

# The Decline and Fall of the Pribilof Fur Seal (*Callorhinus ursinus*): A Simulation Study

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Trites, A. W., and P. A. Larkin. 1989. The decline and fall of the Pribilof fur seal (*Callorhinus ursinus*): a simulation study. *Can. J. Fish. Aquat. Sci.* 46: 1437–1445.

A mathematical model incorporating the basic life history features of the North Pacific fur seal (*Callorhinus ursinus*) approximated the decline of the Pribilof Islands population by reconstructing pup estimates and counts of adult males over the period 1950 to 1987. Simulation results suggest that commercial female harvesting and a series of poor juvenile survival rates were responsible for causing and maintaining the observed decline in pup production on St. Paul Island from 1956 to 1970. A more recent drop in pup production since 1976 is also attributed to poor juvenile survival, but with the addition of higher natural mortalities of adult females. It appears that the natural mortality of adult females may have increased by 2 to 5% beginning in the mid 1970s. We suspect reductions in the fur seal food base and entanglement-related mortality associated with commercial fishing in the North Pacific are contributing to the current decline, although neither possibility has yet been clearly demonstrated.

Un modèle mathématique intégrant les caractéristiques fondamentales du cycle de vie de l'otarie à fourrure (*Callorhinus ursinus*) a permis d'obtenir une approximation du déclin de la population des îles Pribilof en reconstituant les estimations du nombre de nouveaux-nés et les dénombrements de mâles adultes entre 1950 et 1987. Les résultats de simulation indiquent que la récolte commerciale de femelles combinée à une série de faibles taux de survie des jeunes adultes ont causé et maintenu le déclin observé de la production de nouveaux-nés sur l'île Saint-Paul entre 1956 et 1970. Une chute plus récente dans la reproduction depuis 1976 est également attribuée à un faible taux de survie des jeunes adultes, mais également à une mortalité naturelle plus élevée des femelles adultes. La mortalité naturelle des femelles adultes semble avoir augmenté de 2 à 5 % à partir du milieu des années 1970. On croit que la réduction des sources alimentaires de base de l'otarie, et la mortalité due à l'empêchement dans les filets lors des pêches commerciales, dans le Pacifique Nord, contribuent au déclin actuel bien qu'aucune de ces deux possibilités n'ait été clairement démontrée.

Received July 12, 1988  
Accepted March 23, 1989  
(J9808)

Reçu le 12 juillet 1988  
Accepté le 23 mars 1989

The number of northern fur seals (*Callorhinus ursinus*) that return each summer to the Pribilof Islands rose from between 200 000 and 300 000 in 1911 to over 1.5 million in the late 1940s and early 1950s (Kenyon et al. 1954; Lander and Kajimura 1982). Growth of the population and the concomitant increase in the commercial harvest of immature males was initially rapid, but slowed markedly during the 1940s. The apparent reduction in growth rate appeared to be due to reduced rates of reproduction (Kenyon et al. 1954) and lower juvenile survival (Chapman 1961) arising from competition for a limited food supply around the Pribilof Islands. Mathematical models incorporating concepts of density dependent regulation (Nagasaki 1961; Chapman 1961) led to the conclusion that greater productivity could be achieved from a smaller population. As a consequence, between 1956 and 1968 the herd was reduced by 315 000 females in addition to the continued male kill (Lander 1980a).

The maximum sustainable yield that was projected for the reduced herd was never attained. Annual pup production and recruitment of harvestable males declined during the herd reduction program and continued after its completion, falling

far short of predicted levels (Chapman 1981). Lowering herd size was supposed to have increased productivity through density dependent changes in population vital rates. It failed to do so. In 1984 there were just over 800 000 animals alive, only about half the peak abundance of the early 1950s (NPFSC 1985).

A large fraction of the decline in pup production during the late 1950s through early 1970s may be explained by the harvesting of adult females (Eberhardt 1981; York and Hartley 1981) and possibly by a poor survival of pups during the mid 1950s (Eberhardt 1981). It has not been possible to account for the decline of the Pribilof population during this period in terms of simple models of self regulation (Eberhardt 1981; Smith and Polacheck 1984), nor have there been any satisfactory explanations for the continued herd decline (see Fowler 1986). There is no indication that the sustained harvest of males has altered pregnancy rates or the survival of pups on land. Similarly there is no evidence of genetic changes in the size of reproducing males because of harvest selection. Predation, disease, parasites, and heavy metal contaminants have not been demonstrated to be significant sources of mortality. It is speculated

that the herd decline might be due to a high incidence of entanglement of seals in fishing debris. Other possibilities that have been examined and rejected are emigration to other areas, human disturbance of rookeries, incidental catch in fishing gear, and commercial overfishing of major fur seal food resources about the Pribilof Islands. None of these possibilities has been shown to explain the decline of the Pribilof population (see Fowler 1986).

One approach to understanding why the Pribilof Island population has been declining since the mid 1950s, is to mathematically reconstruct historical observations during the years of herd decline. Along with offering possible explanations for the decline, simulation results may also suggest implications for future management and research. A simulation model was therefore developed that attempted to reproduce data sets spanning the period 1950 to 1987.

We begin by briefly reviewing the biology of the fur seal and discuss the available data base. A mathematical model is subsequently proposed to reconstruct observed bull counts and pup estimates over the period 1950 to 1987 on St. Paul Island. The reliability of model predictions and the impact upon herd dynamics of altered population parameters are investigated using techniques of sensitivity analysis. The results are shown to offer explanations for past herd dynamics and suggest directions for future management and research.

