Canadian Stock Assessment Secretariat Research Document 99/107

Not to be cited without permission of the authors¹ Secrétariat canadien pour l'évaluation des stocks Document de recherche 99/107

Ne pas citer sans autorisation des auteurs1

Recent Trends in the Population of Northwest Atlantic Harp Seals, Phoca groenlandica

G. B. Stenson, B. Healey, P. A. Shelton and B. Sjare

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

¹ This series documents the scientific ¹ La présente série documente les bases basis for the evaluation of fisheries scientifiques resources in Canada. addresses the issues of the day in the time traite des problèmes courants selon les frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the Les documents de recherche sont publiés official language in which they are provided to the Secretariat.

des évaluations As such, it ressources halieutiques du Canada. Elle échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

> dans la langue officielle utilisée dans le manuscrit envoyé au secrétariat.

ISSN 1480-4883 Ottawa, 1999

Canadä

Abstract

Trends in the abundance of Northwest Atlantic harp seals (*Phoca groenlandica*) for the period 1960 to 1998 were estimated using survey estimates of pup production, and annual estimates of pregnancy rates and age structure of the catch. These data were fit to a two parameter age structured population model under two different assumptions of pup mortality. In one model formulation pup mortality was assumed to be equal to that of seals one year of age and older (1+) while in the second pup mortality rate was assumed to be 3 times the 1+ mortality rate. The uncertainty associated with the population trajectory from the first formulation was estimated by randomly resampling from within the sampling error of the available pup production estimates. Replacement and sustainable yields were estimated using both model formulations under differing assumptions of the age structure of the harvest. The impact of assuming different levels of unreported mortality on population trends was also examined.

Based upon the first model formulation, the total population was estimated to be approximately 5.5 million (95% C. I. 4.3 - 6.7) in 1998 while assuming higher pup mortality results in a slightly lower estimate of 5.3 million. Under both models, the population was estimated to have increased from the early 1970s until 1996. Since then the population has been relatively stable, growing at less than 0.5% per year. Using the current age structure of the harvest, the estimated 1999 replacement harvest was estimated to be approximately 407,000 animals under the assumption of constant mortality and 402,000 under the assumption of higher pup mortality. The estimates of population size and instantaneous mortality are reduced slightly if unreported mortality is added. Assuming low or moderate levels of additional unreported mortality result in slightly declining (0.2 – 0.8%) populations. Assuming a high level of unreported mortality resulted in an estimated 2% decline in the population in 1998, but the level of loss for young seals in Atlantic Canada used for this run is greater than the current data supports. Given the uncertainty associated with the model estimates the differences among the various model runs rates are not significant.

Résumé

Les tendances de l'abondance du phoque du Groenland (*Phoca groenlandica*) dans le nord-ouest de l'Atlantique pendant la période 1960 à 1998 ont été déterminées à partir de la production de jeunes estimée par relevés et des estimations annuelles du taux de gravidité et de la structure des âges des captures. Ces données ont été ajustées à un modèle de population à deux paramètres structuré par âges en fonction de deux hypothèses de mortalité des jeunes. Dans l'une des formulations, la mortalité des jeunes a été supposée égale à celle des phoques d'un an ou plus (1+) et, dans l'autre, à trois fois le taux de mortalité des 1+. L'incertitude liée à la courbe de la population de la première formulation a été estimée par un ré-échantillonnage aléatoire de l'erreur d'échantillonnage des donnés disponibles d'estimations de production de jeunes. Le rendement de remplacement et le rendement soutenu ont été estimés à l'aide des deux formulations du modèle selon diverses hypothèses quant à la structure des âges de la récolte. L'incidence de divers niveaux de mortalité non déclarée sur les tendances de la population a aussi été examinée.

Selon la première formulation du modèle, la population totale estimée s'élevait à 5,5 millions environ (I.C. 95% de 4,3 - 6,7) en 1998, alors qu'en supposant un niveau plus élevé de mortalité des jeunes, on obtient une estimation légèrement inférieure, de 5,3 millions d'individus. Selon les deux modèles, la population a augmenté du début des années 1970 jusqu'à 1996. Depuis, elle a été relativement stable, s'accroissant de moins de 0,5 % par an. Utilisant la structure actuelle des âges de la récolte, on obtient une récolte de remplacement estimée à 407 000 animaux environ pour 1999, si l'on suppose une mortalité constante, et de 402 000 animaux, selon l'hypothèse d'une mortalité plus élevée des jeunes. Les estimations de l'effectif de la population et de la mortalité instantanée sont réduites légèrement de par l'ajout de la mortalité non déclarée. L'utilisation de taux faibles ou moyens de mortalité supplémentaire non déclarée donne lieu à un léger déclin des populations (0,2 - 0,8 %). Un niveau élevé de mortalité non déclarée se traduit par un déclin estimé de 2 % de la population en 1998, mais le taux de perte de jeunes phoques dans le Canada atlantique utilisé pour cette analyse est supérieur à ce que supportent les données actuelles. Étant donné l'incertitude associée aux estimations du modèle, les écarts entre les résultats des diverses exécutions ne sont pas significatifs.

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, used either the survival index approach (for examples see Sergeant 1971; Winters 1978; Cooke 1985) or virtual population analysis (VPA, 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).

The most recent attempt to estimate the abundance of Northwest Atlantic harp seals was carried out by Shelton et al. (1996). Their model, described in Cadigan and Shelton (1993), 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). Two formulations were considered, Formulation 1 in which the natural mortality rate on pups was the same as that of seals one year of age and older (1+), and Formulation 2 in which the natural mortality on the pups was assumed to be 3 times the mortality on the 1+ population.

