



Fisheries and Oceans Canada  
Pêches et Océans Canada

Science

Sciences

**CSAS**

**Canadian Science Advisory Secretariat**

**SCCS**

**Secrétariat canadien de consultation scientifique**

**Research Document 2009/114**

**Document de recherche 2009/114**

**Abundance of Northwest Atlantic harp seals (1952-2010)**

**Abondance du phoque du Groenland dans l'Atlantique Nord-Ouest (1952-2010)**

M.O. Hammill<sup>1</sup> and G.B. Stenson<sup>2</sup>

<sup>1</sup> Fisheries and Oceans Canada, Maurice Lamontagne Institute, P.O. Box 1000, 850 route de la Mer, Mont-Joli, QC G5H 3Z4

<sup>2</sup> Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, PO Box 5667 St. John's, NL A1C 5X1

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time 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.

La présente série documente les fondements scientifiques des évaluations des ressources et des écosystèmes aquatiques du Canada. Elle traite des problèmes courants selon les 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.

Research documents are produced in the official language in which they are provided to the Secretariat.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at:

Ce document est disponible sur l'Internet à:

<http://www.dfo-mpo.gc.ca/csas/>

ISSN 1499-3848 (Printed / Imprimé)

ISSN 1919-5044 (Online / En ligne)

© Her Majesty the Queen in Right of Canada, 2010

© Sa Majesté la Reine du Chef du Canada, 2010

**Canada**



---

**Correct citation for this publication:**

Hammill, M. O. and Stenson, G. B. 2010. Abundance of Northwest Atlantic harp seals (1952-2010). DFO Can. Sci. Advis. Sec. Res. Doc. 2009/114. iv + 12 p.

**ABSTRACT**

A population model was used to examine changes in the size of the Northwest Atlantic harp seal population between 1952 and 2009. The model incorporated information on reproductive rates, reported removals, as well as estimates of non-reported removals and losses through bycatch in other fisheries to determine the population trajectory. The model was fitted to eleven estimates of pup production beginning in 1952, including two survey estimates of 2008 pup production, by adjusting the initial pup production size and estimates of adult mortality. Juvenile mortality was fixed at three times adult mortality rates. Fitting the model to the low estimates of 2008 pup production resulted in an estimated pup production in 2009 of 1,113,900 (95% CI=968 400 to 1,268 100) while total population size was 6 851 600 (95% CI=5 978 500 to 7,697 200). When the data are fitted to the high 2008 survey estimate, the estimated pup production increased to 1,316,000 (95% CI=1,090,200- 1,524,100) and the total population increased to 8,238,500 (95% CI=6,774,300 to 9,540,300), but the fit to the data was poor. The model fit to the high estimate of pup production was improved if we assumed reproductive rates in 2008 were the same as those observed in 1970.

**RÉSUMÉ**

Un modèle de population a été utilisé pour étudier les changements de taille de la population du phoque du Groenland de l'Atlantique Nord-Ouest entre 1952 et 2009. Le modèle comprenait des données sur le taux de reproduction, les prélèvements déclarés, ainsi que des estimations des prélèvements non déclarés et des pertes par les prises accessoires des autres pêches afin de déterminer la trajectoire de la population. Le modèle a été ajusté selon onze estimations de production de petits à compter de 1952, incluant deux estimations par relevé de la production de petits de 2008, en ajustant la quantité initiale de la production de petits et les estimations de la mortalité chez les adultes. Le taux de mortalité juvénile a été établi comme étant trois fois le taux de mortalité adulte. L'ajustement du modèle aux faibles estimations de production de petits de 2008 a donné une estimation de production de 1 113 900 petits pour 2009 (IC de 95 % = entre 968 400 et 1 268 100), tandis que l'estimation de la population totale a été de 6 851 600 individus (IC de 95 % = entre 5 978 500 et 7 697 200). Lorsque les données ont été ajustées selon l'estimation élevée du relevé de 2008, la production estimée de petits a augmenté à 1 316 000 (IC de 95 % = entre 1 090 200 et 1 524 100) et la population totale a augmenté à 8 238 500 (IC de 95 % = entre 6 774 300 et 9 540 300), mais la correspondance avec les données a été faible. L'ajustement du modèle selon l'estimation élevée de la production de petits a été amélioré si l'on supposait que le taux de reproduction de 2008 était le même que celui qui a été observé en 1970.

---

---

## INTRODUCTION

In 2001, the Eminent Panel concluded that the replacement yield approach, where Total Allowable Catches (TAC) were established at levels to maintain a constant population were not sufficiently risk adverse to avoid a decline in the population if the full TAC was to be taken in every year (McLaren et al. 2001). Instead the committee suggested that a framework that incorporated benchmarks and harvest control rules be established. In response, the Department developed and implemented an approach in 2003 that used two precautionary ( $N_{70}$  and  $N_{50}$ ), and a limit ( $N_{30}$ ), reference levels set at 70%, 50%, and 30% of the largest population size known to identify when certain management actions were to occur (Anon. 2003, 2006). The basis of the framework was that harvest levels were to maintain an 80% probability that the population would remain above  $N_{70}$ . If the population fell below  $N_{70}$ , then the TAC was to be reduced to ensure an 80% likelihood that the population would recover above  $N_{70}$  within 10 years. If the population level fell to  $N_{30}$ , then commercial harvesting was to end until recovery of the population was observed (Hammill and Stenson 2007). Development of this framework moved the management of harp seals towards a Precautionary Framework, although simulation testing to determine the robustness of the framework to uncertainty was still required to meet the objectives of a true Management Procedure. This work has recently been initiated (Hammill and Stenson 2009).

