NOT TO BE CITED WITHOUT PRIOR
REFERENCE TO THE AUTHOR(S)

Northwest Atlantic Fisheries Organization

Serial No. N4289 **NAFO SCR Doc. 00/55**

SCIENTIFIC COUNCIL MEETING – JUNE 2000

Estimating Pup Production and Population Size of the Northwest Atlantic Harp Seal (*Phoca groenlandica*).

by

B. P. Healey and G. B. Stenson

Science Branch, Department of Fisheries and Oceans
P. O. Box 5667, St. John's, Newfoundland, Canada AlC-5Xl

Abstract

Pup production and population size of Northwest Atlantic harp seals *(Phoca groenlandica)* for the period 1960 to 2000 were estimated using independent survey estimates of pup production, annual estimates of pregnancy rates, and age-structured removals. Removals included reported catch, estimated by-catch and assumed levels of seals killed but not landed (struck and lost). These data were fit to a three-parameter age structured population model that allows for differing assumptions of pup mortality. The two parameters estimated in the model are the pup selection parameter (s) and unaccounted mortality (m). The impact of assuming that the mortality of young seals (age class 0) was greater than that of seals one year of age and older (1+) was illustrated by using a fixed parameter (γ) as the ratio of age class 0 mortality to that of older seals. Replacement yields were estimated using differing assumptions of the age structure of the harvest. The uncertainty associated with the estimates was determined by randomly re-sampling from within the sampling error of the pup production estimates.

Assuming that the unreported mortality of age class 0 seals is 3 times that of 1+ animals, the total population was estimated to be approximately 5.2 million, with a 95% confidence interval of 4.0 to 6.4 million seals in 2000. Assuming different γ-values changes the estimates slightly, but differences were minimal. The population was estimated to have increased from less than 2 million in the early 1970s until 1996; since then the population has been relatively stable. Using the current age structure of the removals (~70% young of the year), the 2000 replacement harvest was estimated to be approximately 533,000, with 95% confidence interval (C.I.) 373,000, to 693,000. Assuming that the levels of by-catch and the Greenland harvest remain at their 1999 levels, and accounting for struck and lost, the corresponding replacement level of seals that can be landed in southern Canada at the proportion of pups observed in 1999 (90%) is 257,000; (95% C.I. 102,000, to 342,000). This level would be reduced slightly if the proportion of young in the harvest decreases.

Introduction

Various approaches have been used to estimate the size of the harp seal *(Phoca groenlandica)* population in the Northwest Atlantic (see Roff and Bowen, 1983 or Shelton *et al*., 1996 for reviews of the different methods). Earlier estimates, based primarily on interpreting age composition data, use either the survival index approach (e.g. Sergeant, 1971; Winters, 1978; Cooke, 1985) or sequential population analysis (e.g. Lett and Benjaminsen, 1977; Winters, 1978). More recent efforts have focused upon fitting various forms of a two-parameter population model (variation of a Leslie model) to independent field estimates of pup production for several years (termed the population model approach, e. g. Roff and Bowen, 1983, 1986; Shelton *et al*., 1992, 1996; Stenson *et al.*, 1999).

Shelton *et al*. (1996) estimated the population of Northwest Atlantic harp seals using the model described in Cadigan and Shelton (1993), which involved fitting a population model to independent estimates of pup production. With the exception of the methods used to obtain initial pup production and parameter estimation, the model used by Shelton *et al*. (1996) was very similar to that of Roff and Bowen (1983). Based upon annual estimates of age-specific reproductive rates and catch-at-age up to 1993 and six independent survey (mark-recapture and aerial) estimates of pup production (1978, 1979, 1980, 1983, 1990 and 1994), total population was estimated to be approximately 4.8 million if the natural mortality was assumed to be constant across ages, and 4.5 million if the mortality rate of young of the year seals was assumed to be 3 times that of seals one year of age and older (1+). Warren *et al*. (1997) estimated that the 95% confidence intervals associated with the constant mortality model were 4.1 – 5.5 million. The population was then estimated to be growing at 5% per year.

Since 1996 Canadian catches increased dramatically from an average of 52,000 from 1983 - 1995 to over 240,000 during 1996 - 1999 (Stenson *et al*., 2000a). Also, based on new methods of reporting catches, the estimates of removals in Greenland during the late 1980s and early 1990s were revised upward from the ~16,000 assumed in Shelton *et al*. 1996 to over 50,000 (Anon. 1999a). Similar to the Canadian catch, catches in Greenland continued to increase: over 53,000 seals were landed in 1993, compared to an estimated harvest of 103,000 in 1999, an average increase of 12% per annum (Stenson *et al*., 2000a).

Stenson *et al*. (1999) explored the impact of these increased catches on the population estimates and estimated 1998 population size using reproductive and catch data up to 1998, but pup production data which terminated in 1994. They also estimated the impact of incorporating several assumed levels of struck and lost (i.e. seals that are killed but not landed and therefore not included in the reported landings). Reviewing these estimates, the National Marine Mammal Peer Review Committee (Anon 1999b) concluded that, based on the 1994 pup production survey, the population was on the order of 5 million, but that a new pup production survey was necessary in order to determine the current population size. The committee also recommended that future estimates be made with models that included variable mortality for different age classes and that as many sources of unreported mortality as possible be incorporated explicitly in the population model. The committee suggested that until additional information is available, future modeling assume that 5% of the total numbers of young of year killed in southern Canada are lost while 50% of older animals and all age classes in the northern areas (Arctic and Greenland) are not recovered.

Surveys were carried out in March 1999 to estimate pup production of harp seals in the Northwest Atlantic. Stenson *et al*. (2000b) estimated that 997,900 (SE=102,100) pups were born off Newfoundland and in the Gulf of St. Lawrence during 1999. Also, Walsh *et al*. (2000) estimated the numbers of seals caught incidentally in lumpfish fishing gear in Newfoundland since 1978 while Sjare and Stenson (2000) provided additional information on the levels of struck and lost in the Canadian commercial hunt.

The objective of this study is to estimate current population size of Northwest Atlantic harp seals using an age structured population model, incorporating recent estimates of reproductive rates (Sjare *et al*., 2000), unreported mortality (Waring *et al*. 1999; Walsh *et al*. 2000; Sjare and Stenson, 2000), and pup production. Replacement yields (in units of total removals) and the corresponding levels of reported catch in the Canadian Front and Gulf that would provide such yields are calculated, assuming that other hunt components take the same number of animals as each component did in 1999. In addition, we present an estimate of population size in 2005 and 2010 if these replacement yields are taken in the intervening period. Uncertainty in these estimates was determined incorporating the error associated with the available pup production estimates.

Model Structure

The population model used to estimate numbers-at-age for harp seals in the Northwest Atlantic from 1960 to 2000 is an extension of the model described in Shelton *et al*. (1996) and Cadigan and Shelton (1993). The original model (hereafter referred to as the 'Cadigan-Shelton' model) consists of two components, the first being the population dynamics model while the second involves a statistical model. For comparative purposes, we present a description of both the Cadigan-Shelton model and the extended version used in this study.

