

# Unexpected Changes in Reproductive Rates and Mean Age at First Birth during the Decline of the Pribilof Northern Fur Seal (*Callorhinus ursinus*)

Andrew W. Trites<sup>1</sup>

Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada V9R 5K6

and Anne E. York

National Marine Mammal Laboratory, National Marine Fisheries Service, 7600 Sand Point Way N.E., Seattle WA, 98115, USA

Trites, A.W., and A.E. York. 1993. Unexpected changes in reproductive rates and mean age at first birth during the decline of the Pribilof northern fur seal (*Callorhinus ursinus*). *Can. J. Fish. Aquat. Sci.* 50: 858–864.

From 1956 to 1968, female northern fur seals (*Callorhinus ursinus*) were harvested on the Pribilof Islands, Alaska, in an effort to increase the productivity of the herd. In theory, pregnancy rates should have increased and the age at first birth should have declined as population density was reduced. Instead the opposite happened: pregnancy rates dropped and age of first birth increased. It is unlikely that these changes were caused by shortages of food or poor physical condition of the females, given that body size increased over this period. The most likely explanations for the changes observed between 1958 and 1974 are related to altered age and sex ratios of breeding animals caused by the depletion of females and/or the harvesting of young males. Changes in pregnancy rates and age at first birth are inconsistent with the density-dependence paradigm and suggest that relative densities of mature age and sex classes on the breeding beaches (a product of social interactions and territory size) may be more consequential than absolute population densities in affecting the reproductive biology of northern fur seals.

De 1956 à 1968, des femelles d'otarie à fourrure (*Callorhinus ursinus*) ont été récoltées dans les îles Pribilof (Alaska) afin d'accroître la productivité du troupeau. En théorie, le taux de gravidité aurait dû augmenter et l'âge de la première mise bas aurait dû diminuer suite à cette baisse de la densité de la population. Au contraire, les effets opposés ont été notés : le taux de gravidité a diminué et l'âge à la première mise bas a augmenté. Il est peu probable que ces modifications s'expliquent par un manque de nourriture ou une mauvaise condition physique des femelles, car la taille des individus a augmenté pendant cette période. L'explication la plus plausible des changements observés entre 1958 et 1974 a trait à une modification des rapports des âges et des sexes des reproducteurs découlant du manque de femelles ou de la récolte de jeunes mâles. Les modifications des taux de gravidité et de l'âge à la première mise bas ne concordent pas avec le modèle de la dépendance envers la densité. Cela porte à croire que, en ce qui a trait à la biologie de la reproduction chez les otaries à fourrure, les densités relatives des classes d'âge d'individus matures et des classes de sexes des animaux présents sur les plages de reproduction (qui découlent des interactions sociales et de la taille des territoires) sont plus importants que les densités de population absolues.

Received March 27, 1992

Accepted October 19, 1992

(JB450)

Reçu le 27 mars 1992

Accepté le 19 octobre 1992

The abundance of northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska, increased from 200 000 to 300 000 animals in 1911 to over 1.5 million in the late 1940s under a management policy that protected females but allowed the harvesting of immature males (Kenyon et al. 1954; Lander and Kajimura 1982). When population growth slowed during the 1940s, it was suggested that the herd's productivity had been lowered by reduced rates of reproduction (Kenyon et al. 1954) and juvenile survival (Chapman 1961) arising from competition for a limited food supply around the Pribilof Islands. Mathematical models subsequently suggested that greater productivity (and a larger harvest) could be achieved from a smaller population (Chapman 1961; Nagasaki 1961). As

a result, 315 000 females were killed between 1956 and 1968 in addition to the continued male harvest (Lander 1980a). However, annual pup production and recruitment of harvestable males failed to increase as predicted, and the population declined (Fig. 1; Chapman 1981).

Lowering the herd size was supposed to increase productivity through density-dependent changes in population vital rates. In particular, reproductive rates should have increased and mean age at first birth should have decreased. Whether or not these changes occurred is the subject of our study.

From 1958 to 1974, over 11 000 female fur seals were collected at sea by Canada and the United States as part of a pelagic research program (Lander 1980b). Based on macroscopic observations of reproductive tracts (Lander 1980b), females were classified as nulliparous (female has never been impregnated), primiparous (pregnant only once, regardless of whether the pregnancy is carried to term), and multiparous (previously

<sup>1</sup>Present address: Marine Mammal Research Unit, Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, B.C., Canada V6T 1Z4.

