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One, two, many: how many harp seals are there?

by

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Abstract

Previous attempts at estimating population size and natural mortality rate in harp seals are unsatisfactory because they are based on false assumptions or fail to take sufficient cognizance of the uncertainty in the estimation of population parameters. In this paper we utilize a simulation model, constrained by estimates of pup production in 1971 and 1979 to locate the set of possible combinations of population size in 1979 and natural mortality. We project the model forward five years to examine the effect of different quotas on population size. There is no evidence that under the present quota the population is endangered, but there is a high probability that under the present quota the population will have declined by 1984.

Introduction

The Northwest Atlantic harp seal, Pagophilus groenlandicus, has in recent years been the object 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 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, Mohn and Gray (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 one-year-old seals and older to be approximately 0.1. This rate is quite reasonable for a species living to age 30 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 0.13. 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

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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, Mohn and Gray 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, Mohn and Gray (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, pregenancy 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 in an appendix: 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 to a set of independent observations. The independent observations in this case are the catch statistics from either the large vessel or landsman 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. This Beddington and William did by assuming that selectivities remained constant at least over blocks of 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 0.13 and a later revised estimate of .14 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 (1980) indicates that there might be significant errors in estimation 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 given 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 Beddingtons 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 1980). 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 and it is necessary to reexamine the problem carefully and attempt to discriminate between the various estimates. In this paper we first exaimine 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 circumvents this problem and also avoids the problem of error in the ageing of older animals.

The Population

The Newfoundland population is divided into two sub-populations, one reproducing on southward-drifting pack ice and forming up east of southern Labrador (referred to as the Front herd), the other in the Gulf of St. Lawrence, mainly in the vicinity of the Magdalen Islands (known as the Gulf herd) (Sergeant 1976). By December, seals have largely completed their southward migration and from December to February they feed intenstively. Most whelping occurs over a one week period beginning in the Gulf in late February and on the Front about 8 March.

Following the whelping at the Front, young harp seals drift southward to the rich feeding grounds in White and Notre Dame bays. During this time they lose their fetal white fur and the pups (known as beaters) take on the spotted juvenile pelage. Also present are large numbers of immature (bedlamer) and adult seals which concentrate on feeding shoals before their movement to the moulting areas in April and May. Once moult begins, the seals swim northward to the pack ice, usually east of the Strait of Belle Isle. After moulting the seals migrate northward to the Canadian Arctic and West Greenland.

The pattern of movement in the Gulf is somewhat different. Beaters, bedlamers and adults usually move eastward to the Cabot Strait and then begin their northward migration along the western coast of Newfoundland. Moulting sometimes occurs in the Esquiman Channel, but is highly variable with a proportion Gulf seals also moulting at the Front.

Beaters begin their northward migration in May and reach West Greenland by early June. At this time adults and immatures are fairly well segregated with the mature seals mainly in the Canadian Arctic and the bedlamers and beaters primarily off West Greenland (Sergeant 1973).

Age Structure of Catch

For some populations it may be assumed that the age-specific 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, each with different hunting selectivities, are used to harvest these animals (Lett and Benjaminsen 1977, Benjaminsen and Ørtisland 1975).

Seals shot from small boats and larger vessels up to 20 m in length (long-liners) mainly in White and Notre Dame bays, Newfoundland, consist primarily of bedlamers. The Quebec northshore, southern Labrador and St. Anthony, Newfoundland, net catches consist of mostly older bedlamers and adults.

Together these hunts represent the landsmen catch. The large vessel catch, taken in breeding and moulting patches until 1964 and in moulting patches only from 1965 to the present, is different in structure than the landsmen catch and must be treated separately. Similarly, the age structure of seals caught off West Greenland and the Canadian Arctic must be considered separately. Thus the age distribution of the total annual catch of seals 1-year-old and older (1+) must combine the catch structure of individual hunts in their proper proportions (Lett and Benjaminsen 1977).

We have adopted a method similar to Lett and Benjaminsen (1977) in constructing the catch-at-age data. We differ from these authors by including the Canadian Arctic and Greenland catch and by including age samples of animals 25 years and older in the analysis. Age samples used to construct the catch-at-age data are given in Bowen (1980). Age was determined by the method of Fisher (1954) and was generally based on a single examination of each tooth section. Recent work indicates that significant errors may occur in the determination of age by this method when age is based on a single 'reading' (Stewart and Lavigne 1979). The implications of these errors on the results of our simulations have not been thoroughly analysed, but preliminary work by Doubleday and Bowen (1980) shows that these errors may be important in the estimation of pup production from catch data.

Between 1952 and 1973 landsmen catch-at-age data were produced from samples of the net catches from La Tabatiere, Quebec, St. Anthony, Newfoundland, and Labrador (Sergeant and Fisher 1960; Sergeant 1971, pers. comm.). From 1974 to 1979 the age structure of the landsmen catch was constructed from nets samples as above and shot samples of the longliner - small boat hunts (Sergeant 1976, 1977, 1978; Bowen and Sergeant 1979). During 1952-54 and in 1958, samples of jaws were collected from catches of the large vessels (Sergeant and Fisher 1960, pers. comm). For the remaining years from 1955 to 1960, the average catch-at-age frequencies for years 1952-54 and 1958 were used, although there are possibly serious errors arising from this convention, since the catch of age 1 and older seals by large vessels represented between 87 and 96% of total 1+ catch during this period (Lett, Mohn and Gray, 1979). Age sampling from the large vessel catch of 1+ seals improved after 1961 with the exception of 1972 and is taken from the following sources: Sergeant (1971, 1976, 1978, pers. comm). Bowen and Sergeant (1979), Øritsland (1971, pers. comm), and Benjanimsen and Øritsland (1975, pers. comm.).

Age compositions of the West Greenland hunt were obtained from Kapel (1977, 1979, pers. comm). Age samples of Canadian Arctic catch are available in 1967, 1969, 1976 and 1977 (Sergeant pers. comm., Stewart pers. comm). Total annual 1+ catch of harp seals in the Canadian Arctic between 1962 and 1971 is reported in Smith and Taylor (1977). Yearly estimates of the Arctic catch from 1974 to 1977 were obtained from Sergeant (pers. comm.). Available data suggest that the Arctic kill has been stable with average annual landings of 1,784 1+ seals.

Total annual catches of harp seals were taken from statistical Bulletins of the International Commission for Northwest Atlantic Fisheries (ICNAF) and supplemented by more recent estimates of the present and historical West Greenland harvests (Bowen 1980)).

Age 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... fi... fn, 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... f_{i+1}, ... f_{n+1}, the new incoming cohort being ignored. If the mortality rates are the same on all ages then fi in year t will equal f_{i+1} in year t+1. The two age distributions can be compared using either a x^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 distribution. The hunting mortality on adult seals is far too small 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, 69, 70, 71, 73, 74 and 76. For reasons to be given later we chose to begin our simulation runs in 1967. To obtain the age distribution of 1+ seals in 1967, we took the 1968 age distribution from age 2 through to 9+, (another reason for this choice was that Benjaminsen and Øritsland (1975) suggested that age 1 animals are not correctly represented in the samples). Our initial analysis used the age distribution of 2 through to 15+; we compressed this last class to 9+ in an attempt to reduce the statistical heterogeneity described below. The age distribution 2 to 9+ in 1968 was compared using the G statistic with the age distribution 3 to 10+ in 1968, 4 to 11+ in 1969 and so forth. The results of all pairwise comparisons are shown in Table 1. There are 5 significant G values, indicating that the samples are not random. Correcting for the possible over representation of 2, 3 and 4 year olds in the sample using the correction factors derived by Sergeant (1976) or Bowen and Winters (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 (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 considered representative of the population. Becuase a correct age distribution is necessary for both cohort analysis and the x^2 method of Beddington and Williams, both approaches must be viewed with considerable sceptism. Because of these problems we adopted another approach.