Using annual estimates of age-specific reproductive rates and catch-at-age up to 1993, Shelton et al. (1996) applied their model to six independent survey (mark-recapture and aerial) estimates of pup production (1978, 1979, 1980, 1983,1990 and 1994). The total population of Northwest Atlantic harp seals in 1994 was estimated to be 4.8 million (95% C. I. 4.1 – 5.5 million; Warren *et al.* 1997) under the first model formulation and 4.5 million using the second. The population was estimated to be growing at 5% per year in both formulations. The number of seals that could be taken in 1996 and result in the same total population as in 1995 (i.e. replacement yield) was estimated at 287,000 and 275,000 for model formulations 1 and 2, respectively (Shelton *et al.* 1996).

No new estimates of pup production are available since 1994. However, additional information has become available on catches in Greenland that indicates the level of harvest used in the previous runs of the model for the period 1975-1994 (Shelton *et al.* 1996) was underestimated (Anon 1998). Also, catches in both Canada and Greenland have increased significantly since 1996, to a level near or at the estimated replacement yields (Anon 1999). In addition, a review of the potential level of unreported mortality associated with seals that

are killed but not recovered during the harvest (Lavigne, in press) has raised concerns about the status of this population.

In light of these new data on catches and concerns about the impact of unreported catches, we have attempted to estimate the current status of Northwest Atlantic harp seals using the population model described in Shelton et al. (1996). Updated data on the harvest levels, age frequencies and age-specific reproductive rates have been incorporated into the model in order to estimate the 1998 population and replacement yields in 1999. In addition, the impact of assuming different levels of unreported mortality on population trends was also examined.

Methods

Model Structure

The population model used to estimate numbers-at-age for harp seals in the Northwest Atlantic from 1960 to 1998 is described in Shelton *et al.* (1996) and Cadigan and Shelton (1993). The model consists of two components, the first is a population dynamics model while the second involves a statistical model. This brief description of the model is taken from Shelton *et al.* (1996).

The basic formulation of the population dynamics 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

A = the 'plus' age class (i.e. older ages are lumped into this age class and not dealt with separately, taken as age 12 in this analysis).

In order to estimate numbers-at-age for years prior to the first year for which continuous pregnancy data were available, it was assumed that the annual pup catch was a constant proportion s of the number of pups born (s=(l/exploitation rate)). Thus, for years prior to the first year for which pregnancy data were available (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 A, where A is a terminal (rather than a plus) age (=25 years in the formulations that follow). This equation was applied iteratively to go back in time and fill in the numbers-at-age matrix. The numbers-at-age for the initial years do not have a large influence on model estimates beyond the mid-1970s but do influence perceptions about the decline and recovery of the population.

The statistical component of the model is

$$N_{0,tj} \sim N(n_{0,tj},\tilde{o}^2_{tj})$$

where $N_{0,tj}$ is the ith survey estimate of $n_{0,tj}$ and \tilde{o}^2_{tj} is its estimated variance.

Maximum likelihood (or equivalently least-squares) estimates of the parameters m and s were obtained using PROC NLIN in SAS applying the Newton iterative method. Following the statistical model given above, the survey estimates of pup production were given weights that are inversely proportional to their variance.

The uncertainty in the population trajectory for Formulation 1 was estimated by resampling the pup productions as describe in Warren *et al.* (1997). Each estimate of pup production was assumed to represent a normal distribution based upon the reported standard errors. A 1000 realizations were carried out to estimate the range of potential population trajectories, and mean and 95% confidence intervals of the 1998 population size determined.

A second formulation of the model was used to investigate the impact of assuming that the mortality of age class 0 (m_0) was equal to that of older seals (m_{1+}). (Roff and Bowen (1983) present arguments in favour of assuming that the mortality rate of pups is higher than that of older seals.) In this formulation, m_0 was assumed to be a constant multiplier of m_{1+} . To be consistent with previous studies (e.g. Roff and Bowen 1983, 1986; Shelton *et al.* 1996) and the assumed mortality rates for other harp seal populations (e.g. see Anon. 1999), we have assumed pup mortality is three times that of 1+ animals.

To calculate replacement harvest, the estimated numbers-at-age up until 1998 were projected to year 1999 using the 1998 estimates of pregnancy-at-age (see below). Catch was removed assuming differing proportions-at-age in the catch (Table 1). The average proportion of age-class 0 in the catch from 1994-97 (the years for which age structures are available, see Stenson *et al.* 1999) was 65%. In order to illustrate the impact of differing age structures, replacement yields were also estimated assuming 50% (average age composition from 1984-94) and 80% pups (age composition of the current catch in southern Canadian areas). The age structure of the harvest of seals 1 year of age and older was assumed to be equal to the 1994-97 average of total catches. The 1999 total catch was varied until the total population in 2000 equalled that of 1999 (i.e. catch removes excess production).

The sustainable catch was also estimated by projecting the 1998 numbers-atage forward to year 2050. Pregnancy rates and age structure of the catch (described above) were assumed to be constant. A constant annual catch (i.e sustainable yield) for the period 1999 to 2050 was varied until a constant population size ('sustainable population') was attained.