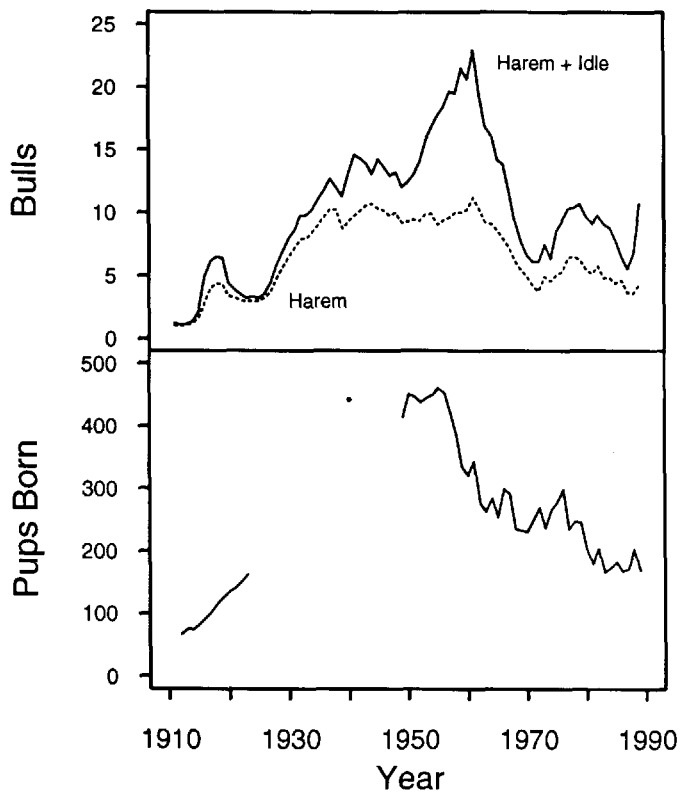


FIG. 1. Numbers of pups born and bulls counted on St. Paul Island (one of the Pribilof Islands) from 1911 to 1989 (in thousands). The data are an index of population abundance and are taken from Lander (1980a), York (1985), and Trites (1989).

pregnant more than once, and either pregnant or nonpregnant at the time of collection). The pelagic samples were all collected in the North Pacific Ocean from California to the Bering Sea, with month and region of sampling varying between years.

Our study used the pelagic data base to test whether reproductive rates increased and age at first birth decreased as the population declined. We estimated annual pregnancy rates and examined the frequency of multiparity among the females sampled. We also estimated the mean age when females gave birth for the first time from 1959 to 1974. Finally we explored the relationship between body size and reproductive condition and considered the influence of fur seal density on reproductive rates.

### Pregnancy Rates

Early analysis of changes in pregnancy rates in the 1950s showed no appreciable change with time (Nagasaki 1961; Chapman 1964). Further analysis of additional pelagic data by Smith and Polacheck (1984) also indicated little change in pregnancy rates over the years 1958–74. However, the authors did not control for geographic effects and other possible sources of sampling bias. Additional analysis by Bigg (1979a) and York (1979) found considerable seasonal and regional variation in pregnancy rates associated with the migratory patterns of females of different ages and reproductive conditions. The highest pregnancy rates were recorded near the breeding beaches during the summer pupping period. Pregnancy rates were lower farther south along the Aleutian chain, while still lower rates were calculated from samples taken in the coastal waters of Washington during winter and spring. In the Gulf of

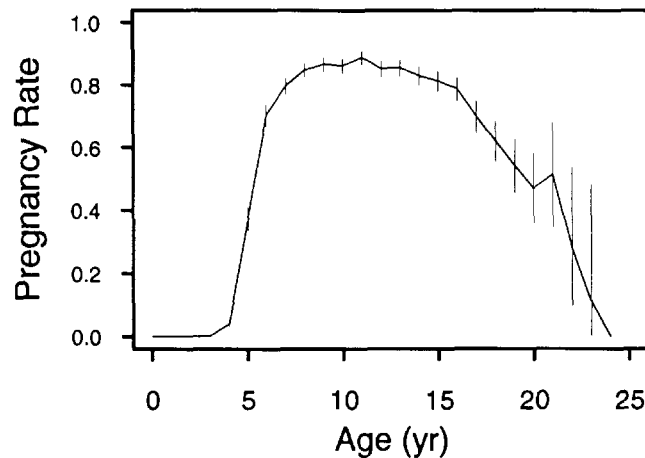


FIG. 2. Age-specific pregnancy rates (including postpartum animals) of 15 020 seals collected at sea in all sampling areas from 1958 to 1974. The vertical bars are 95% confidence intervals. Data from Lander (1981).

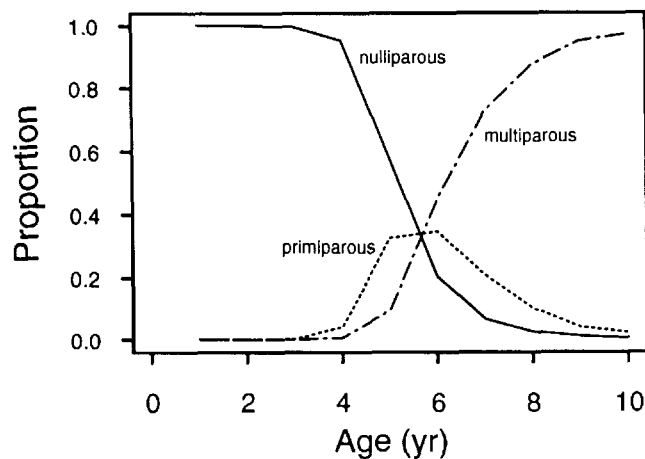


FIG. 3. Age-specific reproductive condition of 10 824 females ages 0–10 yr collected at sea in all sampling areas from 1958 to 1974.

Alaska, the pregnancy rate for sampled females rose and fell as the females migrated northward during late spring/early summer to give birth on the Pribilof Islands.

Pregnant females return to the Pribilofs about 3–4 wk earlier than nonpregnant females (Bigg 1990; Trites 1990). Pregnant and nonpregnant females appear to be more or less randomly mixed from December to March while in the coastal waters of California, Oregon, Washington, and British Columbia (Bigg 1990). They also appear to be randomly mixed from July to September around the Pribilof Islands (55–59°N, 166–174°W). We therefore estimated pregnancy rates for these two regions during the respective time periods. We did not include samples taken from April to June because females were segregated at this time by age and reproductive condition as they migrated northward through the Gulf of Alaska and on by the Aleutian chain.

