RESTRICTED

International Commission for the Northwest Atlantic Fisheries

Serial No. 3718
(D.c.11)

ICNAF Res.Doc. 75/XII/145
(Revised)

SPECIAL MEETING OF PANEL A (SEALS) - DECEMBER 1975

The impact of current management policies on stocks of western Atlantic harp seals, *Pagophilus groenlandicus*

by

P.F. Lett
Department of the Environment
Fisheries and Marine Service
Biological Station, St. Andrews, N.B., Canada

and

D.M. Lavigne
Department of Zoology
University of Guelph
Guelph, Ont., Canada

INTRODUCTION

The harp seal, *Pagophilus groenlandicus*, has formed the basis of an historical sealing industry in the northwest Atlantic for over 200 years (Fisher 1955). From the earliest times, and up to the end of World War II, there were apparently no constraints on the manner in which this hunt was carried out, or on the number of seals taken annually. Regulations controlling aspects of the hunt evolved slowly since that time and, in 1966, a quota system was introduced through the auspices of the International Commission for the Northwest Atlantic Fisheries (ICNAF) (Anon. 1972a).

Recently, conflicting views were expressed on the present status of western Atlantic harp seals. Some suggested that the declining trend in the harp seal population will reach a minimum level around 1976-1977, and subsequently begin to increase in numbers in response to the present quota system of management (Sergeant 1975a, 1975b; Benjaminsen and Øritsland 1975). Others believe that the harp seal has been overexploited for many years (Pimlott 1966; Lust 1967; Davies 1970; Anon. 1972b), and at the present time is a severely threatened and endangered species (Regenstein 1975). New evidence indicates that the population has continued to decline in recent years to a present level of perhaps less than one million animals (Lavigne et al. 1975).

In view of these conflicting viewpoints, it seemed appropriate to utilize modern fisheries assessment techniques (Pope 1972; Doubleday 1975; Lett et al. 1975) to re-analyse the available data. The effects of management strategies, past, present, and future, on the population dynamics of this species were considered.

AMALGAMATION OF DATA

The possibility of obtaining a completely representative age frequency sample from a mammalian population is small indeed (Caughley 1966), and the harp seal is no exception (Sergeant 1959, 1971). Samples of harp seals taken during the southward migration contain few immature animals, while the opposite bias tends to occur in samples of moulting seals collected after the breeding season (Sergeant 1971). However, since there was little justification for subjectively choosing only some of the available data in any given year, all annual age frequency samples collected between 1952 and 1975 were compiled from a number of sources (Sergeant 1959, 1971, 1972, personal communication; Sergeant and Fisher 1960; Øritsland 1971a; Benjaminsen and Øritsland 1975). In total, some 30,057 seals, aged from the annuli of tooth sections (Fisher and MacKenzie 1954), were considered in the present analysis.

Historical records of harp seal catch and effort statistics for the Canadian sealing industry were obtained for the period 1946-1974 (Department of Fisheries of Canada 1968; Department of the Environment 1975). Norwegian sealing efforts and catches in the western Atlantic between 1938 and 1975 were also available (Øritsland 1967, 1969, 1970, 1971b, 1972, 1973; Sergeant, personal communication). These were combined to give total catch and effort for western Atlantic harp seals in recent years.

PRELIMINARY CALCULATIONS

A variety of techniques were, and still are used to hunt harp seals in the western Atlantic. These include the large commercial vessels from Canada and Norway which take the largest proportion of the catch, the small vessel hunt operating along the east coast of Canada, and Canadian landsmen, opportunistic hunters operating from shore when weather permits and ice conditions bring the seals sufficiently close to land. The effort involved is very different for each technique, and there is no common factor to which all effort can be reduced to calculate total effort in a standardized value for each year.

A man-day, selected as the unit of effort, was thus applied only to the large Norwegian and Newfoundland vessels operating in the western Atlantic. Since these vessels took a large proportion of the total catch of seals during the period under consideration, the attendant errors are not considered serious. The amount of effort expended hunting seals aged one and older (1+), was calculated by multiplying the effort by the ratio of the catch of seals aged one and older to the catch resulting from the large vessel hunt.

The annual mean instantaneous total mortality rate (Z) of seals was calculated between years (i, i+1) using the equation:

$$(1) \quad (i,\ i+1)^{Z}(t,\ t+1) = \frac{\sum_{t=3}^{t=17} \mathrm{LOG}_e \left[{}^{i}N_t \Big/ \sum N_i \ \Big/ \ {}^{i+1}N_{t+1} \Big/ \sum N_{i+1} \right]}{n}$$

for cohorts (N) of ages (t) from 3 to 17, where n is equal to 25. In some years, negative mortalities were present for some cohorts, probably the result of sampling and aging problems (Gulland 1969). These values were included in the calculations of the mean total instantaneous mortality, thereby preventing biases resulting from subjectivity. Paloheimo's (1961) linear formula would perhaps

have been the best way to calculate mortality; however, the density of seals does not change as the population contracts. Thus, a unit of effort does not result in the same fraction of the population being exploited.

This change in the catchability, q, (Ricker 1975a) of seals is a problem of considerable importance when trying to derive the relationship between total mortality and hunting effort. Fortunately, independent estimates of harp seal production are available (Fig. 8). The continual decline in population size allows for the regression of time (1950 equals year one) on pup production. By making the assumption that pup production is broadly related to population size, a correction can be made for changes in the catchability by dividing effort by the population index since $q \propto \frac{1}{N}$, producing an estimate of effective effort (E/N). The regression provides estimates of pup production in years when no aerial sensing was carried out.

There are further difficulties in interpreting the relationship between effective effort and total mortality. Hunting pressure was directed off adults in 1966 with the introduction of the quota system (Anon. 1972a) and onto the more valuable pups and beaters. However, with the closure of the Gulf of St. Lawrence fishery in 1972, the quota could no longer be reached by taking only a small proportion of adults. Thus, the hunt was again directed onto adults. Between 1966 and 1972 there was a substantial decrease in the response of total mortality to effective effort, although no significant difference in $\frac{dZ}{d(E/N)}$ could be noted. One possible explanation for this shift is that a directed adult fishery engenders a higher mortality due to losses from wounding and unaccounted death. This effect becomes confounded with the natural mortality rate, biasing it upwards. To alleviate this problem a "dummy" independent variable (Draper and Smith 1966) was added in the regression analysis to account for the directed fishery effect. The following table illustrates the effect of adding the dummy variable:

Year	Total mortality (Z')	Corrected total mortality (Z)	Number aged	Effort man days (E)	Effective effort (E/N)
1952-1953	0.831	0.831	968	232.2	41.46
1953-1954	0.260	0.260	1198	119.8	22.19
1954-1955	0.481	0.481	615	103.8	19.58
1955-1956	0.286	0.286	507	58.2	11.45
1956-1957	0.101	0.101	673	19.0	3.88
1959-1960[a]	0.556	0.556	265	88.6	20.14
1960-1961	0.308	0.308	521	41.0	9.76
1961-1962	0.316	0.316	947	34.8	8.70
1962-1963	0.630	0.630	1655	177.6	45.54
1963-1964	0.221	0.221	2358	75.0	20.27
1964-1965	0.707[b]	0.707	1022	135.7	38.77
1965-1966	0.304	0.595	844	154.6	46.85
1966-1967	0.106	0.397	1066	95.9	29.97
1967-1968	0.100	0.391	2278	79.9	26.63
1968-1969	0.040	0.331	1900	38.2	13.64
1969-1970	0.245	0.536	2388	73.2	28.15
1970-1971	0.293	0.534	3185	35.6	14.83
1972-1973[c]	0.202	0.202	135	12.4	5.90
1973-1974	0.304	0.304	1581	33.7	17.74

[a] 1957-1958, 1958-1959 produced low estimates (Z) for the highest estimates of effort observed; then the calculation of efforts was considered in error.

[b] no estimate from percentage composition data, comparison of CUE's used.

[c] 1971-1972, no positive estimates (Z) were obtained from either percentage composition data or by comparison on the CUE's.

The regression of the effective effort on the corrected values of Z yielded the following equation (Fig. 1):

$$(2) \quad Z = 0.0116\ E/N - 0.1610 \qquad r = 0.84^{1}$$

However, due to the continual drop in recruitment (Ricker 1975a), the estimate of natural mortality, M, is biased downward. The best estimate of the annual instantaneous rate of the decline in recruitment is 0.0524, determined from the logarithm of pup production from cohort analysis with M = 0.21 and a starting F = 0.033. This estimate of the rate of decrease in recruitment agrees well with Ricker's (1975b) of 0.068. Thus, natural mortality, confounded with wounding losses, is between 15 and 19% per year. This value also corresponds well with Ricker's (1975b) estimate of 0.206 or 18.6% per year. As will be subsequently elucidated, an M of 0.21 gave an almost perfect agreement between the simulation and the cohort analysis.

SEQUENTIAL POPULATION ANALYSIS

Sequential population methods (Fry 1949; Murphy 1964; Jones 1964; Gulland 1965; Pope 1972; Doubleday 1975) were developed to estimate fish population sizes and fishing mortalities from catch-at-age data. Although there is no example of this method being used to assess mammalian populations, no assumptions are violated by its use.

For this study, the sequential population analysis developed by Pope (1972), called cohort analysis, was utilized since it assumes that natural and hunting mortality occur somewhat independently, which is true to a great extent in the seal fishery. The method is based on the formula:

$$(3) \quad N_i = C_i\ EXP\ (M/2) + N_{i+1}\ EXP(M)$$

where N_i is the population of a year-class at the i^{th} birthday, C_i is the catch of a cohort at age i, and M is the instantaneous coefficient of natural mortality. This formula is applied sequentially, the population size in each new year depending on the population the year after.

However, some starting values are required. Thus, by expanding equation (3):

$$(4) \quad N_i = (C_i\ EXP(M/2) + C_i\ EXP(3M/2) + C_{i+2}\ EXP(5M/2) + \ldots + (N_t\ EXP(t-i)M)$$

and assuming that hunting does not completely extirpate a particular cohort, the last term for the final year's population is:

$$(5) \quad N_i = \frac{C_i(F_{i+1})}{F_i(1-EXP(-F-M))}$$

This formula is used to calculate the population size in the initial year. Considerable care should be given in estimating

[1] Significant at $P \leq 0.05$

the initial hunting mortality (F) since hunting mortalities are usually low on mammals, and the analysis is sensitive to the initial F in the first few iterations. However, when the data series is long, poor starting values for F are considerably damped as the analysis continues.

