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## Abondance des phoques à capuchon dans l'Atlantique Nord-Ouest (1960 - 2005)

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#### Abstract

A population model incorporating hooded seal pup production estimates since the 1980s, reproductive rates and human induced mortality (catches, by-catch in fishing gear and struck and lost) were used to estimate total abundance for the period 1965-2005. Pup production and total population size are affected by the type of pup production estimates that the model is fitted to. Using only pup production estimates from the Front, pup production in 2005 was 107,900 (SE=18,800; 95\% C.I. $=70,600-143,300$ ) for a total population of 535,800 (SE=93,600; 95\% C.I. $=350,600-711,300$ ). Fitting to pup production estimates from all herds and making assumptions about numbers of hooded seals in the Davis Strait herd for years, when this area was not included in the survey program, results in pup production estimates of 120,100 (SE=13,800; 95\% CI=94,100-147,900) and an estimated total population of 593,500 (SE=67,200; 95\% C.I. $=465,600-728,300$ ). There is considerable uncertainty associated with these estimates which results from a lack of understanding of the relationship between the Davis Strait, Front and Gulf pupping areas, few surveys of all three areas, limited reproductive data and uncertain harvest statistics. Under the Objective Based Fisheries Management plan, hooded seals are considered 'Data Poor', with harvests being set using conservative methods. Recommended harvests are $27,400-32,100$ animals.


## RESUMÉ

On s'est servi d'un modèle de la population incorporant des estimations de la production de nouveau-nés chez le phoque à capuchon depuis les années 1980, les taux de reproduction et la mortalité causée par l'homme (prises, prises accidentelles dans des engins de pêche et individus abattus et non récupérés) pour estimer l'abondance totale de ces phoques entre 1965 et 2005. Les estimations relatives à la production de nouveau-nés chez le phoque à capuchon et à la taille totale de la population sont fonction du type d'estimations sur la production de nouveau-nés qui sont modélisées. Si on intègre uniquement les estimations sur la production de nouveau-nés dans la région du Front, on obtient une production de nouveau-nés en 2005 totalisant 107900 individus (ET $=18$ 800; IC $95 \%=70600-143$ 300) pour une population totale de 535800 individus (ET = 93600 ; IC $95 \%=356600-711300$ ). Après avoir intégré les estimations sur la production de nouveau-nés pour tous les troupeaux et formulé des hypothèses quant aux effectifs de phoques à capuchon dans le troupeau du détroit de Davis pour les années durant lesquelles cette zone a été exclue du programme de relevé, on obtient une production estimée de 120100 individus (ET = 13800 ; IC $95 \%=94100-147$ 900) et une population totale estimée de 593500 individus ( $E T=67$ 200; IC $95 \%=465600$ 728 300). L'incertitude est considérable pour ces estimations en raison d'un manque de compréhension des rapports qui existent entre les aires de mise bas du détroit de Davis, de la région du Front et du golfe, du faible nombre de relevés effectués dans chacune des trois aires, des données limitées sur la reproduction et des statistiques incertaines concernant la récolte. On considère, dans le cadre de la gestion des pêches par objectif (GPO), que le phoque à capuchon est une espèce « peu documentée » pour laquelle les données relatives à la récolte sont calculées au moyen de méthodes prudentes. Les recommandations pour la récolte se situent entre 27400 et 32100 individus.

## INTRODUCTION

The hooded seal is a large phocid inhabiting pelagic waters of the North Atlantic. Whelping occurs on the pack ice around Jan Mayen Island (West Ice), in Davis Strait, off the northeast coast of Newfoundland (Front) and in the Gulf of St. Lawrence (Gulf)(Sergeant 1974). After whelping, hooded seals return to the pack ice off eastern Greenland to moult during June-July, and then they may remain off the eastern Greenland coast, disperse to the Greenland Sea, or Davis Strait over the summer and fall before returning to their respective breeding areas (Sergeant 1974; Folkow et al. 1996; Hammill 1993; Stenson and Sjare 1997).

The relationships between the different breeding groups are poorly understood. Analyses of material from the Front and Jan Mayen herds using DNA fingerprinting (Sundt et al. 1994) and skull morphology (Wiig and Lie 1984), supports the hypothesis of a single population, although limited tag returns suggest that there may be some philopatry amongst adults in the Gulf (Hammill 1993).

Hooded seals are harvested commercially and for subsistence (Rasmussen 1960; Sergeant 1974). Although some regulations were in place to limit opening and closure dates, harvest levels were not regulated until the commercial hunt for hooded seals in the Gulf closed in 1972 (Hammill et al. 1992), and quotas were introduced to limit harvesting at the Front in 1974 (Bowen et al. 1987). At the time, the harvest was directed primarily towards young of the year, also known as bluebacks. This harvest continued until 1982 when the European Economic Community, the primary destination, banned the importation of whitecoats and bluebacks. In 1987, regulatory changes banned the commercial hunt for both the whitecoat and blueback harvests. The harvesting of older animals was permitted, but with the exception of one year when an illegal harvest of bluebacks occurred, harvests were on average much lower than the quota of 10,000 animals allowed (Stenson 2006).

Hooded seals are important predators in the Northwest Atlantic waters around Newfoundland (Hammill and Stenson 2000). However, compared to harp seals, there has been much less effort expended in monitoring changes in hooded seal abundance in the Northwest Atlantic. Prior to 1984, estimates of pup production were obtained using various methods including survival indices, sequential population analyses and catch curves (Stenson et al. 1997). Aerial surveys were flown at the Front and in Davis Strait in 1984, at the Front only in 1985, at the Front and in the Gulf in 1990, and in the Gulf during March1994, and 1996 (Bowen et al. 1987; Hammill et al. 1992; Stenson et al 1997). As a result of this sporadic monitoring, there is considerable uncertainty surrounding hooded seal abundance. The most recent estimates date from 1990, when Hammill and Stenson (2000) suggested that the population may have numbered around 469,900 animals in the Gulf and at the Front, but this estimate is very sensitive to the underlying assumptions and it was strongly recommended by the Eminent Panel to complete a new survey (McLaren et al. 2001). In order to do so, new estimates of pup production were required. These were completed in 2004 and 2005 (Stenson et al. 2006)

Here, we estimate total Northwest Atlantic hooded seal population size, using a general population model structure, that has been modified from the model used in the harp seal assessment (Hammill and Stenson 2005). We provide recommendations for harvest levels that Fisheries and Aquaculture Management (FAM) would like explored, and indicate the impact of these removals with respect to the biological reference points identified under OBFM (Hammill and Stenson 2003).