Data Inputs

Pregnancy-at-age data up to 1993 were presented in Sjare et al. (1996). The pregnancy-rate data used in this model (Table 2) was obtained from Sjare et al. (unpublished data). These data are based upon samples collected up to 1996 and a reanalysis of earlier data. Due to the highly variable nature of annual estimates of age-specific pregnancy rates, the data was 'harmonized' to find the most parsimonious representation of pregnancy rates consistent with the data. The methods used to harmonize the pregnancy data are described in Shelton et al. (1996) and Warren et al. (1997). Reproductive rates in 1997 and 1998 were assumed to be the same as in 1996.

The total annual catch-at-age up to 1998, taken from Stenson *et al.* (1999), are given in Table 3 and illustrated in Fig. 1. This table includes the revised estimates of Greenland catches since 1975 (Anon. 1999).

As in Shelton *et al.* (1996), the models were fitted to the mark-recapture estimates for 1978, 1979, 1980 and 1983 and the aerial survey estimates for 1990 and 1994 (Table 4). The mark-recapture experiments were described in Bowen and Sergeant (1983, 1985) and the 1978-80 results revised in Roff and Bowen (1986). All of these estimates were critically reviewed by Warren (1991), who also took into account the Cooke *et al.* (1985) review of harp seal population dynamics. Bowen and Sergeant (1983) also presented the results of a mark-recapture experiment based on the 1977 marking of seals in the Gulf only, but

this was not included in our analysis since Bowen and Sergeant (1983) concluded the estimates based on Gulf tags only were likely to be negatively biased.

The aerial survey estimates were taken from Stenson *et al.* (1993, 1996). Stenson *et al.* (1993) presents three estimates of pup production at the Front in 1990. However, one of the photographic estimates was known to be incomplete while the other 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 have used a 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).

Although other pup production estimates are available, many of these (e.g. Sergeant 1975; Lett and Benjaminsen 1977; Winters 1978; Cooke 1985) are based upon models that make assumptions about population dynamic processes and so do not provide independent estimates of pup production. Additional aerial surveys were also carried out (e.g. Fisher 1955; Sergeant and Fisher 1960; Lavigne 1976; Lavigne *et al.* 1980, 1982; Myers and Bowen 1989), but unfortunately they did not cover all of the whelping concentrations in a single year.

The model was applied to estimated pregnancy rates back to 1960 and the catch-at-age data back to 1952. Thus the pup exploitation rate parameter was estimated from pup harvests for the eight-year period 1952 to 1959. Ages 12 and older were lumped into a 'plus' age class in the analysis.

Unreported Catches

In order to investigate the influence of unreported catches on model population trajectories and yields, model runs were made assuming differing levels of additional mortality (Table 5). Three levels of mortality were assumed. One represents a low range of possibilities while the high represents the high end of ranges suggested by Lavigne (in press). The moderate level is based upon estimates of struck and lost provided by Sjare and Stenson (1999). In all scenarios it was assumed that the loss rate of age 0 seals in the Front and Gulf region prior to 1983 was low (1%). This is likely since the vast majority of the catches during this period consisted of pups taken on the whelping patch.

Results and Discussion

Estimates of total population size and pup production for the two formulations are given in Table 6 and illustrated in Figs. 2 and 3. Parameter estimates, and estimates of population growth rate (defined as the ratio of

1998/1997 population) are given in Table 7. Approximate replacement harvest, sustainable yield and sustainable population size under differing assumption of the age structure of the catch are given in Table 8. The 1000 population trajectories for Formulation 1 ($m_0 = m_{1+}$) are illustrated in Fig. 4 and the frequency distribution of the estimated population size in 1998 in Fig. 5.

As in previous studies (Roff and Bowen 1983, 1986; Shelton *et al.* 1996), the trajectories for total population estimated from the two formulations were very similar (Fig. 2). The 1998 population was estimated to be approximately 5.5 million (95% C. I. 4.3 - 6.7) using the first model formulation while assuming higher pup mortality (model formulation 2) resulted in a slightly lower estimate of 5.3 million. Under both models, the steady growth in the population observed since the early 1970s has not continued. The population appears to be relatively stable since 1996, growing at less than 0.5% per year (Table 7).

Estimates of total population up to 1994 from the Shelton et al. (1996) are also plotted in Fig. 2 for comparison. As expected, the overall trend in the estimates are similar although the total populations estimated by this study are slightly lower in the earlier period and higher in recent years. This difference may be a result of incorporating higher catches reported in Greenland since 1975 (Anon 1998, 1999). It may also be a result of correcting the manner in which the reproductive data were incorporated into the model in Shelton *et al.* (1996).

The estimates of pup production obtained from the two model formulations were virtually identical (Table 6, Fig 3). Although the general pattern of the pup production trajectories since the mid 1970s were similar to those estimated by Shelton *et al.* (1996), current estimates are lower for the earlier period (Fig. 3). The lower estimates observed at the beginning of the 1960s may have been affected by the longer period over which the selectivity parameter was estimated. In this study it was based on an eight-year period while in Shelton *et al.* (1996) there were only three years between the start of the catch data and the beginning of the model estimates. Although the current estimates suggest that pup production was less than 400,000 in the early 1970s, they are still higher than those estimated by Winters (1978), Roff and Bowen (1983) and Cooke *et al.* (1985).

The population trajectories (Fig 4) and frequency distribution of the 1998 population (Fig 5) indicate that the total population in 1998 was unlikely to be below 4.3 million or above 6.7 million (Table 7). However, this is likely an underestimate of the total uncertainty since Warren *et al.* (1997) found that including the uncertainty associated with the estimates of pregnancy rates increased the confidence limits slightly. Also, the model assumes that there are no errors in the catch-at-age data. Future versions of this model should

incorporate uncertainty in these parameters, possibly through the use of a maximum likelihood formulation (Anon 1997).

