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Estimation of mortality rates and surplus production of Northwest Atlantic harp seals

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INTRODUCTION

Recent analyses of the status of Northwest Atlantic harp seals have provided conflicting estimates of current and historical population levels as well as wide-ranging estimates of mortality rates and sustainable yields. As a result of such differences advice on required conservation measures have ranged from a virtual moratorium on the harp seal hunt (Lett and Lavigne, MS 1975) to a recommended increase in the current kill level (Benjaminsen and Øritsland, MS 1975a). Benjaminsen and Øritsland (MS 1975a) have estimated pup production in 1975 to be in excess of 340,000 with a sustainable yield of 200,000; ultraviolet aerial photography (Lavigne et al., MS 1975), cohort analysis (Lett and Lavigne, MS 1975) and black-and-white photography (Sergeant, MS 1975) all indicate a pup production of about 200,000 animals in 1975. Total (Z) and natural mortality (M) estimates range from Z = 0.26 (Ricker, MS 1975) and M = 0.21 (Lett and Lavigne, MS 1975) to Z = 0.09 and M = 0.08 (Benjaminsen and Øritsland, MS 1975b). Such discrepancies have mainly been due to variability in catch data, errors in age-readings and biases due to changes in recruitment and hunting mortality. Since parameters of mortality and reproductive potential are critical to prognoses of sustainable kill and population change, a reanalysis of most recent data has been carried out and the results are documented below.

1. Calculation of pup production (1954-67) from survival indices

The method used is essentially that described by Sergeant (1971) as modified by Benjaminsen and Øritsland (MS 1975a) and involves relating survival indices of successive year-classes to the number of pups killed of each year-class. In this analysis survival index is defined as,

$$S.I = \frac{\text{Age-group frequency as percent of annual catch}}{\text{Total age-group frequency as percent of total catch}}$$

To avoid smoothing effects due to possible errors in age-reading only age-groups 5 and younger have been considered, and of these, age-group 1 has been excluded because of variability in its contribution to annual kills. Catch-at-age data have been adjusted from Lett and Lavigne (MS 1975) to include total catches (Øritsland and Benjaminsen, MS 1975); these are composite age distributions pooled from a variety of fisheries but are highly comparable to those given for Front samples by Benjaminsen and Øritsland (MS 1975b). Survival indices for age-groups 2-5 for year-classes 1950-71 are shown in Table 1. The mean survival index for each year-class has been computed and related to its pup kill by two-way regression analysis from which a "functional" estimate (Ricker, 1973) of pup production (breeding stock) has been derived (Table 1). The results (Fig 1) indicate that the breeding stock (pup production) peaked at slightly less than 500,000 animals in 1955 and then declined to about 375,000 animals in 1967. Estimates by Benjaminsen and Øritsland (MS 1975b) using Norwegian sampling data from the Front and for a different range of ages (2-10) give essentially the same results in those years for which estimates are available (1962-67). This confirms the comparability of sampling data given in Lett and Lavigne (MS 1975) and that given in Benjaminsen and Øritsland (MS 1975b) and also attests somewhat to the reliability of the regression technique.

Fig 1 also suggests that the level of pup kill has a significant effect on changes in the female breeding stock five years later. The magnitude of this effect has been evaluated by regression analyses of breeding stock change on pup exploitation rate five years earlier (Fig 2). The correlation coefficient ($r = 0.69$) is significant ($P < .05$) which suggests that a substantial proportion of female harp seals whelp at age 5, a conclusion in variance with that of Øritsland (1971) who reported a mean whelping age of 6.5 years for Front females but in agreement with the 5.5 mean whelping age reported by Sergeant (1966, 1971).

2. Calculation of Z and M

Estimates of total mortality (Z) were derived from analyses of catch curves, based on age composition data (both sexes combined) of moulting seals for the years 1968-74 from Benjaminsen and Øritsland (MS 1975b). Age-groups 5-13 only were considered in mortality estimates, since the degree of error in age-readings increases substantially beyond age 13 (Benjaminsen and Øritsland, MS 1975b). Estimates of total mortality (Z_1) (i.e. slopes of regression lines) by this method are summarized in the table below;

Fishery Year	1968	1969	1970	1971	1972	1973	1974	Mean Z
Year-Classes	1955-63	1956-64	1957-65	1958-66	1959-67	1960-68	1961-69	
Z_1	-.100	-.096	-.158	-.038	-.181	-.216	-.147	-.134

The average instantaneous rate of total mortality (Z_1) over the period was 0.134. Table 1 indicates that pup production over the period 1953-69 has been declining and this will have the effect of biasing downwards estimates of mortality from catch curves. To adjust for such biases instantaneous rates of change in recruitment (Ricker, MS 1975) have been calculated for the various year-classes included in the annual catch curves. The basic data are shown in Table 2 and the results are summarized below.

Fishery Year	1968	1969	1970	1971	1972	1973	1974
Year-Classes	1955-63	1956-64	1957-65	1958-66	1959-67	1960-68	1961-69
Inst. Δ Recruitment	-.012	-.048	-.090	-.094	-.095	-.072	-.043
Z_1	-.100	-.096	-.158	-.038	-.181	-.216	-.147
Adjusted Z_1 (= Z_2)	-.112	-.144	-.248	-.132	-.276	-.288	-.190

$\bar{Z}_2 = -.198$

Changes in fishing mortality with time will also produce a bias in mortality estimates from catch curves. One measure of fishing mortality is exploitation rate (μ) which is approximately equal to F at values of $\mu \leq .10$. Estimates of pup production (Table 1) have been converted to total population numbers (age 1 and older) by multiplying by 4 (Sergeant, 1971). Population sizes from 1968-75 have been calculated from interpolation

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assuming a linear decline in pup production from 377,000 in 1967 to 255,000 in 1975. Exploitation rates have then been calculated as the ratio of catch of 1+ seals to population size. Assuming that the distribution of fishing mortality amongst the ages (1+) has remained the same throughout the period under consideration hunting mortalities (i.e. μ) have been accumulated for each year-class from age-group 1 to the year prior to which mortality estimates from catch curves were calculated. The accumulated values were then divided by the number of years involved to produce an estimate of mean fishing mortality exerted on each year-class prior to the year of catch curve analyses. If fishing mortality has remained constant the slope of the regression of average fishing mortality against age for a particular fishery year should be zero. The basic data are given in Tables 3-4 and the results of regression analyses are presented below.

