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Science / Sciences

**C S A S** / **S C C S**

**Canadian Science Advisory Secretariat** / **Secrétariat canadien de consultation scientifique**

**Research Document 2011/100** / **Document de recherche 2011/100**

**Quebec and Newfoundland and Labrador Regions** / **Régions du Québec et de Terre-Neuve et Labrador**

# Historical Abundance of Northwest Atlantic harp seals (*Pagophilus groenlandicus*): influence of harvesting and climate

# Abondance historique du phoque du Groenland dans l'Atlantique Nord-Ouest (*Pagophilus groenlandicus*) : influence de la récolte et du climat

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ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)


Canada

**Correct citation for this publication:**

Hammill, M.O., Stenson, G.B. and M.C.S. Kingsley. 2011. Historical Abundance of Northwest Atlantic harp seals (*Pagophilus groenlandicus*): influence of harvesting and climate. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/100. iv + 16 p.

## ABSTRACT

Reconstructing historical population size provides useful information for management and conservation by providing an indication of abundance prior to exploitation. When combined with environmental variables, such estimates can also provide insights into how a species may respond to climate change. The harp seal (*Pagophilus groenlandicus*) is an obligate pack-ice breeder and is arguably the most abundant phocid species in the north Atlantic. Reproductive rates and morphometric data indicate that density-dependent factors are affecting the dynamics of this population although the mechanisms are not clear. Harp seals have been commercially exploited since the early 1700s, although significant catches did not begin until early in the 19$^{th}$ century. Catch data from historical records and recent harvests were incorporated into a surplus production model to reconstruct the dynamics of this population back to the late 18$^{th}$ Century. The initial population was estimated at 11 million (SE=2,000,000) animals. Assuming that the population at that time was stable and at its environmental carrying capacity. This population estimate serves as a proxy for current carrying capacity assuming that environmental conditions in the 18$^{th}$ century were similar to conditions today.

## RÉSUMÉ

La reconstitution de la taille de la population historique fournit des renseignements utiles pour la gestion et la conservation en donnant une indication de l'abondance avant l'exploitation. Lorsqu'elles sont jumelées avec des variables environnementales, ces estimations permettent également de mieux comprendre la manière dont une espèce pourrait réagir aux changements climatiques. Le phoque du Groenland (*Pagophilus groenlandicus*) doit se reproduire sur des banquises et il est permis de penser qu'il est l'espèce de phoque la plus abondante dans l'Atlantique Nord. Les taux de reproduction et les données morphométriques indiquent que des facteurs dépendants de la densité ont une incidence sur la dynamique de cette population, bien que les mécanismes ne soient pas clairs. Les phoques du Groenland font l'objet d'une exploitation commerciale depuis le début des années 1700, bien que les prises importantes n'aient pas commencé avant le début du XIX$^{e}$ siècle. Les données sur les captures dans les dossiers historiques et les récoltes récentes ont été intégrées dans un modèle de production excédentaire afin de reconstituer la dynamique de cette population à la fin du XVIII$^{e}$ siècle. La population initiale était estimée à 11 millions (SE = 2 000 000) d'animaux, en supposant que la population à cette époque était stable et à sa capacité de support environnementale. Cette estimation de population sert d'approximation pour la capacité actuelle de soutien, en supposant que les conditions environnementales du XVIII$^{e}$ siècle étaient semblables aux conditions actuelles.

# INTRODUCTION

Long-term population dynamics are shaped by a complex interaction between intrinsic (density-dependent) and extrinsic (environmental stochasticity) forces (Bradshaw 2008). Intraspecific competition for common resources leads to a negative feedback between population size and population growth, expressed through reduced reproduction, increased mortality and/or dispersal (Chamaillé-Jammes et al. 2007). Eberhardt (1977, 2002) proposed that as a population increased and per capita resources became limiting, juvenile mortality rates would begin to increase, followed by an increase in age at first reproduction, a reduction in adult reproductive rates and finally an increase in adult mortality rates. Understanding this complex interaction between intrinsic and extrinsic forces, particularly for large-long lived vertebrates, usually involves long-term studies that monitor a combination of several factors including abundance, age-specific mortality and/or reproductive rates, environmental variables, and other biotic factors such as predation (e.g. Owen-Smith 2006; Owen-Smith and Mills 2006; Bradshaw et al. 2006; Gaillard et al. 1998; Hadley et al. 2007; Chamaillé-Jammes et al. 2007).