## Biology of the Fur Seal

The Pribilof northern fur seal spends approximately two-thirds of its life in a pelagic existence and the remaining one-third on the Bering Sea islands of St. Paul and St. George. The St. Paul population accounts for roughly 80% of the total Pribilof herd (Lander and Kajimura 1982) and is the major focus of this paper.

The seals are present on the islands from late May until early November. The mature males arrive early to establish territories on the rookeries and do not leave their positions during the breeding season (Kenyon and Wilke 1953; Fiscus 1978; Bigg 1986). Mature males unable to enter the rookeries live on the fringes or on adjacent hauling grounds. Most of the seals on these haulouts are 3- and 4-yr old immature males that have traditionally been the object of commercial harvesting because they could be killed without interfering with the breeding animals. Juveniles (0–2 yr) are generally not found on the hauling grounds during the commercial harvest, nor are their whereabouts known during the summer following their birth. Commercial harvesting was stopped in 1972 on St. George Island and 1985 on St. Paul. Today sealing continues only at subsistence levels for Aleuts living on the Pribilof Islands (Zimmerman and Letcher 1986).

Mature females (5–6 yr and older) arrive during June and July. They give birth to a single pup shortly after arriving. The pups remain on land near their site of birth until weaned in mid September (Bartholomew and Hoel 1953; Costa and Gentry 1986).

Estimates of pup production from 1950 to 1960 were based on tagging studies and assumptions about the differential survival of juvenile males and females, the size of the female population, and the rate of pregnancy (Chapman 1964). Since 1961, pup estimates within the summer of birth have been based on a "shearing-sampling" method, a variant of the mark-recapture technique (Chapman and Johnson 1968; York and Kozloff 1987). The estimates have all been widely accepted, although

there exists some controversy over the 1950 to 1960 estimates (Smith and Polacheck 1984).

July estimates of adult male numbers on St. Paul Island comprise the second set of field observations. The male seals of adult size (attained at about age 7) are classified as being either harem masters or idle males. Harem masters maintain a territory with one or more females for an average of one and a half breeding seasons (DeLong 1982). Both prior to and after this period of breeding, adult males contribute to the idle bull count. In contrast to the accuracy of the harem bull counts, there is a great deal of uncertainty about the total number of idle males aged 6-, 7-, and 8-yr old, for some may remain at sea (Chapman 1964; Smith and Polacheck 1984). A second area of uncertainty is the age structure of the harem bull population and how it may have changed over time.

## Mathematical Model

### Methods

A simple age-class model was used to reconstruct the estimated numbers of pups born on St. Paul Island from 1950 to 1987 and the numbers of bulls counted on the rookeries. Both data sets are contained in Trites (1989). The simulation treated the fur seal population as spatially homogeneous and was stratified by sex (male ( $m$ ) and female ( $f$ )) and 25 age-classes ( $x$ ), with pups being the 0 age class. Two sets of population data were retained, one for the number of males ( $N_{x,m}$ ) and one for the females ( $N_{x,f}$ ). No density dependent regulatory mechanisms were assumed to be operational.

The annual cycle of the model began in July of each year and followed the life history of the population, including the actions taken by fur seal managers, such as the harvesting of males and females. The first step was to count the returning bulls.

The total number of bulls counted ( $B$ ) was expressed in terms of the proportion ( $p_x$ ) of males aged  $x$  years of adult size that were on land during the time of the count, i.e.

$$(1) \quad B = \sum_{x=7}^{24} p_x N_{x,m}$$

The simulated bull counts did not distinguish between harem and idle male categories because some mature males may be harem bulls for part of the breeding season and idle bulls at other times (Chapman 1961). Computer generated bull counts were calculated by assuming that all males 8-yr and older were present on land and were counted as bulls. The number of 7-yr olds of adult size was assumed to be 25% of the year class, while males under this age were not considered to be bulls. The proportion of males of adult size was based on the mean body weights of male fur seals sampled by Scheffer and Wilke (1953).

The numbers of males ( $H_{x,m}$ ) and females ( $H_{x,f}$ ) harvested on St. Paul Island since 1950 are tabulated in Trites (1989) and York and Hartley (1981), respectively. The female harvest totals were extrapolated for seals age 8+, 10+, and 11+ by applying the life tables of Lander (1981). The harvests were removed from the simulated population by

$$(2a) \quad N_{x',m} = N_{x,m} - H_{x,m}$$

and

$$(2b) \quad N_{x',f} = N_{x,f} - H_{x,f}$$

The number of pups born during one cycle of the model was determined from

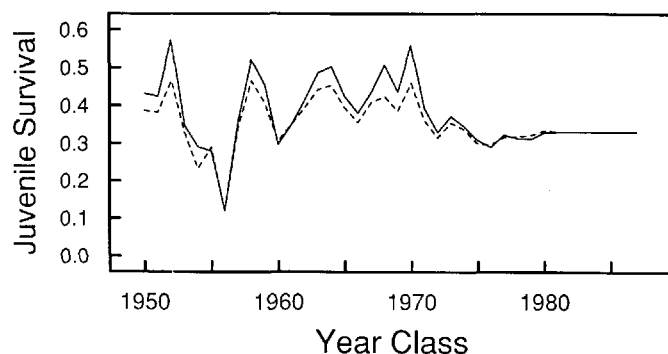


FIG. 1. Estimated rates of survival of juvenile males (birth-2 yr) on St. Paul Island from 1950 to 1987. The two sets of estimates correspond to methods 1 and 3 of Trites (1989) represented by the broken and solid lines, respectively. Survival from 1981-87 was assumed constant.