The basic formulation of the Cadigan-Shelton model is:

$$n_{a,t} = (n_{a-1,t-1}e^{-m/2} - c_{a-1,t-1})e^{-m/2}$$

For $0 < a < A$,

$$n_{A,t} = (n_{A-1,t-1}e^{-m/2} - c_{A-1,t-1})e^{-m/2}$$

For $a = A$, where A-1 is taken as ages A-1 and greater, and

$$n_{a,t} = \sum_{a=1}^{A} n_{a,t} P_{a,t}$$

for $a = 0$;

where $n_{a,1}$ = population numbers-at-age a in year t,
$c_{a,t}$ = the numbers caught at age a in year t,
$P_{a,t}$ = per capita pregnancy rate of age a parents in year t, assuming a 1:1 sex ratio,
m = instantaneous rate of natural mortality, and,
A = the 'plus' age class (i.e. older ages are lumped into this age class and accounted for separately, taken as age 12 in this analysis).

In order to predict numbers-at-age for years prior to the first year for which continuous pregnancy data are available, it is assumed that the annual pup catch was a constant proportion (s) of the number of pups born (s=(1/exploitation rate)). Thus, for years prior to the first year for which pregnancy data were available (year t_0);

$$n_{a,t_0-1} = se^{-ma}c_{0,t_{0-a-1}} - \sum_{i=1}^{a} e^{-m(i-1/2)}c_{a-i,t_{0-i-1}}$$

for a = 1 to $\boldsymbol{A}$, where $\boldsymbol{A}$ is a terminal (rather than a plus) age ($\boldsymbol{A}$=25 years in the formulations that follow). This equation is applied iteratively to go back in time and fill in the numbers-at-age matrix.

The modified form of the Cadigan-Shelton model below allows direct investigation of the impact of assuming that the mortality of age class 0 (m_0) is unequal to that of older seals (m_{1+}). The model has the ability to fix m_0 as a constant multiple of m_{1+}. We denote this multiple as γ (i.e. $m_0 = \gamma m_{1+}$). In general, mammalian biology suggests that γ is greater than or equal to 1.

The modified model has the form:

$$n_{a,t} = n_{a-1,t-1}e^{-(g)m} - c_{a-1,t-1}e^{-(g)m/2}$$

for a =1

$$n_{a,t} = (n_{a-1,t-1}e^{-m/2} - c_{a-1,t-1})e^{-m/2}$$

for $1 < a < A$,

$$n_{A,t} = (n_{A-1,t-1}e^{-m/2} - c_{A-1,t-1})e^{-m/2}$$

for $a = A$, where A-1 is taken as ages A-1 and greater, and

$$n_{a,t} = \sum_{a=1}^{A} n_{a,t} P_{a,t}$$

for $a = 0$, where the variables and subscripts have the same definitions as in the Cadigan-Shelton model. The modification for predicting the numbers at age in the year t_0-1 is as follows:

$$n_{a,t0-1} = se^{-m(g+a-1)} c_{0,t_0-a-1} - (\sum_{i=1}^{a-1} e^{-m(i-1/2)} c_{a-i,t_0-i-1}) - e^{-m(a-1+g/2)} c_{0,t_0-a-1}$$

for a = 2,…,$\boldsymbol{A}$,

$n_{0,t_0-1} = sc_{0,t_0-1}$, and

$$n_{1,t_0-1} = se^{-(g)m} c_{0,t_0-2} - e^{-(g)m/2} c_{0,t_0-2} .$$

Maximum likelihood (equivalently non-linear least squares in this case) estimates of the parameters v_1=log(m) and v_2=log(s) were obtained using PROC IML in SAS applying the Newton-Raphson ridge optimization method. Survey estimates of pup production were given weights that are inversely proportional to their variance, and the predicted pup production was fit to the survey data.

Data Input

There are three sources of input data to obtain model estimates: pup surveys, catch-at-age, and age-specific pregnancy rates. There are currently seven independent estimates of pup production (Table 1). The model was fit to independent estimates of pup production in 1978, 1979, 1980 and 1983 based on mark-recapture experiments (Bowen and Sergeant, 1983, 1985; revised in Roff and Bowen 1986) and aerial survey estimates for 1990, 1994 and 1999 (Stenson *et al*. 1993, 1996, 2000b). The mark-recapture estimates were critically reviewed by Warren (1991), which also took into account Cooke *et al*.'s (1985) review of harp seal population dynamics.

A number of other estimates of pup production in Northwest Atlantic harp seals have been presented but were not included in the fitting procedure. For example, Bowen and Sergeant (1983) also presented the results of a mark-recapture experiment based on the 1977 marking of seals in the Gulf only. However, they concluded the estimates based on Gulf tags only (318,000 ± 48,000) were likely to be negatively biased and so the estimates were not included. Similarly, Stenson *et al*. (1993) presented three estimates of pup production at the Front in 1990. However, one of these estimates was known to be incomplete while another was based on a series of flights made over two weeks and required a variety of assumptions to estimate ice drift over this period. Therefore, we used the 1990 pup production estimate of 577,900 (SE=38,000) based upon the visual surveys at the Front and photographic surveys in the Gulf (Stenson *et al*. 1993).

Attempts were made to estimate pup production using aerial surveys prior to 1990 but they could not be used to fit the model. Unfortunately none of the surveys carried out in 1950, 1951, 1955, 1959, 1960, 1975, 1977 and 1983 (Fisher 1952; Sergeant and Fisher 1960; Lavigne *et al*. 1980, 1982; Myers and Bowen 1989) covered all of the whelping concentrations in the Gulf and off Newfoundland in the same year. Also, none of the surveys covered the northern Gulf ('Mecatina') area, which can account for a significant number of pups in some years (e.g. see Stenson *et al*. 2000b). Given the larger variability in the proportion of pups born in the various whelping areas (Winters 1978; Stenson *et al*. 1996, 2000b) extrapolating the number of pups from one year to another is unreasonable. However, these surveys do provide minimum estimates of pup production for a number of years. Model estimates of pup production were greater than the partial survey estimates for all years where comparisons can be made (post-1960) in each of the model runs.

Using sequential population analysis a number of authors (e.g. Lett and Benjaminsen 1977; Winters 1978) estimated that pup production had declined from approximately 500,000 in the 1950s to approximately 300,000 – 350,000 in the 1970s. Unfortunately, the estimates of pup production are not independent of the assumed mortality and therefore, could not be used to fit to in this model.

Sergeant (1971, 1975), Benjaminsen and Øritsland (1975) and Winters (1978) used the survival index method to estimate average pup production for a various periods between the 1950s and 1970s. Cooke (1985) found that these earlier estimates were not accurate and revised this method to estimate pup production for the periods 1958 - 1967 (400,000 – 500,000) and 1968 – 1977 (300,000 – 400,000) depending upon differing assumptions of errors in the aging of samples. These estimates assume that pup production does not vary over the period being estimated and therefore were not be used in the current model.

The ‘catch’ data that are input to the model (Table 2; Figure 1) are not solely comprised of reported landings (Stenson *et al*. 2000a). These removals also include by-catches from the Newfoundland lump fishery (Walsh *et al*. 2000) and the eastern United States (Waring *et al*. 1999), and animals assumed struck and lost (Sjare and Stenson 2000). The associated rates of struck and lost used (Table 3) are based upon suggestions from the National Marine Mammal Peer Review Committee (Anon 1999b).

The pregnancy rate data used in this study (Table 4) are ‘harmonized’ pregnancy rates (Sjare *et al*. 2000) calculated using the methods of Warren et *al.* (1997). These data are available from 1954-1997. As such, we have assumed that the pregnancy rates in 1998 and 1999 are constant at the 1997 values. For periods in which there are no available data (e.g. 1971-77 for age 5), we have taken the average value of the pregnancy rates immediately prior to and following the gap.