Females begin bearing young as early as age 4 yr (see Fig. 2 and 3). The pregnancy rate rises rapidly until age 8 whereupon it remains relatively constant for the next 5 yr. After age 14, the pregnancy rate declines each year until the seal completely stops reproducing when about 25 yr old.

Erroroneous estimates of pregnancy rates can result from biases hidden in the data (York 1980). For example, 6% (5 of 85) of

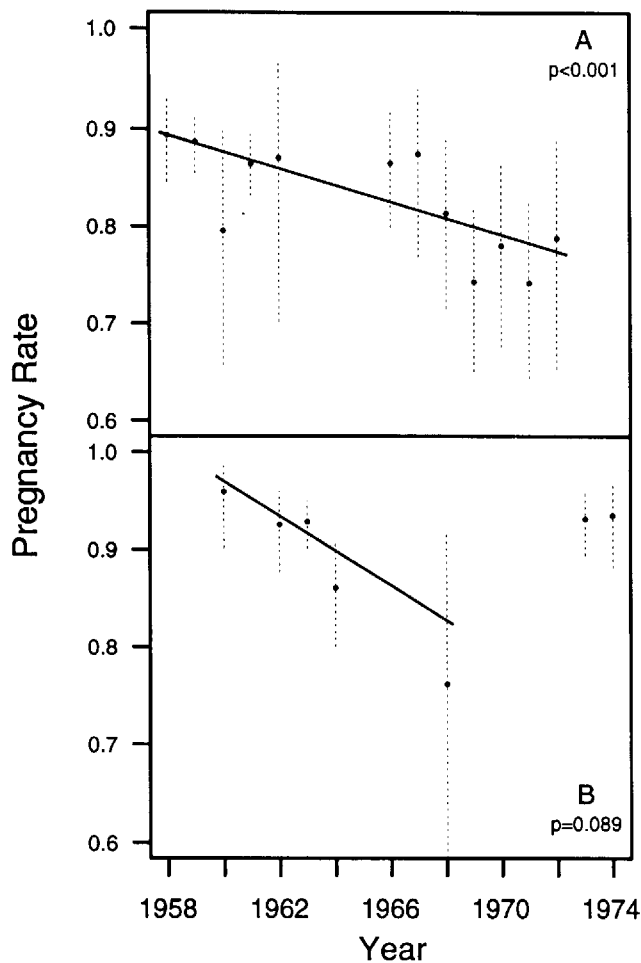


FIG. 4. Annual pregnancy rates of females between the ages of 8 and 13 yr collected from (A) California to British Columbia and (B) in the Pribilof region. The data were fit with weighted linear least squares regressions. Broken lines are 95% confidence limits.

the 4-yr-old females from the 1954 year class were primiparous, implying that the pregnancy rate for 3-yr-olds was 6%. At age 5, 8% (11 of 140) of this year class were primiparous, but not pregnant when captured, and 19% (27 of 140) were multiparous. Thus the pregnancy rate of 3-yr-olds must have been between 19 and 27%, substantially higher than the 6% directly observed. This discrepancy might simply be due to binomial sampling variance. On the other hand, the discrepancy in estimated rates of pregnancy in 3-yr-olds might reflect differential survival rates for pregnant and nonpregnant females or could have arisen if mature females were easier to capture than immature females. Estimates of reproductive rates could also be easily biased by changes in age structure during the intervening time. Hence, we only estimated pregnancy rates for females between the ages of 8 and 13 yr because pregnancy rates vary little for this age group (York 1979; Lander 1981) and because some models for mammalian survivorship (e.g., Siler 1979) suggest that mortality rates should be relatively age constant over this age range (8–13 yr). Furthermore, northern fur seals are at their reproductive prime between 8 and 13 yr based on the size of the fetuses they carry (Trites 1991).

Pregnancy rates of 8- to 13-yr-old females collected in the Pribilof and California – British Columbia regions declined from 1958 to 1972 (Fig. 4; cf. Eberhardt 1990). Weighted linear least squares regressions, with weight inversely proportional to

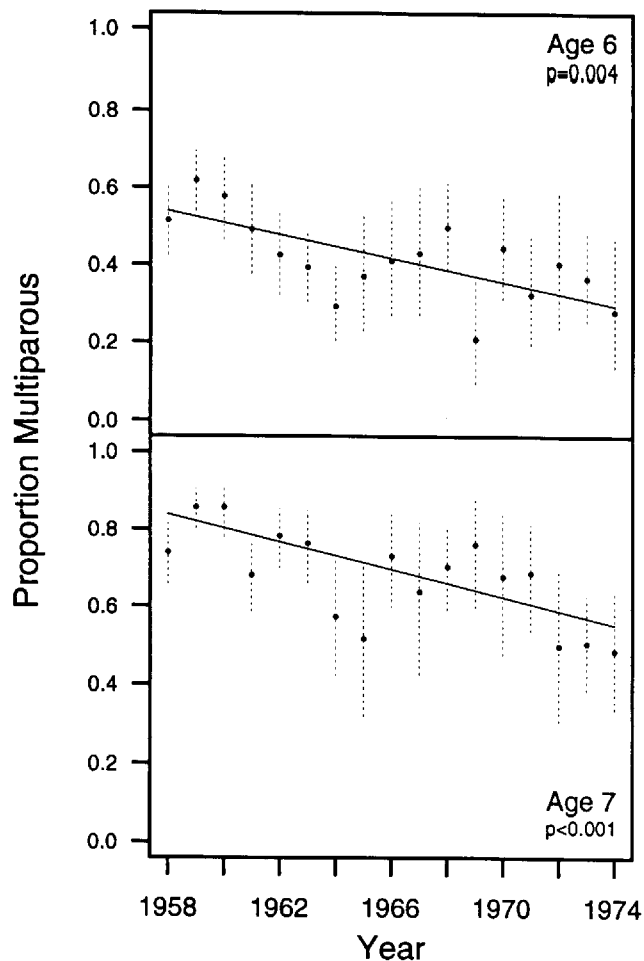


FIG. 5. Proportion of 6- and 7-yr-old females collected in all areas that were multiparous in the 1958–74 pelagic samples. The significance of weighted linear regressions is shown in the panels. Broken lines are 95% confidence limits.