Estimates of replacement and sustainable yields for the two formulations were similar for a given age structure of the catch (Table 8). Generally, yields were higher under catches consisting of a greater proportion of pups. Replacement yields were lower than sustainable yields if the proportion of pups in the catch was high. However, if the catch was assumed to consist of 50% pups, the replacement yield was higher than the estimated sustainable harvest. This is likely due to the large number of juveniles taken under the age structure assumed. Reducing these year classes results in a declining population once they enter the reproductively active age classes.

The estimates of natural mortality (or more correctly, unreported mortality) for the two formulations are similar (Table 7). In Formulation 1, the instantaneous rate of natural mortality (all ages), m, was 0.085, corresponding to an annual survival rate of about 91.5%. In Formulation 2 m_{l+} was estimated to be 0.073, resulting in an m_0 of 0.219 ($3m_{l+}$). These estimates are lower than those of Shelton et al. (1996; 0.107, 0.0898 and 0.269, respectively), but very similar to those of Roff and Bowen (1983) who estimated m = 0.075 for the constant mortality model, and $m_{l+} = 0.0725$ and $m_0 = 0.2175$ for their formulation assuming $m_0=3m_{l+}$. As observed by Shelton *et al.* (1996) and Roff and Bowen (1983), the similarity of the results from the two formulations indicate that the model is relatively insensitive to the assumption of pup mortality and as such, the data does not indicate that pup mortality is significantly higher than that of older animals.

The current data on catches are based upon reports of the number of seals landed in Greenland, the Canadian Arctic and the Front and Gulf regions (Stenson et al. 1999). However, additional mortality occurs from a variety of sources such as animals that are killed, but not landed (struck and lost), and unreported hunting. Based on potential rates of struck and lost provided by Lavigne (in press) and Sjare and Stenson (1999), we estimated the impact of unreported mortality on the population trajectory of harp seals and estimates of current population (Table 9). Generally, the population trajectories assuming reported and differing levels of unreported catches were similar until 1995, but diverge in recent years due to the increased catch levels. To illustrate this, the population trajectories using model formulation 1 are shown in Fig. 6. Adding unreported catches resulted in slightly lower population estimates (Table 9). Low and moderate levels of unreported catches reduced the 1998 estimates from 5.5 million to 5.4 and 5.3 million, respectively, using model formulation 1 and from 5.3 million to 5.2 and 5.1 million, respectively, using formulation 2. In both models the population declined slightly (0.2% - 0.8%) between 1997 and 1998. Assuming a high level of struck and lost, the 1998 population was estimated to be approximately 5.2 and 5 million (model formulations 1 and 2, respectively)

and to have declined approximately 2% in the last year. The latter runs were based upon Lavigne's (in press) estimate that the loss rate for young of the year seals in Canadian waters could be as high as 25% (Table 5). However, available data (Rowsell 1977; Sjare and Stenson 1999) suggests that this level is much lower (<5%) and that loss rates in the Canadian hunt are closer to those used in the moderate runs. Given the slight differences observed and the uncertainty associated with these estimates, the difference among the various model runs are not significant.

Identifying the additional component of mortality reduced the mortality estimated in both models with higher additional catches resulting in lower estimates of instantaneous mortality. These lower estimates of mortality resulted in higher estimates of replacement and sustainable yields than those seen using reported catches only (Table 9). However, it must be remembered that these yields no longer refer to landed catch, but instead refer to total mortality due to hunting and include the assumed level of struck and lost. Therefore, if these estimates are used to set quotas, the allowable catches (TAC) must be adjusted to account for the level of unreported mortality assumed. Given the limited amount of data available on struck and lost, it is important that additional studies be carried out in order to properly quantified the level of unreported mortality that occurs in all components of the hunt.

Acknowledgements

We would like to thank Noel Cadigan, Science Branch, Department of Fisheries and Oceans, St John's for his initial work writing this model and his assistance in modifying it for use during this study.

References

- Anonymous. 1997. International scientific workshop on harp seal fisheries interactions in the Northwest Atlantic: towards research and management actions. 24-27 February, 1997. Canadian Center for Fisheries Innovation, St. John's, Newfoundland. 43p.
- Anonymous. 1998. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals. Int. Coun. Exp. Sea CM 1998/Assess:3.
- Anonymous. 1999. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals. Int. Coun. Exp. Sea CM 1999/ACFM:7.
- Bowen, W. D. and D. E. Sergeant. 1983. Mark-recapture estimates of harp seal pup (Phoca groenlandica) production in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 40:728-742.

- 1985. A mark-recapture estimate of 1983 harp seal pup production in the northwest Atlantic. North Atl. Fish. Org. SCR Roc. 85/I/1. Serial No. N9353. 14 p.
- 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. Estimation of harp seal (*Phoca groenlandica*) pup production from age samples. Can. J. Fish. Aquat. Sci. 42: 468-473.
- Cooke, J. G., A. W. Trites, and P. A. Larkin. 1985. A review of the population dynamics of the Northwest Atlantic Harp seal (*Phoca groenlandica*). Final Report, submitted to the Royal Commission on Seals and the Sealing Industry in Canada, June 30, 1985, 139 p.
- Fisher, H. D. 1955. Utilization of Atlantic harp seal populations. Trans. N. Am. Wild. Conf. 20:507-518.
- Lavigne, D. M. 1976. Counting harp seals with ultraviolet photography. Polar Rec. 18:269-277.
- Lavigne, D. M. *In press*. Estimating total kill of Northwest Atlantic harp seals, 1994-1998. Marine Mammal Science.
- Lavigne, D. M., S. Innes, W. Barchard and W. G. Doubleday. 1980. The 1977 census of Northwest Atlantic harp seals, *Pagophilus groenlandicus*. Int. Comm. Northwest Atl. Fish. Sel. Pap. 6:55-70.
- Lavigne, D. M., S. Innes, K. Kalpakis, and K. Ronald. 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. 10 p.
- 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.
- 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.
 - 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.