## MATERIAL AND METHODS

The current model is fitted to survey estimates of pup production by adjusting the initial population size and adult mortality rates to minimize the mean sum of square differences between pup production estimated by the model, and estimates obtained from survey data. Pup mortality is fixed at three times adult mortality. The model is described in Hammill and Stenson (2005) and is briefly reviewed here.

## Model structure

The basic model has the form : $\quad n_{a, t}=\left(\left(n_{a-1, t-1+} W_{t}\right)-\mathrm{c}_{\mathrm{a}-1, \mathrm{t}-1}\right) \mathrm{e}^{-(\gamma) \mathrm{m}}$
for $\mathrm{a}=1$

$$
\begin{equation*}
n_{a, t}=\left(n_{a-1, t-1} e^{-m / 2}-c_{a-1, t-1}\right) e^{-m / 2} \tag{1}
\end{equation*}
$$

for $1<\mathrm{a}<\mathrm{A}$,

$$
\begin{equation*}
n_{A, t}=\left(n_{A-1, t-1} e^{-m / 2}-c_{A-1, t-1}\right) e^{-m / 2} \tag{2}
\end{equation*}
$$

for $\mathrm{a}=\mathrm{A}$, where $\mathrm{A}-1$ is taken as ages A-1 and greater, and for $\mathrm{a}=0$;

$$
\begin{equation*}
n_{0, t}=\sum_{a=1}^{A} n_{a, t} P_{a, t} \tag{4}
\end{equation*}
$$

where $n_{a, 1}=$ population numbers-at-age a in year $t$,
$\mathrm{c}_{\mathrm{a}, \mathrm{t}}=$ 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. P is expressed as a Normally distributed variable, with mean and standard error taken from the reproductive data
$\mathrm{m}=$ the instantaneous rate of natural mortality.
$\gamma \quad=$ a multiplier to allow for higher mortality of first year seals. Assumed to equal 3 , for consistency with previous studies.
$\mathrm{W}=$ is the proportion of pups surviving an unusual mortality event arising from poor ice conditions or weather prior to the start of harvesting.
A = the 'plus' age class (i.e. older ages are lumped into this age class and accounted for separately, taken as age 25 in this analysis).

The model was adapted to function within an EXCEL spreadsheet and incorporated uncertainty in the parameters using an EXCEL add in called @Risk (@Risk, Palisade Corporation 2000). @Risk allows statistical distributions (e.g. Normal, Negative binomial, Triangle, Uniform) to be associated with parameters within the spreadsheet. The parameters can then be resampled repeatedly (Monte Carlo resampling) from within the distributions to estimate the impact of variability in input parameters.

A second feature called RiskOptimizer uses genetic algorithms to search for optimal answers to simulation models (Palisade Corporation 2000). For some model inputs (e.g. reproductive rates) information is available to describe sample variability in our estimates (mean and standard error). To capture some of the variability in these parameters, single parameter values were
replaced by statistical distribution functions with mean and standard error estimated from the available data. In the current fitting of the model, the uncertainty in the population trajectory was estimated using the following re-sampling scheme. The set of pup production estimates were resampled ( $\mathrm{N}=1000$ ) assuming that the survey estimates of pup production, $n_{0, t}$, are normally distributed as:

$$
\tilde{n}_{0, t} \sim \mathrm{~N}\left(n_{0, t}, \tilde{\sigma}_{t}^{2}\right)
$$

where $n_{0, t}$ is the true pup production for year $t$, and $\tilde{\sigma}_{t}^{2}$ is the estimated variance of $\tilde{n}_{0, t}$.
where $N_{0, t}$ is the $j$-th re-sampled estimate of $n_{0, t}$. Samples were drawn from the reproductive rates, and pup survey estimates. For each set of pup production estimates the model was refitted by calculating new estimates of initial population size and adult mortality rates, which in turn were used to generate population trajectories.

## Data Input

The model was fitted to the independent estimates of pup production obtained from the aerial surveys between 1984 and 2005 (Tables 1 and 2).

Removals from the population were incorporated into the model using catch at age data (Tables 3 and 4; Stenson 2006). Reported catches were obtained from Anon (2006) and the DFO Statistics Branch. Prior to the end of the large vessel hunt (1982) it was assumed that 99\% of the Canadian harvest was recovered. From 1983 onward, it was assumed that $95 \%$ of the pups killed in the Canadian hunt and that $50 \%$ of animals aged $1+$ years and $50 \%$ of all animals killed in the Greenland and Canadian Arctic harvests were recovered (Stenson 2006).

The age structure of the harvest was incorporated from Stenson (2006). Two different harvest age structures were examined. Stenson (2006) noted a change in the harvest age structure after 1984. Therefore, we fitted the model to the pup production estimates using an age structure that was split, using one age structure based on samples collected prior to 1985, and a second age structure for the model period from 1985 onwards (Table 3).

Reproductive data were taken from Duffet (2005) based upon samples collected between 1979 and 2003, primarily from females on the whelping patch, with some animals collected from other times during the year. Since it is difficult to obtain post-implantation and late-term females in Canadian waters, the presence of a corpus albicans was used to indicate pregnancy in the year prior to collection (Øritsland 1971,1975). Corpus albicans were used to indicate pregnancy only in the previous year. Further back-calculatons were not carried out because of corpus albicans resorption and the potential for increasing error (Boyd 1984). Pregnancy rates were incorporated into the model as a binomial distribution (Table 4).