the variance, indicate a highly significant drop in pregnancy rates for the large California – British Columbia samples ( $r^2 = 0.688$ ,  $F_{1,10} = 22.03$ ,  $p < 0.001$ ). Pregnancy rates of animals sampled in the Pribilof region were higher than the southern sample and also suggest a decline in pregnancy rates from 1960 to 1968 ( $r^2 = 0.673$ ,  $F_{1,3} = 6.16$ ,  $p = 0.089$ ). Pregnancy rates may have risen abruptly after 1968 (Fig. 4B), although these high estimates may simply be artifacts of sampling too close to the rookeries in 1973 and 1974 (York 1979; Smith and Polachek 1984).

### Proportion of Multiparous Females

Few females have had two or more pregnancies by the age of 5 (Fig. 3). But by the ages of 6 and 7, the proportion of multiparous females is large, until virtually all females are multiparous at age 8.

The conclusion that pregnancy rates declined as the population dropped is supported by the changing proportion of multiparous females captured. The proportion of 6- and 7-yr-old females that were multiparous in the 1958–74 pelagic samples (Fig. 5) declined with time (weighted linear regressions – age 6:  $r^2 = 0.4405$ ,  $F_{1,15} = 11.81$ ,  $p = 0.004$ ; age 7:  $r^2 = 0.5867$ ,  $F_{1,15} = 21.29$ ,  $p < 0.001$ ). This suggests that pregnancy rates must have dropped and/or that the age of females at first estrus increased as the population declined.

TABLE 1. Number of female northern fur seals captured in 1959 and 1960 that were nulliparous, primiparous, and multiparous and the proportion that were currently or previously pregnant  $p_{a,t}$ .

| Age | 1959  |       |       |           | 1960  |       |       |           |
|-----|-------|-------|-------|-----------|-------|-------|-------|-----------|
|     | nulli | primi | multi | $p_{a,t}$ | nulli | primi | multi | $p_{a,t}$ |
| 1   | 79    | 0     | 0     | 0.00      | 26    | 0     | 0     | 0.00      |
| 2   | 55    | 0     | 0     | 0.00      | 63    | 0     | 0     | 0.00      |
| 3   | 46    | 1     | 0     | 0.02      | 72    | 0     | 1     | 0.01      |
| 4   | 101   | 14    | 1     | 0.13      | 50    | 3     | 1     | 0.07      |
| 5   | 45    | 68    | 27    | 0.68      | 32    | 33    | 20    | 0.62      |
| 6   | 14    | 46    | 98    | 0.91      | 12    | 23    | 48    | 0.86      |
| 7   | 5     | 22    | 165   | 0.97      | 2     | 14    | 97    | 0.98      |
| 8   | 1     | 14    | 193   | 0.97      | 3     | 11    | 139   | 0.98      |
| 9   | 0     | 5     | 138   | 1.00      | 0     | 4     | 177   | 1.00      |
| 10  | 0     | 1     | 116   | 1.00      | 0     | 4     | 159   | 1.00      |

The proportion of females estimated to be multiparous represents all regions of the North Pacific and all months. The likelihood of biased estimates arising from segregated migrations was reduced because samples were from a wide geographical and temporal range. Furthermore, while females may segregate on the basis of age and whether they are pregnant or nonpregnant, there is no evidence that they segregate on the basis of parity (Bigg 1990; Trites 1990). Hence, we felt it was appropriate to pool the data.

### Age at First Birth

Early analysis of pelagic data suggested that the age at first birth changed in a density-dependent fashion (Nagasaki 1961; Chapman 1964). Subsequently, York (1983) calculated the average age at first birth for individual year classes (1952–66) and found that it abruptly increased beginning with the 1956 year class. Age at first birth subsequently decreased but never to the level of the 1952–55 year classes. Possible explanations offered were an impact on prey abundance by commercial fishing or a selection during the female harvest towards taking females that matured earlier.

In the current analysis, we modified the methods of DeMaster (1978, 1981) and York (1983) to estimate the mean age at first birth. We calculated the females' mean age at first birth based on the year of collection rather than on the year class as has been done previously. We took this approach because the attainment of sexual maturity is more likely to be a function of annual feeding conditions than accumulated cohort growth (see Discussion).