Variance Estimates

As in the Cadigan-Shelton model, there is a statistical component in the current model. In this study the survey estimates are re-sampled to obtain approximate 95% confidence intervals for the pup and population trajectories, and the replacement yields, similar to Stenson *et al*. (1999), using the methods outlined in Warren *et al*. (1997). Calculating replacement yields for each of the estimated populations provides an approximate 95% C.I. for the estimated replacement yield.

The uncertainty in the population trajectory was estimated using the following re-sampling scheme. The set of pup production estimates were re-sampled 1000 times. The survey estimates of pup production in year t_i, $\tilde{n}_{0,t_i}$, are assumed to be normally distributed as:

$$\tilde{n}_{0,t_i} \sim \mathrm{N}(n_{0,t_i}, \tilde{s}^2_{ti}),$$

where n_{0,t_i} is the true pup production for year t_i, and $\tilde{s}^2_{ti}$ is the estimated variance of $\tilde{n}_{0,t}$. Furthermore, the re-sampled estimates of pup production, are assumed to be specified by the normal distribution:

$$N_{0,t_i} \sim \mathrm{N}(\tilde{n}_{0,t_i}, \tilde{s}^2_{ti}).$$

To calculate replacement harvest, the estimated numbers-at-age for year 2000 were projected forward one year to 2001 using the 1999 estimates of pregnancy-at-age (see Table 4) in the year 2000. The catch in year 2000 was removed assuming the 1+ proportions-at-age from the catch (Table 5) were equal to the 1+ proportions-at-age in the reported landings plus by-catch in 1999 (Stenson *et al*., 2000a). The average proportion of age-class 0 in reported catch plus by-catches from 1996-99 is 70%. In order to illustrate the impact of differing age structures, replacement yields were also estimated assuming 60% (average age composition from 1984-94) and also 80% pups (age composition of the recent catches in southern Canadian areas, respectively). The 2000 total catch was varied until the total population in

2001 equaled that in 2000. The impact of harvesting the harp seal population at these replacement yields for 5 and 10-year periods (i.e. up until 2005 and 2010) was also investigated.

The replacement yield reported here includes by-catch, struck and lost, and all reported catches in Canada and Greenland. In order to estimate the equivalent landed catch in the Canadian commercial harvest (i.e. Front and Gulf), we assumed that the levels of by-catch, struck and lost, Greenland catches and Arctic catches were the same as in 1999. We adjust the calculated replacement yields by these amounts and present the replacement yields in units of Canadian Front and Gulf catch. If the levels of the other removals change, they will impact the estimated Canadian Front and Gulf landings that will achieve the replacement harvest.

Results and Discussion

The rate of unreported mortality (*m*) can be a difficult parameter to estimate in animal populations. Independent estimates of the age structure of the population are difficult to obtain due to potential biases in sampling (e.g. Sergeant 1975; Roff and Bowen 1986) and changes in recruitment and hunting mortality. Roff and Bowen (1983) reviewed the available data on mortality rates of harp seals. They concluded that although there was conflicting evidence about the relative levels of mortality among young of the year and older seals, it was prudent to assume some level of higher mortality among first year animals. The level of mortality that occurs among young seals is not known, but Roff and Bowen (1983, 1986), Shelton et *al*. (1992, 1996) and Stenson et *al*. (1999) assumed that mortality during the first year was 3 times that of older seals. This assumption was also used to estimate population size and sustainable yields of Greenland Sea and White Sea / Barents Sea harp seals (Anon 1999a). We attempted to estimate mortality of young of the year as a multiple of the mortality of older seals (γ), but were unable to fit a 3-parameter model to the limited data available on pup production. It is likely impossible to estimate γ (due to confounding) in this model given that the model is fitting to pup production and that we also estimate unreported mortality *m*. For the 'base case' we use $\gamma = 3$ to make our results comparable to earlier studies. The results obtained when re-sampling the survey data are restricted to the $\gamma = 3$ case.

Anon. (1999a) also examined the impact of assuming that mortality among young seals in the White Sea is higher (5 times that of 1+ seals). In order to investigate the impact of the assumed level of mortality among first year animals, we varied the multiplier used (γ) between 1 (constant mortality for all ages), 3 and 5. Model runs indicate that there is very little difference in predicted pup production (Figure 2; Table 6) for γ = 1, 3, and 5, not surprising considering that the data used in fitting are pup production estimates. Population trajectories also exhibit similar trends, but population size differs slightly for each of the gamma values (Figure 3; Table 7). In the year 2000, the predicted pup production of the three model runs range from 836,000 to 848,000 and the predicted population sizes are approximately 5.41M, 5.22M, and 5.09M for γ = 1, 3, and 5, respectively. Parameter estimates and likelihood values (negative maximum likelihood) corresponding to these estimates are presented in Table 8. Even though the fit improves as γ increases, the (profile) likelihood ratio test indicates that no pair of estimates are significantly different. For γ=3, the mortality estimate indicates that 84% of pups will survive their first year of life, and that the annual survival rate of older cohorts is 94%.

The pup production estimates show that following a slight decline in the mid 1960's to 1970, the population has produced pups at a rate that has increased almost steadily since this period. Some aberrations exist, a result of the declining pregnancy rates (which change abruptly). Using smoother pregnancy rates should result in less 'sharp' changes in the estimated pup production.

The population trajectory also shows a pattern of growth since the mid 1960's but only up to the mid 1990s. Unlike pup production, total population seems to have stabilized at slightly over 5 million since about 1996. Figure 4 shows the results of 988 population trajectories estimated by the 1000 re-sampled the pup production estimates (12 model fits failed to converge) for the base case (γ = 3). The distribution of population sizes in the year 2000 is presented in Figure 5. The mean estimated population size in the year 2000 for this scenario is 5,215,000 with asymptotic 95% confidence interval of 4,022,000 to 6,408,000. This resampling process only accounts for the error in the pup production estimates. As such, the estimated variance and confidence intervals are likely to be underestimated. When the error associated with estimating pregnancy rates is included in the resampling process, the asymptotic confidence intervals will likely expand by only a small amount (Warren *et al*. (1997) and Healey and Stenson (unpublished)).

Based on comparison of the 1996 and 2000 population estimates for each of the 988 trajectories given in Figure 4, the average change in population size over these four years has been –0.7% (95% C.I. -9.9 – 7.7%), which is not significantly different from zero (i.e. no discernable change in population size). During this same period pup production increased by an average of 13.0% (95% C.I. 5.7 – 20.0%). This difference arises since the large catch of young observed in the past four years has not yet impacted the breeding population. It will do so when cohorts mature, at approximately age 5 (i.e. starting in 2001) (Sjare et *al*., 2000).

Estimates of sustainable yield require accurate predictions of reproductive rates and the age structure of the harvest over extended periods of time. These are unlikely to be constant and therefore the use of sustainable yields to determine harvest quotas is questionable. Replacement yields do not require these predictions to extend beyond the near term and therefore, the sensitivity of these predictions on the long-term sustainability of the population is diminished. However, it is important to monitor the annual removals and re-estimate replacement yield on a regular basis.

The replacement yields, and the resultant population sizes in 2005 and 2010 if the replacement yields are harvested in the intervening period are presented for various scenarios in Table 9. The replacement yield reported here includes reported catches in Canada and Greenland, by-catch, and struck and lost. Under the base case of $\gamma = 3$, the replacement yields are 522,000, 531,000, and 541,000 if the proportion of young in the catch is 0.6, 0.7, or 0.8, respectively (Table 9). The frequency distribution of replacement yields corresponding to each of the populations shown in Figure 4 is given in Figure 6. Assuming that 70% of the removals consist of age class 0 animals, the mean replacement yield is 533,000, 95% C.I.:(373,000, 693,000).