An Alternative Approach

Although there is insufficient information to enable simulation model to be tuned to a particular statistic (eg. x^2) there is sufficient information on one parameter to set limits on the trajectory of the model. This parameter is pup production and by utilizing several approaches we are able to set limits for pup production in 1967, 1971, and 1979. The permissable combinations of natural mortality and initial population size are those which produce pup productions that lie within the limits set in 1971 and 1979, the 1967 limits being used to set the limits to the initial population size. Unfortunately, the methods of deriving the pup production limits do not permit the construction of a probability surface and hence all points lying within the limits must be assumed to be more or less equally likely. The methods of estimating pup production are as follows.

A. An absolute lower limit to pup production can be obtained by summing the catches from a single cohort. The pup kill in 1967 and 1971 was sufficiently high that the summed catches for these cohorts provide reasonable lower bounds for pup production. This method was used primarily to provide a check on the second method of estimation.

B. This method of estimating pup production uses the ratio of catches of adjacent cohorts. Let pup production in year t be N_t, the catch of whitecoats be K_t and the catch of beaters be b. Assuming natural mortality rate to be significant, we may estimate the number remaining at t+1 as $(N_t-K_t)e^{-M} - be^{-M/2}$. Now let the kill of whitecoats in year t+1 be K_{t+1} and the catches of the two cohorts in year t+i be $C_{t,\ t+i}$ and $C_{t+1,\ t+i}$. Assuming no age-specific hunting selectivity we have

$$\frac{(N_t-K_t)e^{-M} - be^{-M/2}}{(N_t-K_t)e^{-M} - be^{-M/2} + (N_{t+1}-K_{t+1})} = \frac{C_{t,t+i}}{Ct,t+i + C_{t+1,\ t+i}} = P \qquad (1)$$

Because of the many age groups that contribute to pup production, the high survival rate and the low fertility rate per female (generally only one pup) pup production in year t+1 will be virtually the same as production in year t: over most of the parameter space examined the difference from one year to the next was only of the order of 5% and rarely did it exceed 10%. Assuming N_{t+1} equals N_t we have

$$N_t = \frac{K_t e^{-M} (1-p) + be^{-M/2} (1-p) - pK_{t+1}}{(1-p)e^{-M} - p} \qquad (2)$$

Approximate confidence limits may be set by inserting the upper and lower limits of p. We also examined the importance of assuming $N_t = N_{t+1}$ by inserting in (1) the relationship $N_{t+1} = rN_t$ and calculating N_t for r equals 1.05 and 0.95. N_t is a nonlinear function of p and the confidence limits tend to be large if p lies close to 0.5. For this reason only, years in which adjacent pup kills are very different give useful bounds; 1967/68 and 1971/72 are such years.

C. In 1979 an attempt was made to estimate pup production by mark-recapture. As far as can be measured the underlying assumptions of this method were upheld at the Front (Bowen 1979) and the confidence limits used are statistically valid (Roff unpubl. data). Unfortunately, inclement weather prevented a significant catch of beaters along the coast of western Newfoundland and thus very few tags from the Gulf experiment were recovered. Hence an estimate could only be made for the Front pup production. Even in this case the estimate may be somewhat low since a patch of pups that whelped in the Strait of Belle Isle was observed but not marked and probably had not mixed with the Front animals at the time the second sample of animals was taken (Bowen 1979).

Setting the Limits of Pup Production in 1967, 1971 and 1979

1967

Of the 1967 cohort, 303,527 animals were caught between 1967 and 1980. To estimate pup production from equation (2) we must first estimate p. This can be done by using the 1970, 71, 73, 74, 76 and 79 samples of moulting males for the 1967 and 1968 cohorts. These data and a test for heterogeneity between years and ages are given in Table 2. No heterogeneity is detectable and hence p is estimated by pooling all samples. Using equation (2) and assuming M = 0.1 pup production is 404,440 with a lower 95% bound of 361, 310 and an upper bound of 473,023. Allowing for a 5% variation in pup production between years the lower and upper bounds are 352,996 and 502,710. For convenience we have rounded these values to 350,000 and 500,000 (this rounding makes no difference to the analysis or conclusions). The estimates from this latter method are in accord with what we might expect from the total kill record, taking into account animals dying from natural causes and animals still alive.

1971

Up to 1979, 233,014 animals of this cohort had been caught. The data for the estimation of p are presented in Table 3. No heteorgeneity is detectable. Using equation (2) the expected pup production is 454,816 with 95% limits from 328,919 to 1,217,400. The upper limit is clearly far too high to be of any use in constraining the simulation. The lower limit obtained when 5% variation in pup proudction between years is assumed is 314,706. We rounded this value to 315,000.

1979

To estimate the 1979 pup production we need to consider the following components. Firstly, the lower limit obtained in the mark-recapture experiment. This number, 97,145, comprises the population of pups from the Front herd still alive after the pup hunt. To this we add the number of pups taken at the Front, 76,868. Unfortunately the Gulf production cannot be directly estimated. An indirect method is to use the ratio of Gulf pups to total pup production obtained from aerial surveys. Of all the surveys attempted only three, 1959 and 1960 (Sergeant and Fisher 1960) and 1970 (Sergeant 1971), achieved a complete coverage of both herds. The percentage of animals of the total in the Gulf were 46.8%, 31.9% and 35.6% respectively. To estimate the lower limit of pup production we assumed a value of 30% and ignored the presence of animals in the Strait of Belle Isle since the estimate of its size may be unreliable: this procedure gives an estimate of Gulf production of 74,577. The total minimum pup production in 1979 is thus 97,145 + 76,868 + 74,577 = 248,590, which we have rounded to 250,000. To estimate the upper limit to pup production we took the upper confidence limit from the mark-recpature experiment, assumed a Gulf to total ratio of 0.5 and calculated the production both with and without the estimate of the size of the Strait of Belle Isle patch (~20,000). The two estimates so obtained are 518,132 and 478, 132: we have used a value of 500,000.

Description of the Model

The model is initiated at the time of pup production in 1967. The choice of 1967 for the starting point of our simulations is somewhat arbitrary, however, several reasons make this a convenient choice. First, 1967 is the earliest year for which reliable estimates of pup production could be obtained. Second, large moulting samples between 1969 and 1979 enabled the estimation of the population age structure, but more importantly, the ratio of ages 1-7 to 8+ in the population. Finally, 1967 was recent enough to make it unlikely that density-dependent changes in natural mortality would be important and yet enough in the past to allow reasonable discrimination between different chosen values of natural mortality.

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. 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. A schematic diagram of the process outlined above is shown in Fig. 1. The number of seals of age i remaining after hunting period j in year t, $N_{i,j,t}$, is given by the equation

$$N_{i,j,t} = N_{i,j-i,t}\, e^{-(F_{i,j,t} + MT)} \tag{3}$$

where $F_{i,j,t}$ 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. $F_{i,j,t}$ can be estimated by iteration from the relationship

$$C_{i,j,t} = \frac{N_{i,j-1,t}\, F_{i,j,t}\, (1 - e^{-(F_{i,j,t} + MT)})}{F_{i,j,t} + MT} \tag{4}$$

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

$$N_{i,j,t} = (N_{i,j-1,t} - C_{i,j,t}\, e^{MT/2})/e^{MT} \tag{5}$$

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 $N_{i,j,t}$: 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 1980). For the model we required the relationship between age and pregnancy rate. Data on this are presented in Table 4. There appears to have been no change in the pregnancy rate of seals aged 2, 3 or 4. At age 7 the maximal pregancy rate is achieved and seals age 7 or 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. 2). 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. 2).