In the development of the model for harp seals, variable environmental conditions were considered to have had an impact on mortality rates among years. Specifically, poor ice conditions and extensive storm activity has probably resulted in higher than normal mortality rates for pups (Hammill and Stenson 2005). In many years, the effects of increased mortality are seen in increased numbers of young of the year that are washed up on beaches or are seen
floating in the water. For harp seals, this mortality was applied before animals are harvested. The impact of changes in environmental conditions on the survival of hooded seal pups is not as clear. The development of hooded seal pups is much different from that of harp seals (Bowen et al. 1985; Kovacs and Lavigne 1992; Lydersen and Kovacs 1996; Lydersen et al. 1997). In spite of these differences, access to a stable platform to haul out and rest may still be important until the animals develop their foraging skills. Furthermore, unlike harp seals, the female-pup bond is virtually non-existent. Therefore, any separation from the female prior to weaning due to ice breakup would likely lead to mortality for a very young pup. Higher mortality was included in the model, as $w_{t}$ (equation 1). It was set as 0.25 in 1981 and 2005.

The effects of four different scenarios on estimates of total abundance were examined and presented at the meeting. Two scenarios were retained. The first scenario fitted the model to estimates of pup production at the Front (Table 1) since this is the largest concentration, and there are four aerial survey estimates from this area. A second scenario attempted to fit to estimates of pup production in all areas (Table 2). No aerial survey estimates are available for the Gulf for 1984 and 1985. However, it was considered at the meeting that Gulf hooded seal abundance was probably on the order of 500-800 animals (Hammill et al. 1992). In 1984, hooded seal pup production in Davis Strait was in the order of 19,000 animals. However, surveys in 2005 provided an estimate of 3,300 animals in this area (Table 1). Since we do not know if this change results from movement between colonies, a decline in abundance due to overharvesting in Greenland or an under-estimate because only a single brief survey was completed in Davis Strait in 2005, we set the Davis Strait estimate as an input with uniform distribution, lying between 1,000 and 23,000 animals. This was applied to the data from 1985, 1990 and 2004, years where Davis Strait was not covered by our aerial surveys.

For harp seals, an additional source of uncertainty relates to reported harvest rates in Greenland. Hooded seal harvests are also not regulated. However, catch levels appear to be constant at around 6,000 animals per year.

Under the Objective Based Fisheries Management approach developed for Atlantic seals, hooded seals are considered 'Data Poor'. This means harvest levels should be calculated using the Potential Biological Removal approach, defined by:

$$
P B R=P B R=0.5 \cdot R M a x \cdot F \cdot N M i n,
$$

where RMax is the maximum rate of increase for the population, $F$ is a recovery factor with values between 0.1 and 1 and NMin is the estimated population size using 20th percentile of the log-normal distribution (Wade 1998). RMax is set at a default of 0.12 for pinnipeds unless there is evidence for other more appropriate rates. The recovery factor ( $F$ ) is set at 0.1 in the case of endangered species, 0.5 for depleted or threatened species and 1 for populations at OSP. The default value for RMax was used while the recovery factor was set at 1 .

## RESULTS

The population model fits to the pup production data by adjusting the initial population size and adult mortality. Fitting only to the pup estimates from the Front, resulted in an initial population size of 372,300 (SE=44,800, 95\% C.I. $=289,500-464,600$ ) in 1965 and an instantaneous adult mortality rate of 0.120 ( $\mathrm{SE}=0.006$ )(Tables 1,2). However, these two parameters are highly correlated and change in a way that is best described by a second degree polynomial
relationship (Fig. 1). A linear model provides an adequate fit to the data with a correlation coefficient of $r=1$ and this was incorporated into the model structure.

Fitting the model to the pup production data, incorporating uncertainties outlined above, resulted in estimates of pup production of 73,400 (SE=9,200, 95\% C.I. $=56,400-92,400$ ) in 1965 increasing to 107,900 (SE=18,800, 95\% C.I. $=70,600-143,300$ ) in 2005 (Fig. 2). The total population was estimated to have increased to 535,800 (SE=93,600, 95\% CI= 350,600711,300) in 2005 (Fig 2).

In a second projection, the model was fitted to the pup estimates from all areas (Table 1,2). The initial population and adult mortality parameters were highly correlated and set to 1 (Fig. 1). Adult mortality was 0.130 ( $\mathrm{SE}=0.004$ ). The initial pup production in 1965 was 94,800 (SE=8,700; $78,600-112,600$ ). Pup production increased to about 120,100 (SE=13,800; 95\% C.I. 94,100147,900 ). Total population size was 478,000 ( $\mathrm{SE}=41,800 ; 95 \%$ C.I. $=400,500-564,300$ ) in 1965, increasing to 593,500 (SE=67,200, 95\% CI=465,600-728,300) by 2005 (Fig. 3).

Estimates of PBR range from 27,400 using only aerial survey estimates for the Front, to 32,100 if surveys from the Gulf, and Davis Strait are also included (Table 4).