It is acknowledged that the natural mortality level for pups may be somewhat different from the adult animals. For this reason, the analysis was modified so that pups could experience a natural mortality twice or half as high. However, the analysis was extremely insensitive to the manipulation of this parameter because of the high hunting mortalities experienced by pups.

Hunting mortalities can be calculated by the formula:

$$(6) \quad F_i = \text{LOG}_e \ (N_i/N_{i+1}) - M$$

A much more detailed description of the method and its accuracy is given by Pope (1972).

In order to start the cohort analysis, an instantaneous total mortality was predicted from equation (2), based on the estimated effort expended in 1975 on hunting 1+ seals. Our estimate of natural mortality, M = 0.21, was subtracted from this value to provide a starting level of instantaneous hunting mortality on seals aged one and older, F = 0.033. The population estimates resulting from this analysis are given in Table 1. The annual mean hunting mortalities generated by the cohort analysis, as by equation (6), were significantly correlated with the effective effort (E/N) r = 0.55[1], while the total calculated mortality (Z) was also significantly correlated r = 0.57[1] with the annual mean hunting mortality. However, it is evident from the two parallel aggregations of points in the regression of total mortality on hunting mortality that another variable is clearly missing. This missing variable remains to be elucidated; however, it is probably related to ice conditions.

According to this analysis, the harp seal population declined exponentially from 1952 to 1975 (Fig. 2). Consequently, the population is now only 15% of its size in 1952. Pup production also declined during this period from 974,309 in 1952 to 216,257 in 1975. However, this decline is not nearly as dramatic as the decline in adults (Fig. 2).

CONSTRUCTION OF A MODEL

It appeared that some insights into harp seal population dynamics, and possible reasons for the decline in population numbers, could be acquired by studying the structure of the system as a whole (Fig. 3). The entire western Atlantic was considered one population in the simulation, since harp seals which breed in the Gulf of St. Lawrence, and on the Front off the coast of Newfoundland, spend much of their life together in the Arctic during the summer (Sergeant 1965). Their complete separation into Gulf and Front breeding populations is also not well documented and some mixing of the two stocks is known to occur (Sergeant 1971, 1975c), especially in the younger age classes (Sergeant 1975b).

In our model (Fig. 3), the program is initialized by entering a population of harp seals, the size of which is arbitrary, since the model will eventually stabilize itself at a particular level. These seals are then split into two groups, animals aged 1+ and pups; each group suffers a particular form of hunting.

[1]Significant at $P \leq 0.05$

The catch equation (Beverton and Holt 1957)

$$(7) \quad {}_iC_t = {}_iN_t \frac{F_t}{F_t+M} \quad (1 - EXP - (F_t+M))$$

where F_t is the instantaneous rate of hunting mortality in the t^{th} period, ${}_iC_t$ is the catch and ${}_iN_t$ is the population in the t^{th} period for age i, is used to calculate the catch of both pups and older seals. The catch of pups estimated from this equation is somewhat biased since most of the hunting mortality takes place during the first few weeks of life shortly after whelping. However, some natural mortality also occurs at this time (Sergeant 1975d; Popov and Timoshenko 1965). Furthermore, the hunting mortality on these animals continues throughout the year, some being taken during the Greenland summer "fishery" (Kapel 1973, 1975) and this would interact to a significant extent with natural mortality. Concurrent with the hunting, the number of seals remaining in each group is calculated by the following equation:

$$(8) \quad {}_iN_{t+1} = {}_iN_t \; EXP - (F_t+M)$$

Of these remaining animals, the sexually mature individuals then reproduce.

During construction of the model, it was necessary to elucidate a homeostatic mechanism that would equilibrate the seal population with the carrying capacity of its environment (McLaren 1967). A series of maturity ogives which respond to population density were described by Sergeant (1966, 1973). These maturity ogives, differing somewhat between the Gulf and Front, were amalgamated and assumed to represent the reproductive state of western Atlantic harp seals for a given population size. The total population size of 1+ seals was determined from cohort analysis (Table 1) for the appropriate years in which Sergeant's data applied. The ogives were then plotted on "probit" paper and lines were fitted by eye, giving more weight to points closer to the 50% maturity level. Values were then interpolated for each age from these lines, under the assumption they represented the best fit of the data. These interpolated values were used to determine the following equation (Fig. 4):

$$(9) \quad \text{ARC sine } {}_iM_t = 20.61A - 10.23\, N_t - 21.27$$

where ${}_iM_t$ is the proportion of the population mature for a particular age i and population number $N_t \times 10^{-6}$ in year t, and A is age in years. This model provides for density-dependent maturity, which was assumed to be linear over varying population densities, since no information was available to indicate otherwise. This probability was applied to the females in the population, assuming a sex ratio of 1:1 (Fisher 1952).

No animals less than 3 years of age were allowed to produce pups. Since the shift in the maturity ogive is linear in response to population density, the model is probably over optimistic at low population sizes. For our purposes, each mature female was assumed to produce a pup on an annual basis (Allen 1975).

The simulation was allowed to run for 100 years which was sufficient time to allow the population to stabilize. The implicit time unit of the clock was years, this unit of time being updated immediately following reproduction.

The simulation was used to generate a relationship between the number of 1+ seals and pup production (Fig. 5). The logarithmic relationship agreed well with the values generated previously by the sequential population analysis (Table 1). Harp seals aged 1+ were included in this relationship since the younger year-classes may compete with adult seals for available food, although only the older, mature stock is responsible for reproduction.

The maximum size to which the unexploited population grew in the model was ≈4.2 million seals. At this point, the birth rate balanced the rate of natural mortality. As the population increased in size, the rate of pup production declined. This was caused by the linear shift in the maturity ogives (Fig. 4), coupled with the exponential increase in the numbers at age. The maximum population size attained in the model was very similar to the size of the 1952 population derived from cohort analysis (Fig. 5).

The effect of various hunting strategies was tested in the model. Any hunting on seals aged 1+ had a devastating effect on population numbers. For example, the equilibrium level for the unexploited population (4.2 million seals), was reduced to a level of ≈83,000 seals in the equilibrium condition by a small hunting effort on 1+ seals of $F_a = 0.075$. In reality, hunting mortalities were much higher on 1+ seals, and the seal population never reached an equilibrium condition, but only showed a continual decline. Consequently, without a simulation model it is extremely difficult to visualize the long-term effects of exploitation, since it usually takes the seal population over 100 years to reach an equilibrium condition.

If only pups, i.e., the young of the year, are hunted, the calculated maximum sustainable yield (MSY) is highest when the catch of adults is zero (Fig. 7). This MSY of ≈84,000 pups occurs at a hunting mortality (F_p) of 0.2 which is far below past levels. Between 1952 and 1974 the hunting mortality on pups was never below 0.25, although it was as high as 1.19, in 1971. With the reduction of sealing activities in the Gulf of St. Lawrence in 1972, the level of hunting mortality dropped to 0.57, still well above that which leads to maximum sustainable yield. At the MSY level, the population of seals required is $\approx 1.8 \times 10^6$, almost three times its present level.

As the hunting mortality on 1+ seals increases, the maximum sustainable yield of pups declines in conjunction with a decline in the optimum level of hunting mortality for pups (Fig. 6). This shift in the optimum level of hunting is quite dramatic. The MSY for pups of ≈84,000 at $F_p = 0.2$ with no hunting of 1+ seals drops to a sustainable yield of ≈30,000, $F_p = 0.1$; with a hunting mortality on 1+ seals as low as $F_a = 0.025$. Pup production drops simultaneously from ≈511,000 to ≈340,000.

DISCUSSION

Sealing regulations began to evolve slowly with the resumption of Norwegian sealing efforts in 1946. Initially, opening and closing dates were established for the hunt, and adult females were protected while on whelping patches (Anon. 1972a). The Norwegians stopped sealing in the Gulf in 1965 and, in 1966, sealing on the Front came under the jurisdiction of ICNAF. The season was then shortened and a quota system introduced (Anon. 1972a) for the first time. Finally, in 1971, Canada and Norway signed a formal agreement regarding sealing activities and the conservation of seal stocks in the northwest Atlantic (Anon. 1972a).

The heavy and persistent exploitation of harp seals in the western Atlantic has been well documented in recent years. Nearly 10 million harp seals are known to have been harvested from this population between 1895 and 1946 (Fisher 1955) and another 5.3 million were taken between 1947 and 1964 (Department of Fisheries of Canada 1968; Øritsland 1967). In 1965, the Government of Canada imposed a quota of 50,000 seals on the Gulf of St. Lawrence (Mansfield 1967) and in 1972, Canada and Norway agreed to equally share a quota of 120,000 harp seals on the Front, with an additional estimated catch of 30,000 to the shore-based "fishery" (landsmen) operating along the east coast of Canada from the Magdalen Islands north to northern Labrador (Anon. 1972a), with an additional known catch of 10,000 to the aboriginal hunt in Davis Strait. Between 1965 and 1974, another 2.3 million harp seals were taken by sealers in the western Atlantic (Department of Fisheries 1968; Department of the Environment 1975; Øritsland 1967, 1969, 1970, 1971b, 1972, 1973). The flexibility of the present allottment system for landsmen was demonstrated in 1975 when their take alone exceeded 50,000, and the total kill of harp seals was in excess of 170,000 animals. None of these catch statistics include sealing activities which take place after the harp seal leaves the breeding and moulting areas and heads northward to spend the summer in the Arctic. Here, it is subjected to further sealing activities by native peoples along the east coast of Canada and in the Canadian Arctic. In addition, Greenland (Denmark) has a summer industry which at one time took an average of 50,000 harp seals per year (Fisher 1955). Greenland catches have been on the decline for the past 20 years, ranging from 15,000 to 20,000 during the early 1950's, 16,000 to 18,000 between 1956 and 1965, dropping to between 4,000 and 7,000 animals in recent years (Kapel 1973, 1975). Thus, hunting of seals, though varied in approach, is continuous throughout the year along the complete length of the seal's migratory pathway (Anon. 1972b).

