Northwest Atlantic Fisheries Organization

Serial No. N474

NAFO SCR Doc. 81/XI/166
(Revised)

SCIENTIFIC COUNCIL MEETING - JUNE 1982

Population Dynamics of Harp Seals, 1967-1991

by

Derek A. Roff
Dept. of Biology, McGill University, 1205 McGregor Avenue
Montreal, Quebec, Canada H3A 1B1

and

W. Don Bowen
Research and Resource Services, Department of Fisheries and Oceans
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

Abstract

Previous attempts at estimating population size and natural mortality rate in harp seals are unsatisfactory because they are based on questionable assumptions or fail to take sufficient cognizance of the uncertainty in the estimation of population parameters. In this paper we adopt a maximum likelihood approach to estimate population size and the rate of natural mortality. 'Most likely' estimates and the associated confidence regions are derived. The basis of this method is a simulation model and externally derived estimates of the ratios between pup productions in 1967 and 1968, 1971 and 1972, and estimates of pup production in 1978 and 1979 from mark-recapture studies. We project the model forward ten years to examine the effects of different quotas on population size. There is no evidence that under the present quota the population is endangered, and in fact a significant increase in population size is predicted given the present level of kill.

Introduction

The northwest Atlantic harp seal, Phoca groenlandica, has in recent years been the subject of controversy within both the scientific and popular literature. Much of this controversy concerns the present status of the population and future management policy. Recent assessments of fluctuations in population size from 1952 to the present (Lett and Benjaminsen 1977, Lett, Mohn and Gray 1979, Winters 1978) have been based largely on cohort analysis and a method of estimating pup production from catch-at-age information termed the survival index method (Sergeant 1975, Benjaminsen and Øritsland MS 1975). Estimates of past and present population are in close agreement, Lett and Benjaminsen (1977) estimating the 1977 population size of animals one year and older (1+) to be 1.2 million, whereas Lett et al. (1979) and Winters (1978) both estimate it at 1.3 million. Since there is considerable overlap in methodology employed this agreement is perhaps not suprising. For this reason it is also not suprising that all three papers estimate the natural mortality rate of 1+ seals to be approximately 0.1. This rate is quite reasonable for a species living to age 30 or more and has been generally accepted.

At a recent meeting sponsored by the World Wildlife Fund to examine the biology and management of the northwest Atlantic harp seal population, Beddington and Williams (1980) presented an alternate method of analyzing the historical data. By this method they estimate the natural mortality rate to be 0.1375. This rate is also quite reasonable for the harp seal; any rate between 0.05 and 0.15 might be considered *a priori* 'reasonable'. The analysis by Beddington and Williams (1980) also produces a different historical population trajectory, although by chance their estimate of the 1979 population size coincides with that derived from cohort analysis. Future projections of population size are significantly affected by the cummulative effect of this higher estimate of natural mortality rate. A closer examination of harp seal population dynamics is clearly warranted.

A major failing of cohort analysis is that it depends upon an estimate of natural mortality and an initial estimate of hunting mortality. Because of the highly selective nature of the various hunts on harp seals, estimating these parameters is difficult (Lett and Benjaminsen 1977, Lett et al. 1979) and the methodologies employed questionable because of the assumptions involved. The most serious problem, however, is the failure to adequately investigate the sensitivity of the analysis to uncertainties in the estimated parameters (but see Mohn 1979). This failure is due to an unwarranted belief in the accuracy of the estimates. Lett and Benjaminsen (1977) calculated total mortality rate for two periods from changes in age frequencies within samples of moulting males, presuming these to be representative of the population age structure. Natural mortality was then calculated by solving two simultaneous equations equating hunting mortality and natural mortality to total mortality. This required estimating the proportional change in the hunting mortality for the two periods, which they did by estimating the change in hunting effort, defined without justification, as number of men involved in the hunt X total horsepower of vessels used X number of days the hunt lasted X (tonnage of vessels)$^{-1}$. The standard errors of the estimates of natural mortality and hunting mortality were estimated presuming the above assumptions to be correct. The estimates themselves and their associated confidence limits may be highly biased if one or more of these assumptions is incorrect. Winters (1978) also estimated total mortality using the age composition data of moulting males, again without statistically examining the assumption that these samples are representative of the population age distribution. Hunting mortality was calculated using pup production estimates from the survival index method and natural mortality obtained by subtraction from the total mortality. Once again the confidence limits given do not take into account inaccuracies in the underlying assumptions, most particularly the population age distribution and the pup production estimates.

Lett et al. (1979) calculated the natural mortality rate using pup production estimates from the survival index method and the sampled age distribution of moulting male seals; the possible errors in these components are not considered. They avoided the problem of estimating hunting mortality by instead estimating the terminal population size using the age structure of the population, pregnancy rate and whelping ogive and the pup production. The age structure was estimated from catch-at-age data taken in the moulting patch and the pup production by the survival index method. There is no published mathematical rationale of the survival index method and the sources of error on bias in this method have not been adequately examined. We present such an examination. Suffice it to note here that, at present, confidence limits cannot be given for these estimates and the possible source of bias make the estimates and use of the method in setting the initial conditions for cohort analysis questionable.

The method used by Beddington and Williams (1980) consists of comparing the output of a simulation model with a set of independent observations. The independent observations in this case are the catch statistics from either the large vessel or landsmen's hunt. Since these catches are also used in their simulation they are not strictly independent and the method would be severely compromised if the catches were 'driving' the simulation model. The hunting mortality on 1+ seals, the age groups used by Beddington and Williams, is very low and is unlikely to be a major driving variable and therefore the lack of independence is probably not critical. Another problem in the estimation procedure is that the hunts are age selective and hence a set of selectivities must be added into the model to adjust the predicted population age distribution to the observed catch distribution. Beddington and Williams did this by assuming that selectivities remained constant at least over blocks of five years. After this they estimated the relevant parameter values by minimizing a χ^2 function based on observed and predicted catches. They later derived confidence limits for this estimate. Their 1980 estimate of 0.1375 and a later revised estimate of .1440 are considerably higher than previous estimates. There are four possible reasons for this: their model might be wrong, the estimation procedure might be wrong, the data might be wrong, and all previous estimates might be wrong. The first seems unlikely because the model is basically only a book-keeping model and involves no nonlinear interactions. The second possibility we also reject in principle, but question the robustness of the technique. This is particularly crucial because there is cause for concern over the age distributions. An analysis by Doubleday and Bowen (MS 1980) indicates that there are significant errors in estimation of age for animals older than about 10 or 12 years. The χ^2 technique weights the older age classes very heavily and it may well be that the noise in these age groups leads to an incorrect minimum. It is significant that other weighting procedures used by Beddington and Free (pers. comm.) such as least squares, which do not give great weight to the older age classes, produces a very flat surface with little discrimination between combinations. Nevertheless the results do call into question previous estimates. It is also possible that Beddington's analysis is sensitive to the pregnancy rate of harp seals used to initiate the model in 1952. Pregnancy rate data are generally unavailable for this period, there being only two samples prior to 1964, one covering the period 1951-54 and another in 1952 (Bowen, Capstick, and Sergeant 1981). If the analysis is sensitive to these uncertain initial values the results must be viewed with skepticism.

Given the problems outlined above with all the methods used to derive natural mortality rates, it is necessary to reexamine the problem carefully and attempt to discriminate between the various estimates. In this paper we first examine the assumption underlying all of the procedures except the χ^2 technique, that the sample of moulting males is a random sample from the population. Finding the answer to be negative we present a new approach that largely circumvents this problem and also avoids the problem of error in the age determination of older animals.

The Population

The following account of the biology of the northwest Atlantic harp seal is based largely on Sergeant (1976a). Harp seals are highly migratory marine mammals inhabiting Arctic waters in summer and sub-Arctic waters around Newfoundland in winter. They begin their southward migration in late September when new Arctic ice is forming and by December the first migrants have reached northern Newfoundland. Here the population separates; about one third of the mature seals going into the Gulf of St. Lawrence to breed near the Magdalen Islands (known as the 'Gulf' herd) and the remainder continuing down the east coast of Newfoundland and eventually breeding on southward drifting Arctic ice off southern Labrador (known as the 'Front' herd). During winter most immature harp seals feed in the 'Front' area, although some do migrate into the northern Gulf of St. Lawrence.

Females give birth to a single pup several days after they have hauled out onto the ice, with most births occurring over a one-week period beginning in late February in the Gulf and about March 8th at the Front. Newborn pups are covered with a long white fur from which they derive the name 'whitecoats'. Pups are nursed for about nine days and then are abandoned by their mothers (Stewart and Lavigne 1980). Once abandoned, whitecoats at the Front continue to drift southward to rich feeding grounds in White and Notre Dame Bays, Newfoundland. They also begin to shed their white fur at this time and after about 18 days of age this coat is completely shed and is replaced with the spotted juvenile pelage. Moulted pups are known as 'beaters'.

As soon as females have finished lactation in March, but before they leave the whelping area, they are courted by males which have been waiting nearby in large herds. Mating appears to be promiscuous.

In early April harp seals haul out onto the receding pack ice usually east of Belle Isle to moult. Adult males and immatures, known as 'bedlamers', moult first, following by adult females which begin to moult about the third week of April. After moulting, harp seals age one and older migrate north. Beaters begin their northern migration in May and some reach West Greenland by early June. At this time adults and immatures are fairly well segregated with mature seals feeding mainly in the Canadian Arctic and the bedlamers and beaters inhabiting the waters off West Greenland.

Age Structure of the Catch

For some populations it may be assumed that the age structure of the catch is directly proportional to the population age structure. However, when applied to the northwest Atlantic harp seal population this assumption can lead to serious errors because several different methods are used to harvest these animals, each with different hunting selectivities (Benjaminsen and Øritsland MS 1975, Lett and Benjaminsen 1977). Seals captured in nets from late December through February along the coasts of southern Labrador and Quebec and in the vicinity of St. Anthony, Newfoundland, are mainly mature animals; whereas seals shot from small boats and larger vessels up to 20 m in length during the February-May period are generally immature animals. The large vessel (offshore) catches taken from breeding concentrations prior to 1965 and from moulting patches throughout the sampling period (1952-1980) consist of a mixture of immature and mature animals. For this reason, the age structure of the total annual catches of 1+ seals must take into account the age compositions of catches by different hunting methods in their proper proportions (Lett and Benjaminsen 1977).

Lett and Benjaminsen (1977) produced the first comprehensive age structure of total annual harp seal catches in the northwest Atlantic for the period 1952-75. The present analysis is based on revised catch-at-age data for the period 1952-80 (Bowen 1982). These data differ from those given in Lett and Benjaminsen (1977) in that they include animals 26 years of age and older and catches from the Canadian Arctic and West Greenland. They also correct a bias in the age composition of inshore catches which led to over-estimation of the kill of mature animals, particularly in recent years.

Some biases most likely still exist in the estimated age compositions of the catch. The age of harp seals in the catches was determined by counting dentine annuli (Fisher 1954) and was generally based on a single examination of each tooth. Recent work by Doubleday and Bowen (MS 1980) and R.E.A. Stewart and D.M. Lavigne (pers. comm.) indicates that there is substantial error associated with age determination of harp seals by this method when age is based on a single 'reading'. The implications of these errors on the estimated age composition of catches have not been thoroughly analyzed, but preliminary work shows that these errors may be important in the estimation of pup production from catch data (Doubleday and Bowen MS 1980). Furthermore, the absence of age samples of seals shot by landsmen for the 1963-73 period and the small sample size used to estimate age compositions of other components of the hunt in certain years have led to assumptions which also may introduce bias.