$$(3a) \quad N_{0,f} = \sum_{x=1}^{24} b_{x,f} N_{x,f}$$

and

$$(3b) \quad N_{0,m} = \sum_{x=1}^{24} b_{x,m} N_{x,f}$$

where  $b_{x,m}$  and  $b_{x,f}$  were age specific natality rates contained in Lander (1981). The abundance of males was assumed to have no effect upon reproductive rates.

The simulation removed the number of male ( $P_{x,m}$ ) and female ( $P_{x,f}$ ) seals taken during the pelagic sampling, then determined the numbers that survived natural sources of mortality from one year to the next as

$$(4a) \quad N_{x+1,m} = s_{x,m}(N_{x,m} - P_{x,m})$$

and

$$(4b) \quad N_{x+1,f} = s_{x,f}(N_{x,f} - P_{x,f})$$

The pelagic research kill data as contained in Lander (1980b) was not appropriate for the purposes of simulation: both the year of kill and age assigned to the dead animals had to be adjusted. The standard practice was to assign a birthday on January 1, ignoring the true biological age of the animal (Lander 1980b). In fact it appears that birthdays were assigned in November, such that a pup born in July and killed only 5 mo later was recorded as 1 yr old. Similarly, animals killed at 17 and 28 mo were both considered to be 2 yr old. We corrected the pelagic data to reflect the true biological ages of the samples. We also adjusted the years of kill from January-December to July 1-June 30 to accord with the annual cycle of the simulation model.

Age specific survival rates,  $s_{x,m}$  and  $s_{x,f}$ , were taken from Lander (1981) for seals aged  $2^+$  and were assumed to remain constant over time. Annual rates of male survival from birth to age 2 were taken from Trites (1989) for the years 1950 to 1980 (Fig. 1).

Trites (1989) proposed three approaches for estimating the rate of juvenile survival, and hence three sets of estimates. All three methods reconstructed the numbers of juveniles that were alive at age 2 yr using the number of males killed during the commercial harvest. They differed in the assumptions invoked concerning subadult survival and escapement from the harvest. Rather than restrict ourselves to just one set of estimates we chose the two most divergent. The first set of estimates (Trites

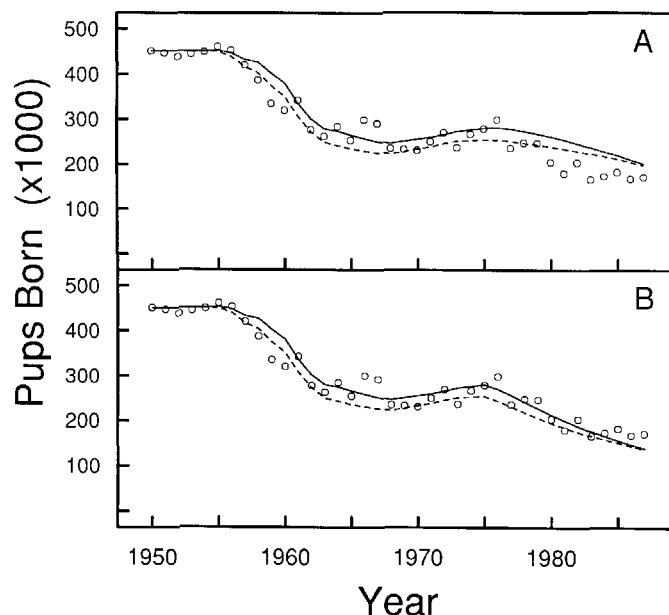


FIG. 2. Field estimates of pups born on St. Paul Island (circles) and simulation results from the pup driven model (lines). The model used the combined field observations of previous years to produce annual estimates of pup production. Broken and solid lines indicate the set of juvenile survival rates used (Fig. 1). Juvenile females were assumed to experience the same survival rates as males. Panel A contains the base run. The result of reducing adult survival by 4% beginning in 1975 is shown in Panel B.

— method 1) was derived using the least refined assumptions, while the second (Trites — method 3) incorporated information from life tables and the annual counts of bulls. The first procedure produced estimates that were generally lower than the second. Further details are provided in Trites (1989). For the purposes of the present simulations, juvenile survival (birth-2 yr) from 1981-87 was set at 33%, the mean rate of survival over the previous 10 yr.

The annual rates of juvenile survival were for males only. It has been a common practice to assume that the survival of juvenile females exceeds that of males by a constant factor ranging from 1.05 to 1.10 (see Chapman 1961, 1964, 1973; York and Hartley 1981; Eberhardt 1981), on the assumption that females experience better environmental conditions during their pelagic life than males. However, there is no direct evidence to support such an assumption of differential survival for juvenile fur seals. For this reason the model was run with both differential (factor 1.10) and equal rates of survival for ages 0 to 2 yr.

The model simulated the St. Paul population from 1950 with the initial herd size having a stable age distribution that produced 454 000 pups. The last year of simulation was 1987.