Total population of harp seals is estimated using a model that incorporates data on age specific reproductive rates and removals with independent, periodic estimates of pup production (Hammill and Stenson 2005, 2008). Previously, the model incorporated eight estimates of pup production since the 70's (1978, 1979, 1980, 1983, 1990, 1994, 1999, 2004). The first four were conducted using mark recapture methods while the last four were aerial surveys. The model assumes a 1:1 sex ratio and annual estimates of age-specific reproductive rates obtained from seals collected during the last quarter of pregnancy. Four different sources of removals were incorporated into the model: 1) the Canadian commercial hunt, 2) the Greenland subsistence harvest, 3) the Arctic subsistence harvest, and 4) the bycatch in commercial fishing gear (Stenson 2009). The reported catch levels were corrected for seals killed but not reported (referred to as 'struck and loss'). Annual estimates of removals are available beginning in 1952. Mortality of young seals due to poor ice conditions was included in the model and incorporated as a proportion of animals surviving. This factor acts on the young of the year (YOY) only and occurs prior to the start of the commercial hunt (Hammill and Stenson 2008). The level of mortality varies among years and is based upon observations of the conditions encountered and reports of dead seals.

During March 2008, the harp seal herd was surveyed to obtain new estimates of pup production. This survey indicated that pup production may be as low as 1,076,574 ( $se=61,279$ ) or as high as 1,648,771 ( $se=118,021$ ) (Stenson et al 2009). Here, we incorporate new information on pup production, removals, and reproductive rates into the population model to obtain an estimate of current population size. We also extended the model back to 1952 by incorporating data on pup production obtained in 1952 and 1960. The model was projected forward to examine three harvest options to determine if the Total Allowable Catch (TAC) would respect the management plan.

---

## MATERIALS AND METHODS

Modelling the dynamics of the Northwest Atlantic harp seal population occurs in two steps. In the first, the model is fitted to the estimates of pup production by adjusting initial population size ( $\alpha$ ) and adult mortality rates ( $M$ ) (Hammill et al. 2009). Referred to as the 'Fitting Model', multiple population matrices are created using Monte Carlo sampling and the parameters  $M$  and  $\alpha$  are estimated. This is done from 1952 until the last year data are available. The second part, referred to as the 'Projection Model', is where the population is projected into the future to examine the impacts of different management options on the population. The projection model is based on the same equations as the fitting model (Hammill and Stenson 2009)

The Projection model predicts the impact of future catch scenarios based upon estimates of current population (abundance at age) and natural mortality assuming:

- Reproductive rates remain constant over the period of the projection
- Mortality from bycatch, the proportion of seals struck and loss, and catches in the Canadian Arctic remain constant
- Greenland catches may vary between 70,000 and 100,000 (uniform distribution), with an average of 85,000 animals
- Ice-related mortality will vary from 0-30% of pup production with an average of 12%
- Pup mortality is fixed at three times 1+ mortality and remains unchanged.

### DATA INPUT

#### Pup production estimates

The model was fit to 11 independent estimates of pup production (Table 1) obtained in 1952, 1960, 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 1952, 1960, 1990, 1994, 1999, 2004 and 2008 (Sergeant and Fisher 1960; Stenson et al. 1993, 2002, 2003, 2005, 2009). The 1952 and 1960 early surveys did not cover the entire area and included estimates of pupping concentrations not surveyed. Also, they did not correct for births occurring after the surveys. Although they are thought to provide some useful information, there is greater uncertainty surrounding these estimates. To reflect this, these surveys were assigned a coefficient of variation of 40%. For 2008, the model was fit to the higher estimate of pup production using the photographic estimate of the main concentration at the Front, as well as the lower estimate using the visual estimate of this concentration (Stenson et al 2009).

Reproductive rate data were obtained between 1954 and 2004 (Sjare et al. 2010) and updated to include data from 2005 to 2007 (Stenson et al. 2009). The data were smoothed using a nonparametric regression estimator (Stenson et al. 2009). Seals 4 years old and younger were considered immature while seals 8 years and older were considered to be fully recruited into the population. The smoothed reproductive rates were extrapolated backwards from 1954 and forward from 2007.

