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

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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 (*Pagophilu*s groenlandicus =ice-lover from Greenland) is an obligate pack-ice breeder and is arguably the most abundant phocid 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 19th century. Catch data from historical records and recent harvests were incorporated into a surplus production model (Pella-Tomlinson) to reconstruct the dynamics of this population to the late 18th Century. Model runs estimated an initial population of 10.8 million (SE=196,000) animals. Estimates of population size were negatively correlated with catches and positively correlated with the winter North Atlantic Oscillation (NAO) index lagged by several years.

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, juveniles 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 longterm 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 (eg 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 distributed throughout the north Atlantic. 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 18th century (Barchard 1987, Ryan 1994). From the beginning of the commercial harvest in Newfounland 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 (av = 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 *et al*. 2003).

During the 1970s, the population declined to reach a minimum of just under 2 million animals, but 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 7.4 million (95% CI=5.0-8.5 million) animals in 2008 (Hammill and Stenson In prep.), 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 rate, harvest, and ice-related mortality information into a population model that is then fitted to estimates of pup production surveys (Sjare and Stenson 2011; 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, resulted in an estimated pup production of 997,900 (SE=102,100) (Stenson et al 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 well understood (Sjare and Stenson 2011). However, in a more recent survey, 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 changes in population dynamics.

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. 1). This, combined with continued harvesting, limit our ability to detect density-dependent changes in the population. Therefore there is a need for an alternate approach to determine if density-dependent factors are affecting the dynamics of this population.

Catch series are an important component of population assessments, along with an understanding of stock structure and present 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 carrying capacity. Stenson (2009) summarizes catches from the Canadian and Greenland harvests from 1952 to the present. However, historical information on catches from hunts in Newfoundland (e.g. Chafe 1923, Coleman 1937, 1949, Barchard 1978, Ryan 1994) and the Gulf of St. Lawrence as well (Gallienne 1963) are available which allow us to explore the long term catch history of Northwest Atlantic harp seals.

Expert reviews provided by the Intergovernmental Panel on Climate Change (IPCC) make it clear that climate change will induce temperature changes and associated adjustments in ocean circulation, ice coverage and sea level. (McCarthy et al. 2001). Such changes are expected to impact marine ecosystems, through changes in population parameters, predator-prey relationships and distribution (Simmonds and Isaac 2007).

Harp seal young of the year (YOY) require ice for suckling and resting for up to the 8 weeks of life (Sergeant 1991). In years, where there is very little ice-cover, mortality (M_{ice}) of nursing and weaned YOY is likely to be quite high. Ice-cover in Atlantic Canada shows considerable inter-annual variation (Drinkwater 2004) and in some years, there is very little ice-cover in the main breeding areas of the Gulf of St. Lawrence (Gulf) and off the northeast coast of Newfoundland (Front).

The North Atlantic Oscillation (NAO) is a measure of the difference in Atmospheric pressure between the low-pressure centre near Iceland and the high-pressure centre near the Azores (Stenseth et al 2003). Changes in the NAO produce changes in mean wind speed and direction over the Atlantic, as well as significant changes in ocean surface temperature and heat content, ocean currents and their related heat transport, and sea-ice cover in Arctic and sub-arctic regions The atmosphere is most dynamically active during the winter and so, fluctuations in the NAO are the greatest between November and April (Stenseth et al 2003). Generally, positive values of the index indicate stronger-than-average westerlies over the middle latitudes and are usually correlated with the presence of more ice in the northwest Atlantic (Johnston et al 2005, Friedlander t al 2010).

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. We also examine an environmental index, the NAO, to determine if changes in NAO are associated with changes in the northwest Atlantic harp seal population.

Materials and Methods

Abundance estimates

Recent estimates of the population (1952-present) are based on fitting of an age-structured model that incorporates annual estimates of reproductive rates, removals and mortality associated to poor ice-conditions into the model structure. The model is fitted to independent estimates of pup production obtained from mark-recapture and aerial survey studies (Fig. 2)(Hammill and Stenson (2011). This model has been used previously to estimate total population of Northwest Atlantic harp seals and details, which are presented in Hammill and Stenson (2011), are not repeated here. This model estimates changes in the population over the period 1952 to the present, a period where we have detailed information on the age-composition of the harvest and age-specific reproductive rates (Stenson 2009; Stenson and Wells 2010). Longterm trends in reproductive rates (Sjare and Stenson 2011. Stenson and Wells 2010) suggest that density dependent factors are operating on the dynamics of this population. There does not appear to be any difference in estimated population trends between models that assume exponential population growth and models assuming density dependence with K = 8 million or more up to 1993 (Fig. 3). Therefore, we used estimates of the total population obtained from the assessment model for the period 1952 to 1993 as our reference or true population size.