Fishery Year	1968	1969	1970	1971	1972	1973	1974
Z_2	-.112	-.144	-.248	-.132	-.276	-.288	-.190
Instant. Δ in F	.012	.021	.019	.020	.032	.042	.055
Adjusted Z_2 (=Z_3)	-.100	-.123	-.229	-.112	-.244	-.246	-.135

$\bar{Z}_3 = -.170$

Since 1967, when adult females were protected in the whelping patches, selective hunting has produced an adult kill which comprised mainly males. The above value of $\bar{Z}_3$ therefore represents mainly the mortality characteristics of adult males. The proportion of adult males (age-group 5 and older) as indicated by Norwegian samples of moulting patches (Benjaminsen and Øritsland, MS 1975)shows a general increase from 1969 to 1974, males on the average constituting 82% of the total adult kill. The total mortality calculated above for combined sexes may therefore be considered to be weighted .82 Z_M + .18 Z_F. Landsmen and small vessel kills of adults tend to be less discriminating and a value of 60% males is perhaps reasonable for this component of the hunt. The mean adult kill during the period 1968-74 was 19,000 animals (Benjaminsen and Lett, MS 1975) of which 5000 (Anon., 1975; Kapel,MS 1975) were taken by landsmen and the remainder (14,000) by large vessels. Application of the above sex ratios to the numbers of adults killed by the two components suggests that over the period 1968-74 males have comprised 76% (14,500 animals) of the adult kill.

From the data given in Table 3 the average population size of adult (5+) females during the period 1968-74 is calculated as 310,000 animals. Because of heavier hunting adult males were somewhat less abundant than females and an average level of 230,000 animals has been assumed. Thus an average kill of 14,500 males and 4500 females produced instantaneous hunting mortalities of .063 and .015 for males and females respectively. The combined hunting mortality during the period was therefore (.063) (.82) + (.015) (.18) = .055. Subtracting this from $\bar{Z}_3$ above gives an instantaneous natural mortality rate of 0.115 for both sexes combined. If one assumes that natural mortality is the same for both sexes this implies a value of Z = .181 for males and Z = .130 for females during the period 1968-74.

3. Mortality rate of immatures

Mortality rates of immature (0-4 years) seals can be obtained if estimates of the number of residual pups (i.e. those surviving the pup kill) surviving to age-group 5 were available. Such estimates have been computed by cohort analysis for year-classes 1960-64 using adjusted catch-at-age data (Benjaminsen and Lett, MS 1976) and M = .115. To reduce biases due to errors in age reading and terminal hunting mortality, the population size of each year-class at age-group 5 has been back-calculated from three starting age-groups (9, 10 and 11). The mean value of these estimates has then been compared with the number of residual pups from estimates of pup production by Sergeant's method given in Table 1.

The results (Table 5) indicate a mean instantaneous total mortality level of 0.157 per year for immature seals from age-group 0 to age-group 5 for these year-classes. Hunting mortalities during the 1960's as determined from cohort analysis averaged about .050. Considering the sensitivity of cohort analysis to starting values of F (particularly low values) one can conclude that the natural mortality rate of bedlamer seals is not significantly different from that of the adults.

4. Mortality rate during 1954-66

The average exploitation rate during the period 1954-66 was .047 (Table 3) or an instantaneous rate of .048. Total mortality (Z) (assuming

M = .115) was therefore .163. Application of this mortality rate to pup survivors (Table 1) in 1954-59 will provide estimates of breeding stock size (i.e. pup production) from 1960 onwards (assuming a mean whelping age of 5 years) which can be compared with estimates of breeding stock size from regression analyses. The degree of comparability of the two estimates will provide a test of the reliability of the mortality rates computed above. The results are presented below.

Female breeding stock	1960	1961	1962	1963	1964	1965	1966	1967
Estimated by regression	439	379	416	412	379	384	376	377
Estimated using Z = .163	422	407	371	379	389	373	376	373

Estimates of breeding stock size by both methods are very similar and, in view of the assumptions of constant mortality, 1:1 sex ratios of the adult kill and an age 5 whelp provides supporting evidence for the natural and total mortality rates computed above. However, if the mean whelping age were 5.5 years as suggested by Sergeant (1966) then a $Z < 0.15$ would also provide good agreement in the above simulation.

5. <u>Projection of pup production 1967-75</u>

The total mortality rate of adult females computed above for the period 1968-74 ($Z = 0.13$) has been used to project the adult female population to 1976 from a level of 377,000 animals in 1967 (Table 1) for whelping ages 5 and 6. The natural mortality of juveniles (immatures) is assumed to be the same as for adults (M = 0.115) and to this has been added the average instantaneous exploitation rate (Table 3) for those years in which each year-class was considered immature, e.g. the 1962 year-class was subjected to exploitation rates of .049 as age 1 in 1963, .050 as age 2 in 1964, .035 as age 3 in 1965 and .050 as age 4 in 1966 ($\bar{\mu} = .046$ for a Z in the immature years of .115 + .046 = .161) before entering the whelping population at age 5 in 1967. The results are shown in Fig 3. They suggest that under the assumptions made, pup production in 1976 was of the order of 295,000-310,000 depending on the average whelping age being 5 or 6. The actual level of breeding stock in 1976 may be somewhat higher than derived above depending on whether or not the actual whelping age is less than 5 years.

6. Estimates of stock size and pup production from cohort analysis

Estimates of harp seal pup production and population size by age have been derived from cohort analysis (VPA) for the period 1952-74 using revised catch-at-age data (Benjaminsen and Lett, MS 1976) and natural mortality (M)equal to 0.115. Starting values of fishing mortality (F) in 1974 (.033) were derived from Table 3 and stock sizes were projected to 1975 and 1976 from catch-at-age data for 1974 and 1975. Because of the sensitivity of population estimates in recent years (1971 onwards) to starting values of F, pup production from 1972 onward has been estimated from survival indices assuming a whelping age of 5 years (see Fig 3). The results are given in Table 6 and Fig 4. They suggest that the harp seal population (1+) in the Northwest Atlantic has declined from about 2.3 million seals in the early 1950's to about 1.0 million in the early 1970's but has been increasing since the introduction of quotas in 1972 and is now estimated to be in excess of 1.1 million animals. Estimates of pup production by cohort analysis agree remarkably well with estimates from survival indices (SI) and confirm the validity of the natural mortality rate used (M = 0.115).