Biological sampling of catch has progressively improved over time, particularly after 1966. Consequently, the estimated age compositions of catches from 1952 to about 1965 are least reliable, whereas considerable confidence may be placed on the data from 1974 onwards. The period from 1966 to 1973 may be considered as a period of gradual improvement in the reliability of the estimates (Bowen 1982).

Are Random Samples of Moulting Seals Really Random?

With the exception of the method of Beddington and Williams all previous attempts to estimate the rate of natural mortality presume that samples of moulting male harp seals are representative of the population age structure. These samples have also been used in the subsequent cohort analyses to establish the initial age-specific weighting factors for hunting mortalities.

We can test this assumption in the following way. Suppose in year t we obtain a random sample of animals whose frequencies within the sample are f_1, $f_2 \ldots f_i \ldots f_n$, where i is age and n the final age or age group (eg. 8+ animals). In year t+1 another random sample is taken and we calculate the frequencies f_2, $f_3 \ldots f_{i+1}$, $\ldots f_{n+1}$, the new incoming cohort being ignored. If the mortality rates are the same at each age then f_i in year t will equal f_{i+1} in year t+1. The two age distributions can be compared using either a χ^2 or G test: a significant result indicates either that hunting mortalities are not equal or that the sample is not random. Variation in hunting mortalities will have to be very large in order to generate a shift in the distribution since it is necessary to shift the population age distribution. The hunting mortality on adult seals is far too small (Lett and Benjaminsen 1977; Winters 1978) to be capable of causing such a shift and hence a significant G value indicates non-random sampling.

Reasonably large samples of moulting males are available for the years 1968, 1969, 1970, 1971, 1973, 1974 and 1976. Our initial analysis used the age distribution of 2 through to 15+. Numerous pairwise comparisons are available: we used the following procedure to select one particular set. To compare 1968 to other years we used the 2 to 9+ age distributions in 1968; thus this age distribution was compared to the 3 to 10+ in 1969, 4 to 11+ in 1970 and so forth. To compare 1969 to other years we used the 3 to 10+ age distribution in 1969; thus this age distribution was compared to the 4 to 11+ in 1970, the 5 to 12+ in 1971 and so forth. The same methodology was employed in comparing years 1970-74 to other years. Each comparison has 8 classes. There are a total of 21 possible comparisons; of these 7 were significantly heterogeneous, indicating that the samples are not random (Table 1). Correcting for the possible over representation of 2-, 3- and 4-year-olds in the sample using the correction factors derived by Sergeant (MS 1976b) or Bowen and Winters (MS 1979) did not remove the significant deviations. A detailed examination of the data indicates that the deviations are not caused by any systematic bias in the data, but rather by particular age groups being over- or under-represented in the sample. One way this could arise is if animals of the same age tended to herd together. In fact this appears to be the case. Sergeant (1965) and Øritsland (MS 1971) report that in late March moulting patches are composed of immatures of both sexes and adult males in separate patches. Later these age groups mix to a greater extent. Adult females enter the moulting patches more gradually and become fully represented only by late April. Whatever the reason, it is clear that the age distributions of moulting samples cannot be assumed to be representative of the population.

The Survival Index Method

As defined by Winters (1978) the survival index is

$$SI_{a,t} = \frac{\text{Total Catch} \times C_{a,t}}{\sum_j C_{j,t} \sum_i C_{a,i}} \qquad (1)$$

where $C_{a,t}$ is the catch of animals of age a at time t and the two denominators are the column and row totals respectively of the age matrix. SI is plotted against pup kill and an estimate of pup production obtained from the pup kill at which SI equals zero. It is clearly necessary in applying this method to assume that pup production does not change significantly over the period of time being considered. For this reason Winters (1978) used only blocks of 5 years. But what other assumptions are inherent in the method?

Confining our attention initially to a single group, we can show that $SI_{a,t}$ is proportional to the frequency of that age group in the population provided that the partial recruitment multiplier shows no systematic trend over time, i.e. on average the multiplier remains the same. This is the same assumption made by Beddington and Williams (1980) in their χ^2 method. This assumption may be reasonable, but it has never been rigorously tested. Since pup production is assumed constant, it is reasonable to assume a constant population size N. Hence

$$f_{a,t} \propto \frac{[N_{o,t-a} - C_{o,t-a}]e^{-\sum_{i=1}^{t}(F_i + M)}}{N} \qquad (2)$$

where $f_{a,t}$ is the frequency, $N_{o,t-a}$ pup production in year t-a, $C_{o,t-a}$ the pup kill in that year and F_i and M the hunting and natural mortality rates from i=1 to i=t.

The last term will be approximately the same for cohorts of the same age and hence

$$f_{a,t} \propto \frac{N_{o,t-a} - C_{o,t-a}}{N} \qquad (3)$$

which verifies that there should be a linear relationship between the survival index and pup kill, at least when only a single age group is considered. Now suppose the population is changing with time, say as some function g(t): we have

$$f_{a,t} \approx \frac{g(t-a)p - C_{o,t-a}}{g(t)} \qquad (4)$$

where p is the proportion of the population pregnant. The ratio g(t-a)/g(t) is likely to be close to 1 permitting the approximation

$$f_{a,t} \simeq p - \frac{C_{o,t-a}}{g(t)} \qquad (5)$$

From the above it can be seen that the estimate of pup production depends not only upon the change in population size but also in the direction of the change in the pup kill. If the population is decreasing and the kill increasing the intercept on the X (pup kill) axis will be reduced whereas if the kill is decreasing the intercept will be extended. During the period 1950 to 1970 the pup kill fluctuated widely from 150,000 to 350,000 but did not show any trend. Thus while individual estimates may be over- or under-estimates due to these fluctuations there should be no consistent bias. Because of the averaging over blocks of 5 years, we would expect the estimate to lag behind the correct value when the population is in a slow decline, a phenomenon found in the simulation study of Beddington and Williams (1980).

To be able to combine survival indices for the same cohort over a number of years we require that they all estimate a common value.

Now

$$SI_{a,t} = \frac{\text{Total Catch } \times f_{a,t}}{\sum_i f_{a,t} E_i N_i} \qquad (6)$$

where E_i is the exploitation rate. We thus require that

$$\frac{f_{a,t}}{\sum_i f_{a,t} E_i N_i} \quad \text{and} \quad \frac{f_{a+1,t+1}}{\sum_i f_{a+1,t} E_i N_i} \qquad (6)$$

estimate a common value, which in general, they do not.

Can we get there from here?

It is a consensus among published analyses of harp seal population dynamics that by 1952 the population was depleted. Thus we may assume

(a) that at some time in the past the population was larger and

(b) that if hunting mortality were removed the population would increase in size.

Any model that attempts to simulate harp seal population dynamics should show an increase in population size after 1952 if hunting mortality is set to zero. Similarly a population in a stable age distribution in which the life table components are set at the 1952 level should increase in the absence of hunting. In a stable age distribution we have

$$\sum_{a=1}^{\infty} e^{-M_o} e^{-M(a-1)} P_a = 1 \qquad (7)$$

where M_o is the mortality rate in the first year, M the mortality rate in subsequent years and P_a the age-specific pregnancy rate. Using the pregnancy formula for the early 1950's of Beddington and Williams (1980) and assuming a 1:1 sex ratio we have

$$\sum_{a=6}^{a=8} 0.5\, e^{-M_o - M(a-1)} P_a + \sum_{a=9}^{a=\infty} 0.5e^{-M_o - M(a-1)} P_{max} = 1 \qquad (8)$$

where P_{max} is the maximum proportion pregnant, achieved by age 9. Substituting in the appropriate values and rearranging,

$$0.5\,(0.23e^{-5M} + 0.59e^{-6M} + 0.80e^{-7M}) + \frac{0.85e^{-8M}}{2(1-e^{-M})} = e^{M_o} \qquad (9)$$

If mortality in the first year of life equals that in subsequent years, then $M_o = M = 0.155$. Beddington and Williams (1980) derived $M_o = .45$ and $M = 0.1375$; substitution of M_o in equation (9) yields a maximum value for M of 0.131. Beddington and Free (pers. comm.) derived $M_o = 0.35$ and $M = 0.144$; from equation (9) we obtain $M = 0.139$ when $M_o = 0.35$. In both cases the maximum value of M theoretically possible is less than that derived by Beddington and his coworkers. Given the life history parameters estimated by Beddington, a population would decline indefinitely and hence could not exist in principle. Hence we conclude that there is something seriously wrong with the analyses of Beddington and Williams (1980) and Beddington and Free (unpublished).

A Maximum Likelihood Approach

Suppose that we have a simulation model in which there is one unknown, say natural mortality M. Now suppose we have two estimates of population size at times t and t+i. Consider a simulation run in which $M = M_j$ and the predicted population sizes at time t and t+i are N_t and N_{t+i} respectively. From the probability distribution functions of the observed estimates we can estimate the probability that the actual population size at t and t+i are N_t and N_{t+i}; let these probabilities be $P_t(M_j)$ and $P_{t+i}(M_j)$. We can now define a likelihood function, $L(M_j)$ for each M_j,

$$L(M_j) = P_t\, P_{t+i} \qquad (10)$$

and the best estimate of M_j is that which maximizes $L(M_j)$.

The approach outlined above can be extended to any number of unknowns although clearly the more unknowns there are the greater will be the number of possible combinations. We estimate two parameters, the natural mortality rate and the pup production used to initiate the simulation. It must be stressed that the validity of the simulation model is assumed and is not directly tested by this method. However, if the model produced either a probability surface with multiple peaks or failed to produce predictions that were reasonably close to the observed values we would have cause to suspect the model (or the estimates).

We have used two metrics to fit the population model. The first is derived as follows. Let $N_{a,t}$ be a sample of seals of age a taken at time t. Then $N_{a,t}/N_{a,t}+N_{a-1,t}$ is the proportion of cohort a relative to its adjacent cohort, a-1. By the central limit theorem this proportion, say Q, can be assumed to be normally distributed with mean Q and variance $Q(1-Q)/N_{a,t}+N_{a-1,t}$. In the absence of hunting or when the kill history of adjacent cohorts is very similar Q will be close to 0.5. Under these circumstances changes in the natural mortality rate or the initial pup production will have little influence on the value of Q predicted by the simulation model. This can be seen from the following approximate formula for estimating pup production using $N_{a,t}$ and $N_{a-1,t}$. Let $N_{0,t}$ be the pup production in year t and $C_{0,t}$ the kill of whitecoats and beaters. Since the majority of these animals are killed over a short period of time we have, approximately

$$\frac{(N_{0,t} - C_{0,t})e^{-M}}{N_{0,t+1} - C_{0,t+1}} \simeq \frac{N_{i,t+i}}{N_{i-1,t+i}} \qquad (11)$$

In adjacent years $N_{0,t} \approx N_{0,t+1}$ and rearranging equation (11) we have

$$N_{0,t} \simeq \frac{C_{0,t}e^{-M} - rC_{0,t+1}}{e^{-M} - r} \qquad (12)$$

where $r = n_{i,t+i}/n_{i-1,t+i}$.

As $C_{0,t}$ approaches $C_{0,t+1}$, r approaches e^{-M} and equation (12) becomes very sensitive to sampling fluctuations, the confidence limits increasing rapidly. In order that confidence limits be small enough to be of any use $C_{0,t}$ and $C_{0,t+1}$ must be quite different.