Table 1: Pup production surveys used as input into the population model. <sup>1</sup> Assumed a coefficient of variation of 40%.

| Year    | Estimate  | Standard Error | Reference                |
|---------|-----------|----------------|--------------------------|
| 1951    | 645,000   | 322,500        | Sergeant and Fisher 1960 |
| 1960    | 235,000   | 117,500        | Sergeant and Fisher 1960 |
| 1978    | 497,000   | 34,000         | Roff and Bowen 1986      |
| 1979    | 478,000   | 35,000         | Roff and Bowen 1986      |
| 1980    | 475,000   | 47,000         | Roff and Bowen 1986      |
| 1983    | 534,000   | 33,000         | Bowen and Sergeant 1985  |
| 1990    | 577,900   | 38,800         | Stenson et al. 1993      |
| 1994    | 702,900   | 63,600         | Stenson et al. 2002      |
| 1999    | 997,900   | 102,100        | Stenson et al. 2003      |
| 2004    | 991,400   | 58,200         | Stenson et al. 2005      |
| 2008 hi | 1,648,771 | 118,021        | Stenson et al. 2009      |
| 2008 lo | 1,076,574 | 61,279         | Stenson et al. 2009      |

### **Catches**

Recent catches were taken from Stenson (2009). Harvest levels from the Canadian commercial hunt, Greenland and Canadian subsistence harvests were corrected for unreported harvests (i.e., seals struck and killed but not landed or reported) and were incorporated into the model along with estimates of bycatch (Stenson 2005; Sjare et al. 2005). It was assumed that 95% of the YOY and 50% of the animals aged 1+ years in the Canadian commercial hunt (Front and Gulf) were recovered, 50% of all animals killed in the Greenland and Canadian Arctic harvests were assumed to be recovered and reported (Stenson 2009).

Poor ice conditions are believed to result in increased mortality ( $M_{ice}$ ) that affects animals prior to the hunt (Hammill et al. 2009). This is incorporated into the model as a survival term. In most years  $M_{ice}$  was set to 1, but in years where particularly poor conditions were noted or observed and reports of large numbers of carcasses or animals disappearing, this factor was adjusted (Table 2).

Table 2. Year where unusual ice mortality is expected and values input to the model to account for this mortality.

|      |      |
|------|------|
| 1969 | 0.75 |
| 1981 | 0.75 |
| 1998 | 0.94 |
| 2000 | 0.88 |
| 2002 | 0.75 |
| 2005 | 0.75 |
| 2006 | 0.90 |
| 2007 | 0.78 |

### **Projections:**

Fisheries and Aquaculture Management requested that three scenarios be examined to determine if they respected the management plan (Table 3).

Table 3. Harvest scenarios examined in the population model.

| Scenario | 2010    | 2011    | 2012    |
|----------|---------|---------|---------|
| A        | 300,000 | 300,000 | 300,000 |
| B        | 275,000 | 275,000 | 275,000 |
| C        | 250,000 | 250,000 | 250,000 |

Each of the projections was run assuming that the level of subsistence catch in the Canadian Arctic, bycatch in fishing gear and the age structure of the harvest remained unchanged, and the age composition of the Canadian commercial catch was 95% young of year (YOY) to reflect the structure observed in the catch (Stenson 2009).

We assumed that extra mortality related to poor ice conditions in 2009 and future years could be described by a uniform distribution with a mean value of 12% but varied between 0 and 30% (0, 0.1, 0.30, 0.20, 0). A value was randomly chosen from this matrix and applied prior to the beginning of the hunt.

An additional source of uncertainty relates to reported harvest rates in Greenland. The Greenland harvest has varied greatly in recent years with reported harvests ranging from as low as 70,000 in 2004 to a high of just under 100,000 in 2000. The Greenland harvest is not limited by quota; therefore we entered the Greenland harvest into the model as a uniform function with a range of 70,000 to 100,000 for a mean harvest of 85,000 animals.

## RESULTS

Fitting the model to the low estimates of 2008 pup production resulted in an estimate of initial pup production of 593,867 (SE=16,597; 95% CI=563,085 to 627,184), and a total population of 2,667,736 (SE=59,725; 95% CI=2,557,974 to 2,788,312) in 1952. Adult mortality ( $M_{1+}$ ) was estimated to be 0.051 (se=0.003). Pup production increased to 1,060,686 (SE=55,149; 95% C.I.=950,215 to 1,166,381) and total population size increased to 6,525,948 (SE=391,812; 95% C.I.=5,734,321 to 7,260,206) in 2008. In 2009, estimated pup production would be 1,113,907 (SE=77,267; 95% CI=968,448 to 1,268,068) while total population size would increase to 6,851,550 (SE=447,648; 95% CI=5,978,477 to 7,697,225) (Fig. 1).

When the data were fitted to the high 2008 survey estimate,  $M_{1+}$  declined to 0.047 (se=0.004), the estimated pup production in 2009 increased to 1,316,012 (SE=113,842; 95% CI=1,090,185 to 1,524,052) and the total population increased to 8,238,521 (SE=730,044; 95% CI=6,774,263 to 9,540,322)(Fig. 2).

To determine if overestimating ice mortality had an impact on pup production, the data were fitted to the high 2008 survey and  $M_{ice}=0$ . When this was done,  $M_{1+}$  was estimated to be 0.048 (se=0.003), the estimated pup production in 2009 increased slightly to 1,360,423 (SE=108,198; 95% CI=1,147,795 to 1,567,962) and the total population increased to 8,905,009 (SE=703,494; 95% CI=7,540,346 to 10,255,889 )(Fig. 3).