## DISCUSSION

The most recent aerial surveys resulted in a pup production estimate of 107,00 (SE = 7,600) for the hooded seal pupping at the Front in 2005. An additional 6,600 ( $\mathrm{SE}=1,700$ ) pups were estimated to have been born in the Gulf and $3,300(S E=2,200)$ in Davis Strait for a total of $116,900(S E=7,918)$ in the Northwest Atlantic (Stenson et al, 2006). Incorporating information on reproductive rates and estimates of removals from the population into a model and fitting this model to the Front survey data only, resulted in pup production estimates of 73,400 (SE=9,200, $95 \%$ C.I. $=56,400-92,400$ ) in 1965, at the start of the modeling period, increasing to 107,900 (SE=18,800, 95\% CI=70,600-143,300) in 2005, depending on model assumptions. The total population at the Front has increased from 372,300 (SE=44,800, 95\% C.I. $=289,500-464,600$ ) in 1965 to $535,800(\mathrm{SE}=93,600,95 \% \mathrm{CI}=350,600-711,300)$ in 2005 . If survey estimates from all breeding areas are pooled, and certain assumptions are made about the abundance of hooded seals in the Gulf and in Davis Strait, during years, when these areas were not surveyed, then pup production in 1965 was 94,800 (SE=8,700; 78,600-112,600). Pup production remained relatively stable throughout the remainder of the 1960s and 1970s then began to increase again in 1985 again attaining 120,100 ( $\mathrm{SE}=13,800,95 \% \mathrm{CI}=94,100-147,900$ ) animals in 2005. The total Northwest Atlantic hood seal population size has increased from 478,000 (SE=41,800; $95 \%$ C.I. $=400,500-564,300$ ) in 1965 to 593,500 (SE=67,200, 95\% CI=465,600-728,300) in 2005. Adult mortality rates varied from 0.12 to 0.13 , which are much higher than adult mortality rates estimates of 0.06 for harp seals using the same modeling approach (Hammill and Stenson 2005).

The marked differences in adult mortality rates observed between harp and hooded seals might reflect real differences in life history patterns, result from uncertainties associated with the small number of reproductive tract samples, the size of the Greenland harvest, and uncertainty in the age structure of harvested animals. Harvesting patterns of this species have changed drastically over the last 45 years, in response to changes in harvesting objectives (blueback vs subsistence hunt). In trying to build the catch tables, it was necessary to search through several different sources to obtain catch data and information on the age structure of the catches. We included in the model some uncertainty associated with poor environmental conditions, but the
impacts of varying ice conditions on young survival are difficult to quantify. Finally, there is considerable uncertainty associated with the catch data. Currently, the majority of harvesting now occurs in Greenland and the reporting of harvest data are often one to two years behind. There is also some uncertainty as to the how accurate the reported harvests actually are.

Two important sources of uncertainty that could have an important impact on our estimates as well as on our PBR estimates are the uncertainty associated with current stock relationships. Unlike harp seals which show some separation between the Northwest and Northeast Atlantic harp seal herds, there does not appear to be any separation among Davis Strait, Northeast and Northwest Atlantic herds of hooded seals (Coltman, Stenson and Hammill, unpublished data). One mechanism for this might be the movement of small numbers of juveniles between herds. Hooded seal juveniles are notorious for their wandering habits (Hammill 1993). This would reduce genetic differences between herds, yet still allow for philopatric behaviour among adults, as is observed in many other ice breeding phocids. Finally, we have assumed that adult male and female hooded seals have similar mortality rates. Among hooded seals there is substantial sexual dimorphism (Hammill et al. 1997; Hammill and Stenson 2000). In other pinnipeds, this is often associated with differential survival in favour of females. Unfortunately, we have no information on how adult male mortality rates might differ from females.

Estimated PBR levels range from 27,400-32,100 animals. When setting the Canadian harvest, reported removals by the Greenland hunt, as well as hunting losses and other human-induced mortality in both the Canadian and Greenland hunts must be taken into consideration.

## LITERATURE CITED

Anonymous. 2006. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP). ICES CM 2006/ACFM:6.

Bowen, W.D., O.T. Oftedal, and D.J. Boness. 1985. Birth to weaning in 4 days:remarkable growth in the hooded seal, (Cystophora cristata), Can. J. Zool. 63:2841-2846.

Bowen, W. D., R. A. Myers and K. Hay. 1987. Abundance estimation of a dispersed, dynamic population: hooded seal (Cystophora cristata) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science 44:282-295.

Boyd, I.L. 1984. Development and regression of the corpus luteum in grey seal (Halichoerus grypus) ovaries and its use in determining fertility rates. Can. J. Zool. 62:1095-1100.

Duffett, K. A. 2005. Trends in pregnancy rates and mean age at maturity in hooded seals (Cystophora cristata) from 1979 - 2003. B. Sc. Thesis. Memorial University of Newfoundland, St. John's, NL. 33p

Folkow, LP, P-E Mårtensson, A.S. Blix. 1996. Annual distribution of hooded seals (Cystophora cristata) in the Greenland and Norwegian Seas. Polar Biol 16:179-189.

Hammill, M.O. 1993. Seasonal movements of hooded seals tagged in the gulf of St. Lawrence. Polar Biol. 13:307-310.

Hammill, M.O., G. Stenson, and R.A. Myers. 1992. Hooded seal pup production in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 12:2546-2550.

Hammill, M.O, C. Lydersen, K.M. Kovacs and B. Sjare. 1997. Estimated Fish consumption by hooded seals (Cystophora cristata) in the Gulf of St Lawrence. J. Northw. Atl. Fish. Sci. 22:249-257.

Hammill, M.O. and G.B. Stenson. 2000. Estimated prey consumption by harp seals (Phoca groenlandica), grey seals (Halichoerus grypus), Harbour seals (Phoca vitulina) and hooded seals (Cystophora cristata). J. Northw. Atl. Fish. Sci. 26:1-23.

Hammill, M.O. and G.B. Stenson. 2003. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals: A Discussion Paper. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/067. 23 p. Available at: http://www.dfo-mpo.gc.ca/csas/

Hammill, M.O. and G.B. Stenson. 2005. Abundance of Northwest Atlantic harp seals (19602005) . DFO Can. Sci. Advis. Sec. Res. Doc. 2005/090. 38 p. Available at: http://www.dfo-mpo.gc.ca/csas/

Kovacs, K.M. and D.M. Lavigne. 1992. Mass-transfer efficiency between hooded seal (Cystophora cristata) mothers and their pups in the Gulf of St. Lawrence. Can. J. Zool. 70:1315-1320.