The harp seal is a medium–sized phocid species distributed throughout the north Atlantic (Fig. 1). The northwest Atlantic population is hunted in Greenland, the Canadian Arctic and Atlantic Canada (Sergeant 1991, Stenson 2009) and has been harvested commercially in Canada since the 18$^{th}$ century (Barchard 1978, Ryan 1994). From the beginning of the commercial harvest in Newfoundland in 1723 through to the end of the century, annual catches averaged approximately 27,000 seals. In the early 1800s (1800-1819) catches increased to an average of 115,000 seal per year. Large scale hunting began in the 1820s with an annual average catch of over 399,999 seals each year from 1820-1859 and 293,000 from 1860-1914. Over 650,000 seals were reported killed in a number of years during this period. Catches were lower during the 1920s and 30s (average = 163,00 $yr^{-1}$, 1919-1939) and then declined to less than 33,000 during World War II. Following the war, Canadian catches increased again to over 273,600 per year until quotas were introduced in 1971. From the early 1950 through 1970, catches in Greenland ranged from 5,000 – 16,000, averaging 11,500 harp seals (Stenson 2009). Throughout the mid to late 1970s, catches in Greenland and Canada ranged from 156,000 – 191,000. Although Greenland catches increased, overall catches fell to 50,000 to 60,000 animals in the mid 1980s due to a decline in Canadian catches as a result of the ban on the importation of whitecoat pelts into the European Economic Community. In 1996, Canadian commercial catches increased significantly due to a renewed interest in seal pelts and for the next decade combined catches reported from the Canadian commercial hunt, Greenland and Canadian subsistence hunts were over 300, 000 animals annually making this the largest marine mammal harvest in the world (Stenson 2009).

Population trends in Northwest Atlantic harp seals from 1952-2010 were estimated by Hammill and Stenson (2011). The population declined during the 1950s and 60s to reach a minimum of just under 2 million animals in the early 1970s. However, it has increased steadily since 1971 when harvest quotas to limit the hunt were implemented (Sergeant 1991). In spite of continued harvesting, the population has continued to increase, with recent estimates of 8.0 million (95% CI=5.0-8.5 million) animals in 2008 (Hammill and Stenson 2011.), indicating that the population has more than tripled over the last 4 decades.

Estimates of abundance of the Northwest Atlantic harp seal population are obtained by incorporating information age-specific reproductive rates, harvest, and ice-related mortality information into a population model that is then fitted to estimates of pup production (Sjare and Stenson 2010; Stenson 2009; Stenson et al. 2003). Surveys completed in 2004 resulted in pup production estimates of 991,400 (SE=58,200), which were essentially the same as estimates obtained from surveys flown in 1999 (997,900, SE=102,100)(Stenson et al. 2003, 2005). These results suggested that pup production was levelling off possibly due to a combination of the high harvests and density-dependent changes in the dynamics of the population. An analysis of reproductive rate data collected between 1954 and 2004 showed that reproductive rates had been declining since the mid-1980s, which also provided support for density-dependent regulation of the population, although the mechanism was not understood (Sjare and Stenson 2010). However, Stenson et al (2011) estimated 2008 pup production to be 1.63 million animals (SE=110,400), which was much larger than expected, particularly for a population supposedly undergoing density-dependent limitation.

The survey to count pups born on the ice represents the primary metric to monitor changes in production in this population. Unfortunately, the number of surveys is limited and they are only completed every 4-5 years (Fig. 2). This, combined with continued harvesting that focuses on young animals, limits our ability to detect density-dependent changes in the population.

Catches are an important component of population assessments, along with an understanding of stock structure and abundance. In particular, they allow the estimation of the unexploited population size (Higdon 2010), which, if certain assumptions are made, can then be used as a measure of historic population size and perhaps carrying capacity. Stenson (2009) summarizes catches from the Canadian and Greenland harvests from 1952 to the present. Historical information on catches from hunts in Newfoundland (e.g. Chafe 1895, Mosdell et al. 1923; Coleman 1937, 1949, Barchard 1978, Ryan 1994) and the Gulf of St. Lawrence (Gallienne 1963) are also available that allow the reconstruction of the long-term catch history of this population.

In this paper, we use catch data extending back to the 1700's to reconstruct the historical population and trajectory of the Northwest Atlantic harp seal population.

## MATERIALS AND METHODS

### ABUNDANCE ESTIMATES

The historical harp seal population was back-calculated from the present to 1720 using a non-age structured surplus production model (Pella and Tomlinson 1969). Parameters in the Pella-Tomlinson (P-T) model were adjusted to minimize differences between the predicted population size and the recent (1952-1993) estimates of population size.