In conducting a population assessment, the critical parameter, and one of the most difficult to accurately assess, is the level of natural mortality. Our estimate of the instantaneous rate of natural mortality for western Atlantic harp seals was 0.21 ± 0.11 (2.2 S.E.), i.e., an average annual mortality rate of 19%. This represents an average mortality rate for all age groups, since data are not now available to provide age-specific natural mortality rates for harp seals. This rate is higher than previous estimates of harp seal natural mortality. Fisher (1952) suggested that natural mortality for harp seals during the 1940's was probably not more than 15%. Allen (1975) used a rate of 0.08, while Benjaminsen and Øritsland (1975) assumed rates of 0.12 and 0.13. Our mean estimate does fall within the 10-20% mortality level arrived at by the Committee on Seals and Sealing (Anon. 1972b).

In general, there is a paucity of information on rates of natural mortality for pinnipeds. Our estimate, however, is rather similar to the few estimates of natural mortality which were calculated for other species. For example, Chapman (1961) calculated annual natural mortality in northern fur seals, *Callorhinus ursinus*, in 1958, 1959, and 1960, to be 0.18, 0.20, and 0.25, respectively (mean, 0.21). Annual mortality rates for Weddell seals, *Leptonychotes weddelli*, were estimated at 0.17 for females and 0.24 for males (Stirling 1971), i.e., a mean annual natural mortality rate for adult Weddell seals of 0.21. Annual mortality rates for ringed seals *Phoca hispida*, in the Canadian Arctic, and for harbour seals, *Phoca vitulina richardi*, on Canada's west coast were estimated at about 0.17 (Smith 1973) and 0.20 (Bigg 1969), respectively. The latter two figures, however, include some hunting mortality. These mortality figures are all of the same order of magnitude, represented by the instantaneous rate of natural mortality of 0.20 found in many fish populations (Beverton and Holt 1957). By comparison, female Himalayan thar, *Hemitragus jemlahicus*, studied by Caughley (1966) have an annual natural mortality rate of 0.25.

From a knowledge of the natural mortality rate, it is possible to calculate other populations characteristics. For example, using the equation given by Caughley (1966), mean life expectancy at birth for harp seals in the unexploited condition is only 4.76 years, even though the maximum life span would appear to be about 25 to 30 years (Fisher 1955; Sergeant 1971; Øritsland 1971a).

The use of an instantaneous rate of natural mortality is nevertheless a compromise in the absence of age-specific natural mortalities. It assumes that natural mortality takes place at a constant rate throughout the life span of the population. There is good evidence, however, that natural mortality in some mammals is initially higher in young animals, declining with age, and later increasing again after maturity is reached (Caughley 1966). This may not, however, be the case for all mammals, and does not appear to apply to all pinniped species. Bigg (1969) found that young harbour seals did not suffer appreciably higher mortality than older year-classes. Similarly, natural mortality in northern fur seals was found to be actually lower in young animals than older year-classes (Chapman 1961). It must be noted that natural mortality may be a density-dependent characteristic of a population which may change over time. Age-specific natural mortality may increase in earlier ages at high population levels, especially in some social species such as fur seals, sea lions, grey seals, *Halichoerus grypus*, and elephant seals, *Mirounga* sp., where young may be crushed and killed in densely populated rookeries. Similarly, natural mortality rates of older animals may increase under these conditions, because of intraspecific competition for territories and limited food supplies.

Cohort analysis utilizes an estimate of the instantaneous rate of natural mortality, and catch data for specific age classes over the time sequence for which such data are available. When this type of analysis is applied to fish populations, it is not possible to truly validate the results in quantitative terms. A mammalian population, such as the harp seal, studied over a number of years, provides an opportunity to compare the findings, both qualitatively with what is known about the species' biology in general, and quantitatively with previous estimates of population size and annual production.

In the early 1950's Fisher (1955) estimated that the population of harp seals in the western Atlantic numbered about 3.3 million animals, and estimated annual production to be 645,000 seals. The present cohort analysis produced a population estimate for 1952 of 4.2 million seals aged one and older, with production of about 970,000. Fisher's (1955) estimates, however, were based on aerial survey data using black and white photography. Recently, this has been found to underestimate the number of white-coated pups on ice and snow by as much as 48% because of the lack of contrast between the animal and its background (Lavigne and Ronald 1975). It seems, on this basis alone, that Fisher's results may have underestimated production, and thus the total population numbers. Fisher (1955) also noted other possible sources of error in his estimates.

Regardless, Sergeant (1975d) concluded that the population in the early 1950's was near its asymptotic stock size. Our model supports this view, suggesting a maximum stock size under the carrying capacity existing during 1952-1975 of about 4.2 million seals, the 1952 population estimate from cohort analysis.

Furthermore, Sergeant and Fisher (1960) suggested that between 1950 and 1960 the population was virtually cut in half. This, again is supported by the cohort analysis, the population declining from 4.2 million to 1.9 million seals. Similarly, Øritsland (1971a) concluded that the harp seal population declined by 60% during the period 1955 to 1970. The present cohort analysis suggests that the decline during this period was in the order of 75%.

The drastic reduction in sealing activities between 1939 and 1946, with no sealing in 1943, is reflected in the present analysis by the strong cohorts in the 1952 population between the ages of 6 and 13. It is also evident that these strong year-classes maintained the stock for some time (Table 1).

Estimates of annual production of western Atlantic harp seals during the period 1950-1975 have been made using a variety of techniques. These include estimates made from aerial surveys of whelping and moulting seals, capture-recapture experiments, and greatest catch (Sergeant 1975c), catch and survival estimates (Sergeant 1975c; Benjaminsen and Øritsland 1975), and recently from an aerial census using ultraviolet photography (Lavigne et al. 1975). Comparison of these estimates with those obtained from cohort analysis indicate that the latter provides higher estimates than the techniques used previously (Fig. 8).

Underestimates of annual production by photographic surveys may be attributed to the techniques used and the problems of conducting an aerial census (Fisher 1955; Sergeant 1975c, 1975d; Lavigne and Ronald 1975). The differences between our estimates and previous calculations (e.g. Sergeant 1975c; Benjaminsen and Øritsland 1975) are more difficult to explain, but may be due to the smaller, and perhaps more biased, samples used by these authors. Despite the differences, both sources of estimates for annual production indicate similar declining trends and, in fact, at the present time (1970-1975) the differences are only of an academic nature with respect to management considerations. The trend is clear. Extrapolation of either trend, which must occur if current management strategies are continued, leads to zero production in the near future.

The most recent aerial census, incorporating ultra-violet photography to detect pups (Lavigne and Øritsland 1974; Lavigne and Ronald 1975), suggests that pup production was probably less than 200,000 in 1975 (Lavigne et al. 1975). The present analysis produced a similar figure, ≈216,000, and indicated that the total western Atlantic population of harp seals now numbers less than one million animals (Table 1).

Our results support the view, expressed by many in recent years, that the harp seal cannot sustain present levels of exploitation. A number of conservationists and humane groups have actively campaigned to have harp seal hunting reduced to sustainable yield levels or abolished completely (Pimlott 1966; Lust 1967; Davies 1970; Amory 1971; Regenstein 1975). A number of others have expressed concern over the continued exploitation of the harp seal (Anon. 1972a; Breummer 1975; Lavigne et al. 1975).

The Special Advisory Committee on Seals and Sealing made recommendation for a 6-year moratorium based in part on the results of a life table model for the harp seal, produced in 1971 (Allen 1975). Allen also recommended a reduction in annual harvest to stop declining trend in population numbers. The results of the Allen model were, however, somewhat more optimistic than the results of the present analysis. The reasons for these differences are obvious. Allen's model assumes a natural mortality rate of only 8% per annum, much lower than the observed mortality rates for the few pinniped species for which comparable data exist, and less than half our calculated level of natural mortality for harp seals. In addition, the Allen model has no density-dependent self-regulating mechanisms. If unexploited, the population expands indefinitely, never reaching equilibrium with the carrying capacity of the environment.

It should be stressed that the present model may still be on the conservative side in its predictions. Every mature female in the population, determined by the oscillating maturity ogive in response to population size, was permitted to produce a pup. In reality, only about 90% of mature females produce pups (Sergeant 1971; Øritsland 1971a). Our estimates, both of total population numbers and annual production are higher than

previous estimates throughout the period under consideration. Annual production in 1975 may thus have been less than 200,000 animals as indicated by an aerial census (Lavigne et al. 1975).

In contrast with these views, fishermen may wish to escalate the hunt to further reduce a seal population that damages fishing gear and competes with them for common food resources such as herring, *Clupea harengus*, cod, *Gadus morhua*, and capelin, *Mallotus villosus* (Fisheries Council of Canada 1974, 1975). In addition, sealers are naturally anxious to preserve what they believe to be their traditional right to harvest a renewable natural resource. A recent analysis has, in fact, suggested that the sustainable yield of harp seals in the western Atlantic is higher than previously believed and recommended a take of 200,000 seals in 1976 (Benjaminsen and Øritsland 1975).

The population numbers in the early days of the hunt may have been considerably higher than the present calculated maximum population size of 4.2 million animals. There is a suggestion that the carrying capacity of the environment has been reduced during this period. It would also appear that the harp seal in the western Atlantic, like many other exploited populations (Gulland 1971), would have been exterminated by the present time except for the ability of the population to respond and compensate for declining numbers by increasing their reproductive potential (Sergeant 1966, 1973). At the present time, it would appear that this response, the early maturation of animals, has probably reached a limit. The population will probably be unable to respond any further in this way as population numbprs continue to decline. The severity of the present situation may be attributed in part to the continued practice of taking substantial numbers of adult seals each year. In the early 1950's, Fisher (1952, 1955) warned that continued exploitation of older animals would lead to a dramatic decline in population numbers, and recommended that, if the hunt continued, it should concentrate on taking young-of-the-year. Our results suggest that, to maximize yield, in terms of the numbers of seals taken, the exploitation rate on pups alone should be in the order of 17% at the MSY population level, considerably less than the 30% to 45% suggested by Sergeant (1975d), but in much better agreement with Ricker's (1975b) estimate of 20%. Any exploitation of seals aged 1+ has a drastic effect on resultant equilibrium population size. If older animals are included in the catch, the number of pups taken must be reduced significantly (Fig. 9A, B), or the population will inevitably decline.