The final component of the model is the initial age distribution. As discussed previously samples taken from the moulting patches are not random and hence these distributions are only biased approximations of the true distribution. However, since the distributions do not show a systematic bias pooling acorss years will tend to reduce the bias. Furthermore the most important consideration is the ratio between 8+ animals, which are fully mature and the younger immature age groups (the 7-year-old age groups was omitted initially from the pooled adult class because we thought this age not to be fully mature. Later more detailed analysis indicated otherwise. To test the hypothesis that the moulting samples are not biased with respect to the ratio of 'immatures' (1 to 7 year olds) to 'matures' (8+ animals) in 1967 we proceeded in the same manner as previously described for the extended distributions (see p. 6): the data for this analysis are presented in Table 5. The G value is not significant at the 5% level and hence all years may be pooled to give an estimate of the desired ratio. A similar analysis for the 1 to 7 year olds, presented in Table 6 indicated that the removal of the 8+ class did not eliminate the bias in sampling. However, since the major contribution to pup production is from the 8+ class and the contribution of the 1 to 7 year olds is distributed slowly across years as these groups mature the relative frequencies within the 1 to 7 age group is not critical; substantial changes in this distribution do not effect the population trajectory. Because the method of collecting does not lead to larger moulting samples being necessarily collected from a larger area or from more patches of seals it is not evident that larger samples more closely approximate the true distribution. We therefore calculated the distribution both using sample size as weighting factor and using no weighting (Table 7). Because there is little difference between the two methods we used the unweighted distribution.

Given a particular pup production in 1967 the population size at this time can be calculated from

$$N = \frac{2 \times PUPS\ (1 + RATIO)}{(RATIO \times 0.87) + Q}, \qquad Q = p_4f_4+p_5f_5+p_6f_6+p_7f_7 \qquad (6)$$

where N : Population size in 1967
PUPS : Pup production in 1967
RATIO: Ratio of 8+ to 1-7 year olds in 1967
pi : Proportion of age group i pregnant in 1967
fi : Frequency of age group i within the 1-7 age grouping in 1967

Analysis

Initially we shall assume that mortality in the first year of life is the same as all other years. As outlined earlier we ran the model from 1967 to 1979 for a range in pup production in 1967 from 3.5×10^5 to 5.0×10^5 and a range in natural mortality from 0.05 to 0.15. Combinations of these two parameters were rejected if they failed one or more of three criteria:

(i) the observed catch of an age group of seals exceeded the predicted number in that age group,

(ii) the pup production in 1971 was less than 3.15×10^5 animals, and

(iii)the pup production in 1979 was less than 2.5×10^5 or greather than 5.0×10^5.

The population size in 1979 as a function of all combinations of pup production and natural mortality initially considered possible is shown in Fig. 3. Combinations excluded by one or more of the above criteria are hatched: note that for the higher values of natural mortality rejection is due to all three criteria not being met. The region remaining is still quite large, the 1979 population size of 1+ animals lying anywhere between about 8×10^5 and 2×10^6 animals. Significantly, however, the natural mortality rate of .13 and pups production 430,000 in 1967 proposed by Beddington and Williams (1980) is unlikely, it lying beyond the extreme edge of the acceptable set of combinations.

Of concern is what will happen to population size if the present quotas are maintained. Given the uncertainty about any density-dependent mechanisms thay may limit population growth it is unwise to attempt any analysis of equilibrium population size. Instead we ask the question: what will be the population size five years hence given the present catch structure? The stated policy of the Federal Government of Canada is to restricted catches to levels below the replacement yield such that slow increases in the population may be expect to occur. If there is a significant probability that under the present management quota the population in 1984 will be less than or equal to that in 1979 the quota may need revision. To project forewards we made the following assumptions: (a) the age specific pregnancy rates will remain at the same values as in 1979 and (b) the catch structure remains the same as in 1979. This means that the proportion of the catch taken by each hunt remains at the 1979 figure and that each hunt maintains the same age specific hunting selectivities.

The predicted population sizes and the ratio of population size in 1984 to size in 1979 are shown in Fig. 4. The predicted population size in 1984 lies between about 6.0×10^5 to 2.8×10^6. Even under the worst scenario there is no danger of a catastrophic collapse due to hunting, although as shown by Fig. 4b the population may be declining at this time as a result of overharvesting. Examples of three possible trajectories, marked on Fig. 4b, are shown in Fig. 5; all three result from acceptable combinations of parameters. What is clearly evident from these trajectories is that in all cases the population was declining prior to the introduction of quotas in 1972. The increase in the quota in 1974 may have caused the population to decline. For these three cases what population size would result from changes in the quota? To examine this question we increased or decreased the quotas on all hunts by a constant factor. The effect on population size in 1984 of varying the quota in this way is shown in Fig. 6. Over the range considered there is almost a linear relationship between population size and the proportional change in the quota. Furthermore the slopes of the three lines are very similar. Population size will increase or decrease by approximately 60,000 for every 10% increase or decrease in the quota. In considering the full set of permissable combinations two probabilities need consideration. Firstly, what is the probability that the population will be increasing or stationary by 1984? Secondly, what is the probability that the population will be greater than 1×10^6 animals in 1984? These probabilities are shown in Fig. 7 as functions of the future quota. Given the present quota there is a probability of 0.43 that the population will be decreasing by 1984 and a probability of 0.26 that the population will be less the 1×10^6. A 20% reduction in the quota will decrease these probabilities to .30 and .18 respectively.

If natural mortality is age specific the most likely point at which it differs from the adult rate is during the first year of life. To examine the consequences of a higher than adult rate during the first year we ran the simulation with first year rates as high as 5X the adult rate. The response surfaces for population size in 1979 and 1984 are shown in Fig. 8 for this extreme rate. Changes in the first year mortality do not alter the possible set of population sizes either in 1979 or 1984: what they do is to shift the region of acceptable combinations downwards. Thus for any particular initial pup production the maximum and minimum acceptable adult natural mortality rates are reduced. While changes in first year survival rates therefore change the set of probable combinations they do not affect the results of changes in the quota. These conclusions, however only apply to differences in the first year rate that are constant and for proportional changes in the quota. Any analysis of long-term strategies will need to consider the consequences of temporal changes in mortality rates and changes in the structure of the hunt.

Discussion

Despite the fact that the data base for harp seals is probably one of the most detailed and accurate that is available for a "fishery", the degree of uncertainty in the rate of natural martality and population size is very high. This reflects the lack of information on critical parameters, most particularly the age distribution of the population. If such distributions were available the model could be constrained by these and confidence regions obtained. Simulation runs using assumed age distributions do show the the samples sizes required to achieve reasonable confidence bounds are feasible. It is not, however, clear that the present method of collecting moulting sample can be changed to achieve a random sample. The alternative, that of constraining the population by pup production may be as effective if reasonable estimates of these can be obtained. The best methods of estimating pup production are marked-recapture and photographic aerial survey (Bowen 1979, Lavigne, Innes and Barchard 1980). But the success of methods depends very heavily on suitable weather conditions and there is a high probability that bad weather will prevent one segment of the population being estimated. Even after these difficulties are surmounted it seems likely that the best estimates of pup production will have confidence bounds at least 25% (Bowen 1979). Thus we may have to live with the fact of a high degree of uncertainty in the basic population parameters required to manage the stock. Fortunately the large numbers of age groups and stability in reproductive success (offspring production does not fluctuate violenty as it does in certain fish species such as haddock) prevent the population from catastrophic declines. But it is possible for the population to be declining for a number of years before the change could be detected.