Recent estimates of the population (1952-present) are based on fitting of an age-structured (AS) model that incorporates annual estimates of reproductive rates, removals and mortality associated to poor ice-conditions into the model structure. The AS model is fitted to independent estimates of pup production obtained from mark-recapture and aerial survey studies (Fig. 2)(Hammill and Stenson 2011). The years 1952 to the present, represent a period where we have detailed information on the agecomposition of the harvest and age-specific reproductive rates (Stenson 2009; Stenson and Wells 2010).

Post-1993 population trajectories are affected by model assumptions (i.e. exponential or density-dependent growth). Therefore, 1993 was selected as a cut-off (Fig. 3).

A discrete time parameterisation of the Pella and Tomlinson (1969) model was used because of uncertainty surrounding the age structure of catches, and a lack of age-specific reproductive rate data that are required to produce a more detailed model. With the Pella and Tomlinson model, the estimated population size (Nt+1) at time t+1, is described by:

$$N_{t+1}=N_t+ N_t (\lambda_{max}-1)(1-( N_t /K)^{\theta})-b H_t$$

Where:

- $N_t$ is the population size at time t,
- K is the estimated carrying capacity
- $\theta$ is a shaping parameter of the density dependent response, set at 2.4 (Trzcinski et al. 2006).
- $\lambda_{max}$ is the maximum rate of increase, set at 1.12 (Wade 1998)
- $H_t$ is the reported harvest and
- b is a parameter to account for animals killed but not reported

Reported catch data are available from current catch statistics and catch data gleaned from a variety of sources (Fig. 4). Recent catches were taken from Stenson (2009). Data were updated to include the 2008 data on the Canadian commercial harvest (DFO Statistics Branch). Reported catch levels from the Canadian and Greenland hunts 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 (Sjare et al. 2005). The levels of struck and loss applied were the same as used previously, which results in an average overall correction of 1.1 applied to the reported catch from 1952 to 1985, and 1.2 applied to the reported catch from 1986 to 1993

Historical catch data (Fig. 4) were available from a number of sources. Barchard (1978) compiled a list of Newfoundland catches beginning in 1723. The catches prior to 1796 were estimated based upon the reported volume of seal oil exported. Ryan (1994) summarized catches in the Newfoundland hunt from 1810 to 1914. Chafe (1895), Mosdell et al (1923) and Colman (1937, 1949) also provide data on the number of seals taken in Newfoundland.

The number of seals taken in the Gulf of St. Lawrence has not been compiled previously. Catches by hunters from the Magdalen Islands between 1858 and 1884 were reported by Gallienne (1963) while Canadian (i.e. non-Newfoundland) catches between 1885 and 1937 were obtained from the Fisheries Statistics of Canada (Anon 1888-1940). ICNAF (1970) provided catch statistics for the period 1938-1951. Gulf catches are not available prior to 1858.

The catches reported by Barchard (1978) and Ryan (1994) were cross-checked with the original sources (e.g. Chafe 1895, Anonymous 1888-1940, Mosdell 1923, Coleman 1937) whenever possible and were evaluated as reliable, questionable, or no evaluation. Generally, catches reported by the various sources were similar. Newfoundland catches prior to 1895 were taken primarily from Barchard (1978). Data on catches were not available for some of the early years (prior to 1800). To correct for missing data, we followed Barchard (1978) by interpolating the average of the two flanking points as catch for the missing year.

From 1895 onward, catches were taken from the original sources to ensure that hooded seals catches were not included in the totals. Prior to this date, the number of hooded seals taken were not reported and so could be included in the total number of seals taken. However, catches of hooded seals were generally low in most years accounting for ~5% of total catches between 1863 and 1962.

All catches from 1952-2008 were taken from Stenson (2009). Catches in the Canadian Arctic and Greenland are not included prior to 1952. However, they are likely low in comparison to the numbers of animals taken in the commercial hunt. (Fig. 4). Similarly, early data (i.e. prior to 1952) do not include corrections for struck and loss and is estimated by the model.

Changes in estimated population size were determined by adjusting *K* and the non-reporting factor prior to 1952 to minimize the sum of squares differences between estimates of total population obtained from the P-T model and those from the age structured model using Risk Optimizer (an EXCEL add-in, Palisade Corporation, Newfield, NY, USA). One hundred simulations were conducted by randomly selecting a starting initial population size and non-reporting coefficient. Mean values and confidence limits for *K* and the non-reporting coefficient were estimated from the distribution of the 100 runs.