In summary, management of harp seal stocks in the western Atlantic has failed to protect and conserve a renewable natural resource, and to ensure sustained yields to support an historical sealing industry. Some attempt is now needed to discern the prospects for future management. With this in mind, the simulation was modified so that a specific number of pups could be removed, consistent with the present quota system of management, and hunting mortality on 1+ seals was kept low (0.016) to approximate the incidental catch of native hunters only. The starting population was that represented by cohort analysis in 1975, and M was held at 0.21. When 150,000 pups were removed, the population reached extinction by 2,004; furthermore, with only 100,000 pups removed annually, it became extinct by approximately the same time (Fig. 9A). When only 50,000 were killed, the population still declined rapidly and was extinct by approximately 2015. With the removal of only 10,000 pups, the population began to build up slowly. With no pup hunt or incidental catch, the population expanded at 2% per year. At this rate, the population required ≈40 years to reach the MSY level. With only the incidental catch (F_A = 0.016) it would take ≈65 years to reach an MSY population size.

If the hunting on adults is completely stopped, allowing for some aboriginal catch, the natural mortality used to predict future prospects possibly is as low as 0.16 because of no wounding mortality. In this case, the catch of 50,000 pups leads to a very slow decline in population with a catch of adults of 0.016 (Fig. 9B). When the pup catch is 10,000 the populations builds up at 4% per year; no pup catch results in a population build-up at 5% per year. The MSY level of population is reached by the year 2000, demonstrating that hunting must be stopped at the bare minimum for 25 years. In addition, it is necessary to point out that natural mortality may be density-dependent (Sergeant 1966) and, in this case, at low population sizes, natural mortality may decline, allowing for a more rapid build-up of the population. However, small changes in natural mortality resulting from density dependence would never be sufficient to rehabilitate the population at present levels of exploitation.

The continued decline of the present breeding population for the next few years is inevitable. The low escapement of pups in recent years will be insufficient to merely replace losses through natural mortality. If we have learned anything from the depletion of other marine mammal stocks (Gulland 1971; Scheville 1975), the only viable management recommendation at the present time is to abolish all harp seal hunting, excepting perhaps the aboriginal summer hunt in the eastern Canadian Arctic and off western Greenland.

In the future, continued assessments should be made to provide more data to validate the model and to ensure continued protection of this natural resource. If any future hunting of the population is permitted, it should be restricted to pups only, and be held within conservative sustainable yield predictions based on the best data available at the time.

ACKNOWLEDGMENTS

Additional financial support was provided through the Committee on Seals and Sealing to the Minister of State for Fisheries, and through a grant from the Donner Canadian Foundation to the University of Guelph.

Although the analyses and conclusions expressed in this paper are those of the authors, we thank T. Øritsland, Sea Mammal Section, Institute of Marine Research, Directorate of Fisheries, Bergen, Norway, and D. E. Sergeant, Arctic Biological Station, Fisheries and Marine Service, Ste Anne de Bellevue, Quebec, Canada, for supplying previously unpublished data for inclusion in our analyses.

A number of individuals commented on our results and offered constructive suggestions. We especially thank H. D. Fisher, S. J. Holt, L. Boerema, K. Ronald, W. Doubleday, R. Halliday, and G. Winters, for their input.

REFERENCES

Allen, R. L. 1975. A life table for harp seals *Pagophilus groenlandicus (Erxleben)*. Symposium on the Biology of the Seal, Guelph, Canada, August 1972. Rapp. P-v Reun. Cons. per. int. Explor. Mer. (In press).

Amory, C. 1971. The slaughter of baby seals. Earth 2(9): 29-35.

Anon. 1972a. Canadian-Norwegian agreement on sealing. Polar Record 16: 268-271.

1972b. Interim report to the Minister of Environment from the Committee on Seals and Sealing. Fisheries Information, Fisheries and Marine Service, Environment Canada.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations, Ser. II, Vol. 19, 533 p.

Benjaminser, T., and T. Øritsland. 1975. The survival of year-classes and estimates of production and sustainable yield of northwest Atlantic harp seals. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/121.

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

Breummer, F. 1975. A year in the life of a harp seal. Natural History 84(4): 42-49.

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

Chapman, D. G. 1961. Population dynamics of the Alaska fur seal herd. Trans. 26th North American Wildlife Conf.: 356-369.

Davies, B. 1970. Savage Luxury. The Ryerson Press, Toronto, 76 p.

Department of Fisheries of Canada. 1968. Canadian Atlantic coast harp and hood seal catch statistics: an historical series by regions, methods of capture, types of pelts, areas of catch, 1946-1967. Economic Service, Department of Fisheries of Canada, Ottawa.

Department of the Environment. 1975. Canadian sealing statistics - 1968-1974. Fisheries and Marine Service, Environment Canada, Ottawa.

Doubleday, W. G. 1975. The least squares approach to analysing catch at age data. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/35.

Draper, N. R., and H. Smith. 1966. Applied Regression Analysis. John Wiley and Sons, Inc., New York, N.Y., 407 p.

Fisher, H. D. 1952. Harp seals of the Northwest Atlantic. Fish. Res. Board Can. Circ. General Ser. No. 20, 4 p.

1955. Utilization of Atlantic harp seal populations. Trans. 20th North American Wildlife Conference: 507-518.

Fisher, H. D., and B. A. MacKenzie. 1954. Rapid preparation of tooth sections for age determinations. J. Wildl. Manage. 18: 535-537.

Fisheries Council of Canada. 1974. Resolutions passed at annual meeting in Ottawa. Seals. Fisheries Council of Canada Bull. May, 1974: 3-4.

1975. Resolutions passed at annual meeting in Halifax. Seals. Fisheries Council of Canada Bull. May, 1975: 3.

Fry, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 27-67.

Gulland, J. A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. ICES C. M. 1965(3) (Mimeo).

1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Manuals in Fisheries Sci. No. 4, 154 p.

1971. The effect of exploitation on the numbers of marine animals. Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970), p. 450-468.

Jones, R. 1964. Estimating population size from commercial statistics when fishing mortality varies with age. Rapp. P.v. Cons. perm. int. explor. Mer 155, 38: 210-214.

Kapel, F. O. 1973. Age analysis and catch of harp seal in northwest Greenland. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/54.

1975. Recent research on seals and seal hunting in Greenland. Symposium on the Biology of the Seal, Guelph, Canada, August 1972. Rapp. P-v Reun. Cons. per int. Explor. Mer. (In press).

Lavigne, D. M., and N. A. Øritsland. 1974. Ultraviolet photography: A new method for remote sensing of mammals. Can. J. Zool. 52: 939-941.

Lavigne, D. M., and K. R. Ronald. 1975. Improved remote sensing techniques for evaluating seal populations. ICES C. M. 1975/N: 12.

Lavigne, D. M., S. Innes, K. Kalpakis, and K. Ronald. 1975. An aerial census of western Atlantic harp seals *(Pagophilus groenlandicus)* using ultraviolet photography. UN/FAO/ACMRR Working Party on Marine Mammals, Ad Hoc Group III, Doc. 31, Sept. 1-6, 1975, Seattle, Washington.

Lett, P. F., A. C. Kohler, and D. N. Fitzgerald. 1975. The role of stock biomass and temperature in the recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua*. J. Fish. Res. Board Can. 32: 1613-1627.

Lust, P. 1967. The Last Seal Pup, the Story of Canada's Seal Hunt. Harvest House, Montreal, 152 p.

Mansfield, A. W. 1967. Seals of arctic and eastern Canada. Fish. Res. Board Can. Bull. 137. (Second edition, revised).

McLaren, I. A. 1967. Seals and group selection. Ecology 48(1): 104-110.

Murphy, G. I. 1964. A solution of the catch equation. J. Fish. Res. Board Can. 22: 191-201.

Øritsland, T. 1967. Revised catch and effort statistics for the Norwegian seal hunt in the Front and Gulf areas off Newfoundland, 1937-1967. Int. Comm. Northwest Atl. Fish. Serial No. 1959.

1969. Catch and effort statistics for Norwegian sealing in Front area, Newfoundland, 1968 (revised) and 1969. Int. Comm. Northwest Atl. Fish. Res. Doc. 69/37.

1970. Provisional catch and effort statistics for Norwegian sealing in Front area, Newfoundland, 1970. Int. Comm. Northwest Atl. Fish. Res. Doc. 70/93.

1971a. The status of Norwegian studies of harp seals at Newfoundland. Int. Comm. Northwest Atl. Fish. Redbook 1971, Part III: 185-209.

1971b. Catch and effort statistics for Norwegian sealing in Front area, Newfoundland, 1971. Int. Comm. Northwest Atl. Fish. Res. Doc. 71/132.

1972. Catch and effort statistics for Norwegian sealing in Front area, Newfoundland, in 1971 (revised) and 1972 (provisional). Int. Comm. Northwest Atl. Fish. Res. Doc. 72/127.

1973. Effort and catch statistics for Norwegian sealing in Front area, Newfoundland, in 1973. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/122.

Paloheimo, J. E. 1961. Studies on estimation of mortalities I. Comparison of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645-662.

Pimlott, D. H. 1966. Seals and seal hunting in the north Atlantic. Can. Audubon 28:33-39.

Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. 9: 65-74.

Popov, L. A., and Ju.K Timoshenko. 1965. Nekotorye dannye O grenlandskom tiulene N'iufaundlendskogostada. [Some data on the Greenland seal of the Newfoundland stock]. *In* Morski Mlekopitaiushchie, p. 158-170. Moscow.

Regenstein, L. 1975. The Politics of Extinction. MacMillan Publ. Co. Inc., New York, 280 p.

Ricker, W. E. 1975a. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 19, 382 p.

1975b. Mortality and production of harp seals, with reference to a paper of Benjaminsen and Øritsland (1975). Int. Comm. Northwest Atl. Fish. Res. Doc. 75/XII/143.

Scheville, W. E. [ed.]. 1974. The whole problem, a status report. Harvard University Press, Cambridge, Mass., 419 p.

Sergeant, D. E. 1959. Studies on the sustainable catch of harp seals in the western north Atlantic. Fish. Res. Board Can. Arctic Unit Circ. No. 4: 1-38.

1965. Migration of harp seals *Pagophilus groenlandicus* in the northwest Atlantic. J. Fish. Res. Board Can. 22: 433-464.