- Rowsell, H. C. 1977. 1977 sealing activities by Newfoundland landsmen and ship on the Front. Rep. To Comm. Seal Sealing and Can. Fed. Humane Soc. 24p.
- Sergeant, D. E. 1975. Estimating numbers of harp seals. Int. Coun. Exp. Sea Rapp. Proc. -Verb. 169: 274-280.
- Sergeant, D. E. and H. D. Fisher. 1960. Harp seal populations n the western North Atlantic from 1950 to 1960. Fish. Res. Board Can. (Arctic Unit, Montreal, Que.) Circ. No 5: 58p.
- Shelton, P. A., N. G. Cadigan, and G. B. Stenson. 1992. Model estimates of harp seal trajectories in the Northwest Atlantic. Can. Atl. Fish. Sci. Adv. Coun. 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. North Atl. Fish. Org. Sci. Coun. Studies. 26: 1-14.
- Sjare, B. and G. B. Stenson. 1999. Comments on struck and loss estimates for harp seals in Northwest Atlantic. Dept. Fish. Oceans Can. Stock Ass. Sec. Res. Doc 99/106.
- Sjare, B. G. B. Stenson, and W. G. Warren. 1996. Summary of female reproductive parameters in the Northwest Atlantic. North Atl. Fish. Org. Sci. Coun. Studies. 26: 41-46.
- 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. North Atl. Fish. Org. Sci. Coun. Studies 26:47-61.
- Stenson, G. B., R. A. Myers, M. O. Hammill, I.-H. Ni, W. G. Warren, and M. C. S. Kingsley. 1993. Pup production of harp seals, *Phoca groenlandica* in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2429-2439.
- Stenson, G. B., B. Sjare, and D. Wakeham. 1999. Catch-at-age of Northwest Atlantic harp seals. Dept. Fish. Oceans Can. Stock Ass. Sec. Res. Doc. 99/105.
- Warren, W. G. 1991. A critical review of mark-recapture estimation of Northwest Atlantic harp seal production 1977-83. Can. Atl. Fish. Sci. Adv. Coun. 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. Pat 1I: 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. Assumed age structure of the catches used to estimate replacement and sustainable yields.

Age Class_]	Percentage of	pups
	50%	65%	80%
0	0.500	0.650	0.800
. 1	0.090	0.063	0.036
2	0.075	0.053	0.030
3	0.065	0.046	0.026
4	0.050	0.035	0.020
5	0.040	0.028	0.016
6	0.030	0.021	0.012
7	0.025	0.018	0.010
8	0.020	0.014	0.008
9	0.010	0.007	0.004
10	0.010	0.007	0.004
11	0.005	0.004	0.002
12+	0.080	0.056	0.032

Table 2. Proportion of females pregnant-at-age, 1960-98 (from Sjare et al. unpublished data).

						Age			
Year	0	1	2	3	4	5	6	7	8+
1960	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1961	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1962	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1963	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1964	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1965	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1966	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1967	0	0	0	0	0.0192	0.1818	0.5435	0.9512	0.874
1968	0	0	0	0	0.0192	0.1818	0.5435	0.9512	0.874
1969	0	0	0	0	0.0192	0.1818	0.5435	0.8143	0.874
1970	0	0	0	0	0.0192	0.1818	0.5435	0.8143	0.874
1971	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1972	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1973	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1974	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1975	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1976	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1977	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1978	0	0	0	0	0.0192	0.5849	0.8889	0.8143	0.874
1979	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1980	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1981	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1982	0	0	0	0	0.1395	0.2054	0.8889	0.8143	0.7763
1983	0	0	0	0	0.1395	0.2054	0.7172	0.8143	0.7763
1984	0	0	0	0	0.1395	0.2054	0.7172	0.8143	0.7763
1985	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1986	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1987	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1988	0	0	0	0	0.1395	0.2054	0.5455	0.6866	0.7763
1989	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.7763
1990	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1991	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1992	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1993	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1994	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1995	0	O	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1996	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1997	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1998	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456

Table 3. Catch-at-age of harp seals in the Northwest Atlantic, based on reported catches 1952-98 (from Stenson et al. 1999)