From this base two kinds of simulations were conducted. The first, the “pup driven model,” used the annual field estimates of pup production. Expected numbers of pups born were calculated in each year of simulation, but were not used to generate future population changes, i.e. the simulated births (equations 3a and b) were replaced with the historical numbers of pups born. The second kind of simulation, the “true simulation,” projected future population trends from the initial set of conditions. This type of model was more prone to propagation of errors over time.

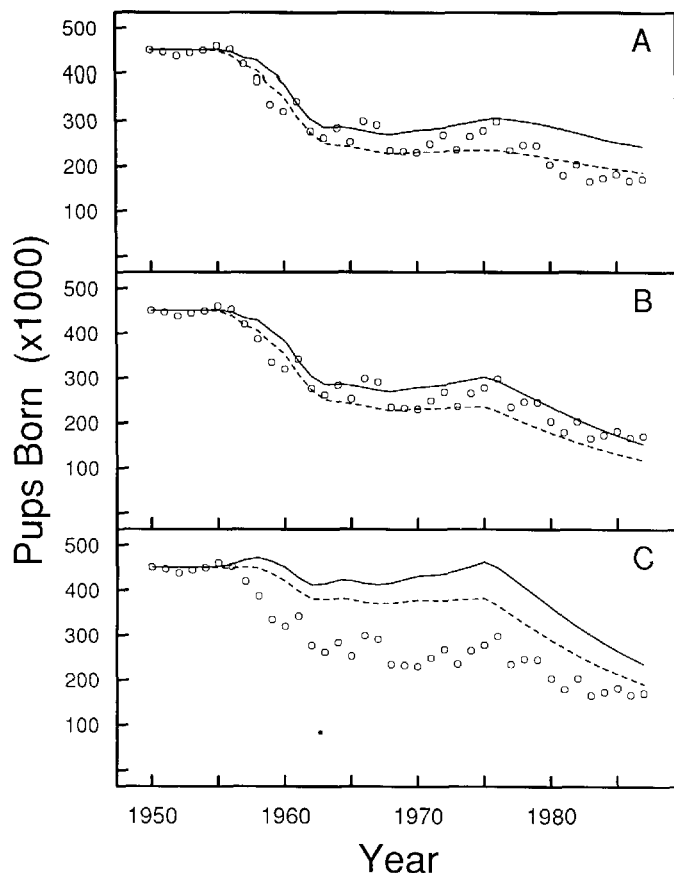


FIG. 3. Field estimates of pups born on St. Paul Island (circles) and simulation results from the true simulation model (lines). The model propagated pup production from the initial model conditions of 1950. Broken and solid lines indicate the set of juvenile survival rates used (Fig. 1). Survival rates of juvenile males and females were assumed equal. Panel A contains the base run. The result of reducing adult survival by 4% beginning in 1975 is shown in panels B and C. Panel C further shows the trend in pup production if females had not been harvested or sampled.

## Results

When the model was driven by field estimates of pup production (the "pup driven model"), the fit of computer generated pups to field observations was good from 1950 till the early 1970s (Fig. 2A). After 1978, pup production declined more than the model predicted. Rerunning the model with lower pregnancy rates during the 1970s and 80s could not approximate the sharp decline observed in numbers of pups born, but increasing adult female mortality did. Reducing adult survival by 4% beginning in 1975 gave a good fit (Fig. 2B) which could have been improved by increasing mortality gradually, rather than by the knife edge approach employed. Experimenting with alternative scenarios led to the conclusion that the observed decline in pup production was consistent with the assumption that adult female survival declined between 2–5% beginning about 1972. It is unclear whether the poor fit in the last 3-yr of simulation is an indication of improving survival or the result of errors in estimating pup production. This should become apparent over the next few years as more data are collected. As for the apparent absence of density dependent processes, note that they may in fact be inadvertently present in this model if the actual numbers of pups born were affected by density dependent processes.

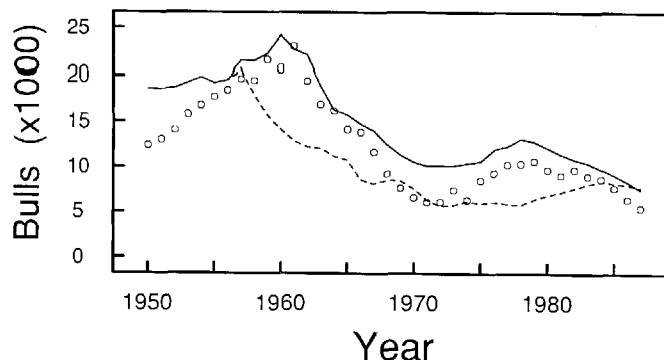


FIG. 4. Field counts of harem and idle bulls (circles) on St. Paul Island and computer counts generated by the pup driven model (lines). As in previous figures, the line types indicate the set of juvenile survival rates used. Simulation results correspond to Fig. 2B.

The results of the second simulation or "true simulation" (driving the model with simulated births) were similar to the "pup driven model" in that the fit to field observations (Fig. 3A) was noticeably improved if the survival of adult females (aged  $2^+$ ) was increased by 4% beginning in 1975 (Fig. 3B). Running the simulation model with no female kill (Fig. 3C) revealed two periods of decrease in pup production during the years 1957–61 and 1975–87. These periods of decline corresponded to periods of low juvenile survival estimates of 1954–56 and 1972–80. The poor survival of female pups from these cohorts reduced the numbers of reproducing females as did the increase in natural mortality of adult females that began in the 1970s. Poor juvenile survival explains about 25% of the decline in pup production from 1950 to 1970. The remaining 75% can be attributed to the commercial female harvest (cf. York and Hartley 1981). The sharp drop in births since 1976 is due to higher mortalities of females at all ages.