We also examined the impact of assuming that there was a sudden upward shift in age-specific reproductive rates in 2008 only, from the low levels currently observed, to levels observed in 1970 (Stenson et al. 2009). Fitting to the high estimate of pup production resulted in a shift in  $M$  to 0.051 (se=0.002). Predicted 2008 pup production increased to 1,586,054 (SE=95,203; 95% CI= 1,406,137 to 1,773,331), but declined to 1,191,164(SE=87,027; 95% CI=1,029,649 to



---

1,363,046) in 2009 (Fig. 4). Total population size increased to 7,809,425 (SE=516,020; 95% CI=6,848,244 to 8,821,180) in 2008 and to 8,092,014 (SE=574,685; 95% CI=7,022,850 to 9,211,374) in 2009.

The three harvest scenarios,(Table 3) were run to examine their impact on the population. All three scenarios would respect the management objective of maintaining an 80% probability of the population remaining above N70, which under the current management plan has been set at 4.1 million animals (Fig. 5 ).

## DISCUSSION

Two estimates of Northwest Atlantic pup production were presented in Stenson et al (2009). One estimate was lower, and in line with expectations from previous modelling with an estimated pup production in 2008 of around 1,000,000 animals (Hammill and Stenson 2008). The second estimate was much higher at around 1.6 million animals (Table 1). The model fit to the low estimate was quite good, while the model fit to the high estimate was very poor.

Two options were examined to determine if the fit to the 2008 high data point could be improved. We assumed that past estimates of ice related mortality were too high. Although this resulted in some increase in pup production, the overall effect was quite low. We also examined the hypothesis that female seals experienced favourable conditions in 2007/2008, with the result that there was a sudden increase in reproduction rates to levels last seen when reproduction was high such as in 1970. The resulting fit to the 2008 survey point was very good, suggesting that this is a reasonable hypothesis. However, analyses of the 2008 reproductive material are needed to confirm this hypothesis. The model used in the analyses was adapted to consider that good years of reproduction would be synchronized across year classes, but the increase in reproductive rates needed to achieve this fit was quite significant. Until the differences between the two surveys can be reconciled, the lower estimate is used to estimate total population size, and to evaluate the impact of the different harvest scenarios on the population.

The Northwest Atlantic harp seal population was last assessed in 2005. At that time it was concluded that the population numbered 5.82 million (95% CI= 4.1-7.6 million)(Hammill and Stenson 2005). This estimate was based on the same approach used in 2009, where information on catches, reproductive rates, and ice related mortality were incorporated into a population model and fitted to estimates of pup production obtained from aerial surveys (Hammill and Stenson 2005). During the 2005 assessment, reproductive rates were assumed to not have changed since 2000 and these were extrapolated forward to 2005 for the assessment. Since then, the same rates were also extrapolated forward to 2009 to evaluate the impacts of different harvest scenarios on the population (eg DFO 2009). For the 2009 assessment, a slightly different model formulation was used (Hammill et al. 2009), and the reproductive rate data from 1954-2007 were re-analysed (Stenson and Hammill 2009). It now appears that reproductive rates have declined since 2000 (Sjare and Stenson 2010, Stenson and Hammill 2009). Incorporating the new reproductive rate data into the population model indicates a higher 2005 population of 6,448,341 (SE=304,175; 95% CI 5862181-7,020,791), which is slightly higher than the earlier estimate of 5.82 million (Hammill and Stenson 2005). Little change was observed in the 2008 population, with a total population size of 6.5 million, increasing to 6.85 million in 2009.

---

Three harvest scenarios were examined for their impact on the population. All three scenarios would respect the management plan objective that there is a probability of 80% that the population remains above N70.

### LITERATURE CITED

- 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(6):728-742.
- Bowen, W.D. and D.E. Sergeant. 1985. A mark-recapture estimate of 1983 harp seal pup production in the northwest Atlantic. Northwest Atl. Fish. Organ. SCR Doc. 85/1/1, Ser., N935. 14p.
- DFO. 2009. A Review of the Harp Seal Total Allowable Catch (TAC) for 2009. DFO Can. Sci. Advis. Sec. Sci. Resp. 2009/006.
- Hammill, M.O. and G.B. Stenson. 2007. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals. ICES J. Mar. Sci., 64: 702–706.
- Hammill, M.O. and G.B. Stenson. 2005. Abundance of Northwest Atlantic harp seals (1960-2005) . DFO Can. Sci. Advis. Sec. Res. Doc. 2005/090. 38 p.
- Hammill, M.O. and Stenson, G.B. 2008. Abundance of Northwest Atlantic harp seals (1960 – 2008). DFO Can. Sci. Advis. Sec. Res. Doc. 2008/077.
- Hammill, M.O., B. Ferland-Raymond, L.-P. Rivest and G.B. Stenson. 2010. Modelling Northwest harp seal populations: modifying an Excel model to R. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/108.
- Hammill, M. O., and Stenson, G. B. 2010. A preliminary evaluation of the performance of the Canadian management approach for harp seals using simulation studies. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/093
- Roff, D.A. and W.D. Bowen. 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. and H.D. Fisher 1960. Harp seal population sin the western North Atlantic from 1950 to 1960 Fisheries Research Board of Canada, Arctic Unit. Circular No. 5.
- Sjare, B. and G.B. Stenson. 2002. Estimating struck and loss rates for harp seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. Mar. Mamm. Sci. 18:710-720.
- Sjare, B. G.B. Stenson and B. Healey. 2010. Changes in the Reproductive Parameters of Female Harp Seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. ICES J. Mar. Sci. 67:000-000.