	_	2	0	0	7	7	80	5	9	œ	9	e	7	0	9	0	2	ဖ	4	8	2	_	œ	4	6	N	က	0	ဖ	Ψ-	υ Ω	7						0	ιO.
	TOTA	32529	29107	28535	35068	40216	26014	31645	33084	29528	20164	33027	35393	35265	24532	33198	34038	20159	29703	26554	23832	13766	13482	15656	18289	17874	16979	18049	18170	19113	22981	19854	8755	61627	44701	56914	86775	13728	11187
	52 +	1794	455	1198	805	549	885	3686	825	1216	208	661	629	2535	736	1095	961	637	744	392	351	142	290	463	72	43	69	240	531	476	427	375	180	269	228	309	875	922	540
	24	1352	499	193	559	383	575	2013	559	824	47	184	454	1478	69	386	319	254	224	201	27	69	29	144	83	41	4	42	82	106	124	93	63	187	153	195	325	460	344
	23	476	665	763	655	422	646	1049	663	926	93	28	530	1018	26	662	507	330	441	268	62	79	22	104	8	22	23	71	93	105	153	188	69	216	192	222	366	369	330
	22	47	983	335	823	496	835	2473	806	1200	118	636	670	1027	268	334	454	809	369	331	124	108	186	170	8	43	25	119	117	169	264	139	25	256	191	240	330	355	538
		1	-		•		•	• •						• •																						281			
	1	1																																		374			
	1	١,		•				•		•				• •				•																		293	•	•	-
		_	_		_		_																													327			
	l		•	•	•		•	٠,	•	٠.		•	•	٠,		•	•		•																	324			
	i												- •																							349			
	l	7		٠,		•	. 4	0,		(.)		. 4	. 4	. 4	•	•	•	•	-								-			_	-	-		-		480			-
		2	~	0	တ	7	ω	/	9		٠,	7	0	ω	_	-	7	_	'n	_	_			_	_			_	_		_		_	_		268			_
lass	13	0 156	8 145	3 262	6 163	1 106	6 178	6 425	9 171	9 248	386	5 102	9 283	8 171	1 335	6 152	4 103	4 920	9 122	796 9	406	185	655	369	250	206	1 234	316	165	468	386	381	3 196	336	3 295	301 339	548	69	3 546
Age C	12	8 193	1 188	5 278	4 217	9 143	4 220	8 723	6 215	5 314	9 43	1 197	9 267	4 225	2 177	0 171	6 133	6 102	4 111	8 123	5 612	357	4 696	3 743	2 61(346	7 254	346	233	99 8	53,	33	373	32,	248	30	3 423	456	428
	1		• •	•	• •	•	٠.		• •	•		•	٠.	• •		• •	•	•	•	•																1 474			
																																				3 541			
	1	1																																		1 493			
		100	.,	.,	٠,	• •	.,	4,	(.,	٧.		٠,	.,	···	4	.,	• •	. 4		ν-			_	_				•		•	Υ			τ-		30 971	_	_	_
	1	ı																																		5 1180			
		Γ		-	•				Ť					_			•		•					•				•		•	•					1505	•	•	•
- 1	l	l						•																												1928			
	4	6646	4396	6360	4947	3118	4822	12522	4667	7184	2919	9139	4305	6997	5340	5163	2491	2026	2706	2790	1342	1737	2547	2003	1931	2966	4077	5003	2420	3767	4105	2867	2694	3431	2456	3008	4954	6261	5225
	က	8671	6645	4951	6858	3974	6081	12222	6051	10402	2667	2866	7255	6303	5229	5419	2958	3321	3353	3167	2710	1786	3345	2420	3495	4604	5609	7418	4198	0999	9699	5399	3812	5481	4378	5340	7881	10073	8483
		1								-																										5380		•	
	1																																			6015			
- 1	1																																						
- 1		Į																																		25777			
	YEAF	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989

Table 3. Con't.

												Age	Age Class													
YEAR 0 1 2 3 4 5 6 7	0	-	2	က	4	2	စ	7	ω	9	0	1	2 13	14	15	16	17	18	19	20	21	22	23	24	25+	TOTAL
1990	39880	13139	10616	10802	7502	5874	3616	~	1617 10	095 10	013 12	89 845	_	3 545	1078	۱	l	1	424	870	402	200	535	276 1	295	108819
1991	49640	10950	8661	8988	6235	4584	3193	ì	1751 8	885 938	•	1028 653	33 808	8 475	901	598		631	534	969	432	468	352	375	700	107173
1992	51585	16283	12876	10746	7151	5033	4123	_		~	`	1053 552					896	759	912	658	530	418	515		887	126457
1993	24157	12655	10444	9429	5830	4039	3209	"	•			878 456	56 627				_	635	299	616	490	413	436	344	929	82028
1994	33905	14206	12337	13911	10305	8228	6389	_	3345 19	1948 15	1505 15	1559 12	1278 160	-	9 1906	5 1019	600 و	296		643	874	703	414		988	125919
1995	43715	14957	12969	14301	10231	8031	6224	$\overline{}$	•					3 973		2 1034	1034 967	979	792	200	877	717	455		975	136792
1996	196285	26403	20053	14170	10216	8259	6883		٠.	2803 35		2275 248	2481 1777	-	9 2232	2 1815	1984	2003	1660	1549		1576	780	•	2615	326660
1997	231848	23359	18112	13626	9394	7387	6077	-	4829 23		2968 19	1967 199	94 1531			1 1572	1677	1696	1414	1364	1020	1331	717	• •	127	347619
1998	248010	24984	19350	14546	10027	7890	6489	~		2531 310		2095 21;	2122 163		4 2046	3 1676	1788	1810	1508	1451	1088	1421	764	666 2	272	371616

Table 4. Survey estimates of pup production of harp seals in the Northwest Atlantic. Methods refer to either mark recapture (MR) or visual and/or photographic survey (AS) techniques.