Thus for the simulation model to be able to discriminate between combinations of parameters we require estimates of Q that are markedly different from 0.5. There are a number of years in which the pup kills are sufficiently different to permit reasonable estimation: of these we selected the pairs of years 1967/1968 and 1971/1972. Earlier pairs were discarded because we chose to initiate the simulation model in 1967. The reasons for this choice are:

1. Øritsland (MS 1971) and Benjaminsen and Øritsland (MS 1975) noted that the pup kill in 1967 was extremely large and by adding to this all those seals from this cohort caught since then we can place an absolute minimum bound for pup production in 1967. Up to 1980 a total of 295,658 of the 1967 cohort had been taken.

2. Few reliable data on age-specific pregnancy rates are available before 1964. This is an important component of the simulation model and since there has been a shift in these rates an earlier start to the model would necessitate adding the earlier pattern of pregnancy as a variable to be estimated: the possible increased uncertainty due to the extra parameters would unlikely be offset by the increased time span available.

3. By 1967 it is generally assumed that the population was substantially reduced from its pristine levels. It therefore seemed unlikely that density-dependent changes in mortality rates have occurred since then and thus we could reasonably assume a constant rate. The analyses of Winters (1978), Beddington and Williams (1980) and Beddington and Free (pers. comm.) suggest that at least since the early 1970's pup mortality, M_o, has equalled adult mortality, M. We have examined both the case in which $M_o = M$ and the case in which M_o is greater than M. In all cases M_o and M are assumed to be constant over time.

What data are available to estimate Q? As discussed earlier the male moulting samples although heterogeneous as a whole do not appear to show a trend in the pattern of bias. We therefore used these data and tested for possible bias by a G test. Six pairs of years are available; there is no significant heterogeneity and no sign of any trends ($G = 10.73$, $P>0.05$). Three years were available for the 1971/1972 combination and again no heterogeneity is detectable ($G = 0.386$, $P>0.05$). Since there is no heterogenity in the sample these can be pooled to yield estimates of Q of 0.2804 ($n = 321$) and 0.3803 ($n = 213$) for 1967/68 and 1971/72 respectively. The respective estimates of standard deviation are 0.0251 and 0.0333. Approximate estimates of pup production, from equation (12), assuming $M = 0.1$ are

N = 370,743 for 1967/68 and N = 411,074 for 1971/72. We estimated Q for the other pairs of years between 1967 and 1979, but these were too close to 0.5 to be of any value and in some cases the samples available to estimate Q were significantly heterogeneous.

The second metric is mark-recapture estimation of pup production. Two estimates are available, one for 1978 and another for 1979. A discussion of the validity of these estimates is given elsewhere (Bowen and Sergeant MS 1981, 1982). For 1978 the estimate is 468,571 with a standard error of 26,179 and for 1979 the estimate is 476,302 with a standard error of 36,361.

Description of the Model

The year is divided into four periods with pup production occurring as a 'point event' at the interface of two of these periods. This division is based on the type of hunting occurring during different times of the year. Immediately following pup production the 1+ seals are subjected to three months of hunting from large vessels and longliners, the former being the large sealing ships that remain at sea for several months and the latter the smaller land based boats. During this period the adults are slowly migrating northwards and the next component of the model comprises the Greenland and Canadian Arctic hunts which take place over four months during the summer. Thereafter there is a period of two months in which the seals are not hunted. At the end of this period a new calendar year begins and the age vector is updated. In the final period of three months, the seals migrate southwards to their feeding and whelping areas and are harvested by shooting and netting. The hunting schedule on the young of the year (whitecoats and beaters) differs slightly from that on the adults in that pups are taken for one month by the large vessels and as beaters, for two months by landsmen. The number of seals of age a remaining after hunting period j in year t, $N_{a,j,t}$, is given by the equation

$$N_{a,j,t} = N_{a,j-1,t} \, e^{-(F_{a,j,t} + MT)} \qquad (13)$$

where $F_{a,j,t}$ is the hunting mortality rate during the period j, M is the instantaneous natural mortality rate and T is the proportion of the year over which hunt j takes place. $F_{a,j,t}$ can be estimated by iteration from the relationship

$$C_{a,j,t} = \frac{N_{a,j-1,t}\, F_{a,j,t}\, (1 - e^{-(F_{a,j,t} + MT)})}{F_{a,j,t} + MT} \qquad (14)$$

where $C_{a,j,t}$ is the catch of seals of age a and hunt j in year t. Solving for $F_{a,j,t}$ used considerable computer time relative to remainder of the simulation. For this reason we used the approximation given by Pope (1972),

$$N_{a,j,t} = (N_{a,j-1,t} - C_{a,j,t}\, e^{MT/2})/e^{MT} \qquad (15)$$

This approximation is reasonable provided $M < 0.3$ and $F < 1.2$: both of these constraints apply to the present model. For reassurance we made runs differing only in the method of estimating $N_{a,j,t}$: the differences in population size after running the model to 1979 were inconsequential.

At least during the last ten years the age at maturity in seals has declined (Bowen, Capstick and Sergeant 1981). For the model we require the relationship between age and pregnancy rate. Data on this are presented in Table 2. Expecting the 1979 data, there appears to have been no change in the pregnancy rate of seals aged 2, 3 and 4. More data are required to substantiate the apparent increase in the proportion of seals pregnant at age 4 and perhaps age 3 in 1979. In the present analysis we have assumed a constant rate for these age classes. At age 7 the maximal pregnancy rate is achieved and seals age 7 and older have been combined. The percentage pregnant at ages 5 and 6 show a significant increase over time (for age 5, $r = 0.936$, $P < 0.01$, age 6, $r = 0.845$, $P < 0.01$) (Fig. 1). In 1978 and 1979 the maximal pregnancy rate is achieved at age 6 and for the purposes of regression analysis the 6+ groups were used for these two years. As is usual with percentages the dependent variable, percentage pregnant, was transformed using the arcsine square root transformation. The proportions pregnant by age and year used in the model were obtained as follows. The proportion pregnant at age 4 was obtained by pooling across years; the same procedure was used for the 7+ animals except that animals aged 6 in 1978 and 1979 were also included. Thus at age 4, 4.6% of females were pregnant and at age 7+ (6+ in 1978, 1979) 87% of females were pregnant. The percentage pregnant at ages 5 and 6 were calculated using the appropriate regression equations (Fig. 1).

The final component of the model is the initial age distribution. None of the hunts represent random samples of the age distribution of harp seals.

We present two methods that estimate the initial age distribution provided that there exists some age above which the seals are randomly sampled. The first method we shall term the additive method.

The age-specific pregnancy rate reaches a maximum at age 7, remaining constant thereafter. Males also mature by age 7 (Fisher 1954) and hence it seems reasonable to suppose that the relative vulnerabilities within the 7+ group will be the same. Benjaminsen and Øritsland (MS 1975) came to the same conclusion. The hunting mortality on harp seals ages 2 and older is very low and hence the population age structure will not be significantly affected by hunting. Letting C(a,t) be the catch at age a in year t and $\hat{s}(a,t)$ the estimated factor by which this catch should be multiplied to correct for its under- or over-representation in the catch we can write

$$\frac{\hat{s}(a,t)\ c(a,t)}{c(7+,t)} = \frac{c(7,t+7-a)}{C[(7+)-a+7,t+7-a]} \qquad a < 7 \qquad (16)$$

The right hand side of the above formula is the representation of age "a" in the catch when this cohort is 7 years old; for example if a = 2, t = 1967 we have

$$\frac{\hat{s}(2,67)\ C(2,67)}{C(7+,\ 67)} = \frac{C(7,72)}{C(12+,72)} \qquad (17)$$

Therefore

$$\begin{aligned} \hat{s}(2,67) &= \frac{C(7+,67)\ C(7,72)}{C(2,67)\ C(12+,72)} \\ &= \frac{C(7+,67)\ C(8,73)}{C(2,67)\ C(13+,73)} \\ &= \frac{C(7+,67)\ C(9,73)}{C(2,67)\ C(14+,74)} \qquad (18) \\ &= \frac{C(7+,67)\ C(10,75)}{C(2,67)\ C(15+,75)} \\ &= \frac{C(7+,67)\ C(11,76)}{C(2,67)\ C(16+,76)} \end{aligned}$$

To avoid significant problems of errors in age determination, we have extended the calculation only to age 11; estimates of total catches above this age, C(12+,72), C(13+,73) etc. should not be sensitive to errors in age determination since these comprise many ages.

The best estimate of s(2,67) is

$$\hat{s}(2,67) = \frac{C(7+,67)}{C(2,67)} \left\{ \frac{C(7,72) + C(8,73) + \ldots\ldots\ C(11,76)}{C(12+,72) + C(13+,73) + \ldots\ C(16+,76)} \right\} \qquad (19)$$

An assumption of this method is that

$$\frac{C(7,72)}{C(12+,72)},\ \frac{C(8,73)}{C(13+,73)},\ \ldots\ldots,\ \frac{C(11,76)}{C(16+,76)}$$

estimate a common value. Heterogeneity between samples can be tested for with a G or χ^2 test. A significant trend for ages 7 and above to be over- or under-represented in the population should appear as a trend in the estimated ratio. Such a trend might not occur if the age-specific selectivities extended above age 12. However, it seems highly unlikely that seals older than age 12 would show differences in behaviour that would generated an age-specific susceptibility to hunting.

The second method of estimating the initial age distribution we term the multiplicative method.

As before let us assume that ages 7 and older are correctly represented in the sample. We thus have

$$\frac{s(2,67)\ C(2,67)}{C(7+,67)} = \frac{s(3,68)\ C(3,68)}{C(8+,68)} \qquad (20)$$

and likewise

$$\frac{s(3,68)\ C(3,68)}{C(7+,68)} = \frac{s(4,69)\ C(4,69)}{C(8+,69)} \qquad (21)$$

$$\frac{s(4,69)\ C(4,69)}{C(7+,69)} = \frac{s(5,70)\ C(5,70)}{C(8+,70)}$$

$$\frac{s(5,70)\ c(5,70)}{C(7+,70)} = \frac{s(6,71)\ C(6,71)}{C(8+,71)}$$

$$\frac{s(6,71)\ C(6,71)}{C(7+,71)} = \frac{s(7,72)\ C(7,72)}{C(8+,72)}$$

Now s(7,72) = 1 since age 7 is correctly represented and hence making use of the above identities we obtain

$$\hat{s}(2,67) = \frac{C(7+,67)}{C(2,67)} \cdot \frac{C(3,68)}{C(8+,68)} \cdot \frac{C(7+,68)}{C(3,68)}\ \frac{C(4,69)}{C(8+,69)}\ \ldots\ \frac{C(7+,71)}{C(6,71)} \cdot \frac{C(4,69)}{C(8+,72)}$$

$$= \frac{C(7,72)}{C(2,67)} \left\{ \frac{C(7+,67)\ C(7+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,71)}{C(8+,68)\ C(8+,69)\ \ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,72)} \right\} \qquad (22)$$

and making use of the 8 to 11 age groups we have

$$\hat{s}(2,67) = \frac{C(7,72)}{C(2,67)} \left\{ \frac{C(7+,67)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,71)}{C(8+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,72)} \right\} \qquad (23)$$

$$= \frac{C(8,73)}{C(2,67)} \left\{ \frac{C(7+,67)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,72)}{C(8+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,73)} \right\}$$

$$\frac{C(9,74)}{C(2,67)}\left\{\frac{C(7+,67)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,73)}{C(8+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,74)}\right\}$$

$$\frac{C(10,75)}{C(2,67)}\left\{\frac{C(7+,67)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,74)}{C(8+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,75)}\right\}$$

$$\frac{C(11,76)}{C(2,67)}\left\{\frac{C(7+,67)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(7+,75)}{C(8+,68)\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ C(8+,76)}\right\}$$

There is no entirely satisfactory method of combining these estimates: we adopted two methods. In the first we weighted each estimate of the correction factors by the sample size of the numerator occurring outside the brackets (C(7,72), C(8,73), etc.) and in the second we calculated an unweighted average of the estimates.