To project the impact of this assumption on future populations, we have assumed future pregnancy rates and the 1+ age structure of the catch will be constant at their 1999 levels. If the proportion of age class 0’s taken by all components of removals is 60%, then continued removals at the replacement yield level will cause the population to decrease slightly over the next 5 to 10 years. However, if the overall proportion of the age 0 group taken is 0.8 (resulting in fewer older reproducing animals being harvested), then the population size will increase. At the current level of approximately 70% age class 0, the population will remain relatively stable.

In order to estimate the portion of the replacement yield that will become landed catch in the Canadian commercial harvest, we assumed that the levels of catches in Greenland and in the Canadian Arctic, struck and loss associated with these harvests and by-catch were the same as in 1999. We adjust the calculated replacement yields by these amounts and present the replacement yields in units of Canadian Front and Gulf landings. The proportion of young in the Canadian commercial harvest was varied from 70% to 90% to illustrate the impact of changes in the age structure on the replacement yields. The situation for which the overall proportion of age 0’s taken from all hunt components is 70% and the Canadian Front and Gulf harvest is 90% closely matches the data for 1999 (the Canadian Front and Gulf actually took over 95% pups in 1999). Using these assumptions, the replacement yield was estimated to be 531,000, with a corresponding Canadian Front and Gulf yield 257,000, 95% C.I. (102,000, 342,000). If the levels of the northern catches or by-catch change, they will naturally impact the estimated Canadian Front and Gulf landings that will achieve the replacement harvest.

In summary, the results indicate that the estimated population size of the northwest Atlantic harp seal herd is approximately 5.2 million, and the population has been stable at this level for the past few years. Total pup production has been generally increasing since the mid-1970’s. In the coming years the rate of increase is expected to slow as the large pup catches taken since 1996 begin to affect the breeding population.

Acknowledgements

The authors would like to thank Noel Cadigan and Peter Shelton, DFO Science Branch, St. John's, for helpful discussion on the population dynamics model and estimation. Dave MacKinnon, Wayne Penney, Becky Sjare and Dennis Wakeham, DFO Science Branch, St. John's, provided assistance with the data used in this study. Aqqalu Rosing-Asvid kindly provided us with the revised estimates of Greenland harvests.

References

Anonymous. 1999a. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals. ICES CM 1999/ACFM:7.

Anonymous. 1999b. Proceedings of the National Marine Mammal Review Committee Montreal, Quebec. February 1-5, 1999. Can. Stock Assess. Proc. Ser. 99/14. 22p.

Benjaminsen, 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.

Bowen, W. D. and Sergeant, D. E. 1983. Mark-recapture estimates of harp seal pup (*Phoca groenlandica*) production in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 40(6):728-742.

Bowen, W. D. and Sergeant, D. E. 1985. A mark-recapture estimate of 1983 harp seal pup production in the northwest Atlantic. Northwest Atl. Fish. Organ. SCR Doc. 85/I/1, Ser., N935. 14p.

Cadigan, N. G., and P. A. Shelton. 1993. SAS programs for fitting a seal population dynamics model. Can. Tech. Rep. Fish. Aquat. Sci., 1927: 34 p.

Cooke, J. G., 1985. Population estimates of northwest Atlantic harp seal (*Phoca groenlandica*) based on age structure data. Can. J. Fish. Aquat. Sci. 42:468-473.

Fisher, H. D., 1952. Harp seals of the northwest Atlantic. Fish. Res. Board. Can. Atl. Biol. Stn. Gen. Circ. No. 20: 4p.

Lavigne, D. M., Innes, S., Barchard, W., and Doubleday, W. G. 1980. The 1977 census of northwest Atlantic harp seals, *Pagophilus groenlandicus*. Int. Comm. Northwest Atl. Fish. Sel. Pap. 6:55-70.

Lavigne, D. M., Innes, S., Kalpakis, K., and Ronald, K. 1982. An aerial census of western Atlantic harp seals (*Pagophilus groenlandicus*) using ultraviolet photography. Int. Comm. Northwest Atl. Fish. Res. Doc., 75/144, Ser. 3717. 10p.

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

Myers, R. A. and Bowen, W. D. 1989. Estimating bias in aerial surveys for harp seal pup production. J. Wildl. Manag. 53:361-372.

Roff, D. A., and W. D. Bowen. 1983. Population dynamics and management of the northwest Atlantic harp seal *(Phoca groenlandica)*. Can. J. Fish. Aquat. Sci., 40: 919-932.

Roff, D. A. and Bowen, W. D. 1986. Further analysis of population trends in the northwest Atlantic harp seal (*Phoca groenlandica*) from 1967 to 1985. Can. J. Fish. Aquat. Sci. 43:553-564.

Sergeant, D. E. 1971. Calculation of harp seal production in the western north Atlantic. Int. Comm. Northwest Atl. Fish. Redbook 1971, Part III, Res. Doc. 71/7:157-183.

Sergeant, D. E. 1975. Estimating numbers of harp seals. Rapp. P.-v. Reun. Cons. int. Explor. Mer 169:274-280.

Sergeant, D. E. and H. D. Fisher. 1960. Harp seal populations in the western north Atlantic from 1950 to 1960. Fish. Res. Board Can. Arctic Unit Circular No. 5.

Shelton, P. A., N. G. Cadigan, and G. B. Stenson. 1992. Model estimates of harp seal trajectories in the northwest Atlantic. Can. Atl. Fish. Stock Assess. Comm. Res. Doc., No. 89, 23 p.

Shelton, P. A., G. B. Stenson, B. Sjare, and W. G. Warren. 1996. Model estimates of harp seal numbers-at-age for the Northwest Atlantic. NAFO Sci. Coun. Studies. 26: 1-14.

Sjare, B. and G.B. Stenson. 2000. Estimating struck and loss rates for harp seals in the northwest Atlantic. Can. Stock Assess. Sec. Res. Doc. 2000/076.

Sjare, B., G.B. Stenson and W. Warren. 2000. Recent estimates of reproductive rates for harps seals in the northwest Atlantic. Can. Stock Assess. Sec. Res. Doc 2000/077.

Stenson, G. B., Myers, R. A., Hammill, M. O. Ni, I-H., Warren, W. G., and Kingsley, M. C. S. 1993. Pup production of harp seals *Phoca groenlandica*, in the northwest Atlantic. Can J. Fish. Aquat. Sci. 50:2429-2439.

Stenson, G. B., M. O. Hammill, M. C. S. Kingsley, B. Sjare, W. G. Warren, and R. A. Myers. 1996. 1994 pup production of the northwest Atlantic harp seal, *Phoca groenlandica in* the Northwest Atlantic during 1994. NAFO Sci. Coun. Studies 26:47-61.

Stenson, G.B., B. Healey, P. A. Shelton and B. Sjare. 1999. Recent trends in the population of northwest Atlantic harp seals, *Phoca groenlandica*. Can. Stock Assess. Sec. Res. Doc. 99/107. 24p.

Stenson, G.B., B. P. Healey, B. Sjare, and D. Wakeham. 2000a. Catch-at-Age of northwest Atlantic harp seals, 1952-1999. Can. Stock Assess. Sec. Res. Doc. 2000/079.

Stenson, G. B., M. O. Hammill, J.F. Gosselin and B. Sjare. 2000b. 1999 Pup production of harp seals, *Phoca groenlandica*, in the northwest Atlantic. Can. Stock Assess. Sec. Res Doc. 2000/080.