7. Density-dependent changes in whelping age

Sergeant (1966) has previously reported a reduction in mean whelping age of harp seals from 6.5 years in the early 1950's to 5.2 years (weighted mean) in the early 1960's. This decline occurred during a period of heavy exploitation which, according to Sergeant (1966) elicited a density-dependent response from the seal population. The age-specific population estimates of harp seals from cohort analysis given in Table 6 are conducive to estimates of mean whelping age providing data are available on sex ratios. According to Allen(1975) adult kills prior to 1967 comprised 60% males and 40% females. Protection of whelping patches in 1965 resulted in a reduced exploitation rate on adult females leading to adult kills comprised of 75% males and 25% females (see earlier calculations). Rough calculations from ratios of annual mortalities of adult males and females based on the above kill sex ratios suggest an adult harp seal population comprised of 53% females prior to 1967 and 58% females thereafter. Application of these sex ratios to the age-specific population structure given in Table 6 along with a 90% reproductive success rate (Sergeant 1966) permits calculation of the mean whelping age concomitant with the estimated pup production for each year. Estimates of mean whelping age obtained in this manner have been plotted against population size (1+) (5 year running average before 1960 and 4 year running average after 1960 with a 1 year lag for the year of parturition) for the period 1952-71 in Fig 5. The results indicate a substantial non-linear decrease in whelping age as the population declined from high levels in the early 1950's and provide good agreement with empirical data provided by Sergeant (1966). Recent data based on Front sampling in 1976 (Sergeant, MS 1976) suggest a mean whelping age of 4.7 years. This is in excellent agreement with the estimate obtained from the regression line in Fig 5.

8. Surplus production (sustainable yield) of pups

If R denotes the ratio of adult female recruits to pup survivors (i.e. for a whelping age of 5 years, $R = e^{-5Z/2}$) and A denotes annual adult mortality the surplus production (sustainable yield) of pups may be defined as:

$$S.P. = \frac{R-A}{R}$$

Surplus production of pups under various combinations of whelping ages and mortalities are illustrated below.

Whelping age (yrs)	R: Pup kill only (A)	R: Universal kill (B)	Surplus Prod. (sust. yield) (A)	Surplus Prod. (sust. yield) (B)
4	.316	.297	65%	59%
5	.281	.261	61%	53%
6	.251	.229	57%	47%
8	.199	.177	46%	31%
10	.158	.136	32%	10%
12	.126	.105	14%	-
14	.100	.081	-	-
Ann. Mortality	10.9%	12.2%		

Since whelping age of harp seals is a function of population size the above table suggests that changes in maturation rate profoundly affect the rate of surplus production and hence effective regulation of population size. The table also indicates that in the absence of density-dependent changes in natural mortality the harp seal population of the Northwest Atlantic has a whelping age of 13 years at maximum equilibrium (i.e. virgin) population size.

9. Pup production and reproductive stock

The attrition in the harp seal population from the early 1950's to the early 1970's undoubtedly affected pup production, the magnitude of the change however being ameliorated somewhat by density-dependent changes in maturation rate. Since significant numbers of harp seals may whelp at age 4 (Chapsky, 1963; Sergeant, MS 1976), animals age 4 and older may be considered as the potential reproductive stock. Thus a plot of pup production per unit reproductive stock versus reproductive stock (4+) should provide an estimate of the change in reproductive rate since the early 1950's. The results are shown in Fig 6 (upper plot). They suggest that a significant increase in reproductive rate of harp seals has occurred in response to declining population levels, implying a non-linear stock-recruit relationship. This relationship is shown in the lower half of Fig 6 along with data points obtained from Table 6. The stock-recruit curve is of the Beverton-Holt type and indicates a maximum equilibrium pup production of 600,000 animals occurring at a population size (4+) of 3 million animals (approximately 4.0-4.5 million seals age one and older) which is an estimate of the aboriginal population level of Northwest Atlantic harp seals. Actual pup production in individual years may have been greater than or less than 600,000 animals in the aboriginal state depending upon the efficacy of the response lag of reproductive rate to population change.

10. Maximum sustainable yield of Northwest Atlantic harp seals

The above information describes the Northwest Atlantic harp seal population as having a natural mortality rate (M) of 0.115 and a maximum equilibrium reproductive stock of 3.0 million seals (4+) producing 600,000 pups at a mean whelping age of 13 years. Such information combined with the stock-recruit model (Fig 6) and the density-dependent whelping model (Fig 5) (extrapolated to 13 years at 4.0 million seals) allows calculation of maximum sustainable yields as generated by the average hunting mortality exerted on 1+ seals since quotas were introduced in 1972 (F = .028, Table 3). The results (Fig 6, lower half) indicate an MSY of 270,000 animals (approximately

80% pups) from a pup production of 470,000 animals and a potential reproductive stock of 1.3 million animals. Similar estimates based on a pup kill only suggest an MSY of 290,000 animals which is well within the MSY range of 250,000-320,000 pups computed by Allen (1975). With reference to Table 6 the above calculations suggest that the harp seal population was at the MSY level during the mid-1950's. From 1950 to 1972 when quotas were imposed the harp seal population decreased from 2.3 million animals (1+) to 1.0 million animals, i.e. approximately 60,000 animals (1.3/22) in excess of equilibrium yield. The average kill over this period was 305,000 seals indicating a sustainable yield of 245,000 seals. Since the harp seal population was close to MSY population size in the early 1950's, 245,000 is an estimate of MSY under kill conditions as they existed during the 1950's and 1960's (pup kill 73% of total kill; mean hunting mortality $\approx$ .05).

11. Estimates of pup production in 1976

Estimates of pup production by Sergeant's method (Table 1) extrapolated from 1967 to 1976 (see Fig 3) range from 295,000 animals assuming a mean whelping age of 6 years to 310,000 animals assuming a whelping age of 5 years. The stock-recruit model (Fig 6) based on a 1976 reproductive stock (4+) of 685,000 animals (Table 6) suggests a 1976 pup production of 339,000. A mean whelping age of 4.7 years derived from 1976 sampling data provided by Sergeant (MS 1976) implies (from Table 6) a pup production of 338,000 animals in 1976. Since both modelling results and empirical data suggest that whelping age in 1976 is 5 years or less the most reasonable range of pup production in 1976 is 310,000-340,000 animals.