1966. Reproductive rates of harp seals, *Pagophilus groenlandicus (Erxleben)*. J. Fish. Res. Board Can. 23: 757-766.

1971. Calculation of production of harp seals in the western north Atlantic. Int. Comm. Northwest Atl. Fish. Redbood 1971, Part III: 157-184.

1972. Canadian studies on harp seals in 1971. Int. Comm. Northwest Atl. Fish. Res. Doc. 72/59.

1973. Environment and reproduction in seals. J. Reprod. Fert., Suppl. 19: 555-561.

1975a. Results of Canadian research on harp seals, 1974. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/1.

1975b. Interrelations of the Gulf and Front herds of harp seals, *Pagophilus groenlandicus*. Canadian Government-Industry Sealing Meeting, 25 Feb., 1975. Doc. No. R/1.

1975c. Estimating numbers of harp seals. Rapp. P.-v. Cons. int. Explor. Mer 169. (In press).

1975d. History and present status of populations of harp and hooded seals. UN/FAO/ACMRR Working Party on Marine Mammals, Ad Hoc Group III, Doc. 7. Sept. 1-6, 1975, Seattle, Washington.

Sergeant, D. E., and H. D. Fisher. 1960. Harp seal populations in the western north Atlantic from 1950-1960. Fish. Res. Board Can. Arctic Unit, Circ. No. 5: 1-58.

Smith, T. G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Fish. Res. Board Can. Bull. 181, 55 p.

Stirling, I. 1971. Population dynamics of the Weddell seal *(Leptonychotes weddelli)* in McMurdo Sound, Antarctica, 1966-1968. Antarctic Res. Ser. 18: 141-163.

Table 1. The top matrix of numbers represents the catch at age of harp seals between 1952 and 1975. Cohort analysis (Pope 1972) was applied to this data to yield the numbers at age in the bottom matrix. The starting hunting mortality, F, for 1975 was 0.033, while natural mortality, M, was 0.21. The asterisk (*) beside 1971-75 indicates the pup production was estimated by the use of a density dependent maturity ogive.

AGE	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	198,063	197,975	175,034	252,279	341,397	165,498	140,996	238,932	156,168	160,319	207,088	259,819	266,382	182,758	251,735	277,750	154,458	233,348	217,431	210,879	117,031	98,335	114,825	136,618
1	1,506	26,219	33,965	7,418	900	3,513	8,693	2,818	5,959	2,357	15,580	4,034	4,029	2,420	8,859	6,784	4,494	13,757	6,186	4,200	1,150	2,695	8,859	4,538
2	5,270	7,716	13,407	11,977	4,051	5,270	5,643	6,843	20,261	1,695	21,112	6,662	5,640	2,470	8,859	4,504	2,798	3,186	6,862	1,835	875	3,669	5,118	3,680
3	7,098	6,442	3,665	15,068	4,276	6,948	14,030	7,245	33,371	2,131	10,274	6,357	9,449	4,995	5,690	2,447	1,153	4,992	3,109	2,304	875	2,969	1,936	2,418
4	8,389	3,820	7,866	6,182	3,601	7,984	20,283	5,435	10,726	2,664	12,306	4,584	7,691	7,364	5,978	2,502	2,102	4,771	2,956	1,447	2,326	2,720	1,312	1,150
5	10,324	3,820	2,592	8,886	2,701	4,152	15,555	6,843	8,343	856	10,613	3,972	7,398	7,158	6,338	4,393	1,739	4,606	3,189	1,460	875	4,616	1,837	1,283
6	11,615	2,996	3,486	5,023	2,926	3,513	14,183	7,648	10,726	1,114	3,839	3,606	6,739	6,488	6,730	5,005	2,029	3,304	1,796	1,040	987	1,273	3,051	1,115
7	8,819	2,622	3,039	4,250	3,601	5,270	9,150	7,245	7,151	985	5,081	2,751	4,541	3,708	5,474	4,615	2,392	2,717	1,415	775	1,254	1,048	984	1,295
8	8,819	2,996	1,698	5,795	2,926	5,270	9,455	6,440	3,575	614	5,619	2,873	3,223	3,038	3,385	3,225	2,500	4,295	2,192	756	875	1,248	1,214	903
9	6,990	2,922	1,877	1,932	2,251	3,832	7,015	6,038	2,384	614	4,064	2,506	2,710	1,442	2,233	2,689	1,667	3,273	2,192	1,081	575	674	1,214	996
10	6,990	2,098	2,950	1,932	1,575	3,832	7,625	4,428	3,575	694	2,710	2,873	2,930	1,184	1,801	2,857	1,667	2,995	2,432	999	575	549	951	963
11	6,990	2,047	994	1,545	2,026	5,270	6,710	2,818	2,384	420	2,145	2,812	2,344	4,635	2,305	2,335	1,233	2,552	1,595	510	382	699	656	348
12	4,947	1,498	2,592	1,932	900	3,513	5,948	2,013	1,789	388	3,145	2,078	2,124	1,545	1,513	1,613	1,887	1,775	1,355	714	483	624	787	572
13	4,624	1,273	2,592	386	1,350	3,513	4,728	1,610	1,430	339	1,919	2,017	2,051	1,390	1,513	1,501	906	1,775	1,116	612	196	499	755	386
14	3,226	974	1,341	386	900	4,152	4,118	2,818	2,384	226	2,032	2,262	1,904	1,236	1,657	1,946	1,223	1,831	877	387	91	424	558	324
15	3,119	749	1,788	773	1,350	2,475	3,203	1,610	1,192	226	3,839	1,895	1,172	1,359	1,368	1,779	1,015	1,609	1,156	488	392	349	492	180
16	3,441	1,199	1,324	386	900	2,076	2,593	805	1,788	170	1,468	2,017	1,172	824	1,513	1,335	942	1,220	1,836	326	287	274	558	292
17	2,581	974	983	773	675	1,757	2,288	1,208	1,192	1,243	1,694	1,528	1,538	669	1,008	1,335	870	1,498	877	265	196	1,273	459	108
18	2,258	674	268	1	450	1,757	763	805	1,192	65	1,355	917	1,099	566	1,369	1,279	1,015	998	678	245	196	624	328	192
19	1,613	599	1,162	1	225	1,437	1,068	1,208	683	48	790	856	1,318	772	864	1,279	906	1,165	678	265	1	1,572	295	96
20	1,613	974	626	386	225	1,437	2,288	403	1,192	161	1,694	978	586	389	864	1,857	614	777	718	183	287	1,896	164	48
21	1,613	599	268	650	450	318	1,068	1	218	0	226	733	439	612	576	612	999	610	399	122	1	1	197	48
22	860	225	268	1	675	719	1,373	1	596	32	1,016	672	439	206	360	445	544	388	279	82	91	0	197	36
23	860	150	715	1	450	1,176	1,220	403	1	32	226	611	513	103	576	389	254	444	239	82	1	25	98	1
24	108	225	179	1	450	319	1,678	1	1	16	226	428	366	206	288	445	181	222	159	20	1	25	131	36
25	753	150	715	1	450	1	763	403	1	81	452	183	587	206	504	222	109	166	120	61	1	75	98	24