As discussed above the samples of males from moulting concentrations appear to approximate the population age distribution. Application of the test outlined above shows that there is significant heterogeneity between years (Table 3, column A). A major contributor to this heterogeneity is the 1976 sample which comprises samples taken by Norwegian and Canadian collectors. The individual samples were compared to samples taken in 1974, 1975, 1977 and 1978 by a G test with the earlier year in each pairwise comparison consisting of ages 7-12+. In all cases the Canadian sample was not significantly different, whereas the Norwegian sample was (Table 4). We therefore used only the Canadian sample. There is, however, still significant heterogeneity (Table 3, column B). An analysis of the data shows that 1973 contributed most to the remaining variability and elimination of this year leaves only one age showing significant heterogeneity. This remaining variability is due principally to age 7 in one year: we therefore began the calculations at age 8 which produced no heterogeneous series (Table 3). Despite the heterogeneity in earlier series the resulting frequency distributions are remarkably similar (Table 5). No trends are evident in the series suggesting that the heterogeneity arises from age-specific variation in the samples that shows no trend with age. Such noise should be dampened by the averaging procedure as indeed it appears to be. The estimated correction factors are very similar for all samples and show a convergence to 1.0 at age 7 as required by the method (Fig. 2a).

We applied the multiplicative method using the original data, excepting that the 1976 Canadian sample alone was used, and calculated both weighted and unweighted correction factors. The predicted frequency distributions are very similar to both each other and those derived using the additive method (Table 5).

The calculated correction factors are also almost identical to those derived from the additive method (Fig. 2b). We have used the frequency distribution calculated using the trimmed data set (column D of Table 5). This distribution is compared in Table 6 with those previously published. All distributions are reasonably similar.

An assessment of the validity of the predicted age distribution can be made by examining the total number killed in cohorts born from 1961 to 1966 (Table 7). The total number of seals killed of the 1961 and 1962 cohorts are very similar. Since the pup productions for adjacent years should be very similar and assuming that mortality rates are not highly variable from year to year we expect that the predicted frequencies for cohorts 1961 and 1962 will be approximately the same. The predicted frequencies, 6.6% and 7.5% are indeed similar. By the same reasoning we expect the frequencies of cohorts 1963 and 1964 to be similar: here, however, we find a discrepancy. Comparing the observed kills of cohort 1963 to that of 1962 and 1964 to that of 1965 it is evident that it is the predicted frequency of the 1964 cohort that is most likely in error. By a similar reasoning we also conclude that the predicted frequency of age group 1 in 1967 (cohort born in 1966) is too high. Before any attempts at adjusting the initial age distribution, we shall consider the results of proceeding with the unadjusted frequencies.

Analysis

A priori it may seem reasonable to assume that the natural mortality rate decreases at least initially with age. However, there are several reasons for suspecting that this may not be the case for harp seals. Firstly, the environment into which the pups are born is relatively free of predators and secondly, conditions on the ice are relatively antiseptic making death from infection unlikely. Probably the greatest source of mortality during the whitecoat stage is premature break up of the ice or ice-rafting which may kill some pups (Sergeant 1976a). Such a phenomenon does not, however, appear to be a common occurrence (Sergeant pers. comm.). The growth rate in the first year of life is very high, the animal attaining $\approx$ 70% of its adult body length by age 1 and approximately 50% of its maximum weight (Sergeant 1973). If there is any change in mortality with age the major portion is likely to occur in the first year when seals are presumably inexperienced at foraging and are growing at a substantial rate. In the absence of any data on the age-specific mortality rate we have examined two possibilities. Firstly, we have assumed that $M_0 = M$

and secondly, that $M_0 = 3M$, i.e. that mortality in the first year of life is 3 times that of 1+ animals (see Discussion for a comparison of mortality rates in pinnipeds).

Using the maximum likelihood approach outlined earlier we calculated $L(M,N_{67})$, where M is natural mortality and N_{67} is 1967 pup production. For computational convenience $L(M,N_{67})$ was multiplied by a constant, making the maximum value of $L(M,N_{67})$ approximately 12. $L(M,N_{67})$ was calculated for all values of M and N_{67} that exceeded e^{-20}. From the distribution of $L(M,N_{67})$ the probability surface of M,N_{67} can be calculated and hence the confidence zones estimated.

The confidence region for M and 1967 pup production when $M_0 = M$ is shown in Fig. 3a. There is only one peak for each mortality schedule as illustrated in Fig. 3b for $M_0 = M$. When $M_0 = M$ the most likely combination is $M = 0.0975$ and $N_{67} = 380{,}000$ and when $M_0 = 3M$ the results are $M = 0.095$ and $N_{67} = 390{,}000$. There is little difference in either the most likely combination or confidence region between the two mortality schedules. The reason is that the pups born from 1967 to 1977 contribute relatively little to pup production from 1967 to 1978. Thus while the confidence region of M is quite small the range in possible values of M_0 is poorly constrained. The population and pup production trajectories for the two mortality schedules are shown in Fig. 4. In both cases the predicted pup productions for 1977 and 1978 are very close to the estimated means from mark-recapture; the predicted values for the 1967/68 and 1971/72 pup productions are also very close to the estimates obtained from the approximate formula, eqn (12).

However, although the model indicates a decline in the 1+ population size from 1967 to 1972, under both mortality schedules an increase in pup production is predicted for this period. Although such an increase may have occurred due to a shifting age structure this initial increase most probably results from the predicted errors in the initial age distribution. There are two ways in which the error in the estimation of the initial age distribution can be taken into account. Firstly, we might incorporate it directly into the likelihood function. However, at present we have insufficient knowledge of the error in the age distribution to do this. The second alternative is to use several variations and examine the consequences for management. The ratio between pup kills earlier than 1967 can, as described earlier, be used to limit the range in variation. Furthermore, the assumption that pup production and population size declined between 1967 and 1972 can be used to further restrict the plausible range in variation. On the basis of these arguments, we adjusted the frequencies of age groups 1 and 4 by 'trial and error' to obtain a 'reasonable' time trace (i.e. one in which pup production does not increase from 1967 to 1972). This adjustment comprises a reduction in the two aforementioned frequencies and an increase in the frequency of 7+ animals (Table 7). An increase in the frequency of the 7+ group is necessary to produce a decline.

Using the adjusted age frequencies the best combination of M and N_{67} are $M = 0.0825$, $N_{67} = 380,000$ when $M_0 = M$ and $M = 0.0775$, $N_{67} = 380,000$ when $M_0 = 3M$ (Fig. 5). The pup productions under these two schedules remain more or less constant until 1977 when females from the first quota yearclass (1972) entered the breeding population (Fig. 6).

The projected rate of population increase under the present quota increases as the frequency of 7+ animals is increased. The reason for this is that since the model is tuned to independent parameters (the 1967/68 and 1971/72 relative pup productions and the mark-recapture estimates) a marked decline in pup production from 1967 to 1971 implies a low mortality rate to enable the population to increase to the estimated size. We have undertaken detailed analysis with both the original distribution and the adjusted: the results are not significantly different and we shall present the results only for the adjusted distribution.

Both analyses indicate that the population is increasing: this is not surprising since the pup productions estimated independently of the model show an increase from 1967 to 1979. Projecting ahead, assuming a quota the same as in 1981 the 1979 age-specific pregnancy rates and the most likely combination of parameters, the model predicts that the population will continue to increase (Fig. 7) until checked by density-dependent processes or changes in environment conditions. In fact, under either combination of 'most likely' parameters, the population is predicted to increase even with a doubling of the quota. However, management decisions must take into consideration the uncertainty in the estimates and hence should not be based on single projections alone.

To examine the results over the full range of combinations of M and N_{67}, we took an increase in the quota of 25% and projected ahead to 1991. Age-specific pregnancy rates and hunting selectivities were held constant at the 1979 values. Fig. 8 shows the ratio of the 1+ population size in 1991 to that in 1981: values above 1 indicate an increasing population. In the hatched areas one or more cohorts were eliminated and so this region has been left undefined. In both cases there is a negligible probability of the population declining. These results do not imply that the population will increase to the plotted values: density-dependent effects or environmental changes will at some point intervene to slow down population growth. The important point is that the present kill will not by itself cause the population to decline.

Since the present population is well below its pristine level we would predict that as it increases density-dependent effects will come into play to reduce population growth. The predicted population size for 1980 is approximately the same as that previously arrived at for 1952 by Lett and Benjaminsen (1977), Lett et al. (1979), and Winters (1978). It has been suggested that during the period 1952 to 1967 density-dependent changes in pup mortality and pregnancy rate occurred. We tested this proposition by running our model forwards to 1999 using the average kill for the period 1952 to 1972 (an average pup kill of 221,966 and a 1+ kill of 78,819, which we rounded to 222,000 and 79,000 respectively) and the 1967 pregnancy rate. The results are shown in Fig. 9. At the 'best' combinations pup production continues to increase. Therefore, in these cases density-dependent changes are required to bring the pup production down to the 1967 level. Such changes would have to have a lag in order to cause the population to actually decrease. There are, however, numerous combinations of M and N_{67} that lie within the 95% confidence region that lead to a decline in pup production to the 1967 level without the necessity of postulating density-dependent effects. It seems likely that these combinations are closer to the actual values than the two best estimates. However, as shown in Fig. 9 such combinations will not lead to a decline in the population at present harvesting levels.

To calculate the replacement yield, defined on the 1+ population, we used the following approximate method.

$$N_{1+,t+1} = (N_{1+,t} - qRCe^{-M/2})e^{-M} + (N_{o,t} - (1-q)RC)e^{-M_o} \qquad (24)$$

where $N_{1+,t}$: is the number of 1+ seals at time t

$N_{o,t}$: is the number of pups at time t

C: is the total allowable catch; C = 183,000

q: is the proportion of the catch that is allocated to 1+ seals. At present q = 0.2.

R: is the factor by which C must be multiplied to maintain a stable population.

We require that $N_{1+,t+1} = N_{1+,t} = N$, (the last for notational convenience). Substituting and rearranging we have

$$R = \frac{N(e^{-M} - 1) + N_{o,t}e^{-M_o}}{e^{-M/2}qC + e^{-M_o}(1-q)C} \qquad (26)$$

Projections to 1991 of R, population size and pup production for the two 'most likely' estimates are shown in Fig. 10. Equation 25 works well when $M_o = M$ but underestimates R when $M_o = 3M$, in the latter case the population increasing by about 7% by 1991. For all practical purposes the approximation is satisfactory. The replacement factor R is somewhat different for the two mortality schedules. But in either case the replacement yield is greater than is presently being taken. Again we emphasize that management should not be based on these single projections: they are given here for illustration. To take into account the uncertainties in the estimates it is necessary to estimate the replacement yield over the plausible set of combinations of M and N_{67}. The predicted 1982 replacement yield for a set of combinations are shown in Fig. 11. Superimposed on these yield isopleths are the confidence regions for the two mortality schedules. The total allowable catch in 1982 was 186,000, plus an unregulated catch of about 14,000 at West Greenland, for a total of 200,000 animals. The question that is most pertinent to present management of harp seals is "What is the probability that the present kill (200,000) will cause the population to decline?" Using the adjusted age distribution this probability is <0.001 with either mortality schedule.