12. Prognosis of population change under varying kill rates

The 1976 population age structure given in Table 6 has been used as a basis for projections of population change under various kill rates. The 1976 kill (170,000) as well as future kills are assumed to comprise 80% pups (mean representation since 1972); pup production from 1977 onwards has been calculated from the stock-recruit model (Fig 6) under assumptions of polygamous males and continued protection of whelping females. The results (Fig 7) indicate that kills of 150,000 and 200,000 animals can be sustained and will allow the harp seal population to increase to MSY population size albeit very slowly in the latter case. The model also suggests that the sustained yield at present population levels is 215,000 animals. It should be noted that increased protection of adult females will not only increase sustained yields but will also accelerate achievement of MSY population levels. It should also be noted that stochastic variability will diminish the predictive success of the above deterministic model with time and therefore periodic evaluations of population trends are desirable if management objectives are to be achieved.

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Table 1. Survival indices (ages 2-5) and estimated pup production of harp seals for median years 1954-67. Bracketed estimates are those derived from Benjaminsen and Øritsland (MS 1975b).

Year-Class	S.I. at age 2	3	4	5	Mean S.I. (X)	Pup Catch (Y)	Year-Classes	Median Year Pup Production $R_{y.x}$	$R_{x.y}$	G. Mean Pup Production		Correlation Coeff. (r)
1950	.42	.77	.92	1.36	.87	226						
1951	.95	.37	.86	.79	.74	302						
1952	1.34	1.78	.95	.62	1.17	198						
1953	1.44	.96	1.05	1.20	1.16	198						
1954	.94	.79	1.41	1.02	1.04	185	1950-58	412	495	452		0.82
1955	.60	.83	.77	.79	.75	260	1951-59	425	514	468		0.84
1956	.34	.85	.93	.66	.70	347	1952-60	407	504	453		0.82
1957	.80	2.45	1.88	1.28	1.60	172	1953-61	404	502	450		0.83
1958	1.51	1.26	1.34	.83	1.24	149	1954-62	394	498	443		0.80
1959	1.04	.95	.86	1.28	1.03	243	1955-63	393	459	425		0.85
1960	1.98	1.01	1.19	1.61	1.47	164	1956-64	405	476	439		0.86
1961	1.08	1.25	1.49	1.16	1.25	175	1957-65	344	417	379		0.80
1962	.75	.86	1.00	1.05	.92	211	1958-66	380	455	416	(424)	0.83
1963	.42	.80	.54	.63	.60	286	1959-67	380	447	412	(390)	0.83
1964	1.25	.45	.71	1.04	.86	271	1960-68	357	403	379	(350)	0.86
1965	.84	.92	.97	1.05	.92	187	1961-69	356	415	384	(368)	0.83
1966	.82	.86	.87	1.07	.91	255	1962-70	341	413	376	(360)	0.77
1967	.55	.78	.99	.88	.80	280	1963-71	342	416	377	(359)	0.78
1968	1.26	1.29	2.07	2.00	1.66	160					(353)	
1969	1.04	.68	1.05	.91	.92	237						
1970	.69	.99	.59	.98	.81	220						
1971	1.26	.73	.80	( )	.93	213						

Table 2. Basic data used in calculation of instantaneous rate of change in recruitment. The 1968-69 estimates of pup production are from Working Paper 75/XI/3.

Year	Pup Production	Pup Kill	Pup Survivors	Log_e Pup Survivors
1954	452	185	267	5.59
1955	468	260	208	5.34
1956	453	347	106	4.66
1957	450	172	278	5.63
1958	443	149	294	5.68
1959	425	243	182	5.20
1960	439	164	275	5.62
1961	379	175	204	5.32
1962	416	211	205	5.32
1963	412	286	126	4.84
1964	379	271	108	4.68
1965	384	187	197	5.28
1966	376	255	121	4.80
1967	377	280	97	4.57
1968	353	160	193	5.26
1969	362	237	125	4.83

Table 3. Calculation of exploitation rates of 1+ harp seals 1954-74. Bracketed figures are derived from interpolation.

Year	Pup production	Total population (1+)	Total kill (1+)	Exploitation rate (μ)
1954	452	2260	98.8	.044
1955	468	2295	88.8	.039
1956	453	2180	53.5	.025
1957	450	2125	86.5	.041
1958	443	2060	165.1	.080
1959	425	1930	85.7	.044
1960	439	1970	129.1	.066
1961	379	1670	25.0	.015
1962	416	1800	117.0	.065
1963	412	1755	85.4	.049
1964	379	1585	79.8	.050
1965	384	1585	56.1	.035
1966	376	1525	75.6	.050
1967	377	1506	58.7	.039
1968	(360)	1440	39.7	.028
1969	(345)	1380	58.7	.043
1970	(330)	1320	43.2	.033
1971	(315)	1260	23.2	.018
1972	(300)	1200	15.8	.013
1973	(285)	1140	29.6	.026
1974	(270)	1080	36.0	.033
1975	(255)	1020	36.4	.036

Table 4. Basic data used in calculation of instantaneous rate of change in fishing mortality rate with age.

Age (i)	Mean historical exploitation rate ($\bar{\mu} = \sum_{t=1}^{i} \mu / i-1$)							
	1967	1968	1969	1970	1971	1972	1973	1974
5	.046	.043	.039	.040	.036	.031	.027	.022
6	.050	.045	.041	.039	.039	.032	.027	.027
7	.049	.048	.042	.041	.038	.035	.029	.027
8	.047	.043	.045	.042	.040	.035	.032	.029
9	.047	.046	.041	.045	.041	.037	.032	.031
10	.050	.046	.044	.042	.044	.037	.034	.032
11	.050	.049	.044	.044	.041	.040	.034	.033
12	.047	.049	.047	.044	.043	.038	.038	.034
13	.047	.047	.047	.047	.043	.041	.036	.037

Table 5. Calculation of instantaneous mortality rate (Z) of immature harp seals (0-5 years). N_5 is the mean population size at age 5 of each year-class as computed by cohort analysis from terminal ages 9, 10 and 11 (M = 0.115).