## RESULTS

Reasonable fits were obtained between the 'true' population based on the AS model and the P-T model (Fig. 5). The model fitted to the catch time-series resulted in an average *K* of 10,800,000 (SE=1,900,000; 95% CI=7,000,000-14,600,000). The average non-reporting rate (*b*) for the period 1723-1951 was 1.44 (SE=0.26; 95% CI=0.93-1.95)(Fig. 6).

The mean starting population size in 1730 was 8.7 million, which increased throughout the remainder of the century (Fig. 7). This initial increase is a side-effect of seed values used to initiate the model. The population leveled off at 10.8 million animals as indicated above. Harvests began to increase in the late 1700s reaching over 500,000 in the 1820s, causing the population to decline (Fig. 4, 6). The population declined to a minimum of about 4.5 million in 1861, increased to about 5.2 million by 1870, then declined continuously to reach the lowest value in the time series of approximately 1.6 million animals in 1918. A slight recovery, to approximately 2.2 million, was observed during the 1920s, but the population declined again, reaching a minimum of 1.7 million animals in 1940. After this, the population recovered again to 2.7 million by 1947 and then declined to the low of 1.6 million animals by 1971. Since then the population has recovered reaching 8,500,000 (95% CI=5,900,000 -11,800,000) animals in 2008.

## DISCUSSION

The Northwest Atlantic harp seal population has been harvested continuously over the last 300 years. This harvest can be characterized by periods of extensive exploitation leading to population declines punctuated by periods of reduced exploitation due to changes in economic conditions, world wars, and changes in management approaches, that have allowed for recovery (Sergeant 1991). By far the largest harvests occurred during the 1800s, with reported harvests of over 500,000 animals occurring in several years between 1828 and 1873.

Back-calculating the population based upon this history of catches resulted in an estimated population rounded to the nearest million of approximately 11 million animals at the start of this period of intensive exploitation. The apparent increase in population during the $18^{th}$ C is an artifact of the way in which the model is initiated. The population could not sustain the high level of harvest that occurred throughout the $19^{th}$ C, indicating that it is unlikely that there were as many as 20 million animals as some have claimed. Since quotas were first introduced into the Canadian harvest in 1971, the population has been recovering and now appears to be approaching historical levels.

Information on abundance is needed for harvest management, and building ecosystem models to understand the role that seals may play in structuring marine ecosystems. For the Northwest Atlantic harp seal population, population abundance is determined from an AS model that has incorporated information on removals, age-specific reproductive rates and mortality related to poor ice conditions. The model is tuned to independent estimates of pup production that are obtained approximately every five years. Since the 1990s, the model has assumed exponential growth to describe the dynamics of this population. However, this assumption may no longer be appropriate for several reasons: the population has increased, having quadrupled since the early 1970s, growth rates have declined (Chabot and Stenson unpublished data) and there has been a general decline in reproductive rates of mature adults with considerable inter-annual variability (Stenson and Wells 2010). Therefore, it appears that density-dependent factors are affecting the dynamics of this population. Unfortunately, with a combination of very high, and variable, harvests, along with independent estimates of pup production that are only obtained approximately every 5 years and a lack of data on estimates of adult mortality, we are limited in our ability to describe the form of these density-dependence changes and particularly to estimate K. In 2010, a range of possible K values from 10 to 16 million were selected and examined, with K=12 million considered as most reasonable (Hammill and Stenson 2011). This value is very close to our estimate, rounded to the nearest million of K=11 million (95% CI: 7-15 million)

Our estimate of historical population size can act as a proxy for present-day *K*, assuming that the historic population was relatively stable at or near a resource ceiling and that environmental conditions today are similar to those experienced during the $18^{th}$ and $19^{th}$ centuries. These assumptions are questionable, but our approach allows us to establish a tentative K, until we learn more about the population and environmental carrying capacity. Our estimate of 11 million is roughly double the estimated K of 3-5 million animals reported in previous studies (e.g. Barchard 1978). Although previous work acknowledged that there was non-reporting (e.g. struck and loss, or pelts stocked on the ice but not recovered) this was not taken into account. The current study indicates that this is likely to have been quite significant (44%). Vessels that may have sunk before returning to port would not be included in the harvest numbers, which were mostly based upon numbers of pelts or barrels of oil sold. Also, previous reports of historical harvest (e.g. Barchard 1978, Ryan 1994) focused upon the Newfoundland hunt and did not include harvests from other areas (Quebec, Maritimes) which we have included. All of the catch statistics prior to 1952, including ours, did not include subsistence catches although these are likely to be in the order of a few thousand which is small in comparison to the commercial catches. The Greenland catch was also not included prior to 1952. However, at that time catches in Greenland were low in comparison to Canadian catches (~15-20,000 vs 300,000; Stenson 2009) and are unlikely to change the estimates significantly. The Greenland and subsistence catches are partially accounted for within the estimated unreported catch. There are other sources of uncertainty, which we have not considered in our analyses. For example, theta the shaping parameter, was fixed at theta=2.4, and the maximum rate of increase for the population, $R_{max}$ was also fixed in our model at $R_{max}$ =1.12. Consequently, we have underestimated the uncertainty associated with our value of K.