Walsh, D., B.Sjare, G.B. Stenson, and E.H. Miller. 2000. Preliminary estimates of harp seal by-catch in the Newfoundland lumpfish fishery. Can. Stock Assess. Sec. Res Doc. 2000/078.

Waring, G.T., D.L. Palka, P.J. Clapham, S. Swartz, M.C. Rossman, T.V.N. Cole, L.J. Hansen, K.D. Bisack, K.D. Mullin, R.S. Wells, D.K.Odell, and N.B. Barros. 1999. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 1999. NOAA Technical Memorandum, NMFS-NE-153.

Warren, W. G. 1991. A critical review of mark-recapture estimation of northwest Atlantic harp seal production 1977-83. Can. Atl. Fish. Stock Assess. Comm. Res. Doc., No. 59, 12 p.

Warren, W. G., P. A. Shelton and G. B. Stenson. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part II: Uncertainty in the estimates of harp seal population size. J. Northw. Atl. Fish. Sci. 22:289-302.

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

Table 1: Pup production surveys used to estimate pup production

Year	Estimate	Standard Error	Reference
1978	497000	34000	Roff and Bowen 1986
1979	478000	35000	Roff and Bowen 1986
1980	475000	47000	Roff and Bowen 1986
1983	534000	33000	Bowen and Sergeant 1985
1990	577900	38800	Stenson *et al*. 1993
1994	702900	63600	Stenson *et al*. 1996
1999	997900	102100	Stenson *et al*. 2000b

Table 2: Total removals of northwest Atlantic harp seals (reported landings + by-catch + struck & lost), 1952-1999.

	Age													
Year	0	1	2	3	4	5	6	7	8	9	10	11	12+	Total
1952	219536	10876	13941	9642	7359	7771	12593	8684	8456	6238	7130	5955	28398	346579
1953	219447	26292	8458	7595	5086	4924	4086	3368	3373	3231	2840	3160	20152	312012
1954	199519	38327	15053	5993	7151	3920	4686	3932	3584	2512	3478	1572	19229	308956
1955	273296	27225	10561	7776	5617	4841	4484	3641	3749	3033	3440	2916	20793	371372
1956	357914	15935	6365	4682	3634	2845	2761	2334	2415	2083	2234	1827	13828	418857
1957	182432	26232	9775	6887	5411	4328	4188	3543	3551	3067	3436	3034	21413	277297
1958	162465	30211	12029	13248	13308	11059	7505	6648	5615	5297	10263	6089	54395	338132
1959	251899	25194	9584	6699	5137	4373	4310	3629	3592	3135	3478	2925	20834	344789
1960	176927	38286	14839	11380	7894	6453	6447	5187	5008	4320	4930	4213	30142	316026
1961	184800	9159	3621	3402	3463	1488	1678	1445	997	930	1316	782	4243	217324
1962	219330	32755	35492	10658	9642	6765	3218	2869	2898	2828	1422	1453	14459	343789
1963	284999	11568	10023	7963	4807	3841	4054	4035	3730	3427	3983	3742	23113	369285
1964	279868	8001	7018	6965	7499	5119	7119	3963	3135	2944	4490	2408	28559	367088
1965	195499	14106	7161	5883	5828	6776	6138	2673	1299	932	1587	638	10246	258766
1966	261978	15451	12172	5987	5583	5651	5527	5078	3397	1886	2022	2459	16894	344085
1967	285596	15430	7430	3389	2801	3593	4340	3812	2649	1766	1658	1980	15342	349786
1968	166413	7605	5657	3870	2417	2103	1978	2622	2530	1780	1845	1374	12251	212445
1969	243285	22981	4169	3875	3083	3263	2414	2727	3107	2304	2036	1751	13178	308173
1970	226503	9914	8405	3787	3181	3085	1855	1930	1956	1854	2295	1609	10068	276442
1971	220822	9356	3617	3423	1677	1412	974	788	664	991	983	786	4224	249717
1972	126199	6148	3840	2362	2305	1125	962	843	522	270	445	414	3500	148935
1973	110548	9313	5953	4040	2897	3835	1379	1220	1333	781	875	931	5604	148709
1974	125659	13542	7337	2744	2314	2095	3037	1045	1112	1188	877	682	5992	167624
1975	151069	16419	7701	3957	2239	1844	1644	1641	983	772	1024	671	4232	194196

Table 2. Continued

Year	Age 0	1	2	3	4	5	6	7	8	9	10	11	12+	Total
1976	150261	20935	10085	5497	3473	1185	799	745	767	337	559	442	2810	197895
1977	151496	11394	7774	6560	4753	2385	1362	1094	688	336	454	435	2898	191629
1978	136172	27319	14993	9283	5934	4033	3010	997	1352	594	926	458	3811	208882
1979	156317	22747	11646	5995	3358	2226	1708	1152	780	616	502	355	4518	211920
1980	144697	25954	12943	9090	5049	3411	2655	2028	1582	1083	937	998	7368	217795
1981	196515	22477	11404	8692	5660	4104	2856	1926	1541	814	1017	1001	6835	264842
1982	167498	23830	14302	8694	4539	3259	1954	1877	1293	1681	1293	1022	5949	237191
1983	69499	18548	9220	6990	5051	2454	2276	1960	931	1056	1043	750	4954	124732
1984	36460	11362	11983	10284	6132	4016	3073	2513	1961	971	1105	1058	8907	99825
1985	25777	10245	9881	8981	5081	3315	2574	2078	1746	850	1019	770	7450	79767
1986	40913	12506	11120	10873	5982	3879	3025	2397	1964	1022	1090	1008	9125	104904
1987	66411	17985	16143	16201	9763	6148	4760	3565	3053	1642	1666	1578	13529	162444
1988	92908	23563	21742	19129	11269	6978	5079	3769	3319	1534	1530	1334	15016	207170
1989	75550	17477	15847	15313	9475	6466	4744	3495	2909	1451	1459	1323	13006	168515
1990	49985	21659	19199	20162	12090	8057	5590	3984	3044	1641	1752	1711	15197	164071
1991	65607	19701	16160	16508	10667	7751	5535	3995	3276	1598	1706	1753	14447	168704
1992	70003	26669	21685	19015	12119	8439	6793	5292	3782	2473	2034	1806	16362	196472
1993	57944	23585	19537	18507	10837	7625	5922	4552	3738	1912	1827	1690	15171	172847
1994	70227	28998	24014	24697	16673	11325	8715	6293	5679	3030	2678	2689	22017	227035
1995	59028	33521	27826	26307	16074	12513	8960	7582	5248	2641	2398	2457	21560	226115
1996	219087	48683	39473	30427	18458	13419	10334	8504	6741	3460	4030	3764	35775	442155
1997	257129	47907	33296	26759	15778	11083	8558	6796	5540	2678	3679	3120	25004	447327
1998	289592	39448	30127	29757	17136	14079	11075	8752	8219	4347	3566	3962	28866	488926
1999	280819	41801	34454	32655	18839	13341	10238	7974	6841	3158	3215	3094	26985	483414

Table 3: Assumed levels of struck and lost for young of year (0) and older (1+) seals.

	Harvest Area			
	Front and Gulf		Can. Arctic and Greenland	
	0	1+	0	1+
1952-1982	0.01	0.5	0.5	0.5
1983-1999	0.05	0.5	0.5	0.5

Table 4: Harmonized pregnancy rates used in the model (Sjare et *al*. 2000).