The trend of the bull counts generated by the pup driven model was consistent with that observed on St. Paul (Fig. 4). Increasing the natural mortality of adult males in the 1970s did not have an appreciable effect on the computer counts of bulls. The lack of fit in the first 10 yr of simulation may be explained by the stable age structure used as an initial condition of the model. The initial male population could have been chosen with a different age structure to produce a perfect fit for the early years of bull counts.

The model driven by simulated births generated a downward trend of bull counts, but in a few years of simulation the historic male harvest exceeded the numbers available, causing elimination of some year classes. Extinctions did not occur when the model was driven by the historic numbers of pups born. This suggests that much of the year to year variation in the field estimates of pup production is likely real and not a reflection of measurement error alone.

The fur seal population on St. Paul Island will continue to decline unless rates of natural survival improve. Extending the model to the year 2000 using the steady state conditions of 1980–87 suggests that unless mortality rates decrease, pup production would decline exponentially reaching an annual level of about 70 000 in the year 2000. The number of bulls would rise rapidly from 1988 to 1993 in response to the current suspension of the commercial male harvest. Their numbers could reach 25 000 before declining in response to the reduction in pup production.

## Sensitivity Analysis

### Methods

Two procedures were used to determine responsiveness of model output to changes or errors in input parameters. The first procedure calculated relative sensitivities to identify whether input parameters produced a strong or weak effect upon model output. The second procedure (analytic model validation) examined the combined effects of errors in all input parameters on model output. Both procedures were adapted from the works of Majkowski (1981); Miller (1974); Miller et al. (1976); and Mohn (1979).

The simulation model that produced the best fit of simulated pup production ( $X_t^o$ ) to observed data contained eight sets of initial conditions and input parameters, ( $P_i^o$ ;  $i=1...8$ ): (1) juvenile survival, (2) adult survival, (3) reproductive rates, (4) initial population, (5–8) numbers of males and females harvested at sea and on land). A parameter set was changed by fixed amounts  $u_i$  such that

$$(5) \quad P_i = (1 + u_i)P_i^o.$$

The model was then rerun with individually altered parameters to produce new estimates of pup production  $X_t$  at time  $t$  which were compared with  $X_t^o$  by partial deviances,  $D_t$ .

The uncertainty in model predictions and validity of the simulation was analytically quantified for both the true simulation model and the pup driven model. We calculated the distribution of deviances using the analytic procedure formulated by Miller (1974) and Miller et al. (1976), and applied by Mohn (1979); and tested for linearity and independence of input parameters.

### Results

Model output (number of pups born) was most sensitive to survival rates of adult females, followed by birth rates and survival rate of juveniles. Altering survival rates of adult females by as little as 3% changed predictions of pups born by over 100% after 30 yr of simulation. This was in part because adult survival rates were high and a small percentage change produced a large absolute change.

The least critical simulation parameters were the numbers of males and females harvested at sea and on land. Introducing errors of  $\pm 25\%$  did not significantly change the model predictions. Error in the male kill was not important because the model assumed no relation between male abundance and pup abundance. Altering the female harvest was most significant for the years 1959–64 after which the effect of removal had passed. Errors in determining the numbers of females collected at sea proved insignificant. Errors in the initial age structure of the population (i.e. 1950) had a linear effect on model output as might be expected.

Using an estimate of the variance of  $u_i$  and the relative sensitivity coefficients ( $R_{i,t}$ ) from Tables 1 and 2, the standard deviation of input uncertainty was estimated at one-third of maximum error according to Miller et al. (1976). If maximum error was assumed to be 1% then the standard deviation would be 0.00333 and  $\text{Var}(u_i = 1\%) = 0.00001$ .

In the absence of field estimates of input uncertainty, uniform errors of 0–4% were applied to all values and 95% confidence limits on the model predictions were estimated by  $X_t^o \pm 1.96 \times \text{Var}(D_t) X_t^o$ . The widening of the confidence bands of the estimates over time (Fig. 5A) is indicative of a propagation of

TABLE 1. Relative sensitivity  $R_{i,t}$  of model output (pups born) to 1% changes in the eight parameter sets of the pup driven model. The sensitivity coefficients show the response of simulated pup production (measured as a percent change) to 1% errors in model input parameters at time  $t$ . The sensitivity to errors in the kill of males on land and at sea was equal to zero.