AGE	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971*	1972*	1973*	1974*	1975*
0	974,309	999,864	881,923	744,699	866,287	796,283	860,065	684,874	553,941	582,544	556,611	521,058	488,526	435,142	421,835	489,697	430,489	416,839	383,451	278,333	258,280	241,198	225,715	216,257
1	367,344	611,438	631,422	557,285	376,508	394,830	496,452	327,038	340,121	308,414	329,862	364,733	348,440	356,159	380,179	315,290	346,876	296,805	327,802	218,861	83,290	195,622	139,834	154,626
2	565,901	458,525	472,017	481,240	445,048	304,382	316,880	394,590	262,554	278,332	247,873	251,733	210,957	149,119	184,482	144,558	87,244	115,009	156,284	99,825	89,486	66,470	107,567	104,733
3	546,894	453,966	364,726	370,539	379,303	357,101	241,982	251,778	313,687	194,501	217,601	181,914	198,053	165,920	118,695	93,862	113,121	68,288	90,628	122,303	79,265	71,748	50,577	62,536
4	362,600	436,913	362,170	292,341	286,787	303,607	283,267	183,515	197,564	224,225	155,806	167,134	141,734	152,031	139,995	91,809	93,069	88,856	50,859	70,501	97,063	63,463	55,485	39,254
5	274,140	286,365	350,716	286,494	231,401	229,223	238,911	211,302	143,681	150,486	179,355	115,214	131,369	107,962	116,684	99,999	71,583	57,336	67,729	38,569	55,844	76,583	48,993	43,794
6	293,565	212,918	228,684	281,951	224,227	185,139	182,066	179,453	165,117	108,954	121,211	135,827	89,814	99,888	82,068	88,811	77,995	56,458	42,331	52,029	29,942	44,478	57,921	38,059
7	209,604	227,502	169,891	182,229	224,023	179,120	144,900	134,811	138,738	124,185	87,314	94,795	106,853	86,734	75,062	59,617	67,483	60,665	42,718	32,698	41,237	23,600	34,907	44,283
8	186,971	161,961	182,049	134,975	143,886	178,347	140,468	110,843	102,753	106,021	98,775	66,201	74,363	82,525	58,755	55,816	44,170	52,547	45,828	33,334	25,806	32,298	18,024	27,409
9	149,939	143,616	128,586	146,037	104,191	113,997	139,821	105,332	84,050	80,071	85,386	75,997	51,975	57,375	64,158	38,894	42,621	33,553	38,897	35,173	26,341	20,130	25,056	13,517
10	139,563	115,245	113,782	102,540	116,636	82,429	98,954	107,021	79,944	65,983	64,351	65,556	59,346	38,960	45,209	49,995	28,475	32,885	24,751	29,556	27,537	20,834	15,711	19,217
11	174,539	106,834	91,527	89,574	81,378	93,125	63,366	65,240	82,763	61,503	52,860	49,722	50,350	45,467	30,515	35,824	30,673	21,581	23,960	17,467	23,058	21,804	16,396	11,879
12	120,286	135,185	84,035	73,386	71,216	64,140	70,741	45,322	50,343	64,940	49,540	40,916	37,772	38,865	32,682	22,659	26,288	20,239	15,196	17,985	13,700	18,337	17,044	12,698
13	141,570	93,048	108,230	65,784	57,746	56,916	48,828	51,887	34,925	39,199	52,290	38,225	31,295	28,705	30,112	25,129	16,915	20,330	22,913	11,887	13,936	10,670	14,482	13,107
14	62,174	110,591	74,277	85,396	52,976	45,592	62,973	35,322	40,690	27,022	31,469	40,658	29,169	23,521	22,017	23,046	19,018	12,895	14,881	17,568	8,444	11,120	8,200	11,059
15	71,365	47,492	88,766	59,001	68,973	42,131	33,218	31,126	26,094	30,836	21,700	33,679	30,920	21,936	17,953	16,359	16,929	14,403	8,804	11,273	13,892	6,763	8,632	6,144
16	59,853	55,840	37,822	70,343	47,129	54,612	31,922	24,042	23,780	20,079	24,782	14,134	17,488	24,908	16,578	13,321	11,655	12,888	10,220	6,096	8,770	10,908	5,168	6,554
17	68,037	45,418	43,535	29,566	56,671	37,392	42,399	23,841	18,764	17,666	16,125	10,774	9,640	13,120	18,719	12,869	9,596	8,599	9,284	7,358	4,648	6,851	8,595	3,686
18	60,468	52,826	35,938	34,404	22,459	45,329	28,727	32,308	17,995	14,136	13,201	11,538	13,842	6,430	10,033	14,265	8,581	6,995	5,622	6,736	5,725	3,591	4,607	6,554
19	42,286	46,981	42,213	28,889	27,886	17,800	35,161	22,599	25,463	13,512	11,400	9,480	8,527	10,221	6,702	6,901	10,412	6,042	4,771	3,947	5,239	4,464	2,349	3,277
20	32,932	32,825	37,543	33,171	23,416	22,401	13,134	27,540	17,231	20,639	10,910	8,330	6,914	5,725	7,598	3,834	4,442	7,624	3,849	3,257	3,960	4,246	2,203	1,638
21	25,647	25,647	25,730	29,868	26,540	18,788	16,864	8,587	21,960	12,894	16,585	7,318	6,033	5,077	4,362	5,381	1,587	3,046	5,480	2,473	2,475	2,141	1,735	1,638
22	19,974	19,872	20,355	20,615	24,210	21,108	14,934	12,709	6,959	17,800	10,451	13,240	5,272	4,495	3,744	3,817	3,811	863	1,920	4,883	1,895	2,006	1,735	1,229
23	15,556	15,379	15,772	16,205	16,709	19,016	14,462	10,869	10,300	5,105	14,399	7,556	10,127	3,878	3,450	2,711	2,845	2,599	350	1,303	3,236	1,454	1,625	1,229
24	11,211	11,978	12,206	12,557	12,964	13,139	15,413	12,820	8,448	8,348	4,109	11,469	5,575	7,747	3,051	2,285	1,847	1,429	1,707	68	984	2,622	1,196	1,229
25	9 435	8,632	9,507	9,718	10,045	10,371	10,363	10,983	9,985	6,867	6,753	3,127	8,911	4,189	6,094	2,214	1,451	1,334	959	1,341	24	797	2,183	819
Total 1 +																								
meals	4,211,954	3,916,197	3,731,507	3,493,108	3,132,228	2,890,025	2,760,134	2,620,879	2,223,911	1,993,858	1,923,108	1,717,467	1,523,978	1,318,981	1,180,736	1,023,633	924,807	824,471	756,851	741,893	664,787	662,800	649,041	650,878

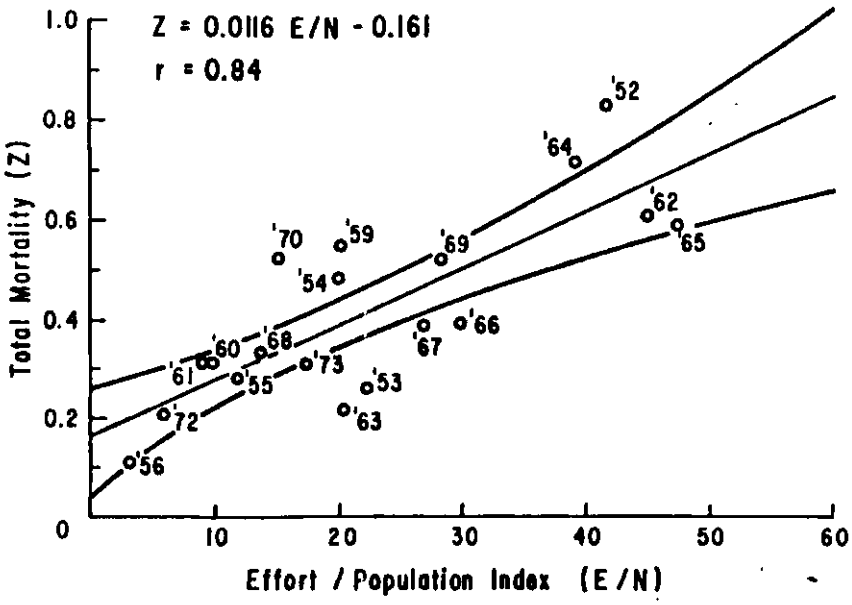

Figure 1. The relationship between effective effort (E/N) and the total mortality (Z). The intercept value of 0.161 is probably a minimum estimate of natural mortality (M) due to a bias resulting from a systematic drop in instantaneous rate of recruitment of 0.052.

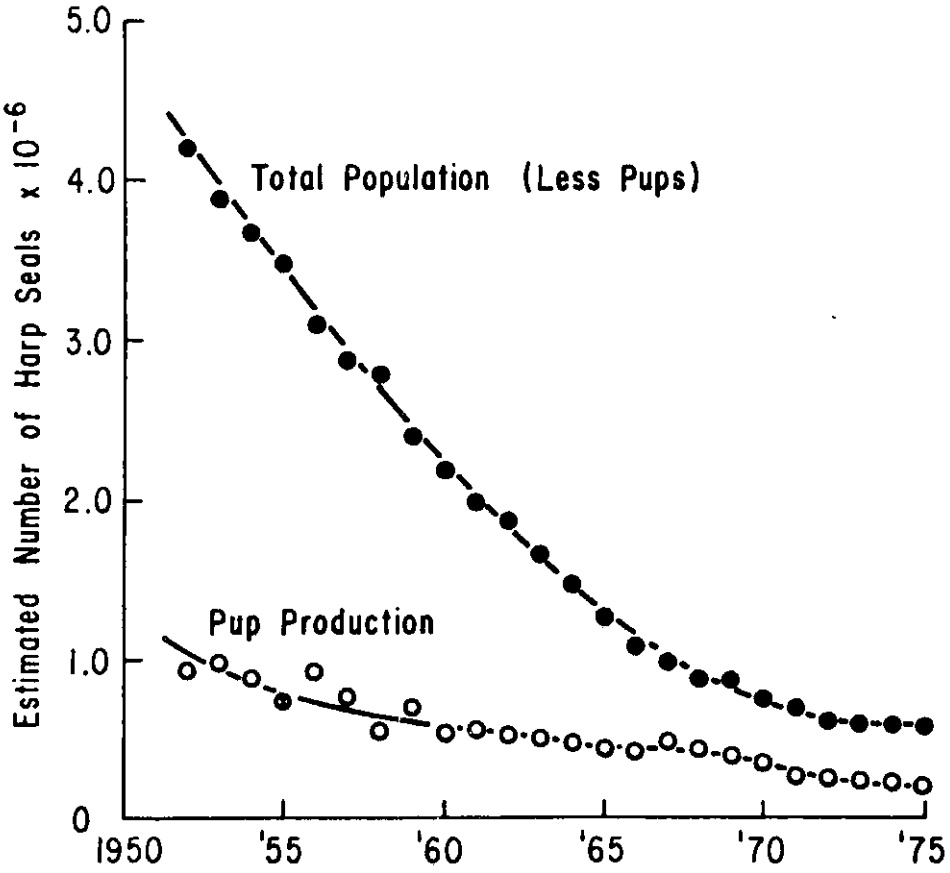

Figure 2. The decline in harp seal *(Pagophilus groenlandicus)* numbers in the western Atlantic between 1952 and 1975 as estimated by cohort analysis. ● - seals aged one and older; O - pup production.