Management policies must therefore take into consideration the probability of decline: management on the basis of 'best estimates' may lead to significant errors in the setting of quotas. To this end it is necessary to determine, albeit arbitarily, acceptable probabilities for future projections. The probabilities given in Fig. 7 are a preliminary attempt toward this goal. These probabilities are based on the assumption that all points in the permissible parameter space are equally likely. This assumption is clearly false. Some combinations of pup production and natural mortality will be more likely than others. It is possible that the population is increasing and future quotas might be substantially increased, but until better information is forthcoming, this may be an optimistic view.

Previous estimates of 1967 pup production fall within the approximate 95% confidence limits given here. Using the survival index method Winters (1978) and Benjaminsen and Øritsland(MS 1975) calculated production of 393,000 and 399,000 pup respectively. These estimates are most likely biased upward about 10-15% (Beddington and Williams 1980). Even so, they fall within the lower 95% limit of 350,000. Lett and Benjaminsen (1977) calculated 1967 pup production based on cohort analysis of about 459,000, whereas Lett, Mohn and Gray (1980) arrived at a value of 348,000. The major shortcoming of these previous estimates is that the methods involved do not permit reliable confidence limits to determined.

Beddington and Williams (1980) and Lett, Mohn and Gray (1980) have reviewed estimates of the instantaneous rate of harp seal natural mortality. Previous estimates have been criticized because of their reliance on the survival index at some point in the calculations (Beddington and Williams 1980) or the assumption that moulting samples are representative of the population age structure (this study). How then do these estimates fall in relation to the permissible parameter space indicated on Fig. 3? We see that the combination of 393,000 pups (predictive regression) and M = 0.10 given by Winters (1978) falls within the permissible parameter space. If, however, we use Winters' functional regression estimate of 363,000 a value of M = 0.10 would be considered unacceptable. Similarly the combination of 357,000 pups and M = 0.10 used by Lett, Mohn and Gray (1980) falls in the unacceptable region of parameter space. Beddington and Williams (1980) combination of 430,000 pups and M = 0.1375 also lies in a region of parameter space considered unacceptable based on our preliminary analysis. By contrast, the combination of 459,000 pups and M = 0.114 given in Lett and Benjaminsen (1977) falls well within the region of acceptable parameter space. Clearly there is considerable uncertainty about the rate of natural mortality in harp seals. This is reflected not only by the size of the acceptable parameter space, but by the fact that only one of the previous combinations of natural mortality falls well within the acceptable region.

We have not attempted in this study to predict long-term changes in the population size. The reason for this are self-evident: given the uncertainty in the population trajectory during a period in which the population is well below levels at which density-dependent factors are likely to operate, projections based on hypothesized regulating factors are very nebulous indeed. Previous analysis have suggested that mortality in the first year has steadily declined with population size (Lett, Mohn and Gray 1979, Beddington and Williams 1980). But since these analyses are based on poor data or models the reality of this change must be called into question. Furthermore changes in the faunal composition of the seals habitat due to climatic changes and/or fishing may alter any density-dependent responses that might act in a pristine environment. An attempt at long-term projections is worthwhile in order to examine the set of possible future states but at the present time there is little indication that they can contribute to optimal management schemes. What they can do is give information on the types of data to be collected and the sorts of questions that need to be addressed.

There is no evidence to indicate that the harp seal populations are endangered. There is evidence that the present quota may be higher than is required to permit the population to increase in the next five years. Even the most optimistic views of the data base and future additions to it suggest that management must deal with a high level of uncertainty.

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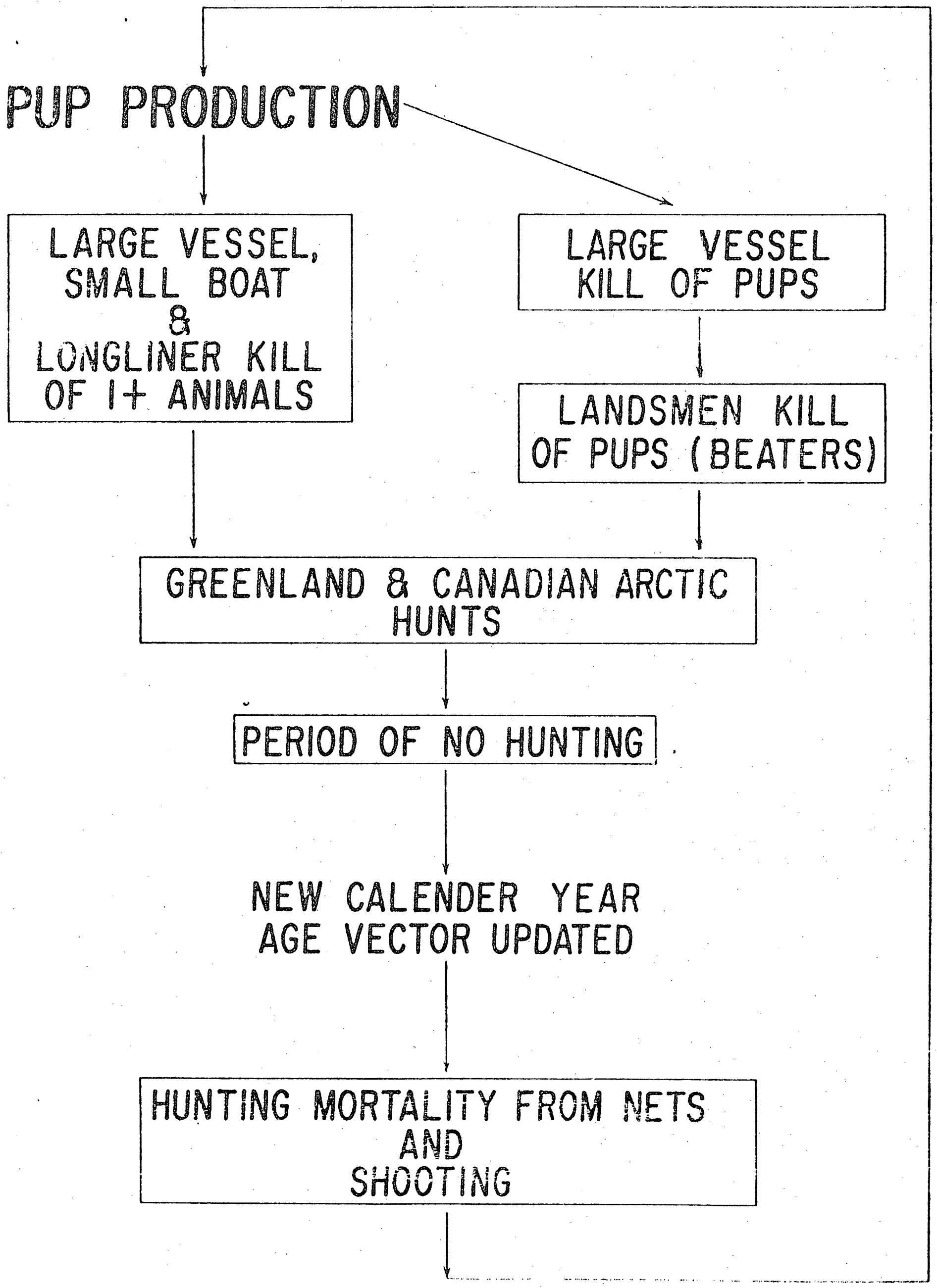

Fig. 1. Schematic diagram of the simulation model.