Discussion

The rate of natural mortality is usually the most difficult parameter to estimate for an animal population. In the case of the harp seal it is difficult to obtain representative age-frequency samples and these are often confounded by changes in recruitment and hunting mortality. Sergeant and Fisher (1960) estimated that the total annual mortality rate for immatures (ages 1-5) was higher than that for adults (ages 6-10), but they were unable to obtain a reliable estimate of first year mortality. Recent authors have suggested that the data are not sufficient to discriminate between the mortality rates of immatures and adults. Generally the average M calculated for adults is assumed to hold for animals of all ages (Allen 1975; Benjaminsen and Øritsland 1975; Lett and Benjaminsen 1977; Winters 1978) or it is assumed that harp seals suffer somewhat higher rates during their first year of life as some function of population size (Lett et al. 1979; Beddington and Williams 1980).

Natural mortality rates in many mammals vary markedly from one age class to another and often males suffer greater rates than females (Trivers 1972; Ralls, Brownell and Ballou 1980). Caughley (1966) reviewed mammalian life tables and concluded that the typical mortality pattern is 'U-shape' consisting of a juvenile phase when the mortality rate is high, followed by a post juvenile phase characterized by initially low but steadily increasing rates of death. However, complete, accurate life tables for both sexes exist for very few species of mammals (Caughley 1966; Rall et al. 1980).

Complete or partial life tables have been proposed for a number of species of pinnipeds: grey seals, Halichoerus grypus (Hewer 1964; Mansfield and Beck 1977); ringed seals, Pusa hispida (Smith 1975); harbour seals, Phoca vitulina (Bigg 1969); southern elephant seals, Mirounga leonina (Laws 1960) and northern fur seals, Callorhinus ursinus (Smith and Polacheck 1981). Life tables for the ringed seal, harbour seal and northern fur seal can be considered most reliable and in each case the mortality rate of immatures is higher than that of young adults. Ralls et al. (1980) found a similar pattern of age-dependent mortality in a number of non-marine species. Thus the assumption of a constant M in harp seals one-year-old and older is unlikely. However, as yet it has not been possible to reliably estimate age-specific mortality rates for harp seals.

The question of whether first year mortality in harp seals is higher than the average rate experienced by older animals is difficult to answer. Winters (1978) estimated the first year M of harp seals to be 0.10, although the validity of this estimate has been questioned. Lett et al. (1979) and Beddington and Williams (1980) found no evidence of higher M in the first year of life during the 1970s; however both studies suggested higher rates may have occurred in the 1950s. Bigg (1969) estimated that first year mortality and average adult mortality in harbour seals were equal, about 0.22.

In most pinnipeds first year mortality is higher than that experienced by older seals and values of 30% to 60% are not uncommon (Smith 1975; Payne 1977; Reijnders 1978; Boulva and McLaren 1979; Landers 1979). Much of this mortality occurs before weaning, usually the result of starvation and/or trauma and varies from 10% to 35% with the exception of the harp seal and possibly the southern elephant seal (Table 8). In harp seals mortality from birth to weaning varies from about 1.0% or less for the northwest Atlantic population to only 3.3% for the White Sea population. Although we can not dismiss the possibility of high post-weaning mortality, harp seals appear to differ from land-breeding pinnipeds in having a low pre-weaning mortality rate. Nevertheless, it seems only prudent to consider higher rates of first year mortality than have been assumed in the past and given what we know about other species, $M_o = 3M$ seems reasonable.

It is generally assumed that male and female harp seals suffer the same natural mortality rates. Lett et al. (1979) stated that this assumption is based on the observation that males and females have similar growth rates and achieve equivalent maximum ages (Sergeant 1973). Ralls et al. (1980) reviewed mortality patterns in seven species of pinnipeds. In each of these, estimated mortality rates of adult males were higher than those of adult females, even in those species like the harp seal, where males and females are similar in size (i.e. harbour and ringed seal) or where females are actually larger than males (Weddell seal). Hence it is likely that male harp seals experience greater mortality rates than do females. Nevertheless, based on data for ringed seals (Smith 1975) and harbour seals (Bigg 1969) these differences are probably small over much of the life span and are unlikely to significantly bias our results.

In projecting to 1991 we do not imply that this is the trajectory that will be followed. Our projections assume present mortality and pregnancy schedules and were made over a 10-year period to allow for temporary changes due to a shifting population age distribution. The analysis indicates that with either mortality schedule, or with doubling of the quota, density-dependent processes or changes in environmental conditions are necessary to halt the population increase.

stabilize the population. However, errors in the estimation of the initial age distribution suggest caution. A more detailed analysis of the selectivity patterns of the hunt is warranted both to improve the accuracy of the initial age distribution and to shed light on possible behavioural changes in the seals and/or changes in the hunt.

The two mortality schedules give somewhat different estimates of replacement yield, the 1982 yield assuming $M_0 = M$ being 339,000 (to the nearest thousand) and that assuming $M_0 = 3M$ being 312,000. Under both mortality schedules there is a gradual increase in the replacement yield due to increasing pup production, a more or less stable state being achieved when the kill is 423,000 for $M_0 = M$ and 392,000 for $M_0 = 3M$. However, these best estimates should not be used as the sole basis for setting the level of kill. Management decisions should take into consideration the probability that the populations will decline under a given catch. As shown earlier, under the present kill this probability is small.

Any simulation model, indeed any analysis, necessarily involves simplifications. We have assumed the natural mortality and pregnancy rates to be deterministic, the former remaining constant, the latter changing linearly with time. These assumptions are undoubtedly not strictly correct but it is unlikely that the variance in these components will be large. If there is any point in the life of the harp seal when mortality might be variable, it is in the first year of life. However, the fact that the survival index method appears to work reasonably well argues against extreme variability. Our greatest source of uncertainty is the relationship between the mortality rate and age. But, because the model is tuned to external observations short term projections of population trends should be reasonably close to reality. Nevertheless the harp seal population, like all natural systems must be managed cautiously with due cognizance of the uncertainty within both the analyses and the natural world.

Even after taking into account the uncertainties described above, the evidence is strong that the harp seal population is large and increasing. It thus provides an excellent opportunity to gain more insight into the biological parameters of the seal population by adaptive management. The most obvious strategy is to vary the quota. A major problem of the present hunt is that because the quota is kept more or less constant over time the relative changes in cohort size that permit the use of such methods as the survival index method are not evident. This is unfortunate since an analysis of the relative sizes of cohorts can be an important source of biological information. From this point of view it would be better to vary the quota, having it high in one year and low in the next. Such a tactic would not endanger the seal population since it is large and is comprised of many age groups, but it may not be economically or socially acceptable.

Our knowledge of the life history parameters and population dynamics of the harp seal is still inadequate to be anything but cautious in deciding upon management schemes. Management policies must take into consideration not only the 'expected' optimum catch, but also the probability of a decline in population size: management based on 'best estimates' alone may lead to significant errors in setting quotas. There are, however, probably few large mammals for which the data base is as good and even fewer populations of large mammals that are as large as the harp seal. Future monitoring of population changes and concomitant changes in physiological and population parameters promises to add very considerably to our understanding of the dynamics of populations of large mammals in general and marine mammals in particular.

Acknowledgments

We are grateful to D. E. Sergeant, F. Kapel and T. Øritsland for providing generous access to unpublished data and for sharing their hardwon knowledge of harp seal biology. We thank R.A.E. Stewart for sending us age composition data for the Canadian Arctic hunt. Dr. W. G. Doubleday provided valuable criticism and suggested examining the question 'can we get there from here?'. Dr. P. Larkin gave useful criticism of an earlier draft. G. King and H. Mullett assisted in preparing the figures. Much of this study was conducted while D. Roff was with the Department of Fisheries and Oceans, St. John's, Newfoundland. Completion of the work was support by a contract (No. OSC80-00315) to D. Roff from the Department of Fisheries and Oceans, St. John's.

References

Allen, R. L. 1975. A life table for harp seals in the northwest Atlantic. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 169: 303-311.

Anderson, S. S., J. R. Baker, J. H. Prime, and A. Baird. 1979. Mortality in Grey seal pups: incidence and causes. J. Zool., Lond. 189: 407-417.

Beddington, J. R., and H. A. Williams. 1980. The status and management of the harp seal in the North-West Atlantic. Report submitted to U.S. Marine Mammal Commission. Washington, D.C. Rep. No. MMC-79/03 127 p.

Benjaminsen, T., and T. Øritsland. MS 1975. The survival of year-classes and estimates of production and sustainable yield of Northwest Atlantic harp seals. ICNAF Res. Doc. 75/121.

Bigg, M. A. 1969. The harbour seal in British Columbia. Fish. Res. Board Can. Bull. 172. 33 p.

Bonner, W. N., and G. Hickling. 1971. The Grey seals of the Farne Islands. Report for the period October 1969 to July 1971. Trans. Natur. Hist. Soc. Northumbia 17: 141-162.

Boulva, J., and I. A. McLaren. 1979. Biology of the harbor seal, <u>Phoca vitulina</u>, in Eastern Canada. Fish. Res. Board Can. Bull. 200 24 p.

Bowen, W. D., 1982. Age structure of Northwest Atlantic harp seal catches, 1952-1980. NAFO Sci. Coun. Studies No. 3: 53-65.

Bowen, W. D., and D. E. Sergeant. MS 1981. Further estimates of harp seal pup production between 1977 and 1980 from mark-recapture. NAFO SCR Doc. 81/XI/153. 6 p.

1982. Mark-recapture estimates of harp seal pup production in the northwest Atlantic. Submitted Can. J. Fish. Aquat. Sci.

Bowen, W. D., C. K. Capstick, and D. E. Sergeant. 1981. Temporal changes in the reproductive potential of female harp seals (<u>Pagophilus groenlandicus</u>). Can. J. Fish. Aquat. Sci. 38: 495-503.

Bowen, W. D., and G. H. Winters. MS 1979. On population size and sustainable yield in Northwest Atlantic harp seals. NAFO SCR Doc. 79/XI/12 (Revised).

Carrick, R., S. E. Csordas, S. E. Ingham, and K. Keith. 1962. Studies on the southern elephant seal, <u>Mirounga leonina</u> (L). III. The annual cycle in relation to age and sex. CSIRO Wildl. Res. 7: 119-160.

Caughley, G. 1966. Mortality patterns in mammals. Ecology. 47: 906-918.

1977. Analysis of vertebrate populations. Wiley & Sons, London, 234 p.

Doubleday, W. G., and W. D. Bowen. MS 1980. Inconsistencies in reading the age of the harp seal, <u>Pagophilus groenlandicus</u>, their consequences, and a means of reducing resulting biases. NAFO SCR Doc. 80/XI/160

Fisher, H. D. 1954. Studies on reproduction in the harp seal, <u>Phoca groenlandica</u> Erxleben in the Northwest Atlantic. Ph.D. Thesis, McGill Univ. 109 p.

Hewer, H. R. 1964. The determination of age, sexual maturity, longevity, and a life table in the grey seal, (<u>Halichoerus grypus</u>). Proc. Zool. Soc. Lond. 142: 593-623.

Ichihara, T. 1974. Populations of northern fur seals. Res. Devel. Dept., Fishery Agency of Japan, Tokyo. p. 1-36. (Translated).

Lander, R. H. 1979. Alaskan or Northern fur seal. <u>In</u> Mammals in the Seas, FAO Fisheries Series No. 5, Vol. 2. Rome, Italy.

Laws, R. M. 1953. The elephant seal (<u>Mirounga leonina</u> Linn.) I. Growth and age. Sci. Rep. Falkland Is. Dep. Surv. 8: 1-62.