Year	Model input parameters					
	Juvenile survival	Adult survival	Birth rates	Initial population	Female harvest	
					Pelagic	Land
1950	0.00	0.00	1.00	1.00	0.00	0.00
1951	0.00	1.00	1.00	1.00	0.00	0.00
1952	0.00	2.01	1.00	1.00	0.00	0.00
1953	0.00	3.03	1.00	1.00	0.00	0.00
1954	0.00	4.05	1.00	0.99	0.00	0.00
1955	0.06	5.03	1.00	0.94	0.00	0.00
1956	0.17	6.02	1.00	0.85	0.00	-0.02
1957	0.30	7.13	1.00	0.77	0.00	-0.08
1958	0.43	7.95	1.00	0.67	0.00	-0.10
1959	0.55	8.93	1.00	0.60	0.00	-0.14
1960	0.65	9.70	1.00	0.52	0.00	-0.17
1961	0.79	10.99	1.00	0.47	0.00	-0.25
1962	0.94	12.06	1.00	0.41	-0.01	-0.34
1963	1.11	12.76	1.00	0.32	-0.01	-0.42
1964	1.22	12.69	1.00	0.23	-0.02	-0.44
1965	1.29	12.56	1.00	0.16	-0.02	-0.43
1966	1.33	12.31	1.00	0.10	-0.02	-0.41
1967	1.36	12.08	1.00	0.05	-0.01	-0.40
1968	1.37	11.78	1.00	0.03	-0.01	-0.38
1969	1.33	11.20	1.00	0.01	-0.01	-0.33
1970	1.29	10.76	1.00	0.00	-0.01	-0.28
1971	1.24	10.44	1.00	0.00	-0.01	-0.23
1972	1.19	10.18	1.00	0.00	-0.01	-0.18
1973	1.15	10.02	1.00	0.00	0.00	-0.14
1974	1.12	9.97	1.00	0.00	0.00	-0.11
1975	1.09	9.91	1.00	0.00	0.00	-0.08
1976	1.06	9.89	1.00	0.00	0.00	-0.06
1977	1.05	9.96	1.00	0.00	0.00	-0.04
1978	1.03	10.05	1.00	0.00	0.00	-0.03
1979	1.02	10.12	1.00	0.00	0.00	-0.02
1980	1.01	10.17	1.00	0.00	0.00	-0.01
1981	1.01	10.18	1.00	0.00	0.00	0.00
1982	1.01	10.19	1.00	0.00	0.00	0.00
1983	1.00	10.18	1.00	0.00	0.00	0.00
1984	1.00	10.14	1.00	0.00	0.00	0.00
1985	1.00	10.10	1.00	0.00	0.00	0.00
1986	1.00	10.05	1.00	0.00	0.00	0.00
1987	1.00	10.00	1.00	0.00	0.00	0.00

error resulting from the structure of the true simulation model. For the model driven by field estimates of pup production (Fig. 5B), the error bands are of the same magnitude over the period because error propagation is constrained by correcting the computer generated births in each year of simulation.

Within 10 yr of the beginning of simulation, adult survival accounts for approximately 98% of the overall model uncertainty (Fig. 5C). The other parameters combined account for less than 2%: birth rates (1.2%), juvenile survival (0.7%), initial population (0.1%), and numbers of males and females killed ( $\leq 0.01\%$ ). Model output is thus extremely sensitive to change in adult survival rates (cf. Smith and Polacheck 1984).

### Discussion

The Pribilof fur seal population had been reduced to low numbers twice before the recent reduction. The first decline,

TABLE 2. Relative sensitivity  $R_{t,i}$  of model output (pups born) to 1% changes in the eight parameter sets of the true simulation model. The sensitivity coefficients show the response of simulated pup production (measured as a percent change) to 1% errors in model input parameters at time  $t$ . The sensitivity to errors in the kill of males on land and at sea was equal to zero.

Year	Model input parameters					
	Juvenile survival	Adult survival	Birth rates	Initial population	Female harvest	
					Pelagic	Land
1950	0.00	0.00	1.00	1.00	0.00	0.00
1951	0.00	1.00	1.00	1.00	0.00	0.00
1952	0.00	2.01	1.00	1.00	0.00	0.00
1953	0.00	3.03	1.00	1.00	0.00	0.00
1954	0.00	4.05	1.01	1.00	0.00	0.00
1955	0.06	5.03	1.06	1.00	0.00	0.00
1956	0.17	6.10	1.17	1.02	0.00	-0.02
1957	0.31	7.42	1.31	1.08	0.00	-0.08
1958	0.43	8.54	1.43	1.10	0.00	-0.10
1959	0.55	9.90	1.56	1.15	0.00	-0.14
1960	0.66	11.13	1.67	1.17	0.00	-0.17
1961	0.81	13.03	1.81	1.26	0.00	-0.25
1962	0.99	15.01	2.00	1.35	-0.01	-0.34
1963	1.22	17.14	2.23	1.45	-0.01	-0.44
1964	1.40	18.48	2.42	1.48	-0.02	-0.46
1965	1.55	19.65	2.56	1.48	-0.02	-0.47
1966	1.67	20.80	2.69	1.49	-0.02	-0.47
1967	1.80	22.24	2.82	1.51	-0.02	-0.49
1968	1.94	23.80	2.96	1.54	-0.02	-0.52
1969	2.05	24.99	3.07	1.54	-0.02	-0.53
1970	2.15	26.13	3.17	1.54	-0.02	-0.52
1971	2.24	27.23	3.26	1.54	-0.02	-0.52
1972	2.32	28.31	3.35	1.53	-0.02	-0.51
1973	2.42	29.42	3.44	1.53	-0.02	-0.51
1974	2.52	30.60	3.54	1.53	-0.02	-0.51
1975	2.63	31.80	3.65	1.53	-0.02	-0.51
1976	2.73	33.00	3.76	1.53	-0.02	-0.51
1977	2.82	34.22	3.85	1.54	-0.02	-0.51
1978	2.91	35.45	3.94	1.54	-0.02	-0.51
1979	3.01	36.68	4.04	1.54	-0.02	-0.51
1980	3.10	37.92	4.13	1.54	-0.02	-0.51
1981	3.19	39.17	4.23	1.54	-0.02	-0.51
1982	3.29	40.43	4.32	1.54	-0.02	-0.51
1983	3.39	41.71	4.42	1.54	-0.02	-0.51
1984	3.49	42.99	4.52	1.54	-0.02	-0.51
1985	3.59	44.28	4.62	1.54	-0.02	-0.51
1986	3.69	45.54	4.72	1.54	-0.02	-0.51
1987	3.79	46.77	4.82	1.54	-0.02	-0.51