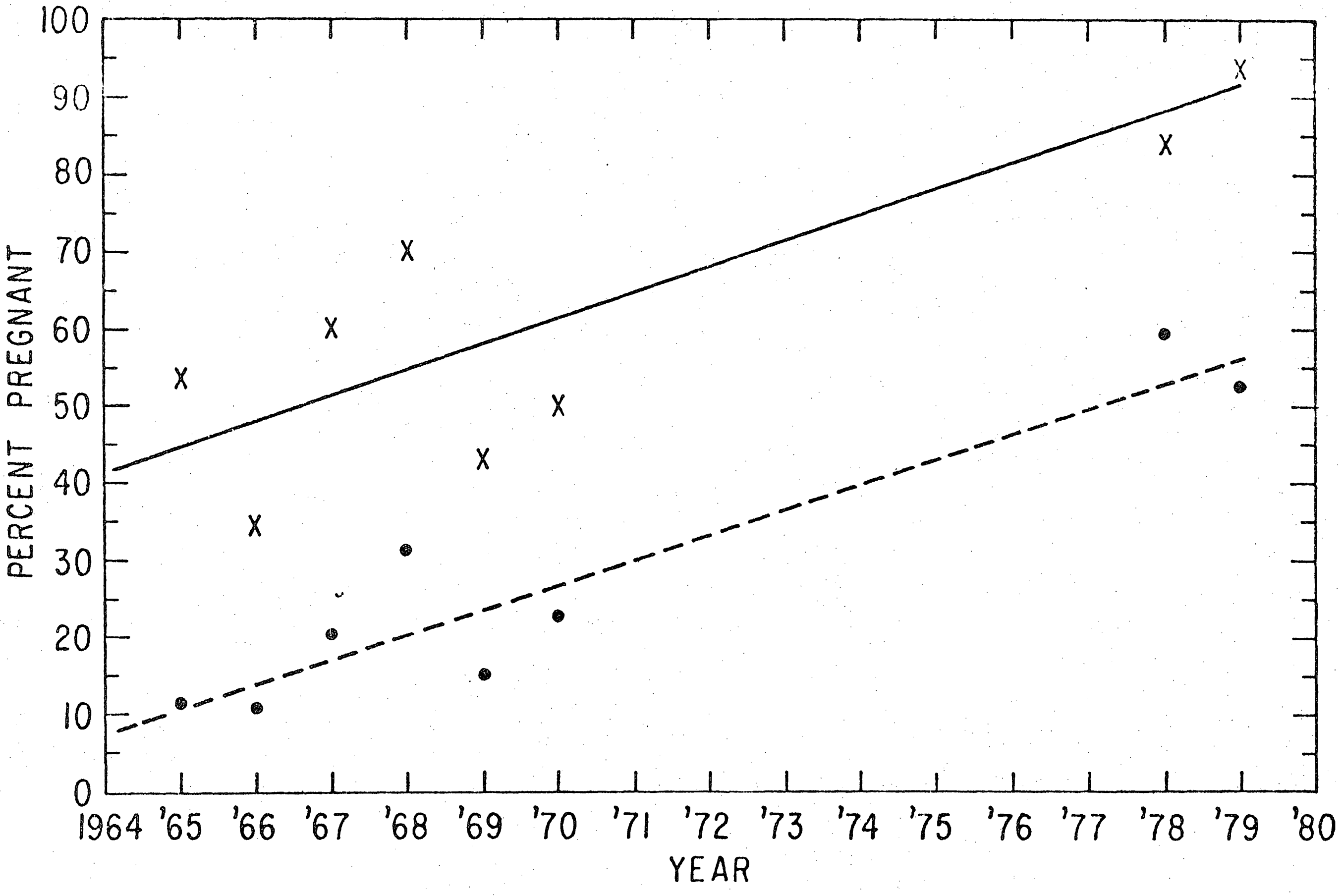

Fig. 2. Proportion of 5-(●) and 6-year-olds (x) pregnant

$\arcsin\sqrt{\%\ \text{Preg}\ 5} = 18.22 + 2.085\ \text{year},\ r = 0.936,\ P < 0.01$

$\arcsin\sqrt{\%\ \text{Preg}\ 6} = 39.50 + 2.091\ \text{year},\ r = 0.845,\ P < 0.01$

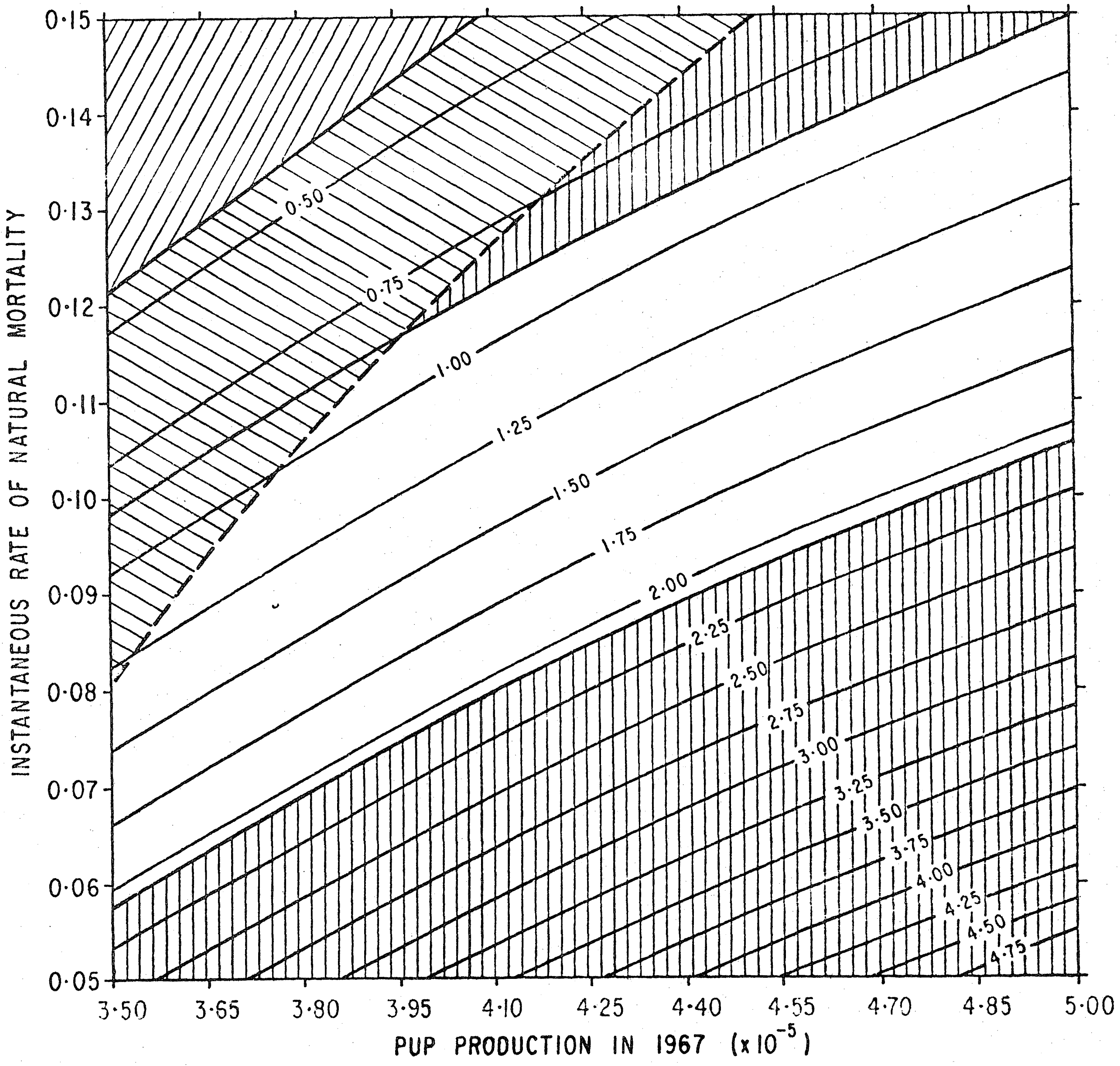

Fig. 3. Population size in 1979 as a function of pup production in 1967 and natural mortality rate.