Mean age at first birth in any given year is estimated as follows. The proportion of females that are pregnant by age  $a$  in year  $t$  is

$$(1) \quad p_{a,t} = \frac{n_{a,t}}{N_{a,t}}$$

where  $n_{a,t}$  is the number of females in the sample that have ovulated at least once in their lifetime (primiparous + multiparous females) and  $N_{a,t}$  is the total number of females in the sample (nulliparous + primiparous + multiparous females). The probability of being pregnant for the first time at age  $a$  in year  $t$  is

$$(2) \quad \hat{p}_{a,t} = p_{a,t} - p_{a-1,t-1}$$

where  $\hat{p}_{a,t} \geq 0$ . From this, the average age at first birth  $\bar{A}$  in year  $t$  is

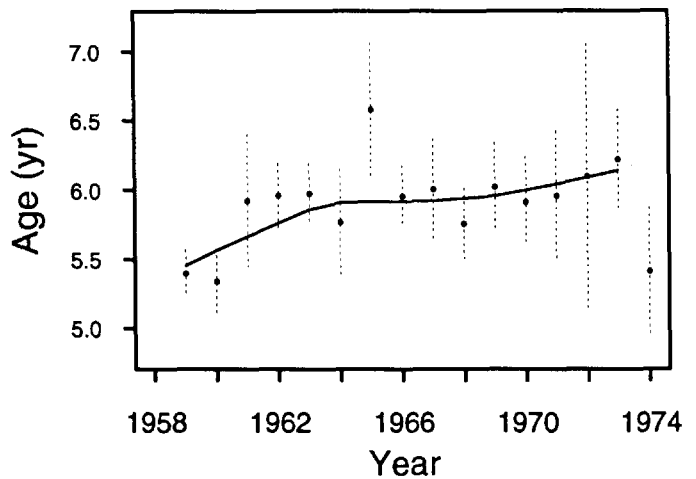


FIG. 6. Mean age at first birth in 1959–74. The trend is shown with a locally weighted robust regression (lowess,  $f = 0.6$ ). Broken lines are 95% confidence limits.

$$(3) \quad \bar{A}_t = \frac{\sum_{a=1}^w a \hat{p}_{a,t}}{\sum_{a=1}^w \hat{p}_{a,t}}$$

To illustrate using the data in Table 1 for the females sampled in 1960:  $\sum_{a=1}^{10} \hat{p}_{a,t} = 0.00 + 0.00 + 0.01 + 0.05 + 0.49 + 0.18 + 0.07 + 0.01 + 0.00 + 0.00$  and  $\sum_{a=1}^{10} a \hat{p}_{a,t} = 0.00 + 0.00 + 0.04 + 0.21 + 2.47 + 1.06 + 0.50 + 0.05 + 0.04 + 0.00$ . Thus the mean age at first birth in 1960,  $\bar{A}_{1960}$ , was 5.34 yr.

The variance of  $\bar{A}_t$  is estimated with the jackknife procedure (Mosteller and Tukey 1977). Based on  $k$  sample observations ( $k = \sum_{a=0}^w [N_{a,t} + N_{a-1,t-1}]$ ),  $k$  estimates of  $\bar{A}_t$  are calculated, each time omitting one sample observation. Next,  $k$  pseudo-values  $J_{i,t}$  are calculated, utilizing the mean age of the full sample  $\bar{A}_t$  and the mean age  $\bar{A}_{i,t}$  obtained by omitting observation  $i$ :

$$(4) \quad J_{i,t} = k \bar{A}_t - (k - 1) \bar{A}_{i,t} \quad i = 1, 2, \dots, k.$$

The variance of the  $k$  pseudo-values  $J_1, J_2, \dots, J_k$  is

$$(5) \quad \text{Var}(\bar{A}_t) = \frac{\sum_{i=1}^k J_{i,t}^2 - \frac{1}{k} (\sum_{i=1}^k J_{i,t})^2}{k(k - 1)}.$$

Degrees of freedom are equal to the number of different pseudo-values minus 1.

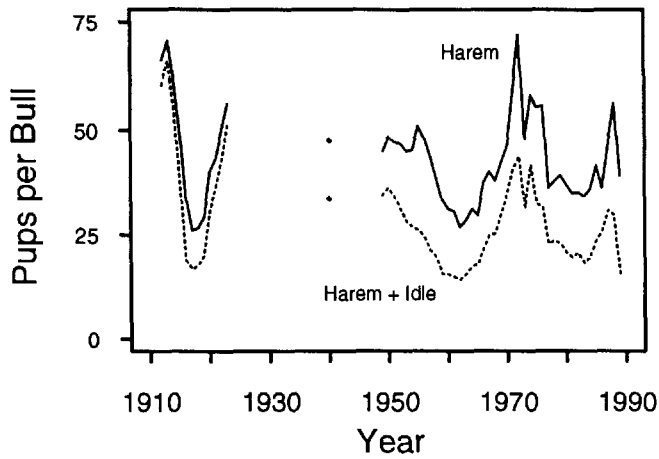


FIG. 7. Ratio of pups born to the number of bulls counted on St. Paul Island. The solid line is a rough measure of harem size based on data from Fig. 1. The broken line shows the ratio of females giving birth to the total number of mature bulls present (harem bulls + idle bulls). Harem bulls actively defend territories with one or more females. Idle bulls are also full grown and defend a territory, but have no females.

The mean age of females giving birth for the first time, as calculated with the above procedure, rose from 1959 and 1974 (Fig. 6). A weighted linear regression, with weight inversely proportional to the variance, indicates that this rise is significant ( $r = 0.56$ ,  $F_{1,14} = 6.41$ ,  $p = 0.02$ ). The anticipated decline in age at first birth in response to the population reduction did not occur.