Year-class	Mean Pop. Size at Age 5 (N_5)	Number of Pup Survivors (N_0)	$\ln N_0/N_5$ (Z)	Z per year
1960	100	275	1.01	.202
1961	96	204	.754	.151
1962	92	205	.801	.160
1963	67	126	.632	.126
1964	64	108	.523	.105
Average			.784	.157

Table 6. Estimates of harp seal population size by age from cohort analysis for the period 1952-76 (M = .115)

	Population Size ('000) at age											
Year	0	1	2	3	4	5	6	7	8	9	10+	No. 1+
1952	555	259	287	247	206	133	201	113	139	91	650	2326
1953	526	318	227	245	213	178	112	167	92	116	610	2278
1954	475	292	264	196	213	186	154	97	147	80	649	2246
1955	520	257	227	222	171	184	163	134	83	128	590	2159
1956	601	229	211	193	192	148	158	140	115	70	613	2069
1957	450	225	195	183	169	169	129	138	122	100	585	2015
1958	455	247	184	166	159	148	145	110	118	105	577	1959
1959	520	267	211	158	133	120	115	115	88	96	543	1846
1960	435	249	219	173	135	118	103	97	92	74	494	1754
1961	424	241	186	178	145	111	99	86	82	78	475	1681
1962	400	222	208	164	156	126	98	87	75	72	482	1691
1963	416	168	172	153	137	130	106	85	75	64	472	1561
1964	423	116	143	145	129	117	112	90	71	63	437	1423
1965	360	136	101	123	123	108	99	93	76	60	400	1319
1966	399	152	114	87	105	104	89	82	80	66	393	1272
1967	381	128	124	92	73	89	87	74	68	68	383	1186
1968	390	91	104	106	80	63	76	73	61	57	374	1085
1969	380	242	75	88	92	70	54	66	63	52	365	1167
1970	334	128	196	64	76	79	59	46	56	53	350	1107
1971	325	101	107	168	55	65	68	51	40	49	341	1044
1972	(334)	100	83	93	147	48	57	60	45	35	329	988
1973	(317)	192	88	73	81	130	41	50	53	39	316	1064
1974	(333)	180	165	76	63	70	112	35	43	46	299	1081
1975	(325)	192	152	141	66	55	61	97	30	37	291	1122
1976	(310)	165	163	131	123	57	48	53	85	26	294	1145

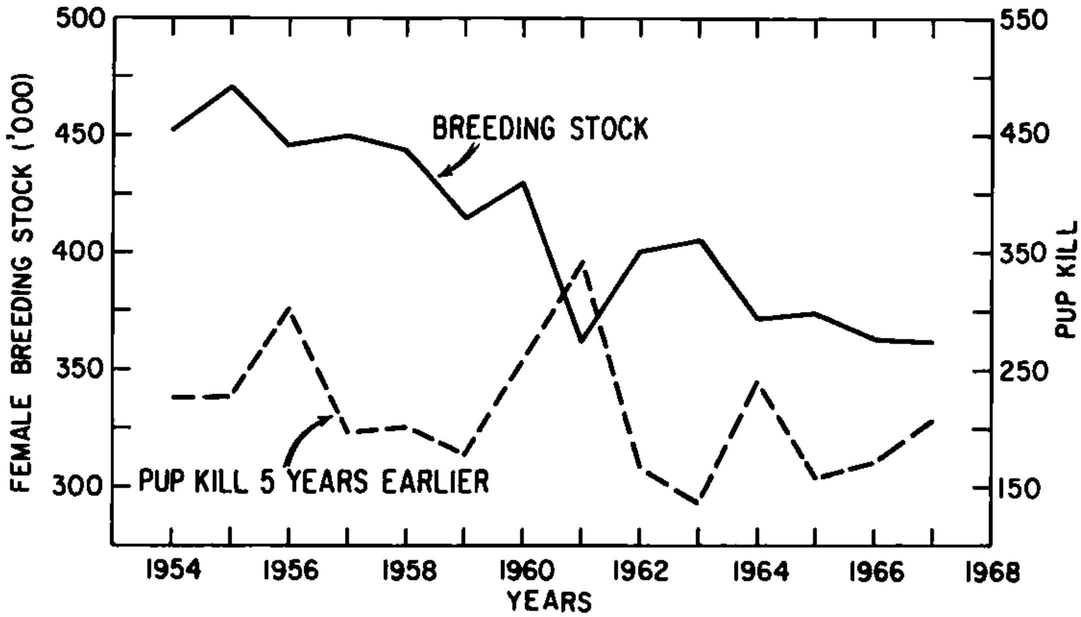

Fig. 1. Regression estimates of female breeding stock size 1954-67 and pup kill with a 5-year lag.

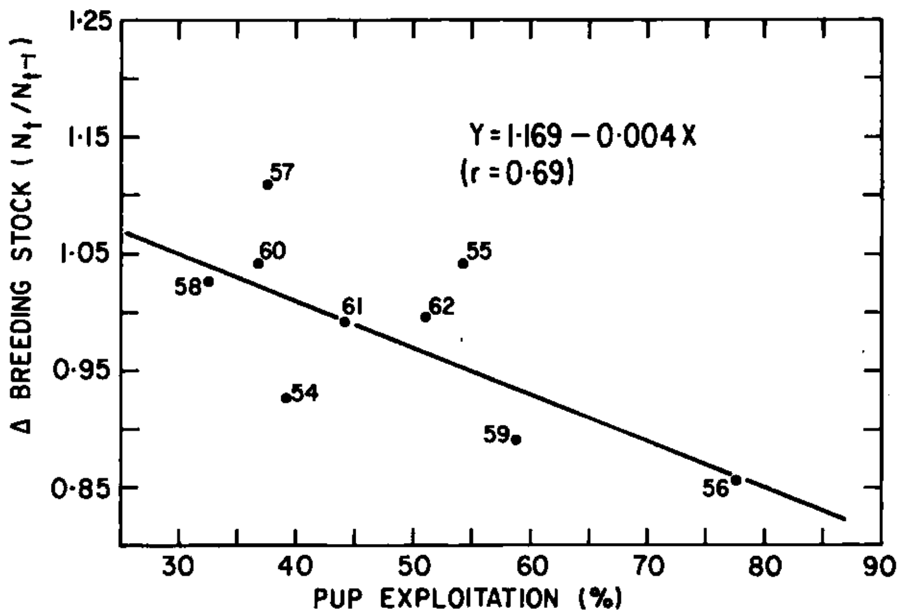

Fig. 2. Relationship between change in female breeding stock and pup exploitation rate 5 years earlier.