Criteria for rejection	Regions in which combinations are rejected.
Catch exceeds predicted numbers	///
1971 pup production less than 3.15 x 10^5	///, \\\
1979 pup production less than 2.5 x 10^5 or greater than 5.0 x 10^5	///, \\\, |||

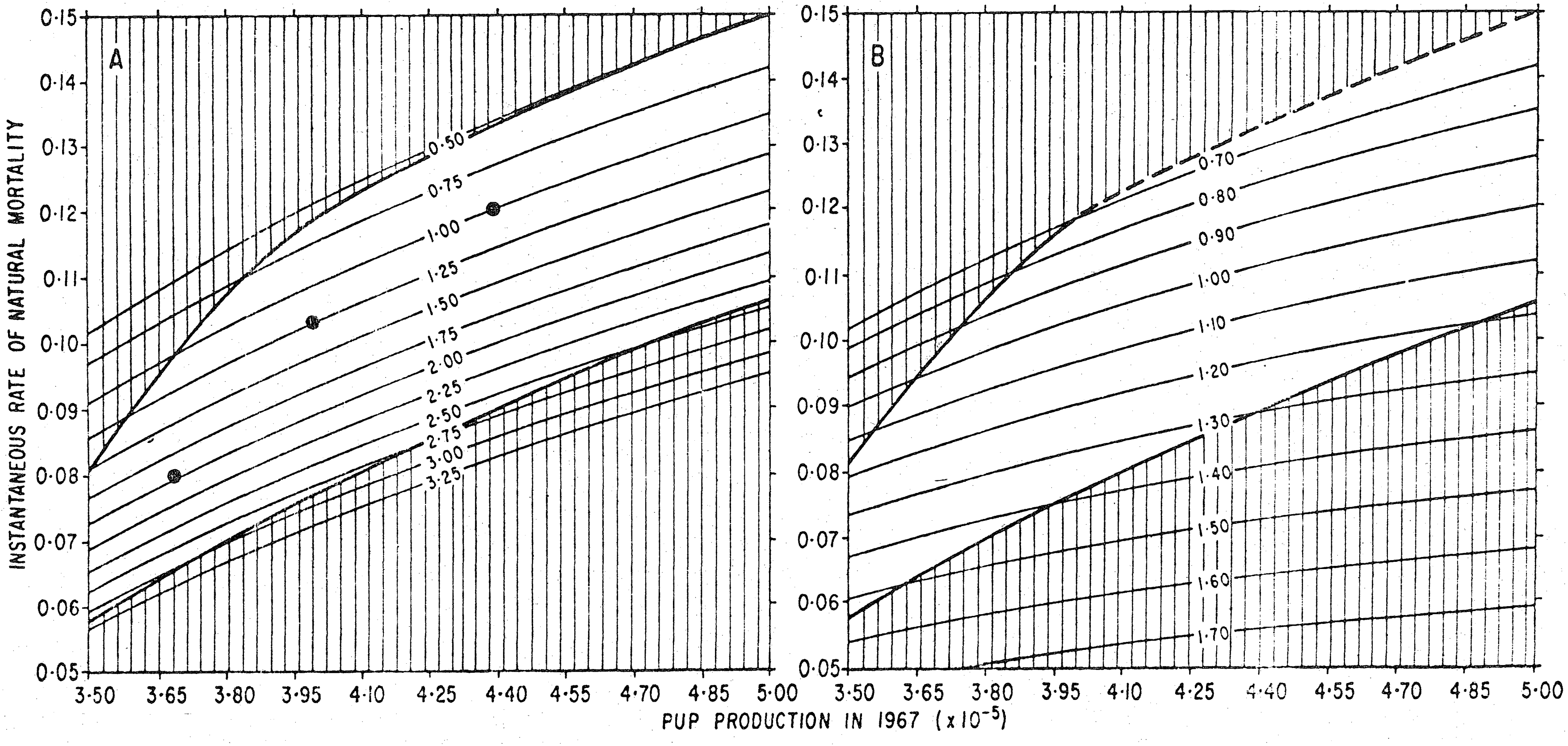

Fig. 4. a) Population size in 1984. Hatched regions are those rejected by previous analysis.

b) Ratio of population size in 1984 to population size in 1979.