- 
- Stenson G. B. 2010. Total Removals of Northwest Atlantic Harp Seals (*Pagophilus groenlandicus*) 1952-2009. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/112.
- Stenson, G.B., M.O. Hammill, and B. Healey. 2010. Reproductive rates of Northwest Atlantic harp seals, 1954-2007. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/113
- Stenson, G. B., M. O. Hammill and J. Lawson, 2010. Estimating pup production of northwest Atlantic harp seals, *Pagophilus groenlandicus*: results of the 2008 surveys DFO Can. Sci. Advis. Sec. Res. Doc. 2009/103.
- 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.W. 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.
- 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.

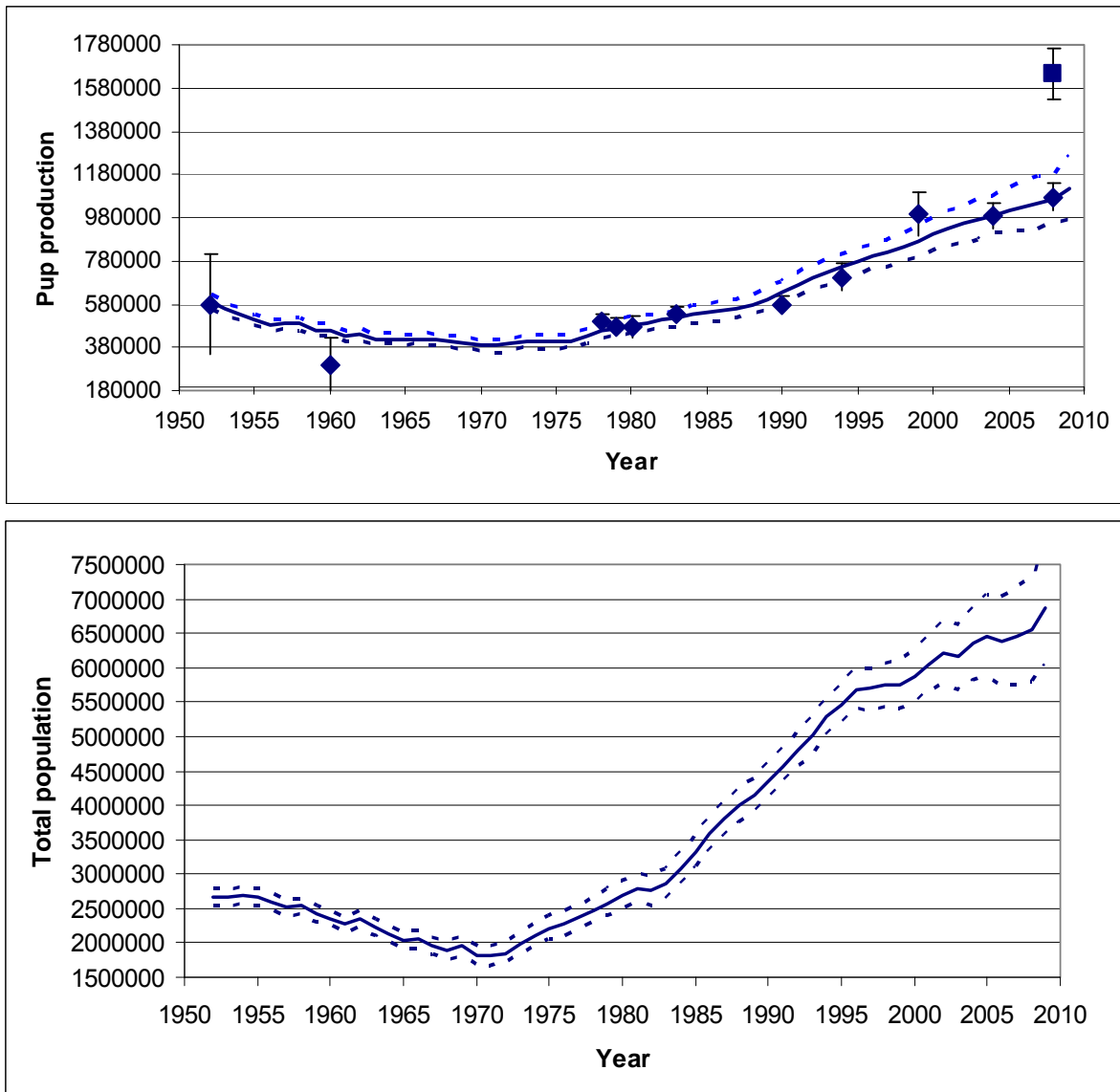


Figure 1. Changes in estimated pup production (mean±95% C.I.) and survey estimates (mean±se) (top) and total population size from 1952 to 2009 (mean±95% C.I.)(bottom), when the model was fitted to the low estimate of pup production from the 2008 survey. The high estimate is also shown (mean±se).