Lydersen, C., K.M. Kovacs, and M.O. Hammill. 1997. Energetics during nursing and early postweaning fasting in hooded seal (Cystophora cristata) pups from the Gulf of St Lawrence, Canada. J. Comp. Physiol. B 167:81-88.

Lydersen C, and K.M. Kovacs 1996. Energetics of lactation in harp seals (Phoca groenlandica) from the Gulf of St Lawrence, Canada. Journal of Comparative Physiology BBiochemical Systemic And Environmental Physiology 166 (5): 295-304

McLaren, I.A., S. Brault, J. Harwood and D. Vardy . 2001. Report of the eminent panel on seal management. 145 pp. Report to the Department of Fisheries and Oceans. Available at: http://www.dfo-mpo.gc.ca/csas/

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

Øritsland,T. 1975. Sexual maturity and reproductive performance of female hooded seals at Newfoundland. Res. Bull. Int. Comm. NW. Atl. Fish. 11:37-41.

Palisade Corporation. 2000. Risk Optimizer: Optimization with simulation for Microsoft EXCEL. 303 pp. Palisade Corporation. Newfield, NY USA.

Rasmussen, B. 1960. On the stock of hood seals in the northern Atlantic. Fish. Res. Board of Canada Translation Series No 387.

Sergeant DE (1974) A rediscovered whelping population of hooded seals Cystophora cristata Erxleben and its possible relationship to other populations. Polarforschung 44:1-7.

Stenson, G.B. 2006. Hunt induced mortality in Northwest Atlantic Hooded Seals. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/066 Available at: http://www.dfo-mpo.gc.ca/csas/

Stenson G. B. and B. Sjare. 1996. Newfoundland hooded seal tag returns in the northeast Atlantic. NAFO Sci. Coun. Studies: 115-118.

Stenson,G.B., R.A. Myers, I-H. Ni and W.G. Warren. 1997. Pup production and population growth of hooded seals (Cystophora cristata) near Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 54 (suppl. 1):209-216.

Stenson, G. B., M. O. Hammill, M. C. S. Kingsley, B. Sjare, W. G. Warren and R. A. Myers. 2002. Is there evidence of increased pup production in northwest Atlantic harp seals, (Pagophilus groenlandicus) ICES J. Mar. Sci. 59:81-92.

Stenson, G.B., M.O. Hammill, J. Lawson, J.-F. Gosselin, and T. Haug. 2005. 2004 pup production of harp seals (Pagophilus groenlandicus) in the Northwest Atlantic. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/037 Available at: http://www.dfo-mpo.gc.ca/csas/

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., L.-P. Rivest, M. O. Hammill, J. F. Gosselin and B. Sjare. 2003. Estimating Pup Production of Harp Seals, (Pagophilus groenlandicus), in the Northwest Atlantic. Mar. Mammal. Sci.. 19:141-160.

Stenson, G.B. M. O. Hammill, J. Lawson. 2006. J. F. Gosselin. Pup Production of Hooded Seals, (Cystophora cristata), in the Northwest Atlantic. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/067 Available at: http://www.dfo-mpo.gc.ca/csas/

Sundt, R.C., G. Dahle and G. Nevdal. 1994. Genetic variation in the hooded seal, (Cystophora cristata), based on enzyme polymorphism and multi-locus DNA fingerprinting. Hereditas 121:147-155.

Wade, P.R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14: 1-37.

Wiig;, $\varnothing$. and Lie, R. W. 1984. Analysis of the morphological relationship between thc Hooded seals (Cystophora cristata) of Newfoundland, the Denmark Strait and Jan MaynJ.Zool., Lond. 203: 227220.

Table 1. Estimated pup production and standard errors of Northwest Atlantic hooded seals from aerial surveys. All estimates are rounded to the nearest hundred.

| Year | Front | Gulf | Gulf ${ }^{1}$ (corrected this study) | Davis Strait |
| :---: | :---: | :---: | :---: | :---: |
| 1984 | $\begin{gathered} 62,400 \\ (43,700-89,400) \end{gathered}$ |  |  | $\begin{gathered} 19,000 \\ (14,000-23,000) \end{gathered}$ |
| 1985 | $\begin{gathered} 61,400 \\ (16,500- \\ 119,500) \end{gathered}$ |  |  |  |
| 1990 | $\begin{gathered} 83,100 \\ (\mathrm{SE}=12,700) \end{gathered}$ | $\begin{gathered} 1,600^{2} \\ (\mathrm{SE}=500) \end{gathered}$ |  |  |
| 1991 |  | $\begin{gathered} 2,000 \\ (\mathrm{SE}=190) \end{gathered}$ | $\begin{gathered} 1,700 \\ (\mathrm{SE}=130) \end{gathered}$ |  |
| 1994 |  | $\begin{gathered} 4,000 \\ (\mathrm{SE}=1,000) \end{gathered}$ | $\begin{gathered} 8,700 \\ (\mathrm{SE}=1,800) \end{gathered}$ |  |
| 1996 |  | $\begin{gathered} 4,678^{2} \\ (\mathrm{SE}=748) \end{gathered}$ |  |  |
| 2004 | $\begin{gathered} 124,000 \\ (\mathrm{SE}=18,600) \end{gathered}$ | $\begin{gathered} 1,400^{3} \\ (\mathrm{SE}=300) \end{gathered}$ |  |  |
| 2005 | $\begin{gathered} 107,000 \\ (\mathrm{SE}=7,600) \end{gathered}$ | $\begin{gathered} 6,600 \\ (\mathrm{SE}=1,700) \end{gathered}$ |  | 3,300 (SE=2,200) |

${ }^{1}$ Published estimates corrected for the temporal distribution of birth using the normal model described in this paper.
${ }^{2}$ Surveys were flown but insufficient stage data were collected to determine temporal distribution of births.
${ }^{3}$ Incomplete counts because animals were missed.