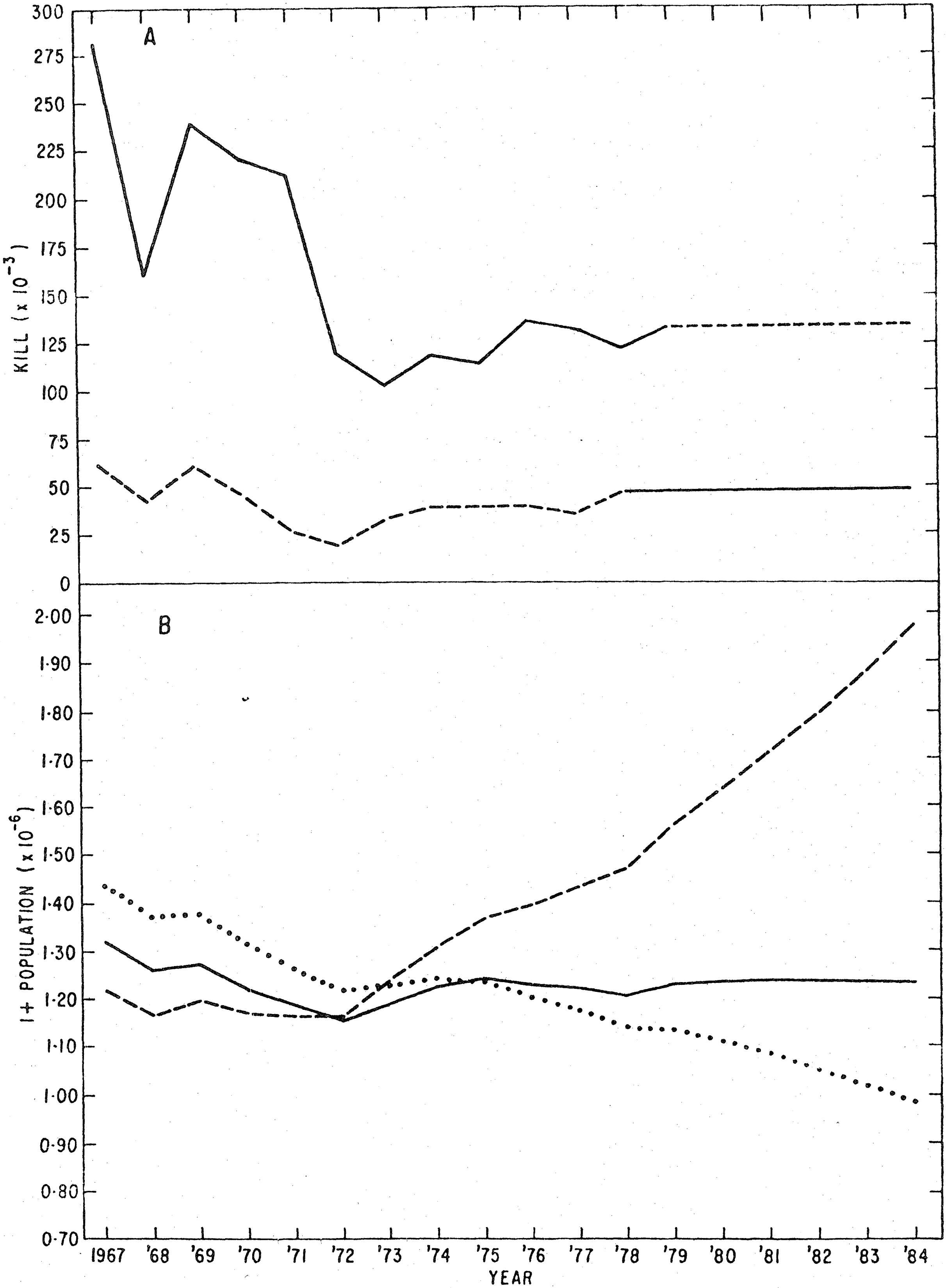

Fig. 5 a) Time trace of pup kill (-) and 1+ kill (---) from 1967 to 1979.

b) Population trajectories for three combinations of natural mortality and 1967 pup production (P): M = .12 and P = 440,000 (....), M = .103 and P = 400,000 (-), M = .08 and P = 370,000 (---). See also Fig. 4a.

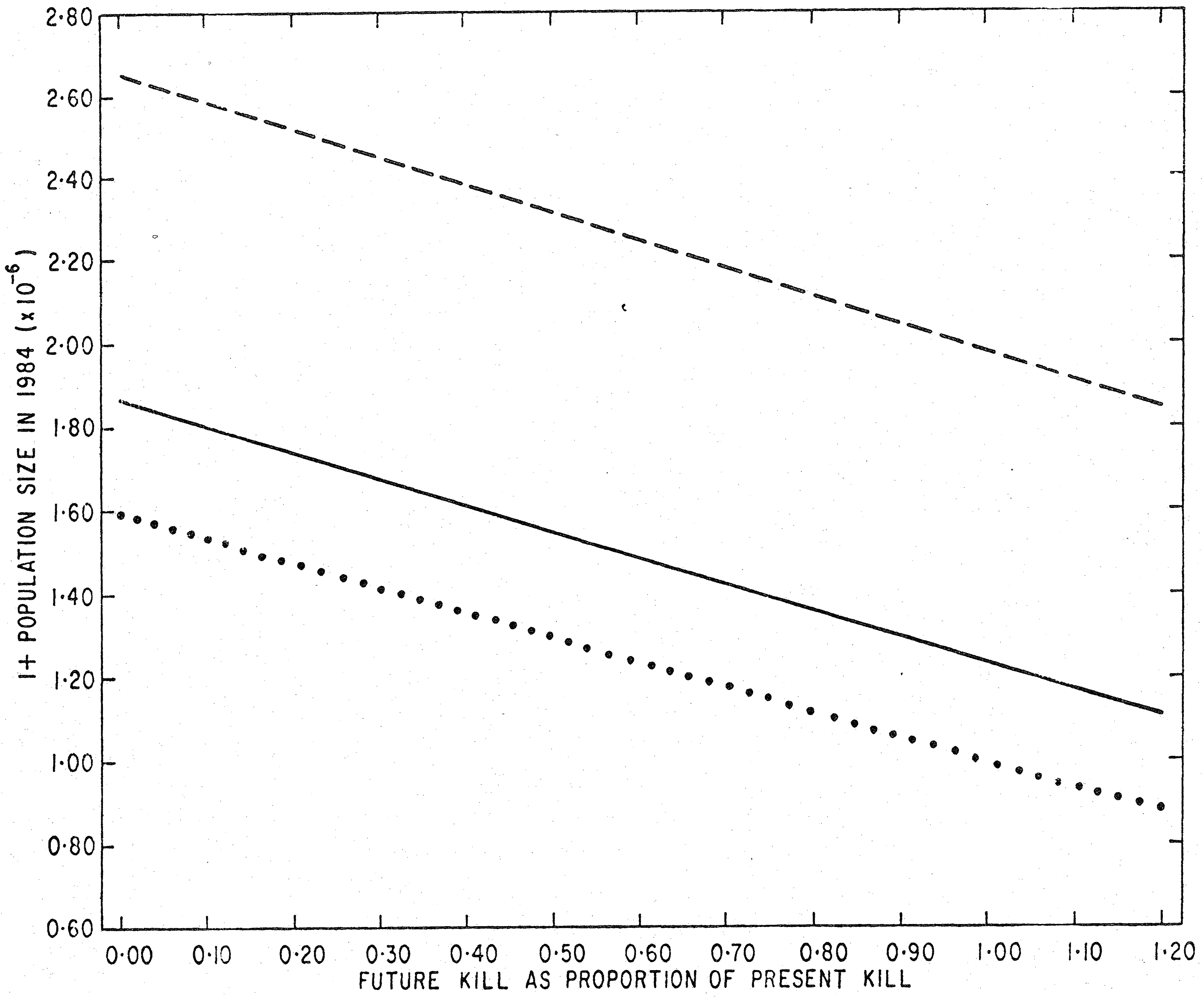

Fig. Fig. 6 Population size in 1984 under different quotas for the three combinations shown in Fig. 5.