Year	Age 4	Age 5	Age 6	Age 7	Age 8+
1954	0.0192	0.1818	0.5435	0.7231	0.874
1955	0.0192	0.1818	0.5435	0.7231	0.874
1956	0.0192	0.1818	0.5435	0.7231	0.874
1957	0.0192	0.1818	0.5435	0.7231	0.874
1958	0.0192	0.1818	0.5435	0.7231	0.874
1959	0.0192	0.1818	0.5435	0.7231	0.874
1960	0.0192	0.1818	0.5435	0.7231	0.874
1961	0.0192	0.1818	0.5435	0.7231	0.874
1962	0.0192	0.1818	0.5435	0.7231	0.874
1963	0.0192	0.1818	0.5435	0.7231	0.874
1964	0.0192	0.1818	0.5435	0.7231	0.874
1965	0.0192	0.1818	0.5435	0.7231	0.874
1966	0.0192	0.1818	0.5435	0.7231	0.874
1967	0.0192	0.1818	0.5435	0.9512	0.874
1968	0.0192	0.1818	0.5435	0.9512	0.874
1969	0.0192	0.1818	0.5435	0.8143	0.874
1970	0.0192	0.1818	0.5435	0.8143	0.874
1971	0.0192	0.3834	0.7162	0.8143	0.874
1972	0.0192	0.3834	0.7162	0.8143	0.874
1973	0.0192	0.3834	0.7162	0.8143	0.874
1974	0.0192	0.3834	0.7162	0.8143	0.874
1975	0.0192	0.3834	0.7162	0.8143	0.874
1976	0.0192	0.3834	0.7162	0.8143	0.874
1977	0.0192	0.3834	0.7162	0.8143	0.874
1978	0.0192	0.5849	0.8889	0.8143	0.874
1979	0.1395	0.5849	0.8889	0.8143	0.874
1980	0.1395	0.5849	0.8889	0.8143	0.874
1981	0.1395	0.5849	0.8889	0.8143	0.874
1982	0.1395	0.2054	0.8889	0.8143	0.7763
1983	0.1395	0.2054	0.7172	0.8143	0.7763
1984	0.1395	0.2054	0.7172	0.8143	0.7763
1985	0.1395	0.2054	0.5455	0.8143	0.7763
1986	0.1395	0.2054	0.5455	0.8143	0.7763
1987	0.1395	0.2054	0.5455	0.8143	0.7763
1988	0.1395	0.2054	0.5455	0.6866	0.7763
1989	0.1395	0.2054	0.5455	0.5588	0.7763
1990	0.1395	0.2054	0.5455	0.5588	0.6456
1991	0.1395	0.2054	0.5455	0.5588	0.6456
1992	0.1395	0.2054	0.5455	0.5588	0.6456
1993	0.0377	0.2054	0.3103	0.5588	0.6456
1994	0.0377	0.2054	0.3103	0.5588	0.6456
1995	0.0377	0.2054	0.3103	0.5588	0.6456
1996	0.0377	0.2054	0.3103	0.5588	0.6456
1997	0.0377	0.2054	0.3103	0.5588	0.6456
1998	0.0377	0.2054	0.3103	0.5588	0.6456
1999	0.0377	0.2054	0.3103	0.5588	0.6456

Table 5. Catch proportion-at-age used to calculate replacement yields. Values of β examined equal 0.6, 0.7, and 0.8.

Age	Proportion of Catch
0	β
1	(1-β)*(0.2133)
2	(1-β)* (0.1665)
3	(1-β)* (0.1501)
4	(1-β)* (0.0876)
5	(1-β)* (0.0647)
6	(1-β)* (0.0502)
7	(1-β)* (0.0398)
8	(1-β)* (0.0344)
9	(1-β)* (0.0171)
10	(1-β)* (0.0177)
11	(1-β)* (0.0171)
12+	(1-β)* (0.1414)

Table 6: Estimated pup production for northwest Atlantic harp seals, 1960-2000.

Year	Survey	γ=1	γ=3	γ=5
1960		349510.8	352755.6	354672.5
1961		358463.2	361895.5	363971.1
1962		372549.3	376465.9	378967.6
1963		410456.7	415169.7	418315.5
1964		422294.6	428686.9	433098.8
1965		421779.9	429798.4	435456.1
1966		413129	422095.5	428514
1967		407304.3	416348.6	422856.9
1968		400118.8	407590.5	412937.7
1969		387205.6	393815.3	398537.7
1970		373905.2	380262	384830
1971		367368.8	372796.9	376686.8
1972		388048.7	391112.5	393257.5
1973		389087.5	392272.9	394478.4
1974		400121.1	403278.8	405444.6
1975		406587.9	409808.5	412008.7
1976		407468.6	410893.8	413245.9
1977		410421.1	414003.3	416486.2
1978	497000	428681.4	431863.2	434091.7
1979	478000	487721	488026.4	488221.5
1980	475000	524036.2	522849.4	521997.9
1981		546908.5	545439.9	544377.4
1982		562896.2	561391.6	560289.5
1983	534000	505664.9	505433.5	505204
1984		509226	509700.1	509992.9
1985		533774	533587.9	533437.1
1986		545865	545667.9	545562.9
1987		580260.8	578405.9	577167.4
1988		615369.2	612174.1	609997
1989		637948.3	634809.7	632669.5
1990	577900	665012.2	662771.2	661236.2
1991		620408.4	616684.6	614040.6
1992		657817.6	654555.8	652219.3
1993		693070.4	690307.2	688330.6
1994	702900	676163	677873.3	679046.7
1995		710795.2	712910.9	714409.3
1996		741398.8	743890.8	745697.3
1997		770117	773187.3	775443.4
1998		793280.8	797022.8	799789.9
1999	997900	818212.2	822719.1	826062.1
2000		836338.8	841871.2	845958.4

Table 7: Estimated population size for northwest Atlantic harp seals, 1960-2000.

Year	γ=1	γ=3	γ=5
1960	2143954	2083793	2042732
1961	2052085	1993559	1953586
1962	2075827	2018362	1979182
1963	2013760	1958023	1920166
1964	1943115	1889456	1853267
1965	1878862	1826338	1791109
1966	1914901	1859538	1822421
1967	1860294	1806709	1770734
1968	1796696	1744483	1709279
1969	1857103	1799744	1760984
1970	1807685	1751011	1712745
1971	1785717	1728882	1690480
1972	1811720	1752742	1712817
1973	1934309	1867168	1821879
1974	2059846	1985340	1935116
1975	2165086	2084653	2030436
1976	2238424	2154332	2097645
1977	2306177	2219416	2160908
1978	2393653	2304497	2244343
1979	2517585	2421455	2356522
1980	2666508	2558916	2486533
1981	2822545	2701198	2619900
1982	2938575	2806169	2717720
1983	3016214	2872822	2777173
1984	3200740	3049598	2948575
1985	3421367	3262156	3155411
1986	3658513	3491139	3378754
1987	3889721	3715028	3597559
1988	4084822	3902095	3779272
1989	4246106	4055692	3927932
1990	4460854	4262765	4130033
1991	4620745	4411996	4272049
1992	4802745	4591788	4450396
1993	4980859	4766458	4622840
1994	5152814	4937343	4793223
1995	5295437	5082912	4940532
1996	5459894	5247833	5105651
1997	5433334	5228467	5091243
1998	5426743	5228064	5095242
1999	5405362	5212286	5083560
2000	5408879	5218753	5092357

Table 8: Estimated parameter values (from estimates of log(*m*) and log(*s*)).

	m	γm	s	Likelihood
γ=1	0.070124	-	2.151185	14.26
γ=3	0.058425	0.175275	2.226661	13.42
γ=5	0.050211	0.260055	2.284662	12.86

Table 9: Replacement yields (in units of 'total removals'), corresponding Canadian Front and Gulf Harvest (assuming γ = 3), and population sizes if the replacement yield is taken for 5 or 10 years, for various age structures of future catch.

