1985b; Smith and Polacheck 1984; Trites 1984). The initial decline may be partially accounted for by the female harvest of 1956 to 1968 (York and Hartley 1981 and present model), but after 1960 it is evident that other factors are involved (Fig. 7). The model results suggest that entanglement mortality can account for the decline after 1960 if the following assumptions are made regarding female mortality (male mortality has no influence on pup production): An additional 15% of juveniles (less than age 3), on average, died from entanglement; an average of 5% of seals over age 3 suffered lethal entanglement; and significant entanglement mortality (at these rates) began in 1960.

The fit of the model to the observed pup counts is improved considerably if entanglement mortality rate is varied as a function of the entanglement rate observed in the subadult male harvest. A variation of $\pm$50% of entanglement rate, i.e., 0.2 to 0.6%, appears to result in $\pm$33% variation in the mean discrepancy between observed male juvenile survival rate and that predicted from line PB in Figure 4 (Fowler 1985a), or $\pm$20% variation in entanglement mortality rate per year. If entanglement mortality rates of all age groups vary to this degree in proportion to

variation in observed entanglement rates, the appropriate curvature in the model pup curve after 1965 is produced.

The best fit is obtained if 2- to 3-year-old females are assumed to have suffered twice the entanglement mortality rates of males of the same age. If females over 3 years of age are assumed to not die at significant rates from entanglement, the decline in pups born since 1960 cannot be accounted for, and the model predicts that a stable population size of 1.49 million seals, 1.06 million females, and 401,000 pups born per year should have been reached by about 1985 (Fig. 10). Higher entanglement mortality of females as opposed to males of the same age could be accounted for if entanglement rate is a function of body size, rather than age as assumed by Fowler (1985a, 1985b). Even at 1 year of age, male fur seals are almost twice the size of females; a 3-year-old male is the same size as a 6-year-old adult female, and the largest females (up to 20 years old) are not as large as a 5-year-old male (Lander 1980a). This suggests that if entanglement is primarily a function of size, adult females could be expected to suffer the same entanglement rates as subadult males, perhaps 5% per year as estimated by Fowler (1985b), and immature females even higher rates. The assumption of 10% entanglement mortality rate for 2- to 3-year-old females is consistent with this hypothesis. Clearly, more information is needed on female entanglement rate and mortality as a function of age. The assumption that males and females of the same age suffer the same mortality rates is unlikely, especially given the disparity in size.

In the above analysis it is assumed that pups on land do not suffer entanglement mortality. In the model, pups of mothers dying from entanglement are assumed to die. Recent evidence reported by DeLong et al. (1988) suggests that mortality rates of pups may be increased by nonlethal entanglement of their mothers, since the females are less efficient at foraging and providing milk for the pup. However, as evident in Figure 3, pup mortality rates on land at a given density do not appear to have changed from 1914-65 to 1966-83, before and after the hypothesized onset of entanglement. Therefore, there is no evidence to support the hypothesis that nonlethal entanglement of lactating females has significantly affected pup mortality on land or the pup population as a whole.

As shown by the model results in Figure 14, a reduction of the current extrinsic mortality rate (due to entanglement or some other cause) by 50% would allow the fur seal population to recover at least partially. If this mortality is in fact due to entanglement, halving the current entanglement rate (to 0.2% from 0.4% of subadult males), which would reduce the annual entanglement mortality rate by 20%, would stop the current decline in pup production, according to model predictions. This suggests that it would be necessary to halve the density of plastic debris in the North Pacific and Bering Sea region to stop the decline and maintain the population at current levels.

The model results reported here suggest that the fur seal population can recover from single-event perturbations such as substantial harvest of the breeding population (females in the case of fur seals) or some other cause of mortality of finite duration. After the fur seal population was

reduced by 1912 to 15% of its carrying capacity level, the population was able to recover fully in 30 years. Recovery would be faster after smaller perturbations. However, long-term, continuous additional sources of mortality, such as lethal entanglement, form a much more serious threat to the population. While single-event perturbations are significant in the short term, chronic sources of additional mortality are much more important when considering the long-term stability of the population.

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