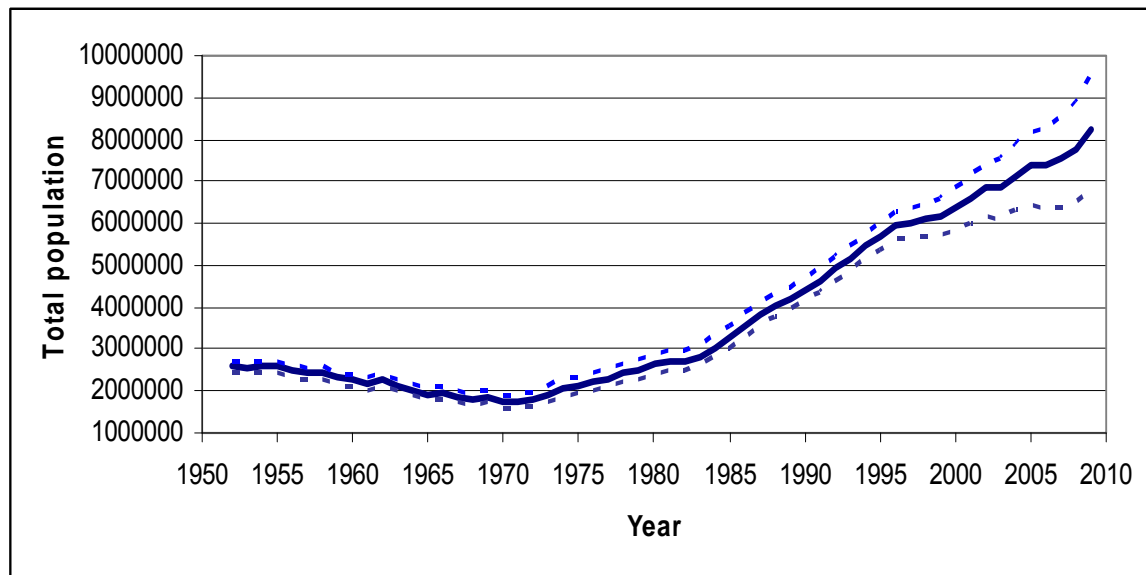
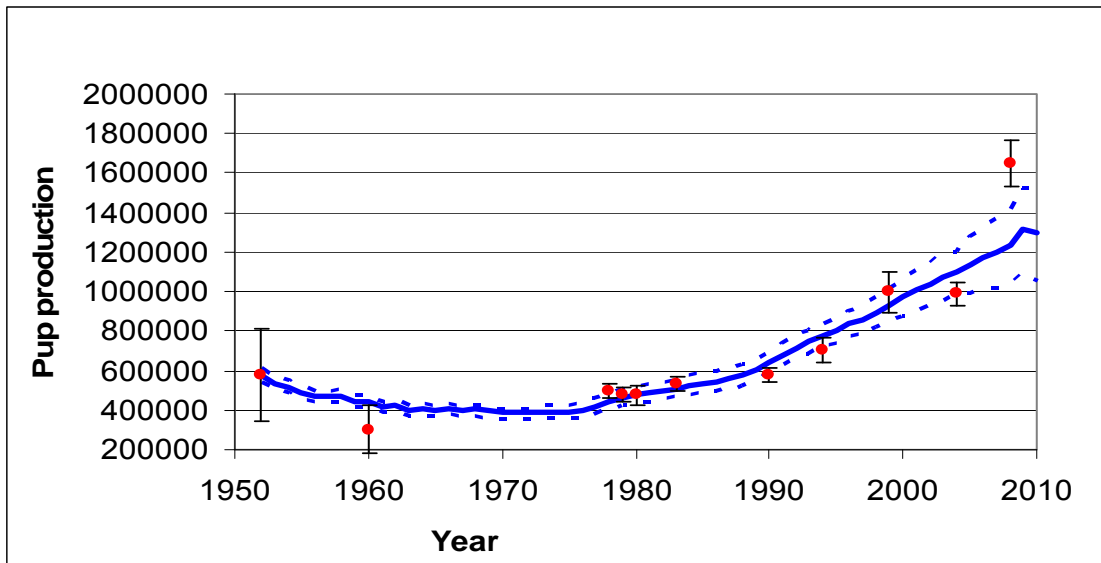


Figure 2. Changes in pup production and survey estimates (top) and total population size from 1952 to 2009 (mean $\pm$ 95%C.I.)(bottom), when the model was fitted to the high estimate of pup production from the 2008 survey.