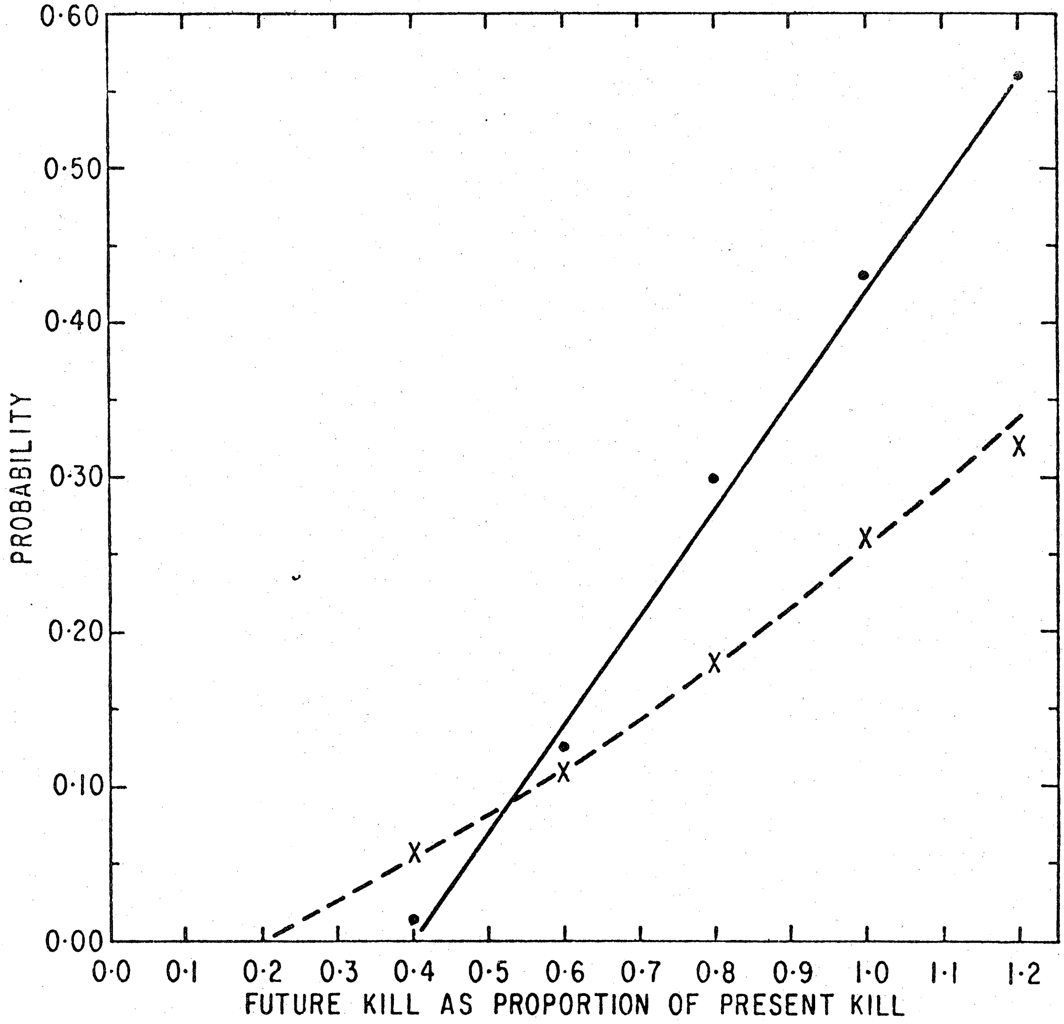

Fig. 7. Probability that 1+ population is less than 1X 10^6 by 1984 (----) and probability that 1+ population in 1984 is less than 1+ population in 1979 (-) as functions of variations in the 1979 quota.

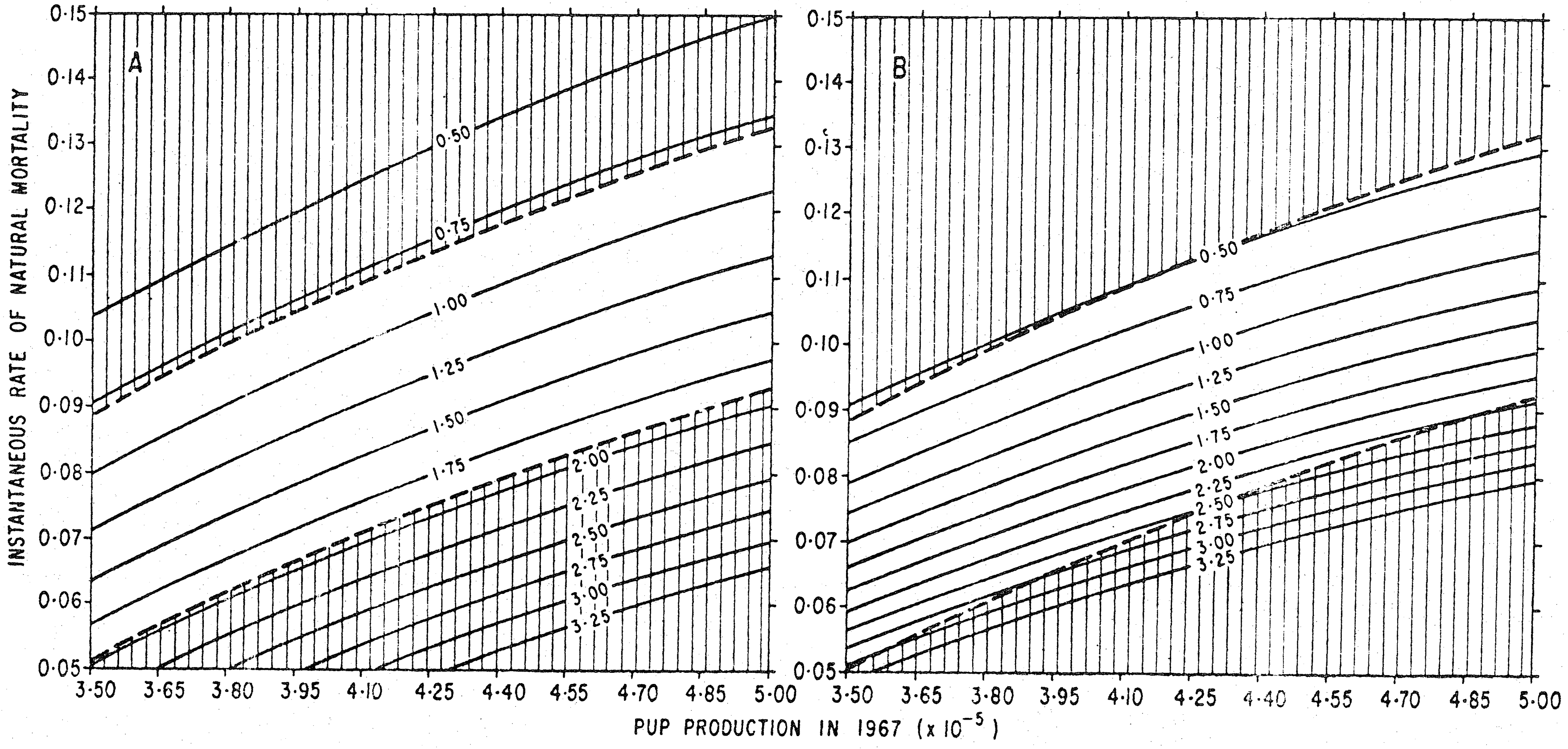

Fig. 8 (a) Population size in 1979 assuming 1st year mortality = 5X adult mortality.

(b) Population size in 1984 assuming 1st year mortality = 5X adult mortality.

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. Testing for bias in the estimation of p for the 1967 and 1968 cohorts.

	1967 Cohort		1968 Cohort	
Year	Age	Number	Number	Age
1970	3	11	25	2
1971	4	15	26	3
1973	6	31	89	5
1974	7	16	70	6
1976	9	8	10	8
1979	12	9	11	11
		90	231	

$G = 10.733$, df = 5, $p < 0.05$

$\hat{p} = 90/321 = 0.2804$

Table 3. Testing for bias in the estimation of p for the 1971 and 1972 cohorts.

	1971 Cohort		1972 Cohort	
Year	Age	Number	Number	Age
1974	3	57	105	2
1976	5	9	15	4
1979	8	15	22	7
		81	132	

$G = 0.386$, $df = 2$, $p < 0.01$

$\hat{p} = 81/213 = 0.3803$

Table 4. 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 5. Testing for heterogeneity across years in the ratio of 1-7 year-olds in 1967 to 8+ in 1967 using moulting patch samples.

	Year							
	1968	1969	1970	1971	1973	1974	1976	Totals
Numbers in age group 1-7 in 1967	77	200	56	67	131	132	44	707
Numbers in age group 8+ in 1967	68	265	49	104	139	132	55	812

$G = 12.41$

$p < 0.05$

Ratio = 1.1485

$1.03865 < p < 1.2709$

Table 6. Test for heterogeneity between years in the age distribution of cohorts aged 1 to 7 in 1967.

	Year						
Year	1968	1969	1970	1971	1973	1974	1976
1968		23.2*	9.6	8.0	9.6	9.9	14.2*
1969			3.6	6.4	21.4*	11.8	2.7
1970				2.0	12.2	5.6	2.2
1971					10.8	7.0	4.4
1973						3.0	9.7
1974							10.1

* G statistic significant at least at the 5% level

Table 7. Age distribution in 1967 based on samples from moulting patch samples in years 1968, 1969, 1970, 1971, 1973, 1976.

Age	% in age group weighted by sample size	% in age group unweighted
1	15.88	16.85
2	16.30	16.20
3	12.71	11.47
4	11.74	11.83
5	14.78	15.27
6	15.19	14.91
7	13.40	13.48