## Discussion

A female's ability to conceive is likely related to food availability and body fat. Many pinniped studies have certainly recognized the importance of growth and nutrition in the attainment of sexual maturity (Laws 1956, 1959; Bryden 1968; Sergeant 1973, 1978; Bowen et al. 1981; Innes et al. 1981; Lett et al. 1981). However, none has considered the critical importance of body fat in relation to body size. Studies of rats and pigs demonstrate that individuals given a high fat diet have first estrus significantly earlier than others fed a low fat diet of equal calories (Kennedy and Mitra 1963; Dickerson et al. 1964; Frisch et al. 1975). Human studies further support the view that females must store at least a threshold or minimum amount of body fat to begin and maintain normal menstrual cycles and hence have the ability to reproduce (Frisch and McArthur 1974; Frisch 1978, 1985).

Nulliparous fur seals ovulate for the first time in August and September (Craig 1964). Based on the studies of rats, pigs, and humans, the weight of the seal in relation to her length probably governs whether or not she ovulates. Thus, high pregnancy rates in one year should correspond to a high ratio of body weight to length the previous year. We attempted to test this by correlating pregnancy rates with body mass of females collected near the Pribilofs from June to August of the previous year. Unfortunately the data were too sparse and no comparison could be made. However, it appears from growth curves that northern fur seals attained larger body sizes as the population declined through the 1960s (Bigg 1979b; Trites and Bigg 1992). Thus, it seems unlikely that the drop in pregnancy rates could be related to body size, given that pregnancy rates dropped as body size increased. Note, however, that there may be a relationship

between the annual growth rate of immature females (fig. 4 in Trites and Bigg 1992) and the proportion of multiparous 6-yr-olds (Fig. 5). These data suggest comparable periodic changes from 1958 to 1974 in both growth rates and the proportion of females that were multiparous.

Another factor that might influence pregnancy rates is a shortage of bulls to service the females (Kenyon et al. 1954; Scheffer 1955). A rough measure of harem size and hence the availability of males is the ratio of pups born to the number of bulls counted (calculated from Fig. 1). As shown in Fig. 7, the average harem size (which excludes harem females without pups) has fluctuated between 25 and 75 females per bull since 1911. Much of this variation is probably associated with the commercial harvesting of males and females. As such, it is difficult to determine what the natural or optimum ratio of males to females is and how this ratio might affect reproductive rates. What is clear, however, is that the harem size increased rapidly from 26.8 females per male in 1962 to 72.0 females per male in 1972. At the same time, pregnancy rates declined (Fig. 4A).

The correlation between harem size and pregnancy rates (ages 8–13 yr, California–British Columbia) is significant (weighted linear regression:  $r^2 = 0.370$ ,  $F_{1,10} = 5.87$ ,  $p = 0.036$ ) as is the relationship between pregnancy rates and females per harem plus idle bulls ( $r^2 = 0.602$ ,  $F_{1,10} = 15.11$ ,  $p = 0.003$ ). However, correlations are weaker if pregnancy rates are lagged by 1 yr (harem:  $r^2 = 0.039$ ,  $F_{1,10} = 0.40$ ,  $p = 0.539$ ; harem + idle:  $r^2 = 0.380$ ,  $F_{1,10} = 6.14$ ,  $p = 0.033$ ). This raises two points. First, idle bulls may have a major impact on pregnancy rates. Second, caution needs to be exerted in interpreting these correlations because both sets of variables contain errors and represent parameter changes in a single direction. More conclusive statements could be made only if pregnancy rates had been estimated through the 1970s as the harem size decreased.

Gentry and Goebel (1982) observed copulations on the breeding beaches and did manipulative experiments with captive males and females to study reproductive behaviour. They found that females enter estrus rapidly and spontaneously between 5 and 7 d postpartum but can be induced by males (cf. Craig 1964). Estrus will only last up to 34 h if the female fails to copulate and will not reoccur later in the breeding season. However, estrus can be terminated within a few minutes of copulation depending upon the diameter of the terminal bulb of the penis and the pattern of pelvic thrusting. Thus, while females are receptive to males ranging in size from 45 to 135 kg (age 5 yr and older, based on growth curves in Trites 1990), the smaller males are not as effective at terminating estrus. Nevertheless, the young males are fertile and successfully impregnate females. This suggests that altering the sex ratio by harvesting immature males could affect the overall rate of reproduction if young males are not available in sufficient number to mate with late arriving young females (Fowler 1990).

The period from the late 1950s to early 1970s was probably one of great turmoil on the rookeries. On one hand, there was a sharp rise and then drop in the numbers of idle bulls seeking females (Fig. 1). On the other, some of the harems were disturbed by rounding up females from the rookeries for harvesting, while others became depleted over time as females harvested from hauling grounds failed to return to their pups (Roppel 1984; Scheffer et al. 1984). The size of the female harvest was large and occurred over a brief period of time (1956–68). Indeed, killing mature females can account for over 70% of the drop in numbers of pups born through the 1960s

(Fig. 1; York and Hartley 1981; Trites and Larkin 1989). All told, these changes during the period of harvesting males and females undoubtedly altered social structure and interaction on the rookeries. This in turn could have lowered pregnancy rates by reducing social stimulus needed to successfully mate or by disrupting mating during the few hours of estrus.

The changes observed from 1958 to 1974 in pregnancy rates and age at first birth were not the anticipated density-dependent responses. Instead of rising, productivity dropped during the years of herd reduction. The most likely explanation for this unexpected result is that reproduction was a function of relative densities of mature age and sex classes in harems rather than absolute population density. The decision to harvest females was based on theoretical concepts of density dependence which have changed little over the past three decades. The failure of the female harvest to achieve its goals contributed to the decline of the herd and demonstrates our incomplete understanding of fur seal population biology. Insights gained from this shortcoming suggest that greater emphasis should be placed upon rookery social structure and fur seal reproductive behaviour in future efforts to manage the northern herds.