Age 0 % (Overall)	Replacement Yield	Age 0% (Cdn. F&G)	Cdn. F&G Landings	Pop'n in 2005 (millions)	Pop'n in 2010 (millions)
0.6	522,000	0.7	213,000	5.19	5.08
		0.8	230,000		
		0.9	249,000		
0.7†	531,000	0.7	220,000	5.25	5.28
		0.8	237,000		
		0.9†	**257,000**		
0.8	541,000	0.7	228,000	5.32	5.49
		0.8	225,000		
		0.9	265,000		

† = Similar to 1999 Proportions

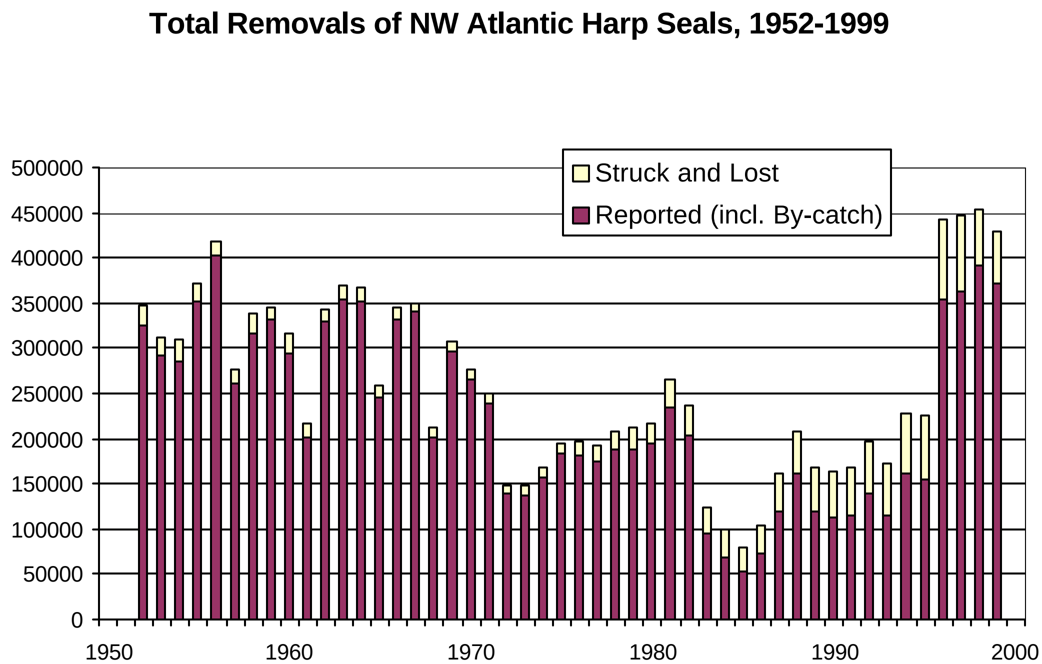

Figure 1: Total removals (reported landings+ by-catch + struck & lost) of Northwest Atlantic harp seals, 1952-1999.

.

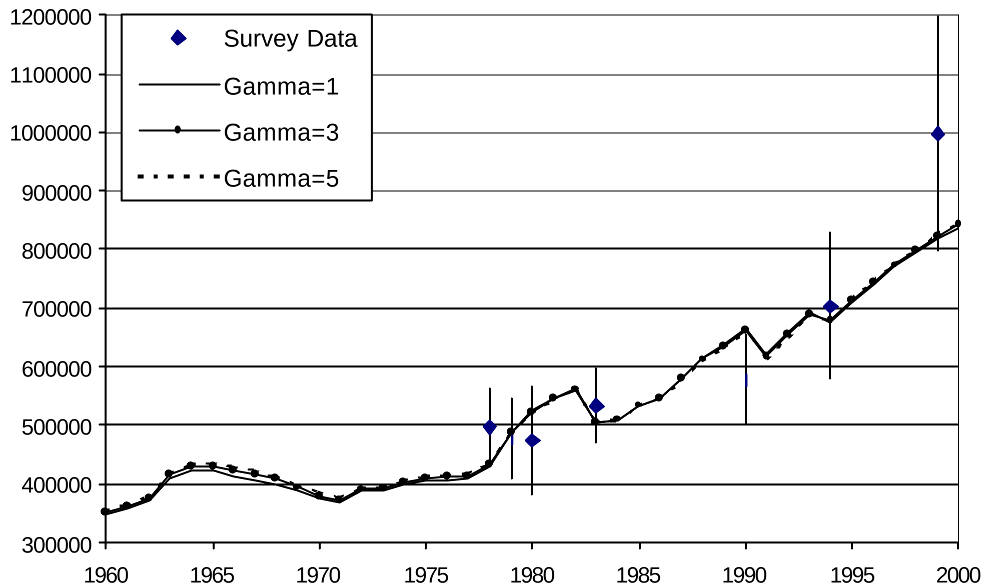

Figure 2: Estimated pup production of northwest Atlantic harp seals under three differing assumptions for first year mortality (gamma), survey estimates of pup production, and asymptotic 95% C.I.'s for the survey estimates.

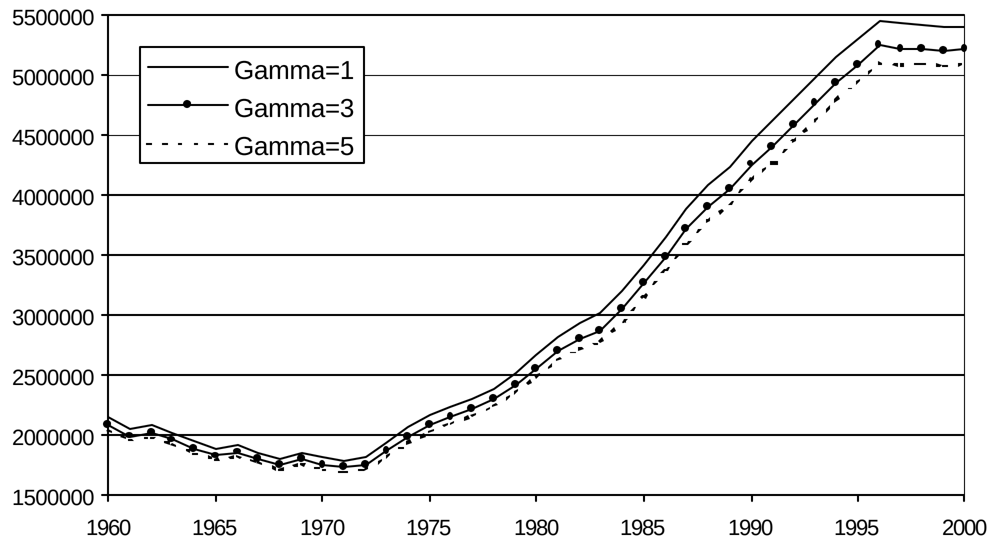

Figure 3: Estimated population size of northwest Atlantic harp seals under three differing assumptions for first year mortality (Gamma).