Year	Method	Estimate	Standard Error	Reference
1978	MR	497 000	34 000	Roff and Bowen 1986
1979	MR	478 000	35 000	Roff and Bowen 1986
1980	MR	475 000	47 000	Roff and Bowen 1986
1983	MR	534 000	33 000	Bowen and Sergeant 1985
1990	AS	577 900	38 800	Stenson et al. 1993
1994	AS	702 900	63 600	Stenson et al. 1996

Table 5. Assumed levels of unreported mortality (%). Prior to 1983 the level of unreported mortality among age class 0 in the Front and Gulf regions was assumed to be 1%.

Scenario		Ha	rvest Area	
	Front	and Gulf	Can. Arctic a	nd Greenland
	0	1+	0	1+
Reported Catch	0	0	0	0
Low	5	33	33	33
Moderate	5	40	50	50
High	25	50	50	50

Table 6. Pup production and total population size estimates for the period 1960 to 1998 for two model formulations.

		M_0 - M_1		$M_0=3M_{1+}$
Year	Pups	Total Population	Pups	Total population
1960	362,895	2,296,610	356,802	2,181,296
1961	380,206	2,206,961	374,232	2,094,780
1962	420,746	2,254,899	415,225	2,144,758
1963	432,903	2,187,811	429,048	2,080,586
1964	432,588	2,103,186	430,386	2,006,055
1965	424,420	2,018,511	423,202	1,930,035
1966	418,539	2,037,703	417,571	1,947,211
1967	414,117	1,967,860	411,738	1,883,240
1968	404,171	1,885,703	401,777	1,809,676
1969	391,434	1,930,513	390,508	1,849,494
1970	382,740	1,871,509	382,651	1,798,015
1971	398,974	1,863,719	397,803	1,794,518
1972	395,503	1,879,182	395,751	1,812,690
1973	401,552	1,995,916	402,118	1,921,058
1974	403,248	2,107,566	404,475	2,023,937
1975	400,499	2,186,550	403,047	2,099,010
1976	403,099	2,236,470	406,589	2,150,462
1977	419,898	2,303,109	423,327	2,217,890
1978	475,565	2,428,573	475,714	2,339,198
1979	507,356	2,565,371	506,101	2,463,715
1980	524,280	2,706,797	523,591	2,594,378
1981	537,170	2,840,577	537,388	2,717,783
1982	482,899	2,872,124	484,360	2,746,727
1983	490,208	2,938,386	492,398	2,814,478
1984	521,778	3,137,206	522,760	3,001,262
1985	536,193	3,359,118	537,522	3,207,097
1986	565,910	3,608,915	566,786	3,440,787
1987	596,273	3,857,051	597,022	3,674,108
1988	611,463	4,071,569	613,156	3,876,380
1989	637,311	4,246,076	639,224	4,044,171
1990	596,322	4,389,747	594,891	4,175,464
1991	635,034	4,563,372	632,733	4,341,301
1992	673,680	4,763,098	670,802	4,531,699
1993	656,434	4,910,845	657,815	4,672,646
1994	692,438	5,122,238	693,830	4,877,703
1995	719,707	5,304,558	721,411	5,053,339
1996	747,314	5,489,232	749,209	5,231,802
1997	768,531	5,498,119	770,426	5,252,277
1998	793,092	5,510,754	795,005	5,277,651

Table 7. Comparison of estimates from the two model formulations.

Model Estimates	, .	$M_0 = M_{1+}$	$M_0 = 3M_{1+}$
Total Population Size	1998	5,510,754	5,277,651
	1997	5,498,119	5,252,277
StD of 1998 population		595,962	
Growth Rate (1998/199	7)	1.0023	1.0048
Pup Production	1998	793,092	795,005
-	1999	819,000	821,000
StD of 1998 pup produc	ction	79,864	
Instantaneous mortality	rate	0.085	0.073
Pups			0.219
Proportion survival rate		0.915	0.927
Pups			0.781
Pup exploitation rate (1	/S) 1952-59	0.4269	0.4132

Table 8. Approximate replacement and sustainable yields under differing assumptions of the age composition of the catch.

Model Estimates	% age class 0	$M_0 = M_{1+}$	$M_0 = 3M_{1+}$
Replacement yield			
-	50	400,000	390,000
	65	407,000	402,000
	80	417,000	415,000
Sustainable yield			
	50	453,000	375,000
	65	482,000	406,000
	80	503,000	447,000
Sustainable Population	on Size (65%)	5,550,000	5,310,000

Table 9. Results of model runs assuming differing levels of unreported mortality. Estimates of replacement and sustainable yields were estimated assuming a catch consisting of 65% age class 0. The rates of additional mortality are given in Table 3.

	Assumed	levels of unrepo	rted catch
	Low	Moderate	High
Model 1 $M_0=M_{1+}$			
1998 Total Population	5,420,000	5,340,000	5,180,000
1998 Pup Production	785,000	778,000	770,000
Instantaneous mortality (M)	0.0762	0.0700	0.0671
Pup exploitations rate (1/s)	0.3912	0.3911	0.3702
Growth rate (1998/1997)	0.9962	0.9923	0.9808
Replacement Yield	453,000	482,000	503,000
Sustainable Yield	462,000	497,000	498,000
Model 2 M ₀ =3M ₁₊		5 140 000	- 000 000
1998 Total Population	5,210,000	5,140,000	5,000,000
1998 Pup Production Instantaneous mortality (M)	786,000	779,000	772,000
1+	0.0649	0.0594	0.05688
Pup	0.1947	0.1783	0.1706
Pup exploitations rate (1/s)	0.3841	0.3842	0.3629
Growth rate (1998/1997)	0.9985	0.9942	0.9830
Replacement Yield	448,000	478,000	497,000
Sustainable Yield	457,000	491,000	494,000