## Acknowledgements

The pelagic data were collected from 1958 to 1974 by the Department of Fisheries and Oceans (Canada) and the National Marine Fisheries Service (United States) under the auspices of the North Pacific Fur Seal Commission. We are grateful to the late Michael Bigg, Peter Boveng, Don Bowen, Howard Braham, Chuck Fowler, Don Ludwig, John Sease, and Carl Walters for their constructive comments and suggestions on earlier drafts of this manuscript. A.W.T. was supported in part by an NSERC operating grant awarded to Don Ludwig at the University of British Columbia.

## References

- BIGG, M.A. 1979a. Preliminary comments on pregnancy rate and age at first pupping, p. 123-142. *In* H. Kajimura, R.H. Lander, M.A. Perez, A.E. York, and M.A. Bigg. Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Submitted to the 22nd annual meeting of the standing scientific committee, North Pacific Fur Seal Commission, April 1979, Washington, DC. (Available from the National Marine Mammal Laboratory, NMFS, 7600 Sand Point Way, N.E., Seattle, WA, 98115)
- BIGG, M.A. 1979b. Preliminary comments on growth by length in female northern fur seals, p. 158-166. *In* H. Kajimura, R.H. Lander, M.A. Perez, A.E. York, and M.A. Bigg. Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Submitted to the 22nd annual meeting of the standing scientific committee, North Pacific Fur Seal Commission, April 1979, Washington, DC. (Available from the National Marine Mammal Laboratory, NMFS, 7600 Sand Point Way, N.E., Seattle, WA, 98115)
- BIGG, M.A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. *Can. Tech. Rep. Fish. Aquat. Sci.* 1764: 64 p.
- BOWEN, W.D., C.K. CAPSTICK, AND D.E. SERGEANT. 1981. Temporal changes in the reproductive potential of female harp seals (*Pagophilus groenlandicus*). *Can. J. Fish. Aquat. Sci.* 38: 495-503.
- BRYDEN, M.M. 1968. Control of growth in two populations of elephant seals. *Nature (Lond.)* 217: 293-299.
- CHAPMAN, D.G. 1961. Population dynamics of the Alaska fur seal herd. *Trans. North Am. Wildl. Nat. Resour. Conf.* 26: 356-369.
- CHAPMAN, D.G. 1964. A critical study of Pribilof fur seal population estimates. *U.S. Fish Wildl. Serv. Fish. Bull.* 63: 657-669.
- CHAPMAN, D.G. 1981. Evaluation of marine mammal population models, p. 277-296. *In* C.W. Fowler and T.D. Smith [ed.] *Dynamics of large mammal populations*. J. Wiley and Sons, New York, NY.
- CRAIG, A.M. 1964. Histology of reproduction and the estrus cycle in the female fur seal, *Callorhinus ursinus*. *J. Fish. Res. Board Can.* 21: 773-821.
- DEMASTER, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. *J. Fish. Res. Board Can.* 25: 912-915.
- DEMASTER, D.P. 1981. Estimating the average age of first birth in marine mammals. *Can. J. Fish. Aquat. Sci.* 38: 237-239.
- DICKERSON, J.W.T., G.A. GRESHAM, AND R.A. MCCANCE. 1964. The effect of undernutrition and rehabilitation on the development of the reproductive organs: pigs. *Endocrinology* 29: 111-118.
- EBERHARDT, L.L. 1990. A fur seal population model based on age structure data. *Can. J. Fish. Aquat. Sci.* 47: 122-127.
- FOWLER, C.W. 1990. Northern fur seals of the Pribilof Islands. *In* The northern fur seal. Species of the USSR and the contiguous countries. USSR Academy of Sciences, Nauka, Moscow. (Available from the National Marine Mammal Laboratory, NMFS, 7600 Sand Point Way N.E., Seattle, WA 98115)
- FRISCH, R.E. 1978. Population, food intake, and fertility. *Science (Wash., DC)* 199: 22-30.
- FRISCH, R.E. 1985. Fatness, menarche, and female fertility. *Perspect. Biol. Med.* 28: 611-633.
- FRISCH, R.E., D.M. HEGSTED, AND K. YOSHINAGA. 1975. Body weight and food intake at early estrus of rats on high fat diet. *Proc. Natl. Acad. Sci. USA* 72: 4172-4176.
- FRISCH, R.E., AND J. McARTHUR. 1974. Menstrual cycles: fatness as a determinant of minimum weight for height necessary for their maintenance or onset. *Science (Wash., DC)* 185: 949-951.
- GENTRY, R.L., AND M.E. GOEBEL. 1982. Behavior and biology. Pribilof Islands, p. 27-32. *In* P. Kozloff [ed.] *Fur seal investigations, 1981*. U.S. Dep. Commer. NOAA Tech. Memo. NMFS F/NWC-37.
- INNES, S., R.E.A. STEWART, AND D.M. LAVIGNE. 1981. Growth in Northwest Atlantic harp seals *Phoca groenlandica*. *J. Zool. (Lond.)* 194: 11-24.
- KENNEDY, G.C., AND J. MITRA. 1963. Body weight and food intake as initiation factors for puberty in the rat. *J. Physiol. (Lond.)* 166: 408-418.
- KENYON, K.W., V.B. SCHEFFER, AND D.G. CHAPMAN. 1954. A population study of the Alaska fur seal herd. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl.* 12: 7 p.
- LANDER, R.H. [ED.] 1980a. Summary of northern fur seal data and collection procedures. Vol. 1. Land data of the United States and Russia (excluding tag recovery records). U.S. Dep. Commer. NOAA Tech. Memo. NMFS F/NWC-3.
- LANDER, R.H. [ED.] 1980b. Summary of northern fur seal data and collection procedures. Vol. 2. Eastern Pacific pelagic data of the United States and Canada (excluding fur seal sighted). U.S. Dep. Commer. NOAA Tech. Memo. NMFS F/NWC-4.
- LANDER, R.H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fish. Res.* 1: 55-70.
- LANDER, R.H., AND H. KAJIMURA. 1982. Status of northern fur seals, p. 319-345. *In* *Mammals in the seas*. Vol. 4. Small cetaceans, seals, sirenians and otters. *Advis. Comm. Mar. Resour. Res.* FAO Fish. Ser. 5. FAO, United Nations, Rome.
- LAWS, R.M. 1956. Growth and sexual maturity in aquatic mammals. *Nature (Lond.)* 178: 193-194.
- LAWS, R.M. 1959. Accelerated growth in seals with special reference to the Phocidae. *Norsk. Hvalfangsttid.* 9: 425-452.
- LETT, P.F., R.K. MOHN, AND D.F. GRAY. 1981. Density dependent processes and management strategy for the Northwest Atlantic harp seal populations, p. 135-158. *In* C.W. Fowler and T.D. Smith [ed.] *Dynamics of large mammal populations*. J. Wiley and Sons, New York, NY.
- MOSTELLER, F., AND J.W. TUKEY. 1977. *Data analysis and regression*. Addison Wesley Publ. Co., Reading, MA. 588 p.
- NAGASAKI, F. 1961. Population study on the fur seal herd. Suisan-cho Tokaiku Suisan Kenkyusho (Fish. Agency, Tokai Reg. Fish. Res. Lab.) Spec. Publ. No. 7: 60 p.
- ROPPEL, A.Y. 1984. Management of northern fur seals on the Pribilof Islands, Alaska, 1786-81. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 4: 26 p.
- SCHEFFER, V.B. 1955. Body size with relation to population density in mammals. *J. Mammal.* 39: 493-515.
- SCHEFFER, V.B., C.H. FISCUS, AND E.I. TODD. 1984. History of Scientific study and management of the Alaskan fur seal, *Callorhinus ursinus*, 1786-1964. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-780: 70 p.
- SERGEANT, D.E. 1973. Environment and reproduction in seals. *J. Reprod. Fert. Suppl.* 19: 555-561.
- SERGEANT, D.E. 1978. Research on harp seals in 1978. *Res. Doc. Int. Comm. Northwest Atl. Fish.* 78/XI/85.
- SILER, W. 1979. A competing risk model for animal mortality. *Ecology* 60: 750-757.
- SMITH, T., AND T. POLACHECK. 1984. The population dynamics of the Alaska fur seal: what do we really know? U.S. Dep. Commer. Natl. Mar. Fish. Serv. NWAFC Proc. Rep. 84-15: 122 p.
- TRITES, A.W. 1989. Estimating the juvenile survival rate of male northern fur seals (*Callorhinus ursinus*). *Can. J. Fish. Aquat. Sci.* 46: 1428-1436.