Table 2. Estimated pup production and standard errors for Northwest Atlantic hooded seals from aerial surveys in years when two or more whelping areas are surveyed. All estimates are rounded to the nearest hundred. In years for which there are no survey estimates for Davis Strait, we assumed a uniform distribution with limits of 1,000-23,000 animals.

|  | 1984 |  | 1990 |  | 2004 |  | 2005 |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | Est | SE | Est | SE | Est | SE | Est | SE |
| Front | 62,400 | 11,700 | 83,100 | 12,700 | 124,000 | 18,600 | 107,000 | 7,600 |
| Gulf |  |  | 1,600 | 500 | 1,400 | 300 | 6,600 | 300 |
| Davis | 19,000 | 2,300 |  |  |  |  | 3,300 | 2,200 |
| St. |  |  |  |  |  |  |  |  |
| Total | 81,400 | 11,924 | 84,700 | 12,710 | 125,400 | 18,602 | 116,900 | 7,918 |

Table 3. Total removals from Northwest Atlantic hooded seal population. Removals are pooled, but the age structure appeared to change after 1984, hence two age structures were incorporated into the catch table-pre-1985 and post-1984 (see Stenson 2006).

| Age | 1960 | 1961 | 1962 | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 3392 | 2374 | 1158 | 4766 | 4780 | 2990 | 17045 | 8566 | 1309 | 9007 | 5469 | 8225 | 7182 | 4792 | 6225 | 7927 |
| 1 | 1870 | 222 | 226 | 249 | 390 | 261 | 368 | 298 | 250 | 292 | 431 | 304 | 764 | 408 | 806 | 589 |
| 2 | 2051 | 356 | 363 | 394 | 606 | 416 | 561 | 456 | 401 | 436 | 632 | 464 | 1018 | 650 | 1086 | 919 |
| 3 | 2528 | 394 | 402 | 437 | 671 | 461 | 622 | 506 | 444 | 483 | 650 | 515 | 1093 | 720 | 1130 | 1018 |
| 4 | 2441 | 457 | 454 | 601 | 1194 | 603 | 1320 | 1022 | 536 | 1221 | 749 | 1066 | 1601 | 934 | 1403 | 1697 |
| 5 | 2139 | 399 | 392 | 557 | 1186 | 550 | 1359 | 1043 | 475 | 1294 | 777 | 1093 | 1484 | 850 | 1352 | 1659 |
| 6 | 1725 | 337 | 322 | 545 | 1328 | 519 | 1617 | 1223 | 418 | 1610 | 704 | 1291 | 1554 | 796 | 1357 | 1806 |
| 7 | 1305 | 282 | 267 | 478 | 1210 | 451 | 1494 | 1126 | 356 | 1502 | 602 | 1190 | 1403 | 690 | 1207 | 1633 |
| 8 | 1035 | 233 | 220 | 402 | 1029 | 377 | 1276 | 961 | 295 | 1288 | 539 | 1016 | 1163 | 577 | 1019 | 1386 |
| 9 | 794 | 198 | 190 | 319 | 774 | 304 | 941 | 712 | 246 | 935 | 442 | 751 | 918 | 467 | 815 | 1054 |
| 10 | 537 | 160 | 152 | 272 | 689 | 256 | 852 | 642 | 202 | 857 | 389 | 679 | 822 | 392 | 647 | 930 |
| 11 | 561 | 151 | 141 | 275 | 732 | 255 | 922 | 691 | 194 | 939 | 343 | 733 | 817 | 390 | 669 | 979 |
| 12 | 536 | 112 | 105 | 195 | 503 | 182 | 626 | 471 | 142 | 633 | 263 | 498 | 593 | 279 | 521 | 676 |
| 13 | 409 | 108 | 105 | 161 | 366 | 156 | 432 | 329 | 131 | 421 | 217 | 346 | 449 | 240 | 397 | 504 |
| 14 | 577 | 110 | 105 | 178 | 435 | 170 | 530 | 401 | 137 | 527 | 210 | 423 | 503 | 261 | 456 | 592 |
| 15 | 246 | 74 | 72 | 107 | 236 | 104 | 275 | 210 | 89 | 266 | 134 | 221 | 285 | 161 | 257 | 327 |
| 16 | 165 | 72 | 71 | 101 | 215 | 100 | 245 | 188 | 86 | 233 | 112 | 197 | 260 | 154 | 252 | 300 |
| 17 | 166 | 34 | 32 | 57 | 142 | 53 | 175 | 132 | 42 | 176 | 67 | 139 | 161 | 82 | 163 | 192 |
| 18 | 272 | 38 | 35 | 73 | 201 | 67 | 256 | 192 | 49 | 263 | 89 | 203 | 206 | 102 | 185 | 267 |
| 19 | 139 | 29 | 28 | 44 | 101 | 42 | 120 | 92 | 35 | 118 | 53 | 96 | 121 | 65 | 101 | 139 |
| 20 | 78 | 30 | 29 | 43 | 96 | 42 | 112 | 86 | 36 | 108 | 48 | 90 | 111 | 65 | 91 | 133 |
| 21 | 47 | 12 | 12 | 21 | 53 | 20 | 66 | 50 | 15 | 67 | 27 | 53 | 56 | 30 | 69 | 72 |
| 22 | 52 | 17 | 16 | 27 | 67 | 26 | 83 | 62 | 21 | 82 | 32 | 66 | 78 | 40 | 67 | 92 |
| 23 | 31 | 16 | 15 | 22 | 46 | 21 | 53 | 40 | 19 | 50 | 25 | 42 | 53 | 33 | 61 | 65 |
| 24 | 56 | 8 | 8 | 14 | 34 | 13 | 41 | 31 | 10 | 41 | 17 | 33 | 36 | 20 | 30 | 46 |
| 25 | 119 | 41 | 40 | 58 | 128 | 57 | 148 | 113 | 49 | 143 | 66 | 119 | 150 | 88 | 147 | 178 |
| Total | 23270 | 6261 | 4958 | 10396 | 17213 | 8498 | 31540 | 19642 | 5988 | 22992 | 13089 | 19853 | 22881 | 13287 | 20514 | 25181 |