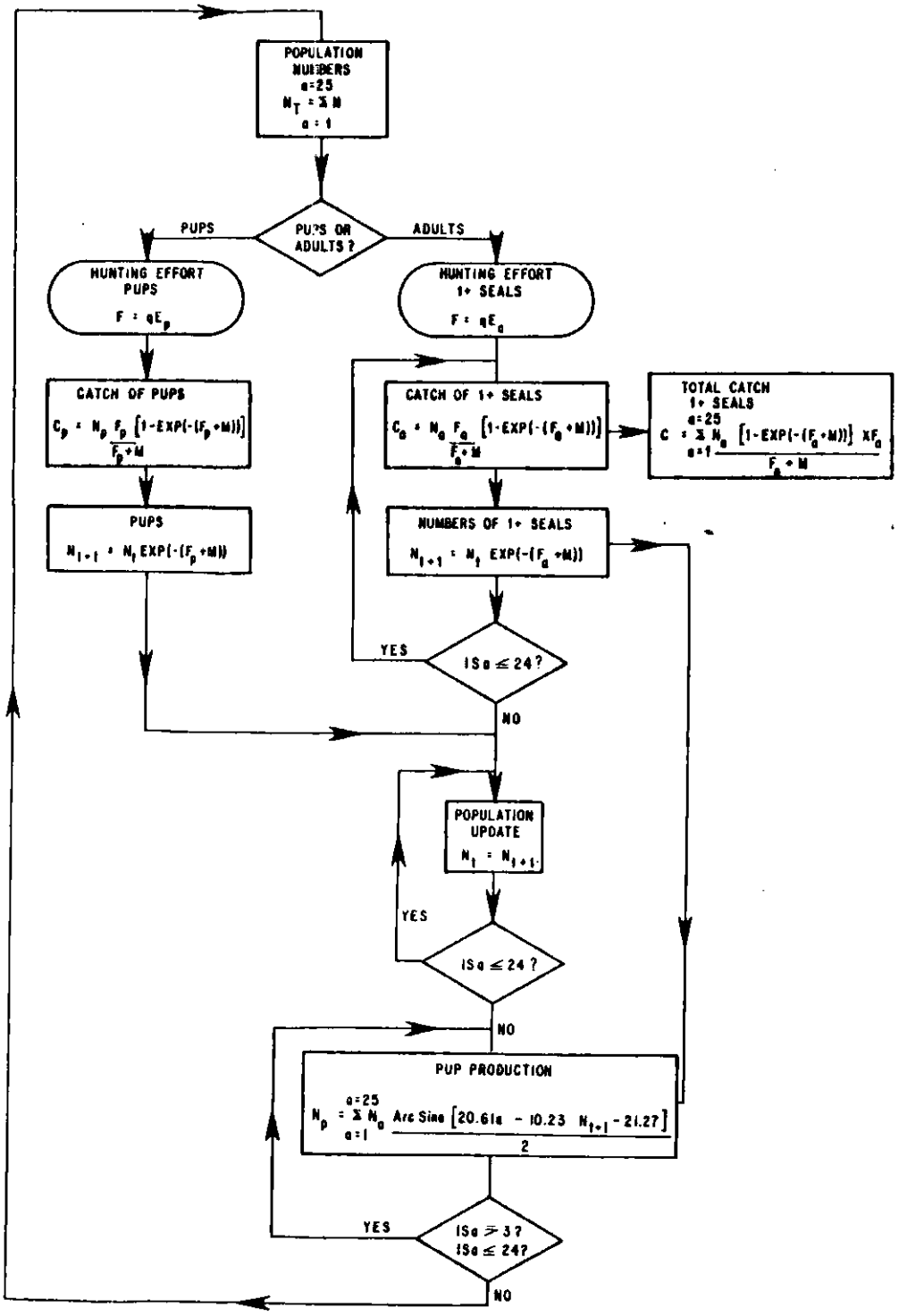

Figure 3. Basic flow chart of a model representing the western Atlantic harp seal *(Pagophilus groenlandicus)* population. Both the Gulf and Front herds were considered to be one population.

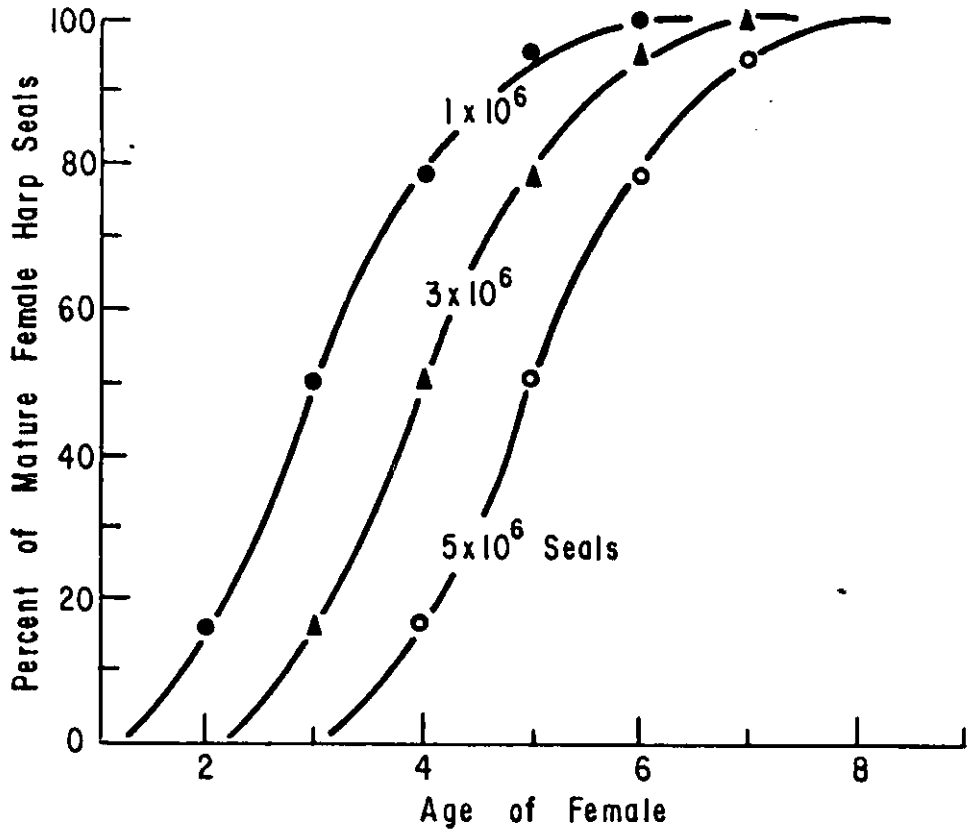

Figure 4. The shift in the maturity ogives of female harp seals, *Pagophilus groenlandicus*, in relation to population density. No female seal less than 3 years of age was permitted to produce an offspring in the model.

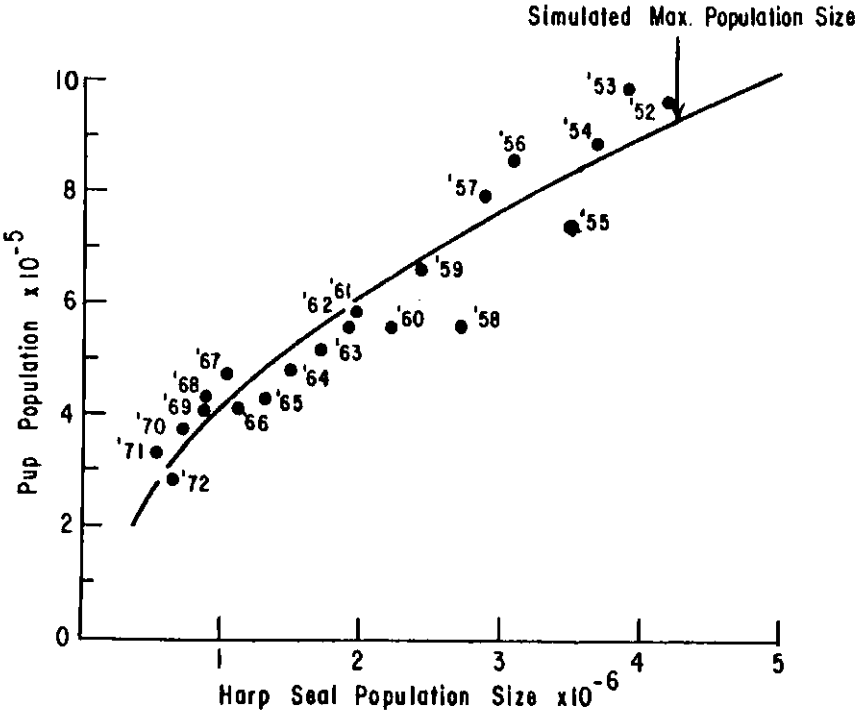

Figure 5. A comparison of the simulated and predicted pup production from cohort analysis in relation to the number of seals aged one and over.

G 7

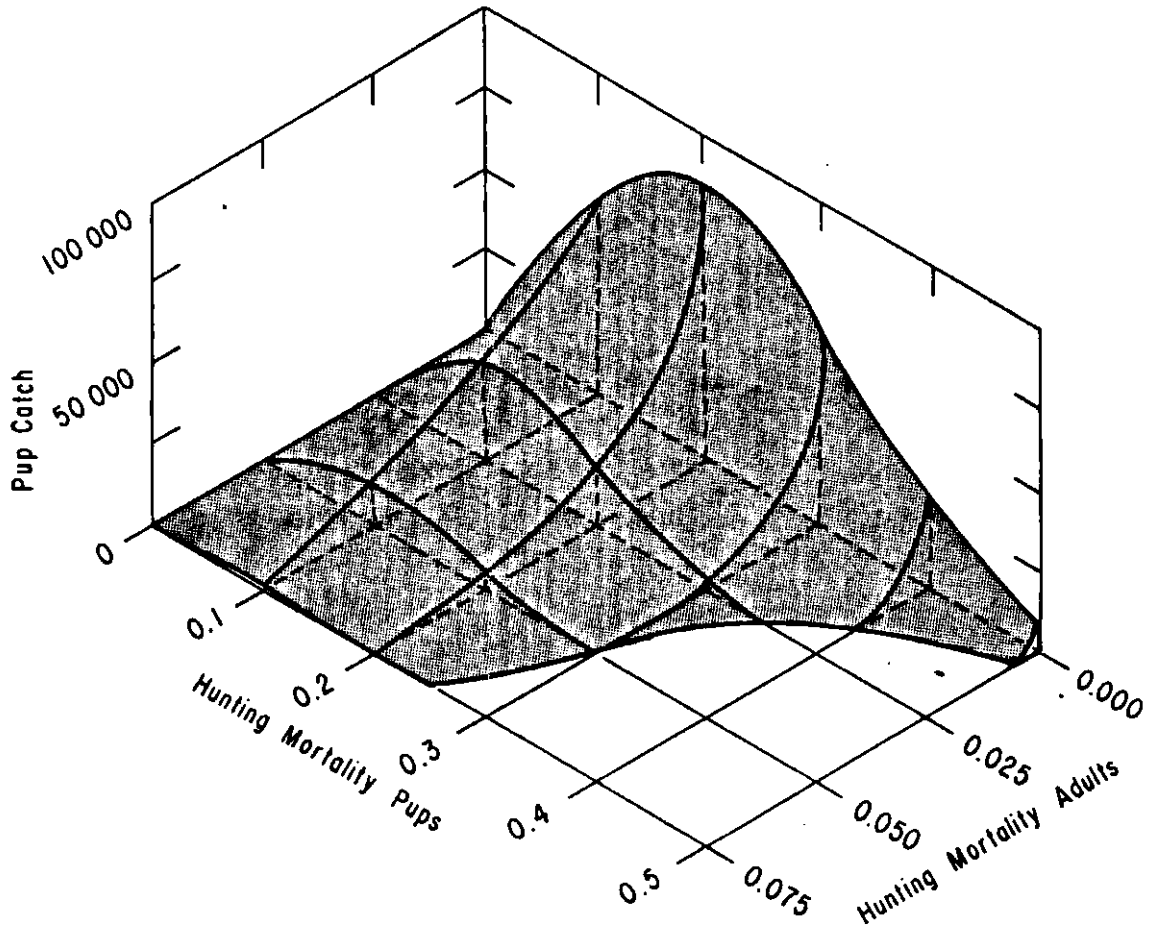

Figure 6. The response of equilibrium pup catch to varying levels of hunting mortality on both pups and adults.