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 in predicted population size and the recent (1952-1995) estimates of population size obtained from the age- structured model. A discrete time parameterisation of the Pella and Tomlinson model (1969) 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 (N_{t+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
θ is a shaping parameter of the density dependent response.
λ_{max} is the maximum rate of increase,
H_t is the reported harvest and
b is a parameter to account for animals killed but not reported

In this study, λ_{max} was set to 1.12, a typical value for pinnipeds (Wade 1998) and θ was set at 2.4 (Trzcinski et al. 2006).

Reported catch data are available from current catch statistics and catch data gleaned from different logbook 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 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 2008.

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) also 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 have not been compiled previously. Catches by hunters from the Magdalene 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, Anon 1888-1940, Mosdell 1923, Coleman 1937) when possible and was 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 (1987). Data on catches were not available for some of the early years (prior to 1800). In order 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 would 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). Twenty thousand runs were completed for each fitting. This was repeated 100 times, 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.

Environmental Index

Several North Atlantic Oscillation time series exist. We used the winter (December through March) index of the NAO available from the Climate Dynamics Division of National Center for Atmospheric Research in Boulder Colorado (http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html).

The NAO is based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. The SLP anomalies at each station were normalized by division of each seasonal mean pressure by the long-term mean (1864-1983) standard deviation. Normalization is used to avoid the series being dominated by the greater variability of the northern station (Fig 5).

Interactions between estimated population size and NAO were examined using Pearson correlation and partial correlation analyses (Version 9, SAS Institute , Cary, NC. USA).

Results

Reasonable fits were obtained between the 'true' population based on the age-structured model and the P-T model (Fig. 6a). The model fitted to the catch time-series resulted in an average K of 10,773,598 (SE=195,646; 95% CI=7,721,919-14,653,244; Range = 7,551,320-15,444,476). The average non-reporting rate (*b*) for the period 1723-1951 was 1.44 (SE=0.026; 95% CI=1.03-1.06; Range=1.01-2)(Fig. 6b).

The mean population size in 1730 was 8.7 million, which increased throughout the remainder of the century (Fig. 6b). Harvests began to increase in the late 1700s reaching over 500,000 in the 1820s, causing the population to decline (Fig. 4, 6b). 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 2.8 million by 1947 and then declined to the low of 1.6 million animals by 1971. Since then the population has recovered reaching 8,497,936 (SE=23,577; 95% CI=5,856,403-11,799,894) animals in 2008.

A weak positive correlation was observed between the number of kills and population size (Table 1). Significant moderate negative correlations were observed between population size and the number of kills lagged by 7-20 years. A positive correlation was observed between the reconstructed population size and NAO lagged by 4-16 years, while a negative correlation was observed between kills and the NAO index. Partial correlation coefficients were also estimated after controlling for the harvest. A positive correlation was observed between the reconstructed population and NAO, and between the population and NAO lagged 1-13 years.

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 of approximately 10.8 million at the start of this period of intensive exploitation.   The apparent increase in population during the 18^{th} C is likely an artefact of the way in which the model deals with an initial population. The population could not sustain the high level of harvest that occurred throughout the 19^{th} C, declining to less than 2 million. 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 a 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, in prep) and there has been a general decline in reproductive rates of mature adults, although considerable inter-annual variability is evident (Stenson and Wells 2010). Therefore, it is expected 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 understand how density-dependence changes might be affecting the dynamics of this population .

Our estimate of virginal population size can act as a proxy for K, assuming that environmental conditions are similar to those experienced during the 18th and 19th centuries. This estimate of 10.8 million is roughly double the estimated K of 3-5 million animals reported in previous studies (ref: Barchard 1978). However, previous work has not taken into account possible non-reporting, which our work indicates is quite significant (40%). In earlier work, Barchard (1978) identified that animals would not be included in statistics if they were shot, but not recovered, and if pelts stocked on the ice were not recovered. 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 trans of oil sold. Previous reports of historical harvest (e.g. Barchard 1978, Ryan 1994) focussed primarily upon the Newfoundland hunt and usually did not include harvests from the Gulf of St. Lawrence 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 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.