The Northwest Atlantic harp seal population is the largest of the three harp seal populations currently recognized with an estimated population of approximately 8 million animals (Hammill and Stenson 2011). Given the large changes in abundance observed in this population, it is expected that increased competition, presumably for food resources will be affecting the dynamics of this population. Current techniques used to evaluate this resource are unlikely to provide insights into *K* before several more years have passed. Management decisions could have an adverse impact on the population if the possibly of density dependent changes in survival and fecundity are not considered. Therefore, there is a need for some proxy of *K*. Fitting a model to catch data from historical records to reconstruct the population, assuming that it was stable and resource limited, provides some insights into pristine population size. We have assumed that the historic environmental conditions that this population was exposed to were similar to current ecological conditions. However, changes in the trophic structure of the northwest Atlantic ecosystem, with the collapse of the groundfish fishery and climate change which are expected to result in a decline in seasonal ice cover could have a significant impact on harp seals (Johnston et al. 2005). This may result in changes in distribution or a different relationship between population and environmental carrying capacity.

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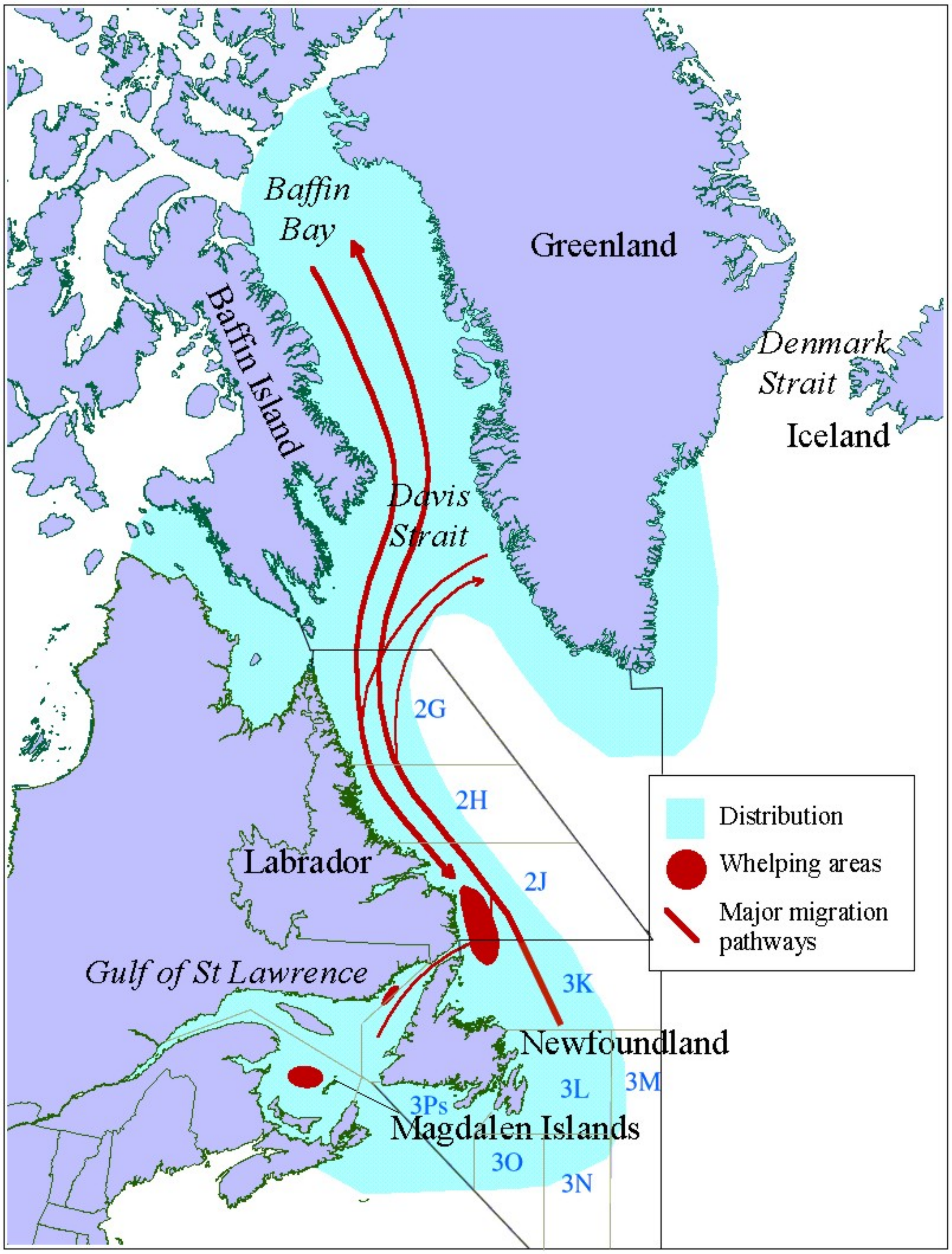