caused by overharvesting, occurred shortly after discovery of the Islands in 1780. Growth of the herd was restored by hunting closures in 1799 and in 1837 by excluding females from the kill (Martin 1946; Roppel and Davey 1965; Roppel 1984; Scheffer et al. 1984). The Russian American company policy of harvesting only polygamous males is believed to have restored the population to its original level when Alaska was sold in 1867.

Within 45 yr of sale of Alaska, the herd of 2.5 million animals had been reduced to fewer than 300 000 by excessive land harvests and commercial kills of males and females at sea. Again the herd grew after hunting closures and the restriction of land harvests to immature males beginning in 1911. The herd increased to 1.5 million seals by the late 1940s and then appeared to stop growing (Kenyon et al. 1954).

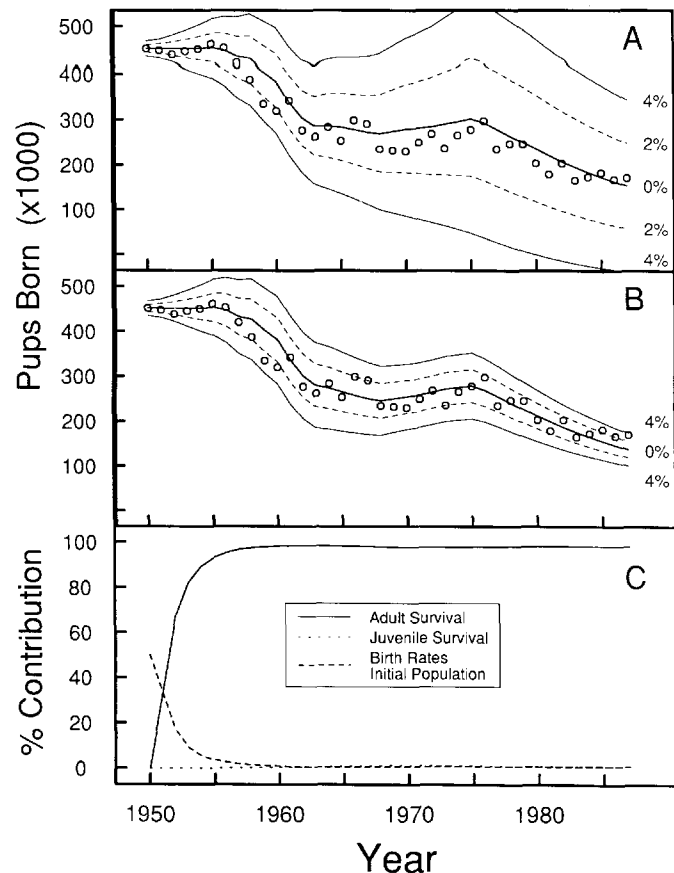


FIG. 5. Uncertainty in model output as measured by pups born if all input parameters contain random errors of 0, 2, or 4%. The bounds are 95% confidence limits placed on the best fit of simulation results (heavy line) to field observations (circles). Panel A shows the results of the true simulation model and panel B the pup driven model. The contribution of input parameter errors to uncertainty in output is expressed as a percentage in panel C. The difference in error contribution is not graphically discernible between the two models. Only the four most significant parameters were plotted. Most of the uncertainty in model output is due to adult survival.

The decision to again harvest females from 1956 to 1968 was based on conjectured concepts of density dependence and a desire to manage for maximum sustainable yield (NPFSC 1962). Reproductive rates and natural survival rates were expected to increase as the population was lowered; but this did not occur (Smith and Polacheck 1981, 1984; York and Hartley 1981; Beacham 1982; York 1983). Instead, the killing of females cut pup production by reducing the number of reproducing animals (Eberhardt 1981; York and Hartley 1981). Stopping the female kill has not restored population growth.

Our simulation study indicates that 75% of the drop in pup production from 1956 to 1962 was associated with the female harvests (cf. York and Hartley 1981), and the remaining 25% with low juvenile survival. Nevertheless, the poor survival of young fur seals is the key factor in low productivity during the 1960s and early 1970s. Pup production would have declined somewhat from 1957 to 1961 even if no mature females had been removed from the population. At best, the population would have remained at a relatively constant level although far below what is believed to be its potential natural upper limit of between 2–2.5 million (Lander and Kajimura 1982). Pup production on St. Paul Island would only have increased if the survival of juveniles had gone above 40% for several years.

The simulations indicate that males and females likely experience similar survival rates over the first 2 yr of life. As the details of pelagic migration during the first 2 yr of life are not understood it is not known whether the sexes are subject to similar sources of mortality.