———— 1960. The southern elephant seal (*Mirounga leonina* Linn.) at South Georgia. Norsk. Hvalfangstiid 49: 466-476 and 520-542.

LeBoeuf, B. J., and K. T. Briggs. 1977. The cost of living in a seal harem. Mammalia 41: 167-195.

Lett, P. F., R. K. Mohn, and D. F. Gray. 1979. Density-dependent processes and management strategy for the Northwest Atlantic harp seal population. ICNAF Selected Papers 5: 61-79.

Lett, P. F., and T. Benjaminsen. 1977. A stochastic model for the management of the Northwestern Atlantic harp seal (*Pagophilus groenlandicus*) population. J. Fish. Res. Board Can. 34: 1155-1187.

Mansfield, A. W., and B. Beck. 1977. The grey seal in eastern Canada. Fish. Mar. Serv. Tech. Rep. No. 704 81 p.

Mattlin, R. H. 1978. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). N.Z. J. Ecol. 1: 138-144.

Mohn, R. K. 1979. Sensitivity analysis of two harp seal (*Pagophilus groenlandicus*) population models. J. Fish. Res. Board Can. 36: 404-410.

Øritsland, T. MS 1971. Progress report on Norwegian studies of harp seals at Newfoundland. ICNAF Res. Doc. 71/8.

Pope, J. G. 1972. An investigation for the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. 9: 65-74.

Popov, L. A. 1971. The causes and dimensions of the natural mortality of young harp seals during the lactation period, p. 159-176. Translated from Russian. Trans. Atlantic Sci. Res. Inst. Fish. Oceano. 39: 1-344.

Ralls, K., R. L. Brownell, Jr., and J. Ballou. 1980. Differential mortality by sex and age in mammals, with special reference to the sperm whale. Rep. Int. Whal. Comm. Special Issue 2: 233-243.

Reijnders, P.J.H. 1978. Recruitment in the harbour seal (*Phoca vitulina*) population in the Dutch Wadden Sea. Neth. J. Sea Res. 12: 164-179.

Sergeant, D. E. 1965. Migrations of harp seals *Pagophilus groenlandicus* (Erxleben) in the northwest Atlantic. J. Fish. Res. Board Can. 22: 433-464.

1973. Feeding, growth, and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 30: 17-29.

1975. Estimating numbers of harp seals. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 169: 274-280.

1976a. History and present status of harp and hooded seals. Biol. Conserv. 10: 95-118.

MS 1976b. Studies on harp seals of the western North Atlantic population in 1976. ICNAF Res. Doc. 76/X/124 (Revised).

Sergeant, D. E., and H. D. Fisher. MS 1960. Harp seal populations in western North Atlantic from 1950 to 1960. Fish. Res. Board Can. Arctic Unit, Montreal, Que., Circular No. 5. 38 p.

Smith, T., and T. Polacheck. 1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms, p. 99-120. *In* C. W. Fowler and T. D. Smith (ed.) Dynamics of Large Mammal Populations. John Wiley and Sons, New York, N.Y. 477 p.

Smith, T. G. 1975. Parameters and dynamics of ringed seal populations in the Canadian eastern arctic. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 169: 281-295.

Stewart, R.E.A., and D. M. Lavigne. 1980. Neonatal growth of northwest Atlantic harp seals, *Pagophilus groenlandicus*. J. Mammal. 61: 670-680.

Trivers, R. L. 1972. Parental investment and sexual selection, p. 136-79. *In* B. Campbell (ed.) Sexual Selection and the Descent of Man, 1871-1971. Aldine Publ. Co., Chicago.

Winters, G. H. 1978. Production, mortality, and sustainable yield of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 35: 1249-1261.

Table 1. Analysis of moulting catches of male harp seals. Pairwise comparison by year using the G statistic of cohorts aged 2 to 9+ in 1968.

Year	1968	1969	1970	1971	1973	1974	1976
1968		27.7*	9.6	14.2	10.4	9.9	15.9*
1969			7.3	6.7	23.4*	18.8*	2.8
1970				7.3	12.9	5.4	3.8
1971					14.5*	15.3*	5.1
1973						6.8	10.2
1974							8.4

* G statistic significant at least at the 5% level

Table 2. Percentage of females pregnant by age and year.

	Year							
Age	1965	1966	1967	1968	1969	1970	1978	1979
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	6.1
4	3.3	0	0	0	4	0	2.5	23.8
5	11.4	11.1	21.1	31.6	16.0	23.1	60.5	53.3
6	54.1	35.3	60.6	70.0	43.8	50.0	90.0*	100.0
7+	83.7	85.0	90.1	88.1	88.0	86.3	82.0	93.3

* combining with 7+ 1978, 6+ : 84.3%

1979, 6+ : 94.3%

Table 3. Tests for homogeneity in the estimation of the 1967 age distribution using the additive method.

	G Statistic			
Age	A	B	C	D
1	17.5*	7.86	1.68	1.68
2	50.3*	17.73*	8.18*	5.21
3	4.1	4.13	3.90	2.00
4	8.5	8.5	1.63	1.56
5	20.7*	20.7*	7.80	5.01
6	6.9	6.9	6.92	4.98
7	-	-	-	2.29

A : All data. df = 4

B : Using only Canadian sample for 1976. df = 4

C : Omitting 1973. df = 3 for ages 1 to 5, df = 4 for age 6

D : Starting at age 8 and omitting 1973. df = 3 for ages 1, 6 and 7, df = 2 for ages 2, 3, 4 and 5.

* Significant at least at the 5% level.

Table 4. Comparison of Canadian and Norwegian samples in 1976 with samples taken in 1974, 1975, 1977 and 1978.

Years Compared	G Value Norwegian	Canadian
1974/1976	11.73*	9.04
1975/1976	18.15**	5.60
1977/1976	16.43**	8.49
1978/1976	18.84**	3.12

* P<.05

** P<.01

Table. 5. Age distributions derived using the additive method under various conditions and the multiplicative model.

Age	Frequency %					
	A	B	C	D	E	F
1	12.2	13.5	12.0	11.7	12.3	11.0
2	13.8	16.3	13.7	12.2	15.6	13.6
3	10.9	10.3	11.0	11.7	9.5	9.8
4	7.2	6.8	6.2	6.3	6.6	6.5
5	7.5	7.1	6.5	7.5	7.4	7.9
6	5.8	5.5	6.1	6.6	5.8	6.3
7+	42.6	40.5	44.5	44.0	42.9	44.8

A : Additive model, all data

B : Additive model, using only Canadian sample for 1976

C : Additive model, omitting 1973

D : Additive model, starting at age 8

E : Multiplicative model, weighted average of selectivities

F : Multiplicative model, unweighted average of selectivities

Table 6. Age distribution in 1967 from various sources.

Age	Additive	Winters	Lett, Mohn and Gray	Beddington and Williams
1	11.7	9.7	7.3	10.6
2	12.2	9.4	7.7	10.1
3	11.7	7.0	10.1	7.5
4	6.3	5.5	11.0	6.9
5	7.5	7.3	6.8	8.0
6	6.6	7.2	9.3	6.7
7+	44.0	53.9	47.8	50.2

Table 7. Comparison of the predicted 1967 age distribution with the total kill of each cohort.

Cohort	Age in 1967	Total killed to 1967	Predicted frequency	Adjusted frequency
1966	1	255273	11.7	8.5
1965	2	201718	12.2	12.2
1964	3	293108	11.7	6.5
1963	4	292251	6.3	6.3
1962	5	235788	7.5	7.5
1961	6	229082	6.6	6.6
	7+		44.0	52.4

Table 8. Natural mortality estimates of pinnipeds from birth to weaning.

Species	Natural mortality at weaning (%)	Source
Harp seal	<1.0-1.0	Sergeant (unpub. data)
	0.9-3.3	Popov (1971)
Grey seal	14.1-35.0	Anderson et al. (1979)
	13.9-27.3	Bonner and Hickling (1971)
Northern fur seal	10.0 ($\bar{x}$)	Lander (1979)
	5.0-20.0	Ichihara (1974)
Southern fur seal		
Arctocephalus forsteri	15.0-26.0[a]	Mattlin (1978)
Southern elephant seal	0.8-6.8	Laws (1953)
	2.0-12.0	Carrick et al. (1962)
Northern elephant seal	15.8	Le Boeuf and Briggs (1977)

[a] birth to 50 days.

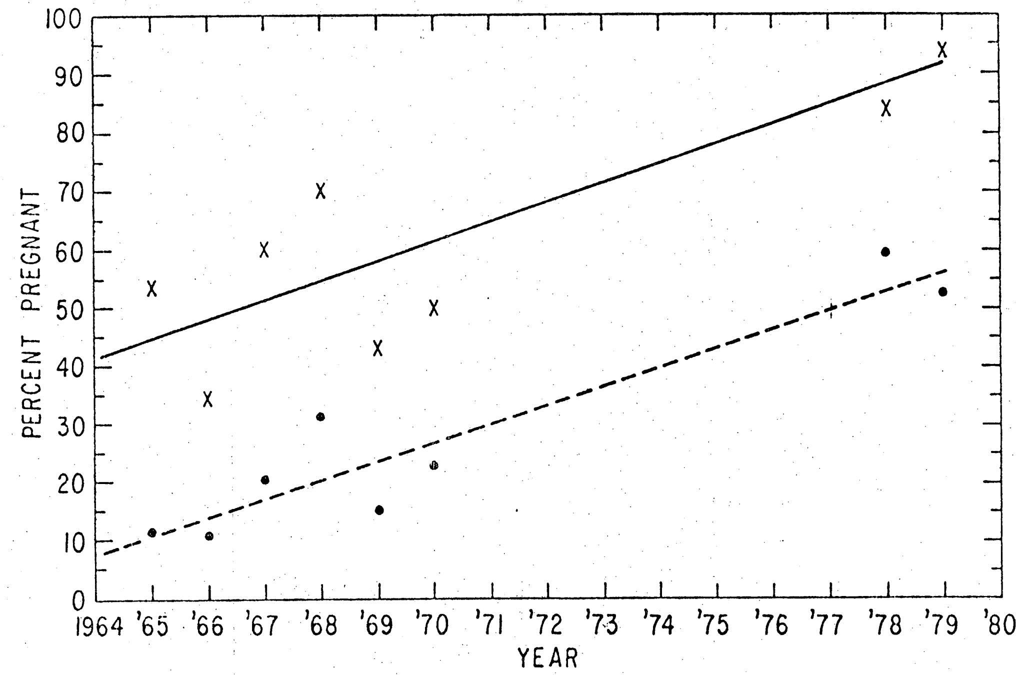

Fig. 1. Temporal changes in the pregnancy rate of seals aged 5(●) and 6(X).

Regression equations given below:

$\arcsin \sqrt{\%}$ Preg 5 = 18.22 + 2.085 year

$\arcsin \sqrt{\%}$ Preg 6 = 39.50 + 2.091 year.