Table 3. continued.

| Age | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 6824 | 9319 | 8323 | 12324 | 11542 | 11036 | 8114 | 237 | 420 | 4624 | 3943 | 4613 | 5073 | 4462 | 4551 | 4661 |
| 1 | 682 | 732 | 1059 | 723 | 780 | 755 | 786 | 739 | 711 | 2683 | 2107 | 2038 | 2297 | 2487 | 2818 | 6206 |
| 2 | 1034 | 1167 | 1636 | 1153 | 1249 | 1205 | 1257 | 1080 | 937 | 1343 | 1158 | 996 | 1247 | 1307 | 1388 | 1905 |
| 3 | 1174 | 1293 | 1689 | 1277 | 1384 | 1335 | 1392 | 1197 | 1038 | 869 | 730 | 649 | 788 | 834 | 902 | 1460 |
| 4 | 1683 | 1649 | 1991 | 1635 | 1664 | 1687 | 1722 | 1314 | 1137 | 886 | 751 | 660 | 810 | 854 | 918 | 1405 |
| 5 | 1596 | 1491 | 1739 | 1480 | 1473 | 1520 | 1540 | 1128 | 981 | 807 | 666 | 605 | 721 | 767 | 841 | 1496 |
| 6 | 1631 | 1376 | 1534 | 1371 | 1292 | 1393 | 1386 | 900 | 786 | 447 | 344 | 341 | 376 | 410 | 471 | 1114 |
| 7 | 1437 | 1189 | 1300 | 1185 | 1097 | 1201 | 1188 | 736 | 640 | 570 | 472 | 427 | 511 | 543 | 593 | 1026 |
| 8 | 1239 | 993 | 1103 | 990 | 911 | 1002 | 989 | 603 | 524 | 416 | 343 | 312 | 372 | 396 | 433 | 761 |
| 9 | 959 | 809 | 894 | 805 | 761 | 819 | 815 | 531 | 463 | 345 | 279 | 260 | 303 | 325 | 360 | 700 |
| 10 | 832 | 675 | 747 | 674 | 623 | 682 | 674 | 419 | 367 | 274 | 215 | 209 | 234 | 254 | 288 | 640 |
| 11 | 844 | 666 | 711 | 666 | 599 | 671 | 657 | 380 | 332 | 339 | 279 | 255 | 302 | 322 | 353 | 636 |
| 12 | 600 | 479 | 523 | 478 | 438 | 483 | 476 | 292 | 258 | 394 | 322 | 297 | 349 | 373 | 411 | 767 |
| 13 | 474 | 419 | 461 | 417 | 405 | 426 | 428 | 301 | 267 | 132 | 86 | 104 | 97 | 112 | 142 | 503 |
| 14 | 535 | 451 | 488 | 449 | 423 | 456 | 454 | 297 | 261 | 54 | 22 | 46 | 27 | 38 | 61 | 363 |
| 15 | 314 | 281 | 314 | 280 | 274 | 286 | 289 | 210 | 188 | 82 | 44 | 68 | 51 | 64 | 91 | 436 |
| 16 | 286 | 271 | 299 | 269 | 268 | 276 | 280 | 212 | 192 | 137 | 87 | 110 | 98 | 115 | 149 | 568 |
| 17 | 183 | 141 | 159 | 141 | 131 | 143 | 141 | 95 | 89 | 129 | 86 | 102 | 97 | 111 | 139 | 471 |
| 18 | 237 | 173 | 180 | 173 | 152 | 173 | 169 | 94 | 84 | 88 | 65 | 68 | 71 | 79 | 93 | 253 |
| 19 | 129 | 113 | 120 | 113 | 109 | 115 | 115 | 83 | 77 | 144 | 108 | 111 | 118 | 130 | 153 | 400 |
| 20 | 132 | 113 | 125 | 113 | 110 | 115 | 116 | 86 | 78 | 44 | 22 | 37 | 26 | 33 | 49 | 250 |
| 21 | 64 | 52 | 59 | 52 | 48 | 52 | 52 | 36 | 36 | 21 | 0 | 20 | 3 | 10 | 26 | 241 |
| 22 | 80 | 69 | 68 | 69 | 64 | 70 | 69 | 48 | 46 | 68 | 43 | 54 | 49 | 57 | 74 | 276 |
| 23 | 62 | 58 | 62 | 58 | 58 | 59 | 60 | 47 | 43 | 61 | 43 | 47 | 48 | 54 | 65 | 195 |
| 24 | 42 | 34 | 38 | 34 | 32 | 35 | 35 | 24 | 23 | 10 | 0 | 9 | 1 | 5 | 12 | 112 |
| 25 | 165 | 154 | 165 | 153 | 151 | 157 | 159 | 118 | 107 | 146 | 108 | 112 | 118 | 131 | 155 | 416 |
| Total | 23238 | 24169 | 25786 | 27080 | 26038 | 26152 | 23364 | 11208 | 10087 | 15114 | 12323 | 12549 | 14188 | 14273 | 15537 | 27266 |