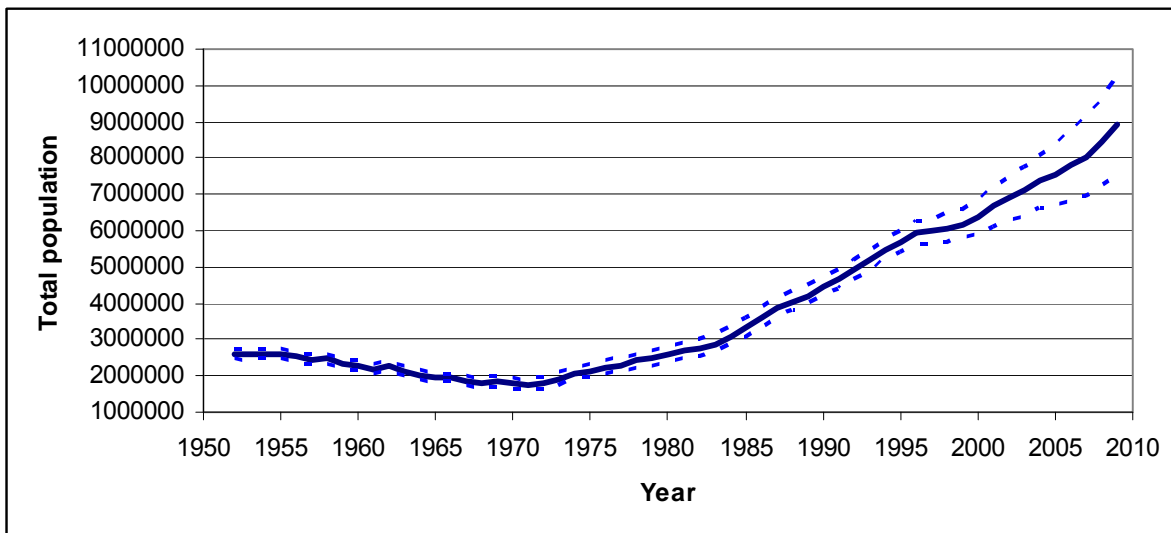
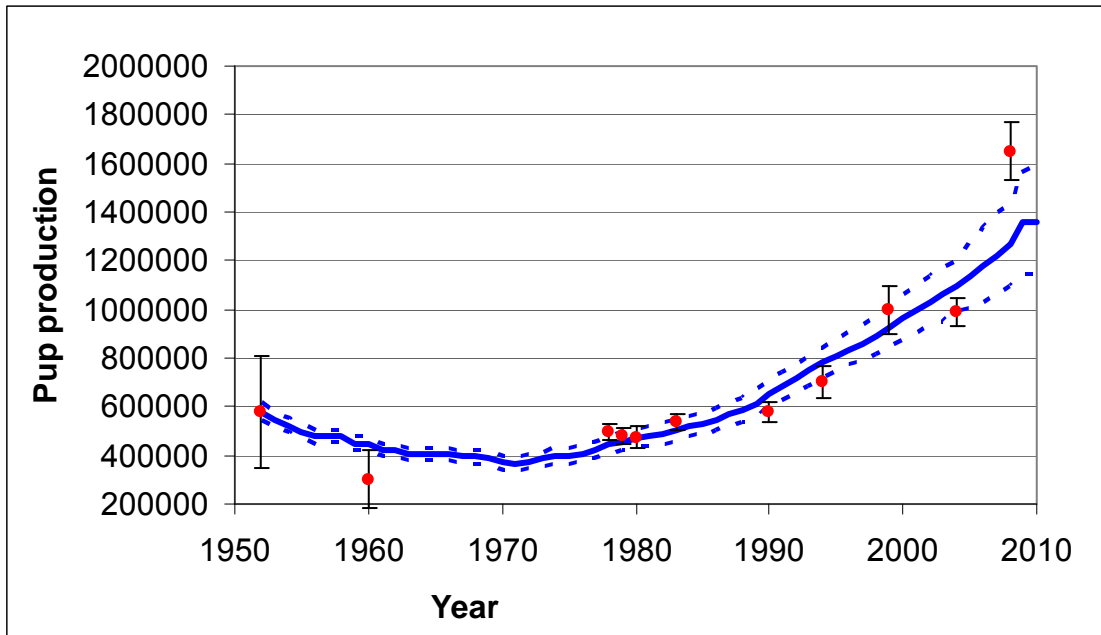


Figure 3. Changes in pup production and survey estimates (top) and total population size from 1952 to 2009 (mean $\pm$ 95% CI)(bottom), when the model was fitted to the high estimate of pup production from the 2008 survey and it was assumed that  $M_{ice} = 0$ .