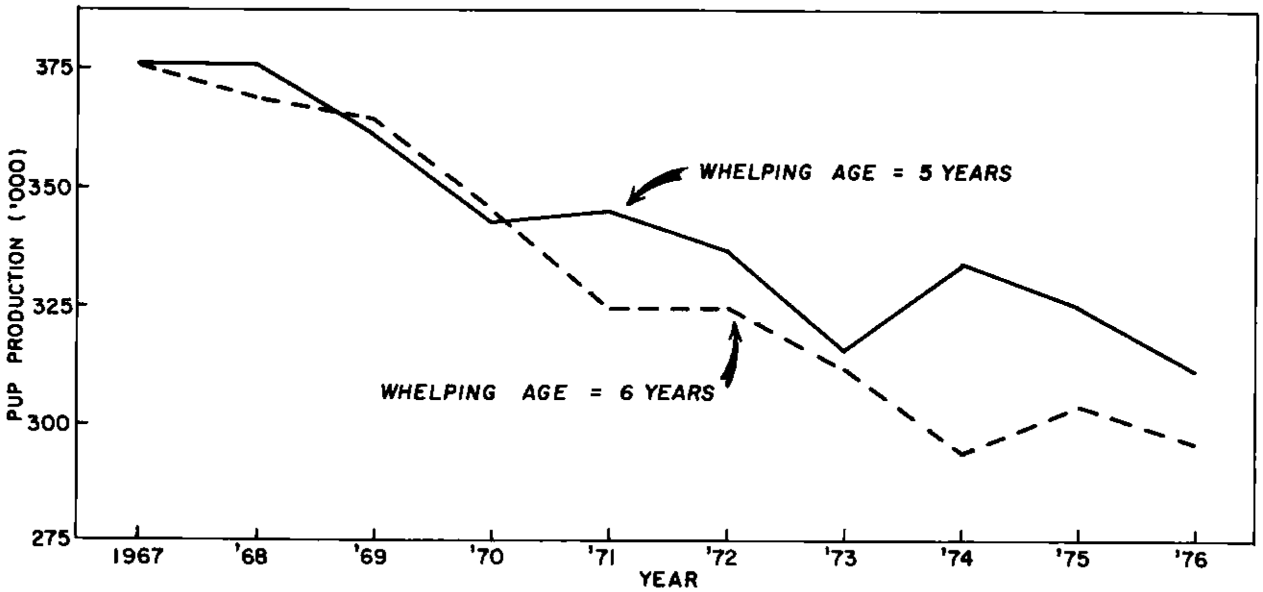

Fig. 3. Projections of pup production 1967-76 according to assumptions of mean whelping age of 5 years and 6 years.

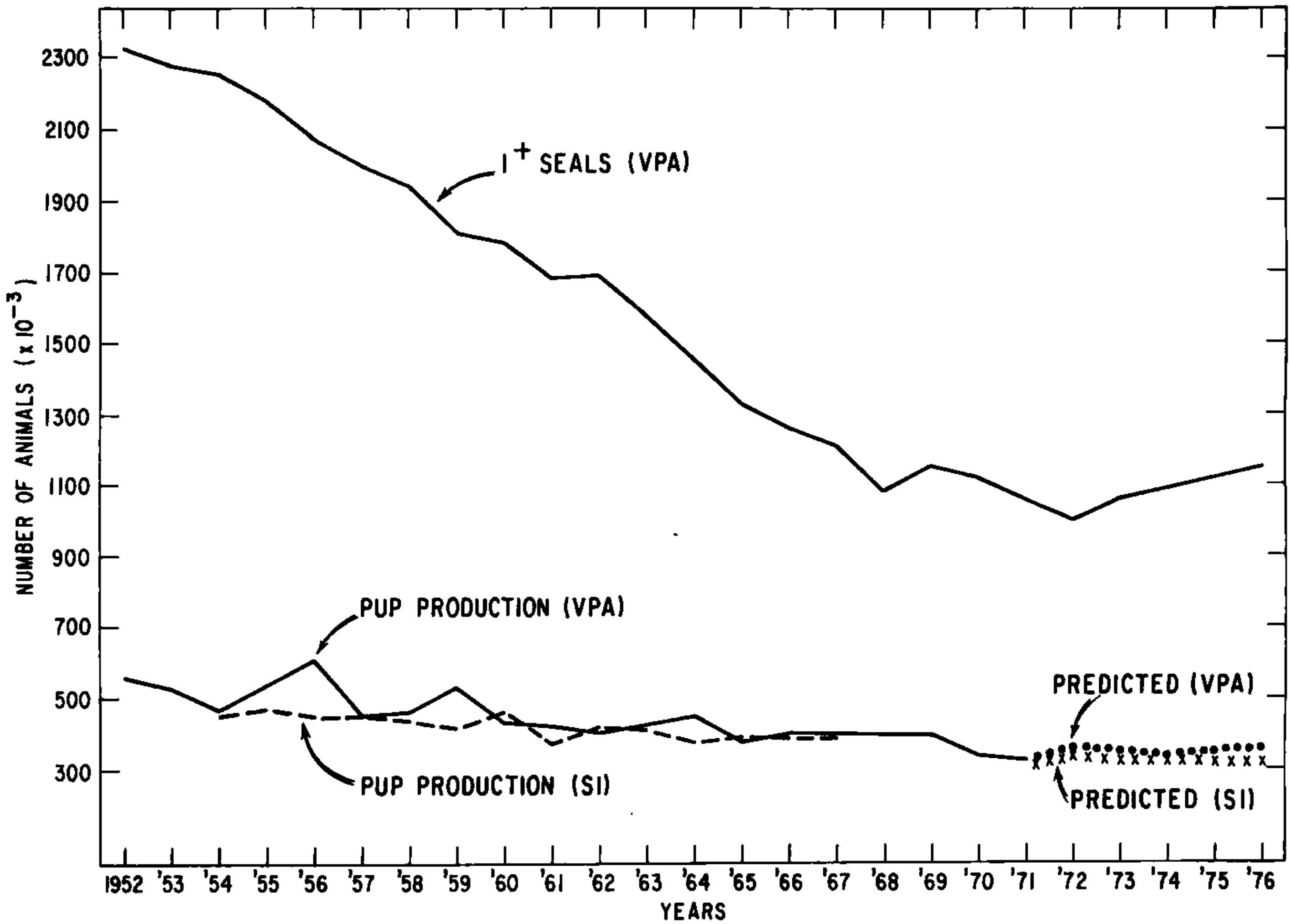

Fig. 4. Estimates of harp seal population size (1+) and pup production from cohort analysis (VPA) 1952-76 with comparison of pup production estimates from Survival Indices (SI) 1954-67.