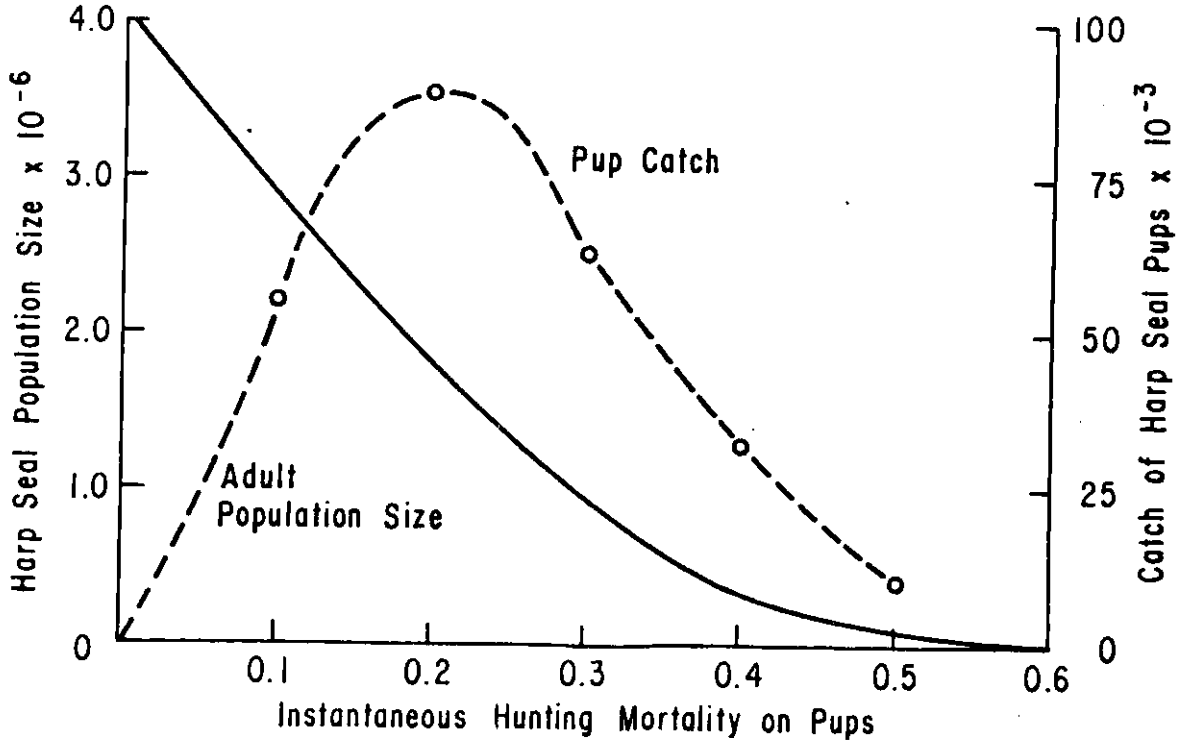

Figure 7. Maximum equilibrium pup catch occurs when there is no hunting on adults and a hunting mortality (F) of 0.2 on pups. This sustains a catch of 83,000 pups from a population of ≈1.7 million adults and represents an exploitation rate of 17% of the total pup production.

G 8

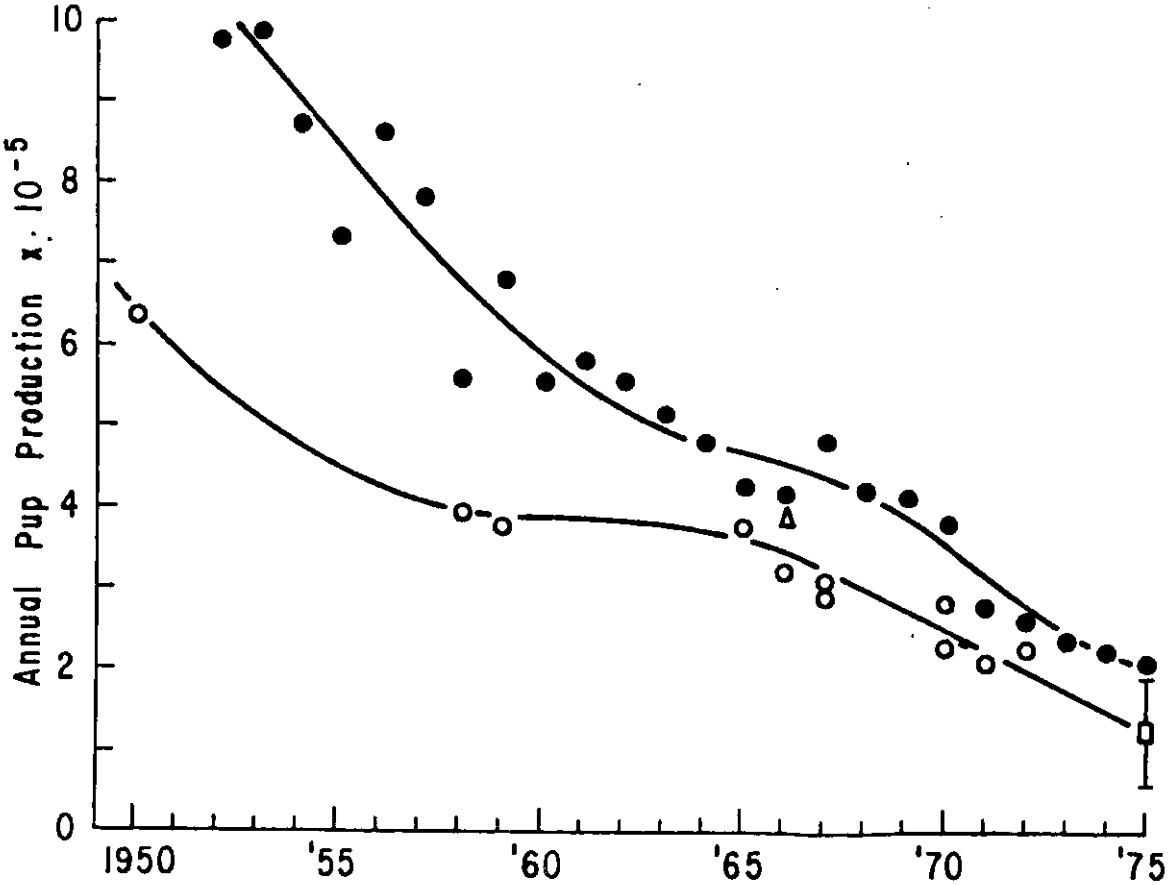

Figure 8. Annual production of western Atlantic harp seals, *Pagophilus groenlandicus*, estimated by aerial survey, capture-recapture experiments, greatest catch, and catch and survival estimates (Sergeant 1975a) O, by survival estimates (Benjaminsen and Øritsland 1975) Δ, by aerial censusing using ultravoilet photography ◘, with error bars designating 95% confidence intervals, and by cohort analysis ●.

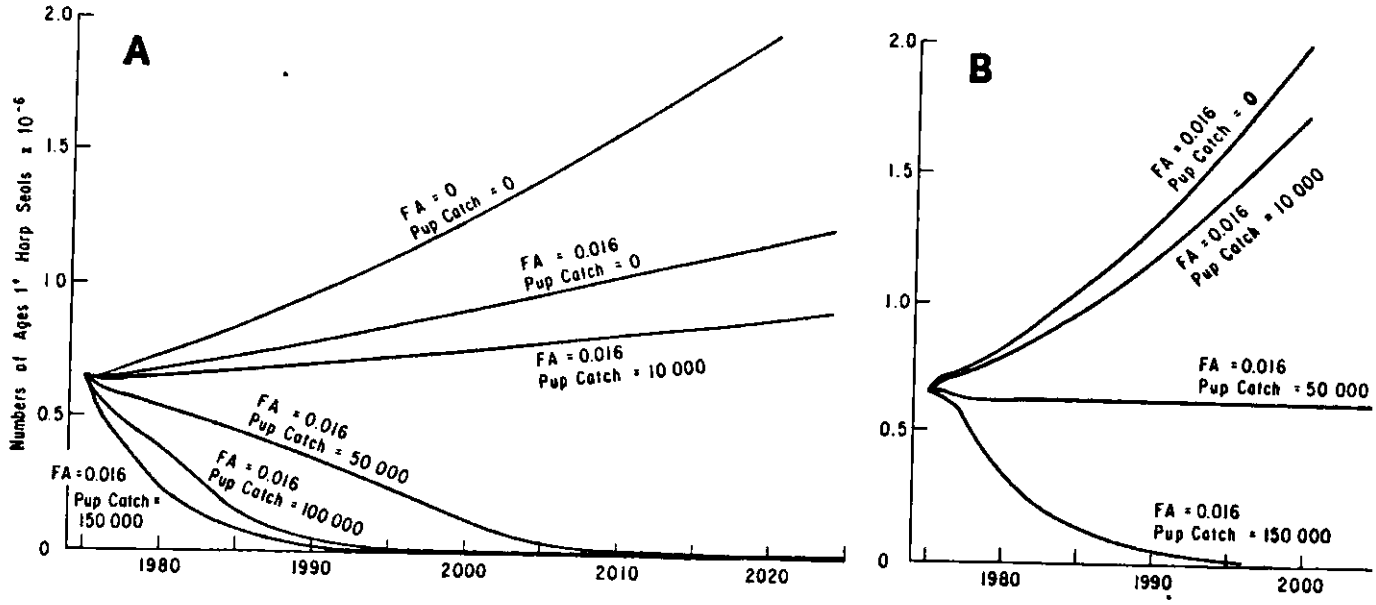

Figure 9. Estimated rates of recovery of western Atlantic harp seals, *Pagophilus groenlandicus*, for different management strategies, based on the 1975 population size predicted from cohort analysis. FA is the hunting mortality on 1+ seals, representing the approximate aboriginal catch in the eastern Canadian Arctic and western Greenland during the summer. Figure 9A assumes a natural mortality of 0.21, while 9B assumes a rate of 0.16.

G 9