- TRITES, A.W. 1990. The northern fur seal: biological relationships, ecological patterns and population management. Ph.D. thesis, University of British Columbia, Vancouver, B.C. 330 p.
- TRITES, A.W. 1991. Fetal growth of northern fur seals: life history strategy and sources of variation. *Can. J. Zool.* 69: 2608–2617.
- TRITES, A.W., AND M.A. BIGG. 1992. Changes in body growth of northern fur seals from 1958 to 1974: density effects or changes in the ecosystem? *Fish. Oceanogr.* 1: 127–136.
- 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.
- YORK, A.E. 1979. Analysis of pregnancy rates of female fur seals in the combined United States – Canadian pelagic collections, 1950–74, p. 50–122. *In* H. Kajimura, R.H. Lander, M.A. Perez, A.E. York, and M.A. Bigg. Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958–74. Submitted to the 22nd annual meeting of the standing scientific committee, North Pacific Fur Seal Commission, April 1979, Washington, DC. (Available from the National Marine Mammal Laboratory, NMFS, 7600 Sand Point Way N.E., Seattle, WA, 98115)
- YORK, A.E. 1980. Maturity and age at first reproduction, p. 64–71. *In* H. Kajimura, R.H. Lander, M.A. Perez, A.E. York, and M.A. Bigg. Further analysis of pelagic fur seal data collected by the United States and Canada during 1958–74. Submitted to the 22nd annual meeting of the standing scientific committee, North Pacific Fur Seal Commission, April 1980, Moscow, U.S.S.R. (Available from the National Marine Mammal Laboratory, NMFS, 7600 Sand Point Way N.E., Seattle, WA, 98115)
- YORK, A.E. 1983. Age at first reproduction of the northern fur seal (*Callorhinus ursinus*). *Can. J. Fish. Aquat. Sci.* 40: 121–127.
- YORK, A.E. 1985. Estimation of the size of the 1940 year class, p. 20. *In* P. Kozloff [ed.] Fur seal investigations, 1982. NOAA Tech. Memo. NMFS-F/NWC-71.
- YORK, A.E., AND J.R. HARTLEY. 1981. Pup production following harvest of female northern fur seals. *Can. J. Fish. Aquat. Sci.* 38: 84–90.