*Figure 1. Distribution, generalized migration pathways and breeding (whelping) areas of Northwest Atlantic harp seals.*

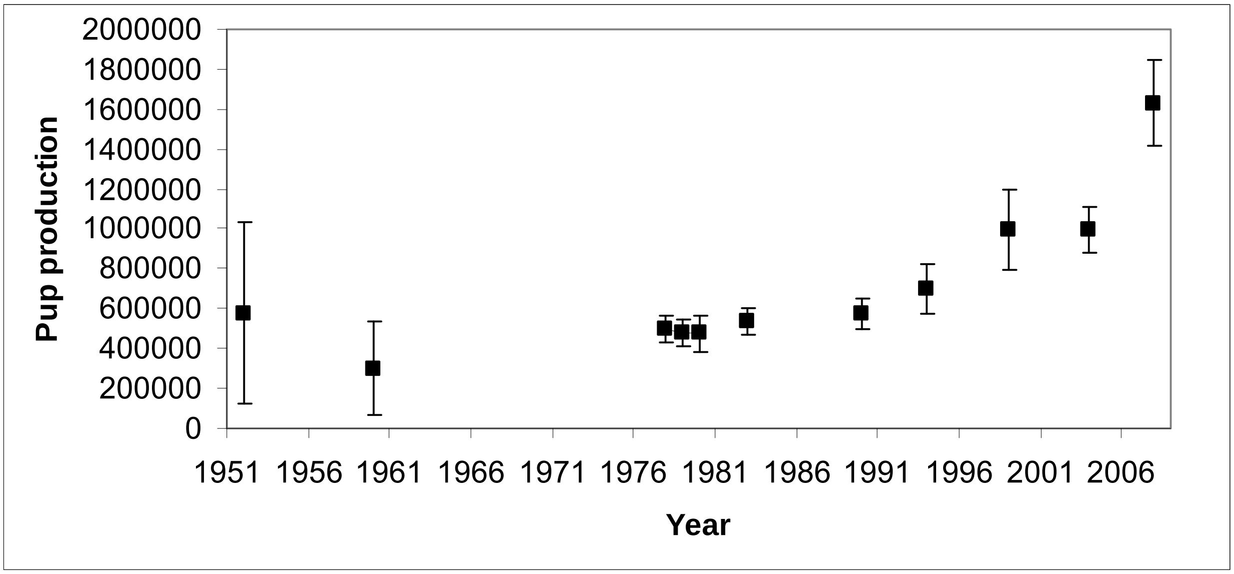


*Figure 2. Estimates of pup production of Northwest Atlantic harp seals from 1952 to 2008. The 1952 and 1960 aerial surveys were incomplete and a CV of 40% has been assigned. The 1977 to 1983 estimates are mark-recapture. Estimates since 1990 are from aerial surveys. These are summarized in Hammill and Stenson (2011)*