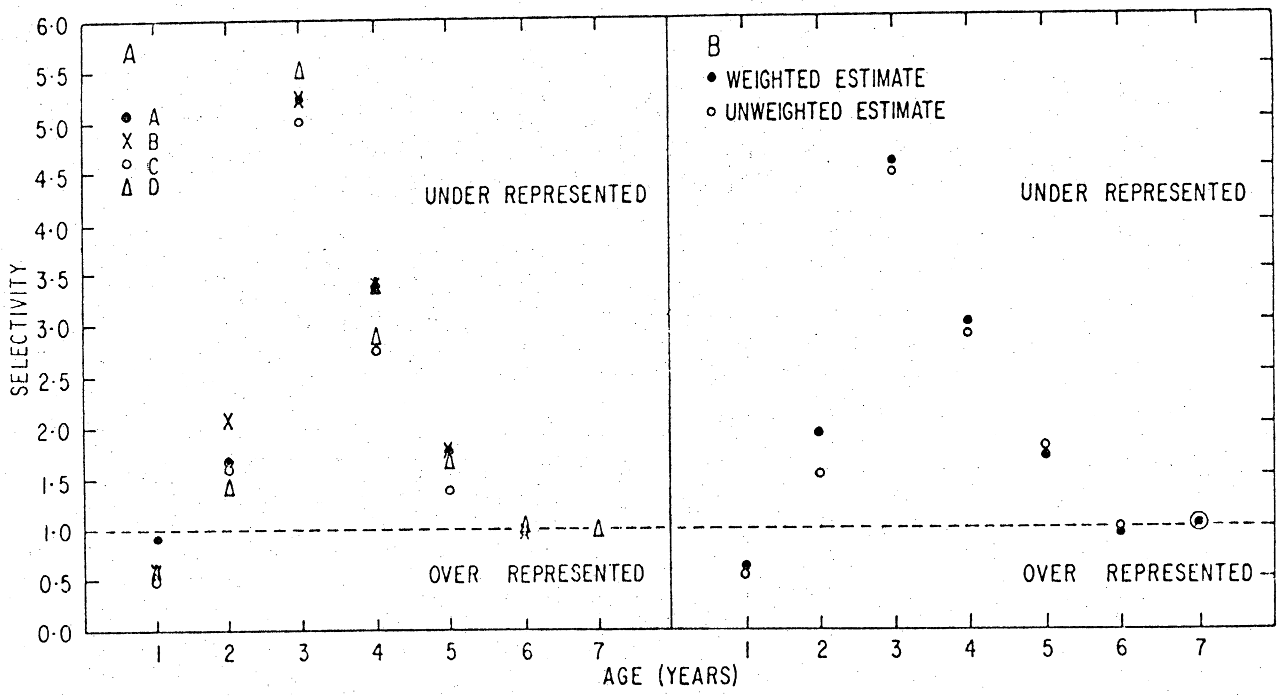

Fig. 2. Correction factors derived using (A) the additive method and (B) the multiplicative method.

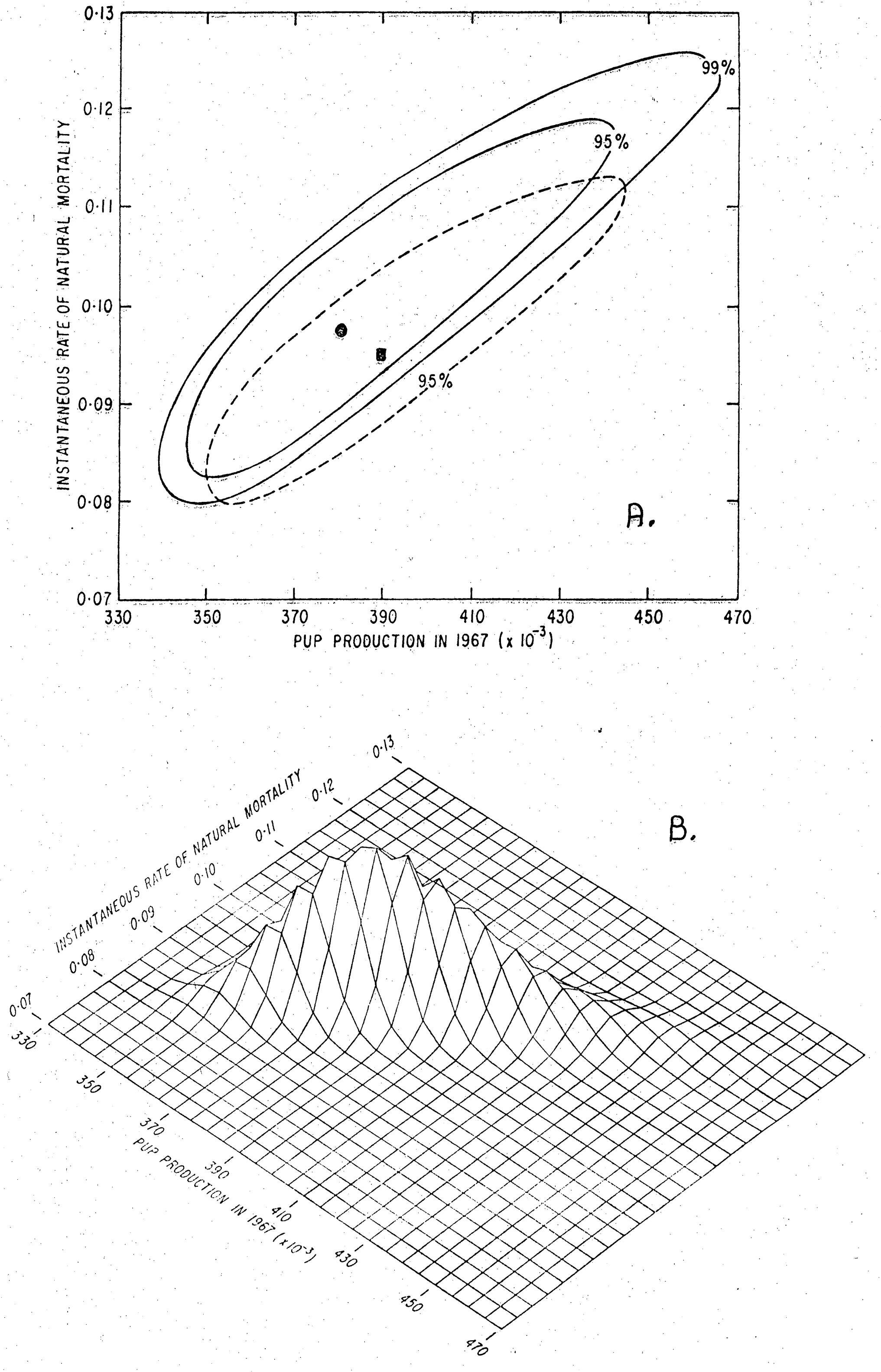

Fig. 3a. Confidence region for the natural mortality schedule, $M_o = M$ (solid line) and $M_o = 3M$ (dashed line) using unadjusted 1967 age distribution.

3b. Three dimensional plot of surface obtained from $M_o = M$.

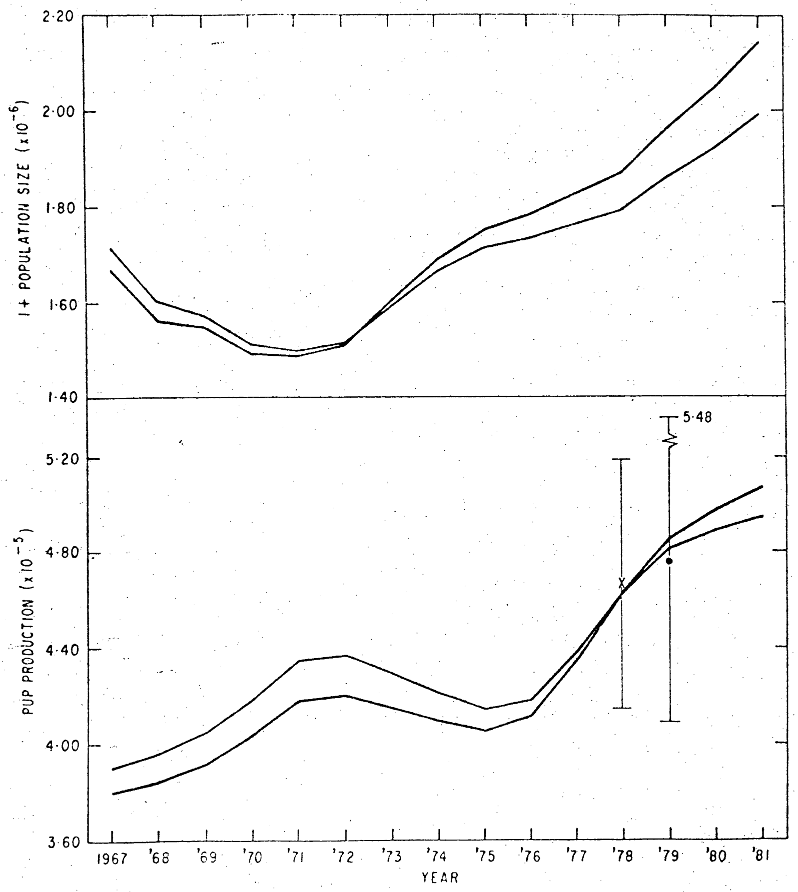

Fig. 4.

Population and pup production estimates from 1967 to 1981 using the 'most likely' estimates of M and N_{67} derived using the unadjusted initial age distribution. 'X' and solid dot represent mark-recapture estimates ±2SE from Bowen and Sergeant (MS 1981).

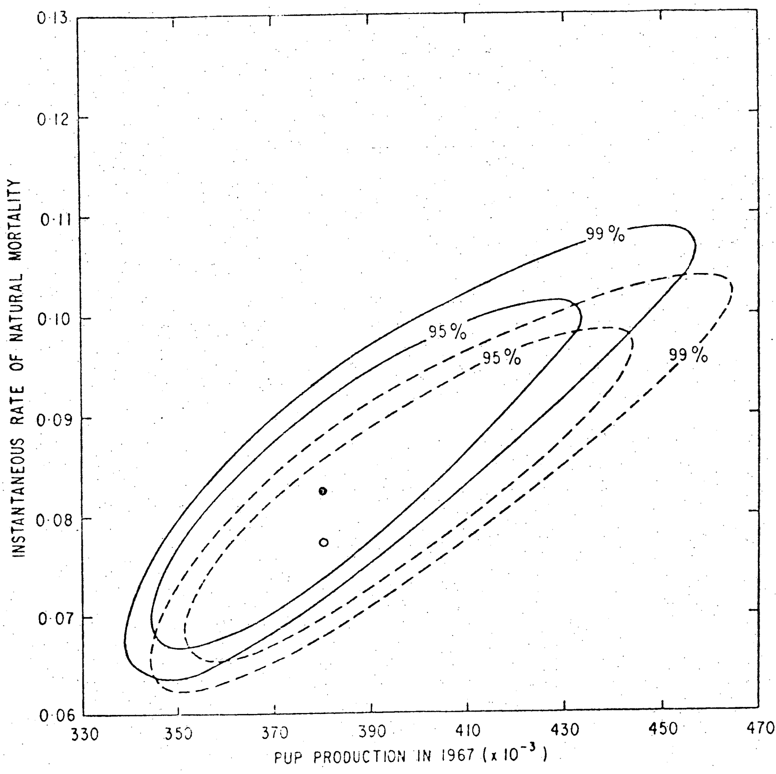

Fig. 5. Confidence regions for the two mortality schedules, using the adjusted 1967 frequency distribution.