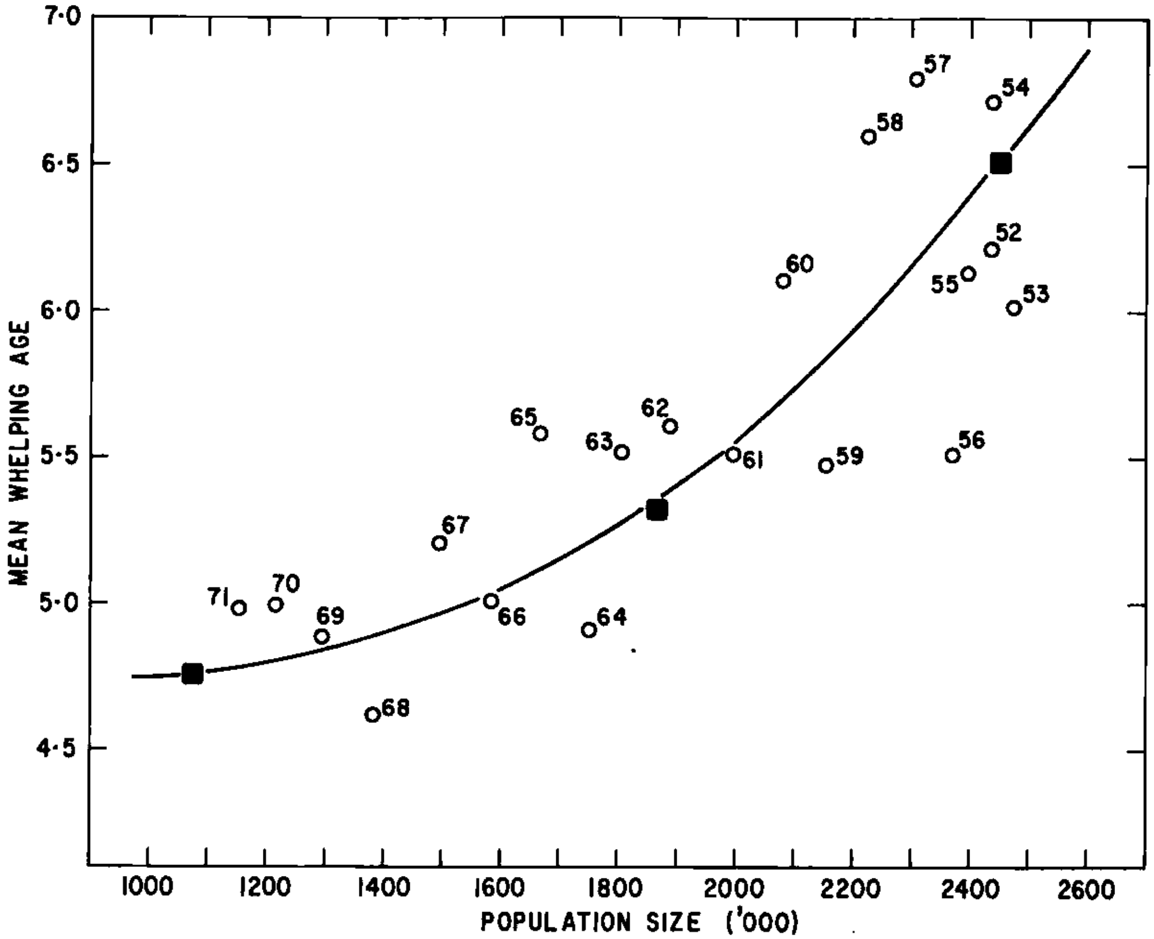

Fig. 5. Relationship between mean whelping age (WA) and the potential reproductive stock size (S) for the period 1951-70. Shaded blocks represent empirical estimates from sampling data (Sergeant, 1966, MS 1976).