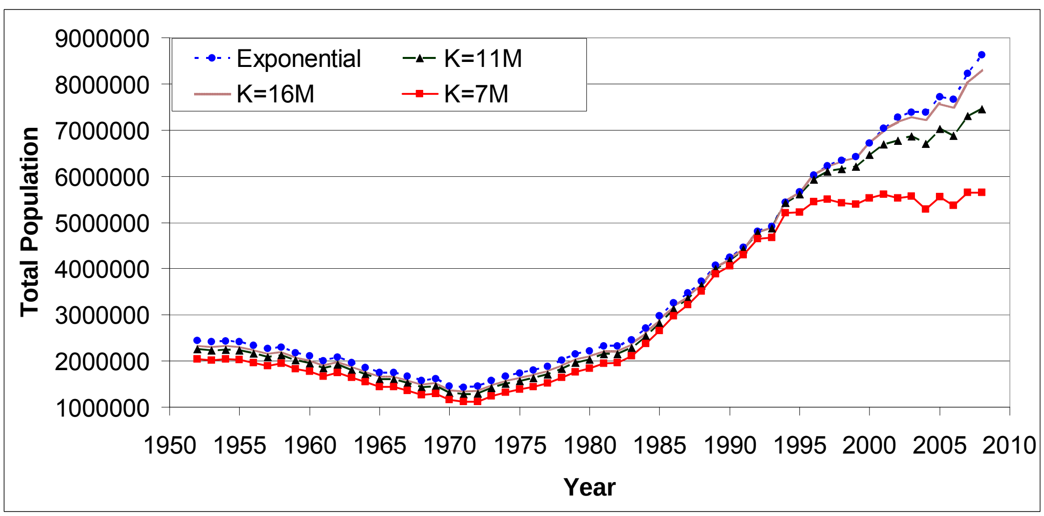


*Figure 3. Changes in estimated population size of Northwest Atlantic harp seals obtained from an age structured model (Hammill and Stenson 2011), under different assumptions of population growth and maximum population size (K).*

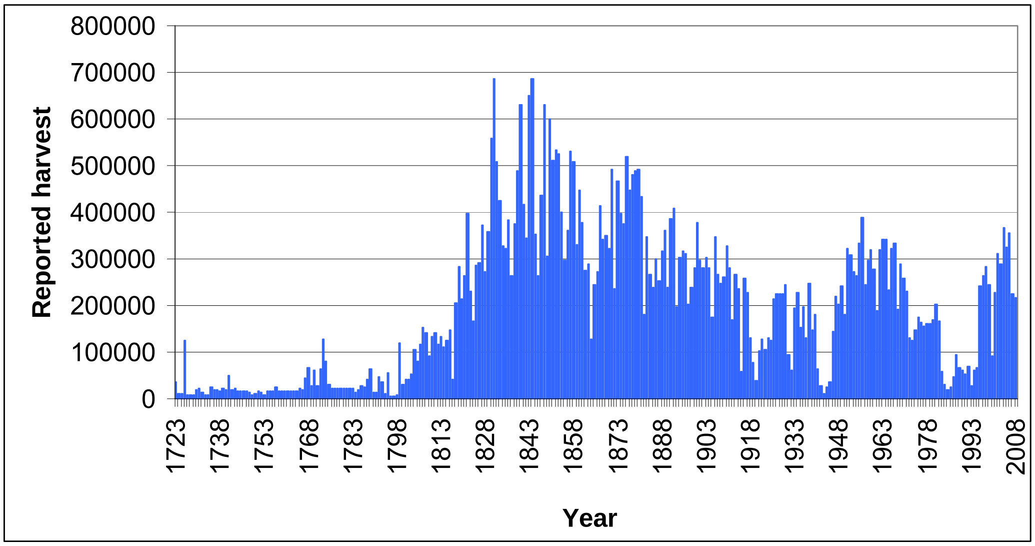


*Figure 4. Reported catches of Northwest Atlantic harp seals in Newfoundland and Canada between 1723 and 2008.*