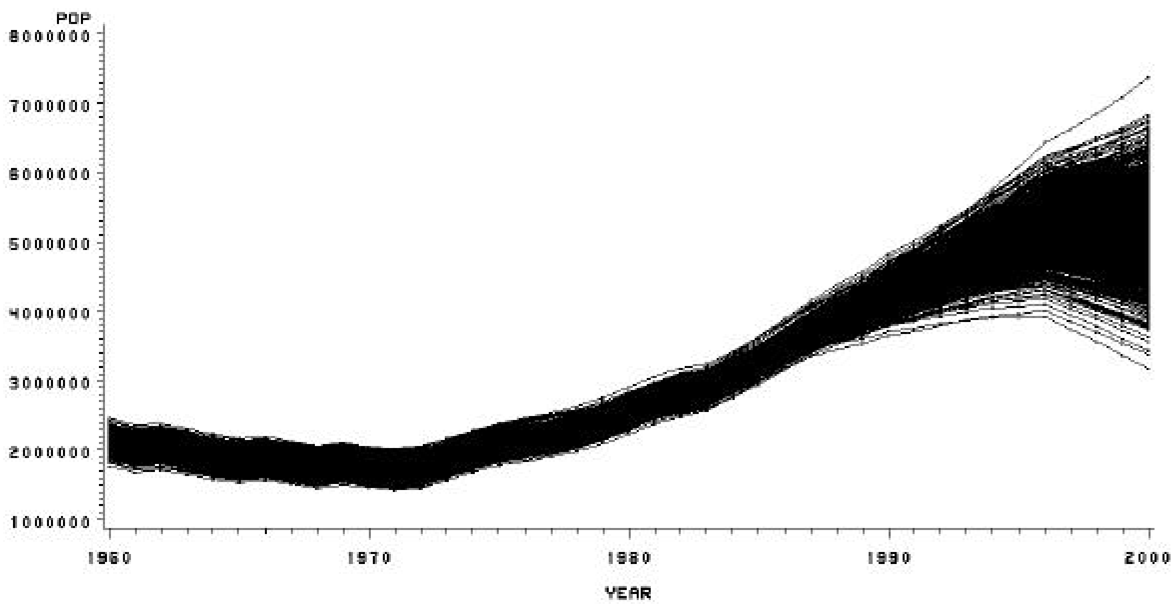

Figure 4: Population trajectories of northwest Atlantic harp seals estimated by 1000 resamplings of estimated pup production.

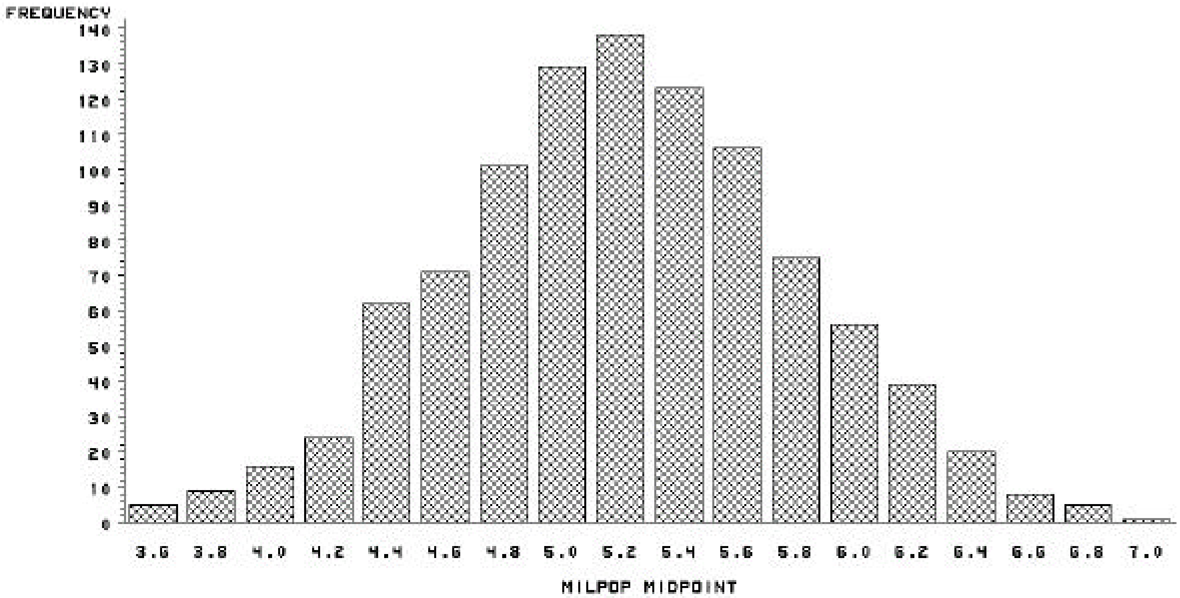

Figure 5: Frequency distribution of estimated population sizes in 2000 based upon 1000 resamplings of pup production estimates. Mean population = 5,215,000 (SE=596,000).

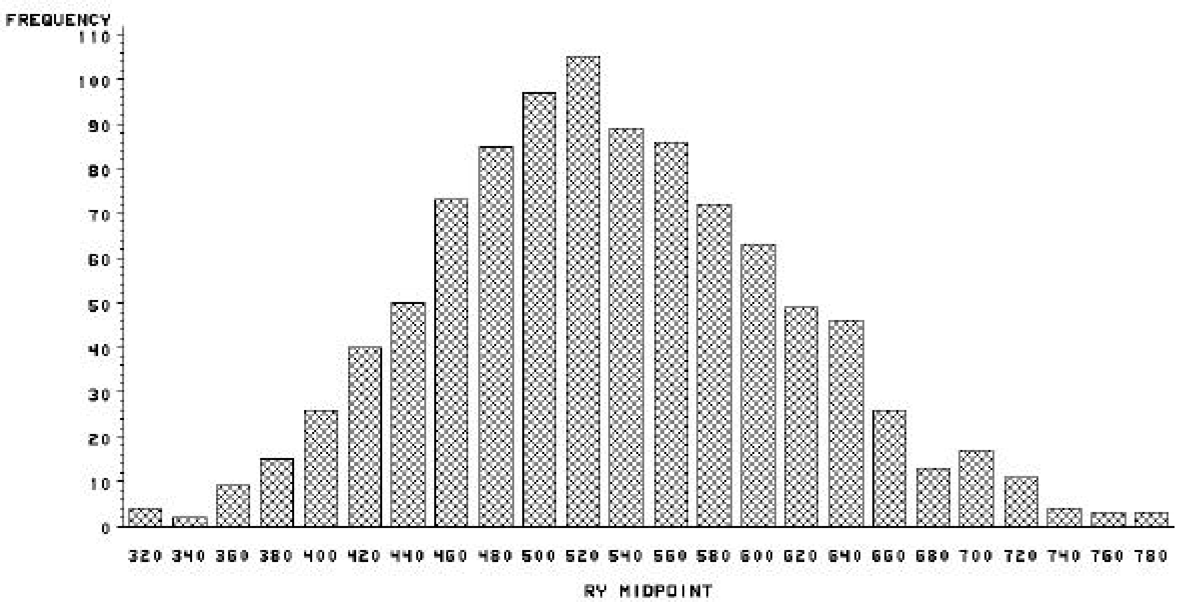

Figure 6: Frequency distribution of estimated replacement yields based upon 1000 resamplings of estimated pup production assuming gamma=3 and 70% of the total removals consist of age class 0. Mean RY = 533,000 (SE=82,000).