Table 3 continued

| Age | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 4851 | 4661 | 5458 | 4795 | 30677 | 4985 | 4235 | 2126 | 3905 | 4198 | 2364 | 4230 | 4290 | 4290 | 4290 |
| 1 | 2683 | 2518 | 3030 | 3069 | 5251 | 6802 | 8210 | 1256 | 2097 | 2330 | 1354 | 2354 | 2525 | 2309 | 2297 |
| 2 | 1436 | 1379 | 1622 | 1487 | 2199 | 2061 | 2098 | 644 | 1153 | 1250 | 710 | 1261 | 1298 | 1268 | 1266 |
| 3 | 911 | 870 | 1029 | 971 | 1504 | 1588 | 1739 | 414 | 726 | 793 | 453 | 800 | 834 | 799 | 797 |
| 4 | 935 | 895 | 1056 | 987 | 1503 | 1526 | 1633 | 423 | 747 | 814 | 464 | 821 | 852 | 822 | 821 |
| 5 | 836 | 794 | 944 | 908 | 1447 | 1632 | 1849 | 383 | 662 | 727 | 417 | 733 | 770 | 729 | 727 |
| 6 | 441 | 412 | 498 | 515 | 904 | 1223 | 1502 | 208 | 343 | 383 | 223 | 387 | 418 | 377 | 375 |
| 7 | 592 | 563 | 669 | 639 | 1010 | 1118 | 1255 | 270 | 470 | 515 | 295 | 520 | 544 | 517 | 516 |
| 8 | 431 | 410 | 487 | 467 | 742 | 829 | 936 | 197 | 342 | 375 | 215 | 378 | 397 | 376 | 375 |
| 9 | 352 | 333 | 398 | 391 | 640 | 766 | 892 | 163 | 278 | 306 | 177 | 309 | 327 | 306 | 305 |
| 10 | 274 | 257 | 309 | 314 | 539 | 702 | 849 | 128 | 214 | 238 | 138 | 240 | 258 | 236 | 234 |
| 11 | 351 | 333 | 396 | 382 | 611 | 694 | 790 | 161 | 278 | 305 | 175 | 308 | 323 | 306 | 305 |
| 12 | 406 | 384 | 458 | 445 | 720 | 838 | 964 | 186 | 321 | 353 | 203 | 356 | 375 | 353 | 352 |
| 13 | 117 | 104 | 132 | 159 | 329 | 556 | 736 | 59 | 86 | 101 | 61 | 102 | 118 | 95 | 94 |
| 14 | 36 | 27 | 40 | 72 | 191 | 403 | 563 | 22 | 22 | 30 | 21 | 31 | 44 | 25 | 23 |
| 15 | 64 | 53 | 72 | 105 | 249 | 484 | 664 | 35 | 43 | 54 | 35 | 55 | 71 | 48 | 47 |
| 16 | 118 | 105 | 134 | 168 | 359 | 628 | 839 | 61 | 86 | 102 | 63 | 104 | 122 | 95 | 94 |
| 17 | 116 | 104 | 131 | 155 | 314 | 520 | 684 | 58 | 86 | 100 | 60 | 101 | 116 | 95 | 94 |
| 18 | 84 | 77 | 95 | 102 | 190 | 279 | 352 | 40 | 64 | 73 | 43 | 74 | 81 | 71 | 70 |
| 19 | 139 | 129 | 157 | 168 | 306 | 440 | 553 | 67 | 107 | 121 | 71 | 122 | 134 | 118 | 117 |
| 20 | 33 | 27 | 37 | 57 | 139 | 278 | 383 | 19 | 22 | 28 | 18 | 28 | 37 | 24 | 23 |
| 21 | 7 | 1 | 8 | 33 | 111 | 268 | 386 | 8 | 0 | 5 | 6 | 6 | 15 | 1 | 0 |
| 22 | 59 | 52 | 67 | 83 | 176 | 305 | 406 | 30 | 43 | 51 | 31 | 52 | 61 | 48 | 47 |
| 23 | 57 | 52 | 64 | 72 | 139 | 216 | 278 | 28 | 43 | 49 | 29 | 50 | 56 | 47 | 47 |
| 24 | 3 | 1 | 4 | 15 | 52 | 125 | 180 | 4 | 0 | 2 | 3 | 3 | 7 | 0 | 0 |
| 25 | 140 | 129 | 158 | 170 | 314 | 458 | 579 | 67 | 107 | 121 | 71 | 122 | 135 | 118 | 117 |
| Total | 15470 | 14671 | 17451 | 16727 | 50616 | 29725 | 33555 | 7059 | 12246 | 13424 | 7703 | 13547 | 14211 | 13473 | 13433 |

Table 4. Age specific reproductive rates and sample size ( N ).

| Age | Mean | N |
| :---: | :---: | :---: |
|  |  |  |
| 3 | 0.217 | 60 |
| 4 | 0.552 | 87 |
| 5 | 0.814 | 118 |
| 6 | 0.860 | 93 |
| 7 | 0.897 | 78 |
| 8 | 0.847 | 59 |
| 9 | 0.897 | 68 |
| $10+$ | 0.881 | 386 |

Table 5. Estimated total population size, source of pup production estimates and harvest age structure to develop model, $\mathrm{N}_{\text {Min }}$, coefficient of variation (CV) and estimated potential biological removal (PBR) harvests for Northwest Atlantic hooded seals.

| Population | Source | Harvest age <br> structure | $N_{\text {Min }}$ | CV | PBR |
| :--- | :--- | :--- | :--- | :--- | :--- |
| 535,800 | Front | Split | 457,000 | 0.17 | 27,400 |
| 593,500 | All | Split | 535,100 | 0.11 | 32,107 |



Figure 1. Relationship between adjustable parameters (Initial population size and Adult mortality) used to fit the population model to the pup survey data. The top panel shows the relationship using only the Front pup production estimates. The bottom figure shows the relationship using pup production estimates from all areas.


Figure 2. Changes in pup production ( $\pm 95 \%$ C.I.) and survey estimates ( $\pm 95 \%$ C.I.) (top) of Northwest Atlantic hooded seals between 1965 and 2005, fitting the model to the Front pup production data only. Total estimated population size and $95 \%$ C.I. are shown in the bottom panel.



Figure 3. Changes in pup production ( $\pm 95 \%$ C.I.) and survey estimates ( $\pm 95 \%$ C.I.) (top) of Northwest Atlantic hooded seals between 1960 and 2007, fitting the model to all pup production data only. Total estimated population size and 95\% C.I. are shown in the bottom panel.