The simulations show no connection between the harvest of immature males and the decline in numbers of pups born. A reduction in male abundance presumably could result in fewer bulls holding harems for longer periods of time because competition for breeding space within the rookeries decreased. There is no indication that the reproductive potential of the herd has been significantly influenced by a reduction in male abundance. Pregnancy rates show no change over the period 1958 to 1972 (Smith and Polacheck 1984) and our simulation results detect no discernable change even during the recent drop in pup production.

The sensitivity analysis showed that small changes in the survival of females have dramatic effects upon population growth (cf. Smith and Polacheck 1984). Population growth is less sensitive to changes in male mortality, reproductive rates, and the age of first reproduction. Similar results have been shown for generalized models of other long lived species (e.g. Goodman 1981).

Lander (1981) estimated the adult female survival rates from the age composition of 16 242 seals collected at sea by United States and Canadian research vessels during 1958–74. The estimates were reexamined by York and Hartley (1981). They compared female survival rates between 1958 to 1965 with the period 1966 to 1974 and could find no significant difference. The pelagic collections of males were inadequate to estimate male survival. Instead, Lander (1981) made an estimate from the limited numbers of breeding males killed experimentally and found dead on land in 1965 by Johnson (1968). The dubious reliability of the male survival rates affects our confidence in the simulated bull counts, but not in the simulated pup production. Pup production was driven entirely by female survival rates; hence we are confident in the predictions of pup production.

The prolonged period of low juvenile survival since 1971 combined with a possible increase in adult mortality of 2–5% beginning in the mid 1970s is decimating the Pribilof fur seal herd. Since 1971 there has been virtually no annual variation in the estimates of juvenile survival (Fig. 1). The estimated average rate of survival over the first 2 yr of life has been 33% from 1971–80, and was assumed in the model to have remained constant ever since. This rate is 7% less than the 40% required to maintain the population at equilibrium and is in sharp contrast to the high survival rates of 40–44% averaged from 1958–71.

There are several sources of mortality that could explain the observed pattern of deaths. One possibility is unnatural causes, such as heavy metal contamination or entanglement in fishing debris. Other known sources of mortality that occur during the pelagic existence are predation by killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*), starvation, weather, parasitism, food poisoning, and infectious diseases (Keyes 1965; Scheffer et al. 1984). Young animals are thought to be most susceptible to starvation and inclement weather (Scheffer 1950; Ichihara 1974).

Much of the variability in juvenile survival from 1950 to 1970 was perhaps due to variability in the availability of food during the winter transition from recent weaning to pelagic foraging in the Bering Sea and Gulf of Alaska. Some of the high

pup mortality experienced in the mid 1950s can be attributed to heavy parasite loads and the harvest of lactating mothers (Scheffer et al. 1984).

The pattern of mortality since 1970, for juveniles and now adults, suggests a response to exogenous factors. The most likely explanations are connected to commercial fishing in the Bering Sea and Gulf of Alaska. Commercial fisheries for groundfish began in the North Pacific Ocean and Bering Sea in the early 1950s with a total aggregate catch of 12 500 t. By 1972 it had risen to over 2.2 million t (OCSEAP 1987; Bakkala and Low 1985; Ito and Balsiger 1983). The intense fisheries suggest that fur seal food resources may have been depleted. Unfortunately the interaction between seals and fisheries is poorly documented (Lowry et al. 1979; Lowry 1982). There are some indications that certain population parameters (survival of pups on land, adult growth rates, and weight at birth) may have increased in recent years as the Pribilof population declined (Fowler 1984, 1985b). However, some of these positive indications may be artifacts of bias and errors in measurements. Conclusions concerning the effects of the intense commercial fisheries on fur seal survival are premature.

There is a growing body of evidence suggesting the assumed increase in mortality in recent times is related to extraneous sources, such as the entanglement of seals in net fragments, plastic bands, and other debris (Swartzman 1984; Fowler 1985a, 1987). As commercial fisheries were developed in the Bering Sea, the number of entangled males observed in the commercial harvest began to rise. The incidence of entanglement among harvested males went from a low of 0.15% in 1967 to a high of 0.72% in 1975. The rate of entanglement dropped sharply in 1976 and has been relatively stable at 0.41% ever since (Scordino and Fisher 1983; Scordino 1985; Fowler 1987). The mortality of young animals (birth to age 2–3 yr) caused by debris entanglement may be as high as 15% of the total number of young animals that leave the Pribilofs (Fowler 1985a, b, 1987).

We suspect that reduced food availability and entanglement in fishing debris are both contributing to the current decline of the Pribilof population through the mortality of fur seals of all ages. However, the significance of each factor has yet to be clearly demonstrated or refuted. A key point to examine is whether the condition of the seals is related to oceanographic conditions and/or the extent of the fishery. A tagging program to estimate survival rates would be useful and the collecting of morphometric measures from pups and harvested animals might reflect feeding conditions. The need to gain further insight into the decline of the Pribilof population is urgent. Unless there is an improvement in their current demographics, the decline of the fur seal could very likely become a fall into oblivion.

## Acknowledgements

We are grateful to Michael Bigg, Doug DeMaster, and Don Robinson for their comments and suggestions on various sections of this work. We also wish to thank Charles Fowler and Anne York for sharing their knowledge of fur seal population dynamics with us. Finally, we thank the referees for their useful comments.

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