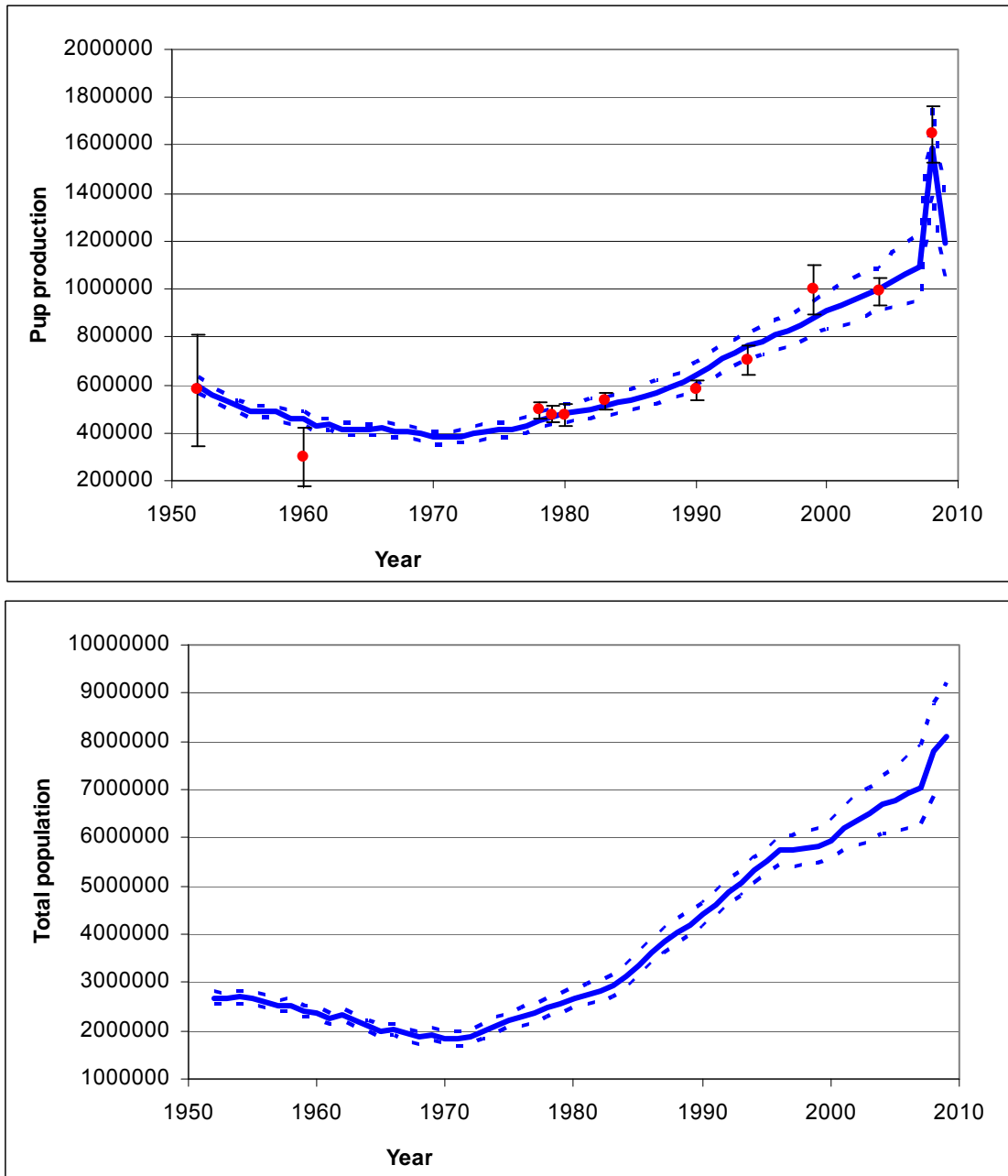


Figure 4. Changes in pup production and survey estimates (top) and total population size from 1952 to 2009 (mean $\pm$ 95% CI)(bottom), when model was fitted to the high estimate of pup production from the 2008 survey, it was assumed that  $M_{ice}=0$ , and that there was an upward shift in reproductive rates to levels observed in 1970 (Stenson et al. 2009).

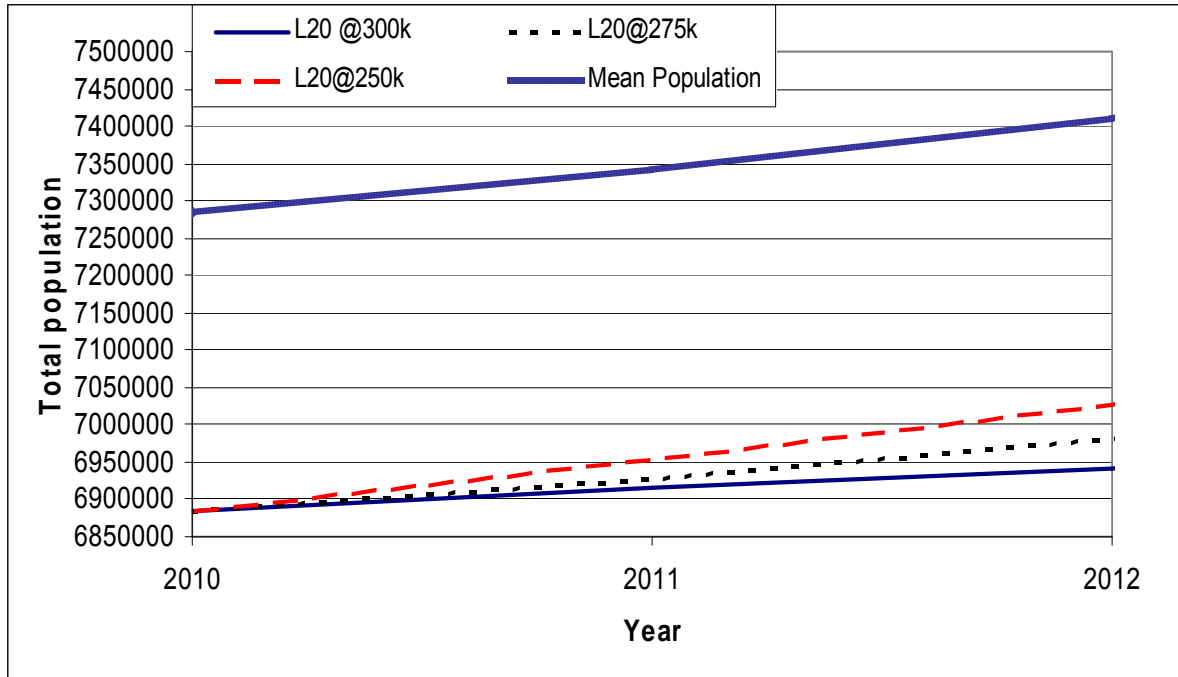


Figure 5. Changes in total population size (mean), and the L20 population size under three different harvest scenarios (Table 2). L20 is the line where there is only a 20% probability that the population is equal to or less than indicated.