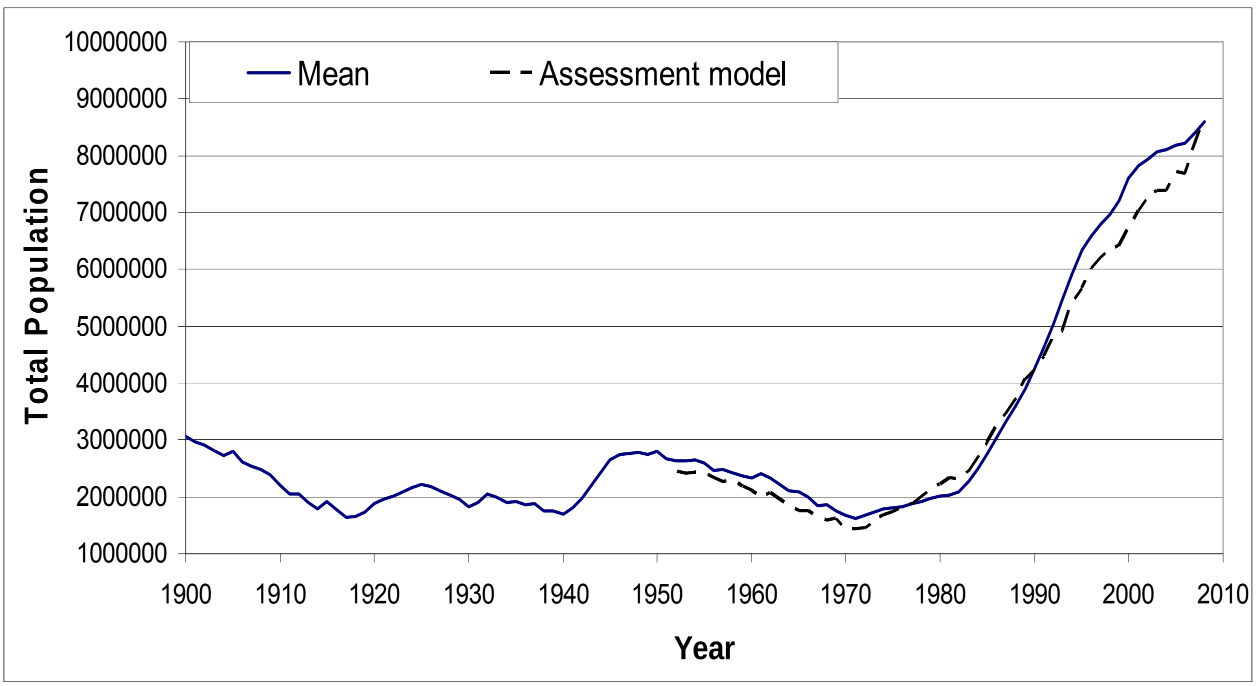


*Figure 5. Estimated abundance of Northwest Atlantic harp seals, showing the fit to estimates obtained from an age structured model 1952-1993.*

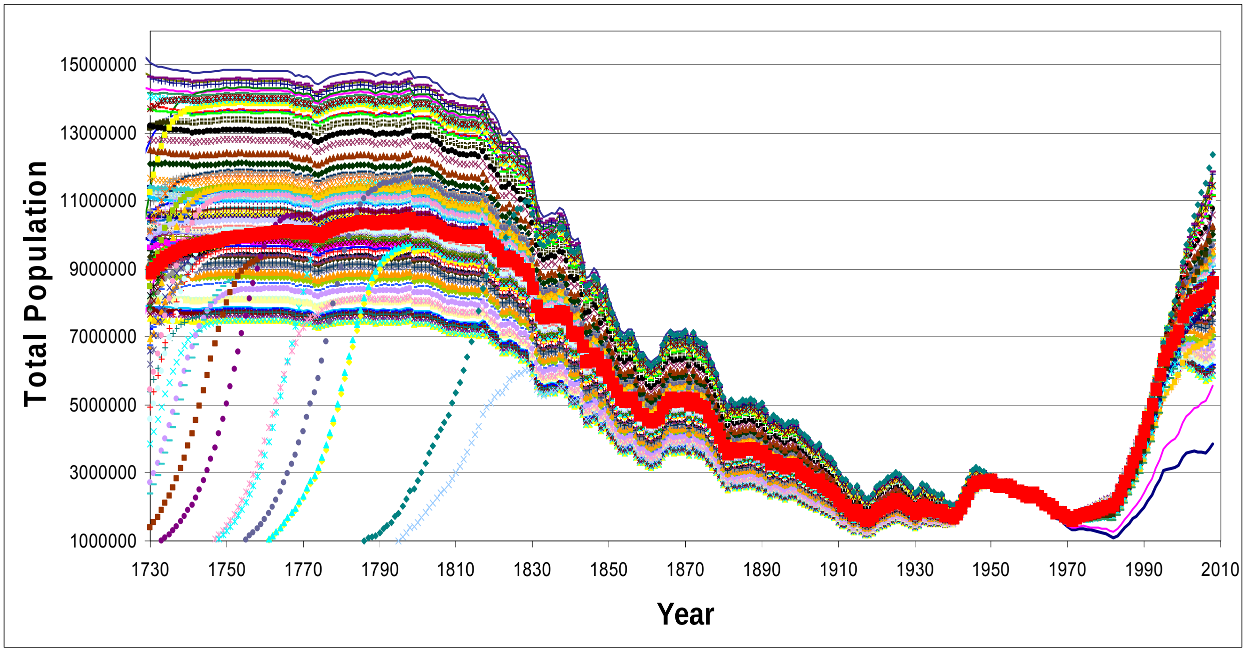


*Figure 6. Estimated abundance of Northwest Atlantic harp seals from 100 trials of the model. The mean is represented by the thick red line. The population shows signs of increasing during the early portion because of the low initial population size introduced into the model.*