———— M_o = M: ● = most likely combination

- - - M_o = 3M: o = most likely combination

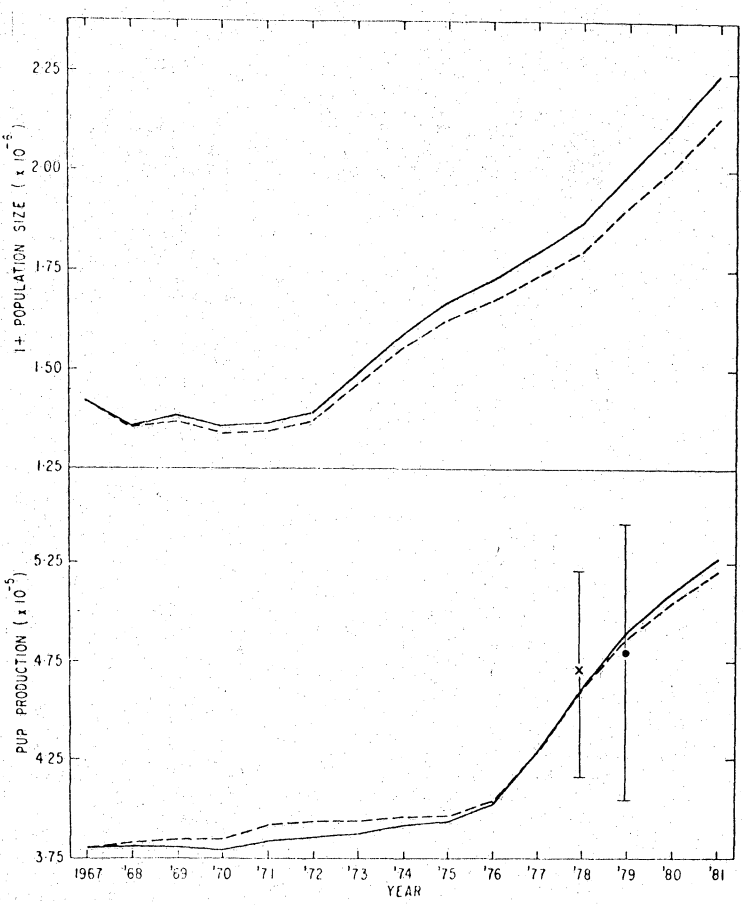

Fig. 6. Population and pup production estimates using the most likely estimates of M and N_{67} shown in Fig. 5. X, ●: mark recapture estimates ±2SE as in Fig. 4.

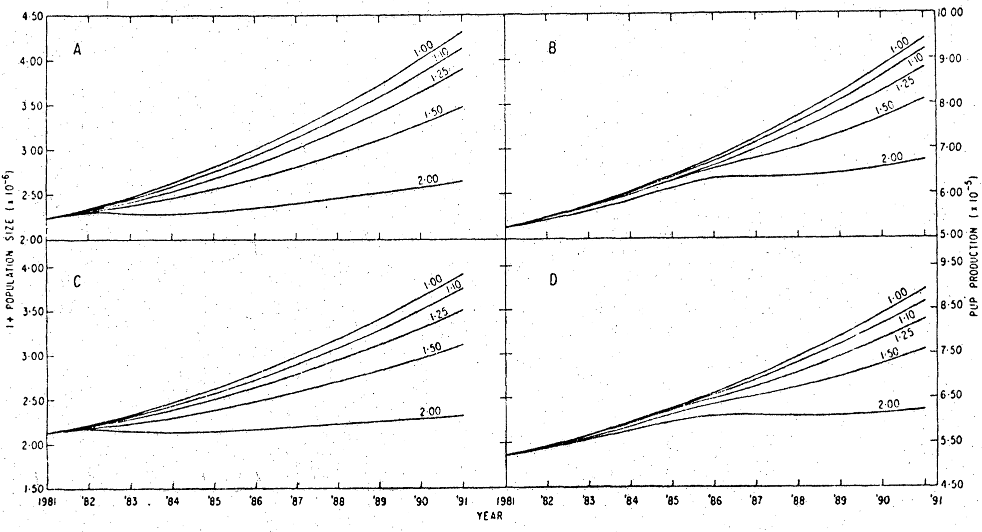

Fig. 7. Projected population growth and pup production assuming a catch that is 1.0X, 1.1X, 1.25X, 1.5X and 2.0X the 1981 total allowable catch of 183,000. Upper panels M_0 = M, lower panels M_0 = 3M.

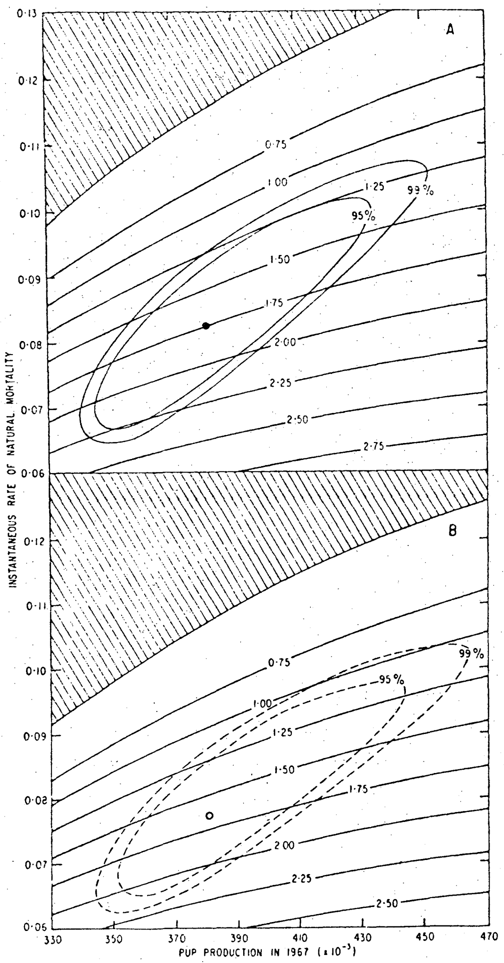

Fig. 8.
Isopleths of the ratio 1+ population in 1991 to that in 1981 as a function of M and N_{67}. The catch is set at 1.25X 1981 quota (i.e. 228,750). Hatched region designates combinations in which the kill in at least one cohort exceeds the size of that cohort. Superimposed on the surface are the 99% and 95% confidence limits of M and N_{67}. A: M_o = M, B: M_o = 3M.

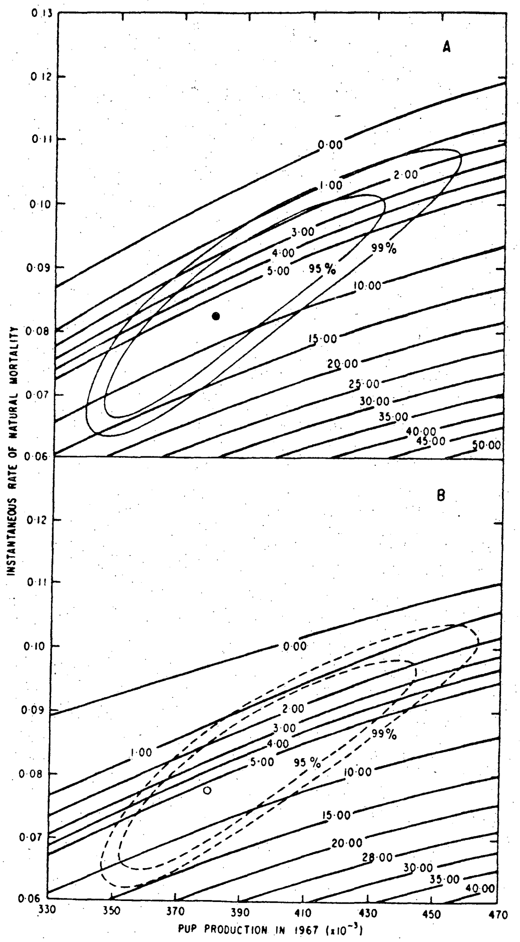

Fig. 9.
Isopleths of pup production ($x10^5$) in 1999 assuming a kill equal to the average from 1952-1971 and age-specific pregnancy rates equal to that in 1967. Superimposed on the surface are the 95% and the 99% confidence limits of M and N_{67}. A: M_o = M, B: M_o = 3M.

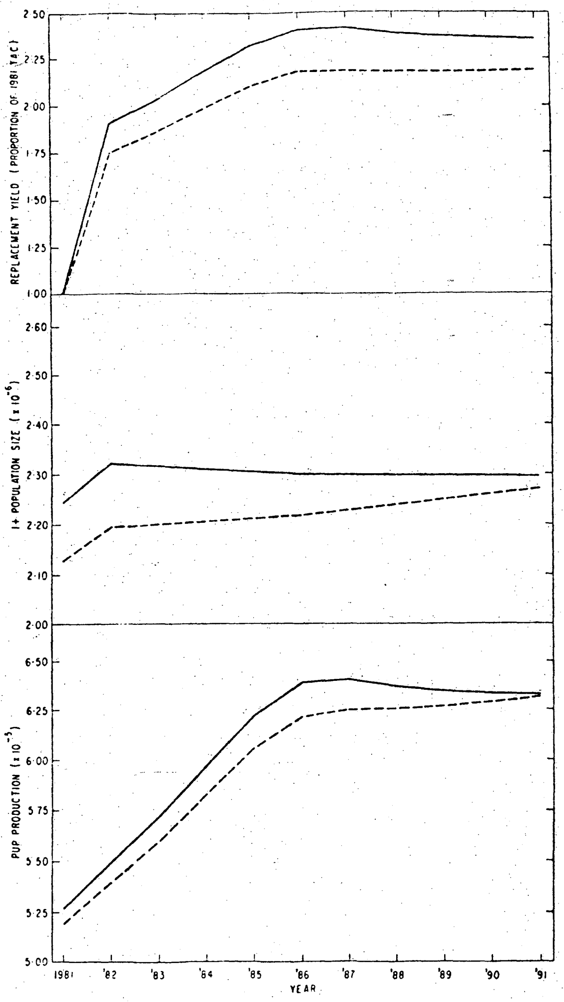

Fig. 10.

Replacement yield estimates as a proportion of 1981 TAC, 1+ population size and pup production, for two mortality schedules, $M_0 = M$ (solid line) and $M_0 = 3M$ (dashed line).

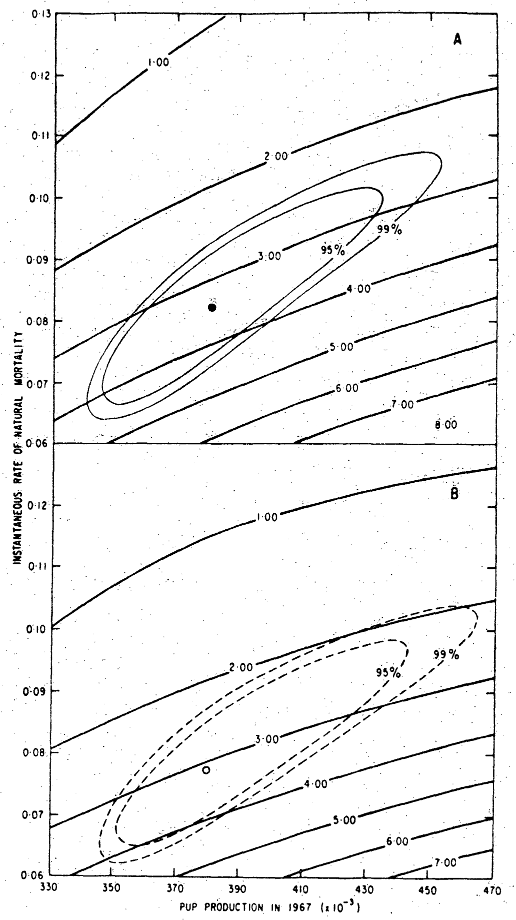

Fig. 11.

Isopleths of replacement yields ($\times 10^5$) for 1982 using the adjusted age distribution. Superimposed on the surface are the 95% and 99% confidence limits of M and N_{67}. A:M_0 = M, B:M_0 = 3M.