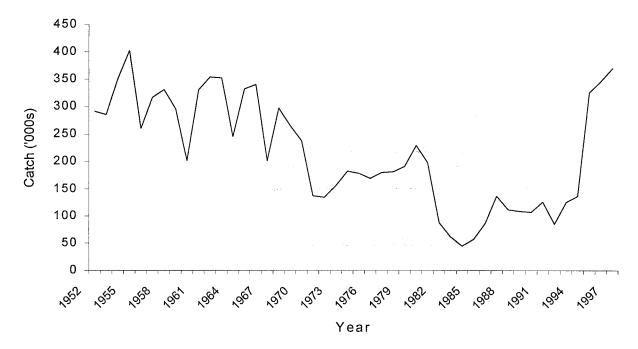


Figure 1. Total catches of harp seals in the Northwest Atlantic, 1952-98.

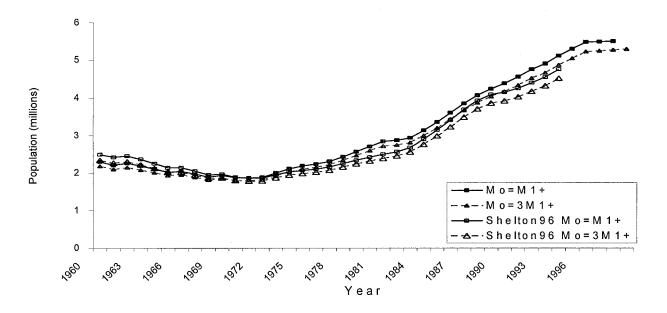


Figure 2. Trajectories of total population size, 1960-98. Estimates from Shelton *et al.* (1996) are shown for comparison.

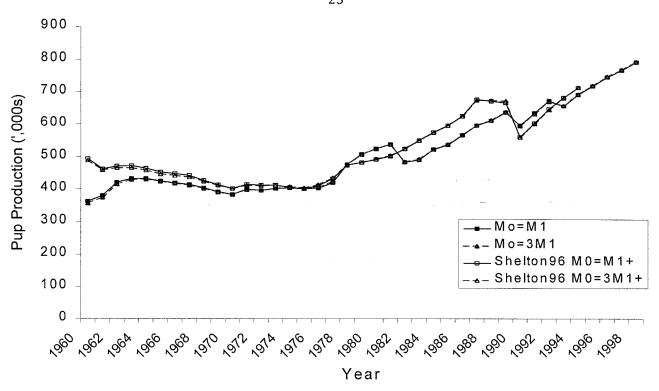


Figure 3. Estimated pup production, 1960-98. Estimates from Shelton *et al.* (1996) are shown for comparison.

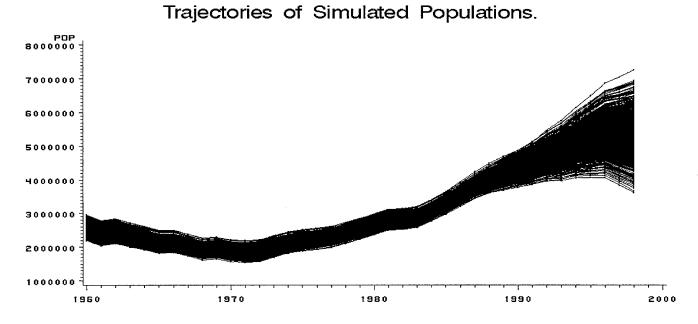


Figure 4. 1000 trajectories of total population size ($m_0=m_{1+}$) based upon resampling independent estimates of pup productions.

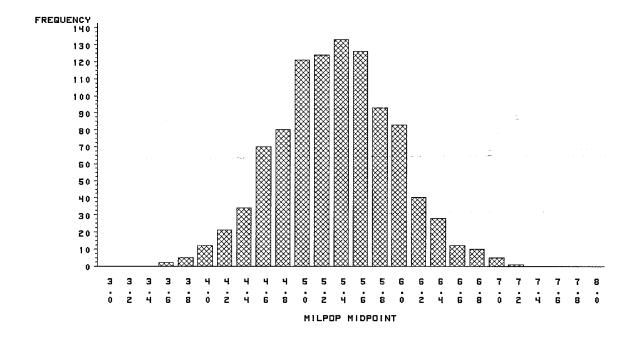


Figure 5. Frequency distribution of estimates for the total population size $(m_0=m_{1+})$ in 1998 obtained by resampling independent estimates of pup production (1000 realisations).

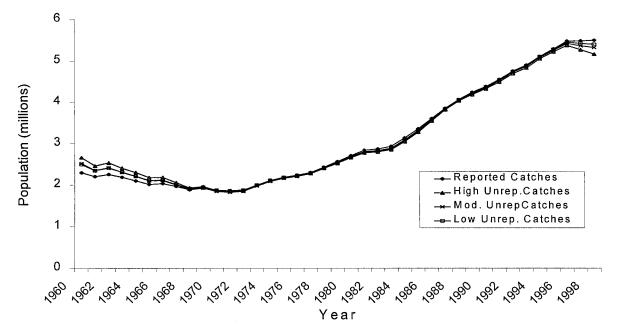


Figure 6. Trajectories of total population ($m_0=m_{1+}$) assuming reported catches and differing levels of unreported mortality. See Table 3 for definitions of unreported catch levels.