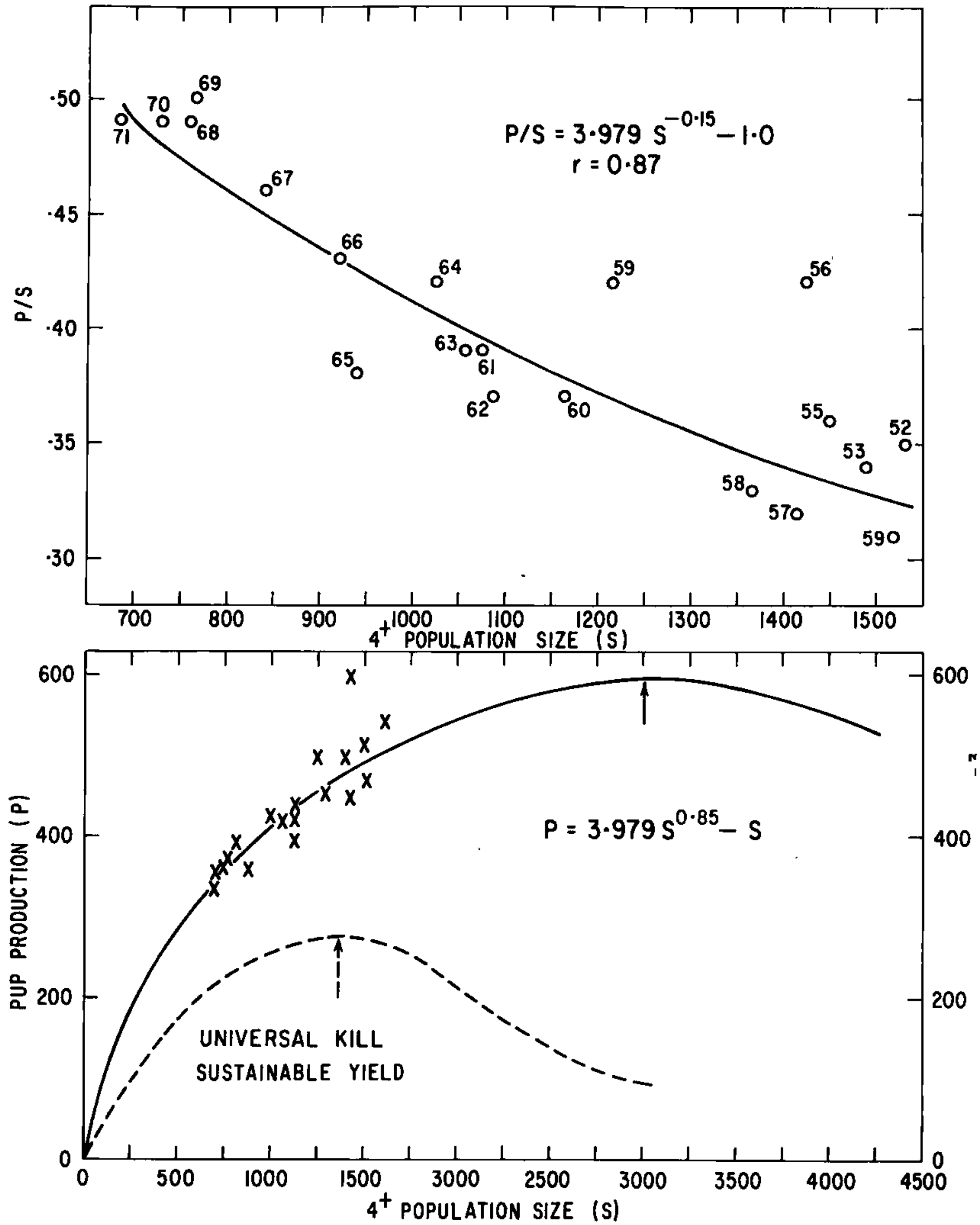

Fig. 6. (Upper). Relationship between reproductive rate (pup production per unit reproductive stock) and the potential reproductive stock (4+). (Lower). Stock-recruit curve and sustainable yields of Northwest Atlantic harp seals as determined from upper graph.

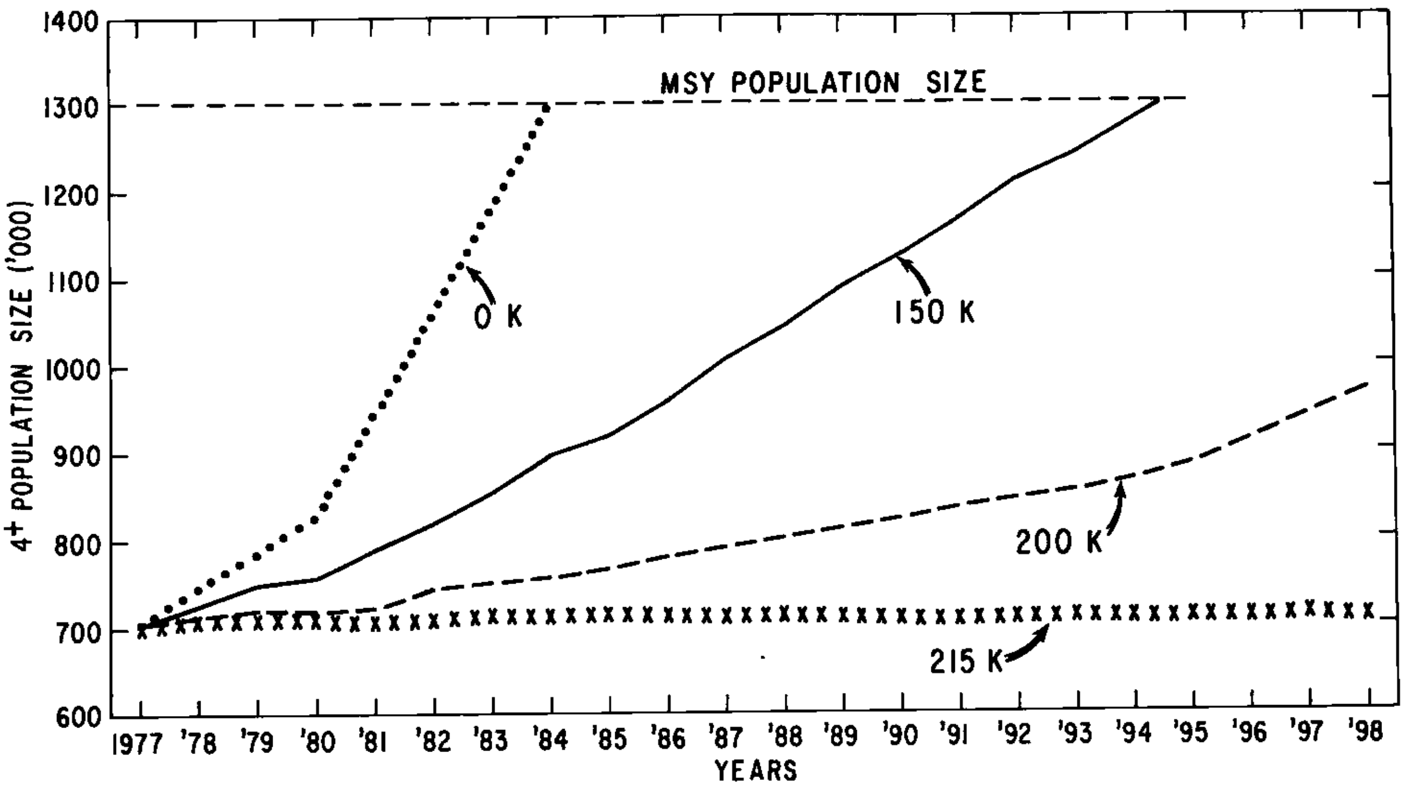

Fig. 7. Prognoses of changes in potential reproductive stock size under various strategies of kill. Pup production is estimated from stock-recruit model and kills are distributed 80% pups, 20% bedlamers and adults. (Kills include aboriginal + Greenland).