Over long evolutionary time scales, marine mammals have survived repeated periods of cooling and warming and have responded primarily through shifts in distribution (Learmonth et al. 2006; Kovacs and Lydersen 2008; Laidre et al. 2008; Moore and Huntington 2008). However, the operating mechanism is not well understood and several hypotheses are possible. For example, do individuals shift in distribution within a season in response to poor ice conditions, moving to alternative sites to have their young? Do animals continue to give birth in traditional areas, with high mortality in areas where ice is poor, while animals having their young in more northerly areas would have lower mortality among their young and hence their numbers would increase? Do animals gradually abandon areas where unsuitable ice conditions persist?

Harp seals require ice for reproduction and it is particularly important as a resting platform for the young of the year (YOY). Years, where there is very little stable ice cover have been associated with very high mortality among young (Sergeant 1991). The decade 1984-1994 was associated with a string of good ice conditions which would have favoured pup production and survival on the ice. However, since 1996, there has been an increase in the frequency of winters with poor ice conditions, (Johnston et al. 2005; Friedlaender et al 2010, Bajzak et al. in press) and this is expected to have a negative impact on YOY survival. Total ice cover in the Gulf of St. Lawrence and at the Front are associated with the NAO, with colder winters associated with a positive phase of the NAO and milder winters associated with a negative phase (Stenseth et al 2003, Johnston et al. 2005, Friedlander et al. 2010).

In this preliminary analyses of factors affecting harp seal abundance we observed a negative correlation between population size and harvest levels that were lagged over several years, which is not unexpected. Our review of historical catches indicated that YOY appear to have accounted for approximately 80% of the historical catches and since harp seals are long living animals that are not recruited into the breeding population before 5 years of age, several weak cohorts would needed before impacts on the population would be detected. Similarly, a positive correlation was observed between abundance and the NAO index, while a negative correlation was observed between catches and the NAO index. This indicates that in heavy ice years, fewer animals were taken, and survival would have been greater which would contribute to population growth.

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. 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, yet there is a need for some proxy of K to provide advice to managers. Fitting a model to catch data from historical records to reconstruct the population provides some insights into pristine population size, which assuming that environmental conditions have remained similar results in an estimate of K of approximately 10.7 million animals. However, changes in the trophic structure of the northwest Atlantic ecosystem and climate change which are expected to result in a decline in seasonal ice cover will have a significant impact on harp seals. Although a shift in distribution may be expected, these changes may also affect the overall carry capacity of the area. and thus the ability of this population to recover to historical levels.

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Table 1. Pearson correlation and partial correlation between estimated reconstructed population size, harvests and NAO. Harvest data are referred to as kill and are lagged by 1 to 20 years. The NAO index is also lagged by 1-20 years. Only correlations that were significant are shown.

	Kill	Kill7	Kill8	Kill9	Kill10	Kill11	Kill12	Kill13	Kill14	Kill15	Kill16	Kill17	Kill18	Kill19	Kill20
Pop	0.17	-.2	-.24	-.26	-.29	-.33	-.37	-.40	-0.41	-0.41	-.40	-.40	-.39	-.38	-.37
	(.04)	(.02)	(.005)	(.003)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)
	NAO4	NAO5	NAO6	NAO7	NAO8	NAO9	NAO10	NAO11	NAO12	NAO13	NAO14	NAO15	NAO16		
Pop	.17	.18	.20	.20	.23	.22	.21	.23	.24	.29	.26	.23	.20		
	(.047)	(.03)	(.02)	(.02)	(.006)	(.01)	(.012)	(.008)	(.005)	(.000)	(.003)	(.009)	(.02)		
	NAO														
Kill	-.27														
	(.001)														
Partial	NAO	NAO1	NAO2	NAO3	NAO8	NAO9	NAO10	NAO11	NAO12	NAO13					
Pop	.26	.25	.22	.20	.20	.22	.20	.25	.20	.25					
	(.008)	(.011)	(.021)	(.026)	(.04)	(.026)	(.04)	(.012)	(.04)	(.01)					

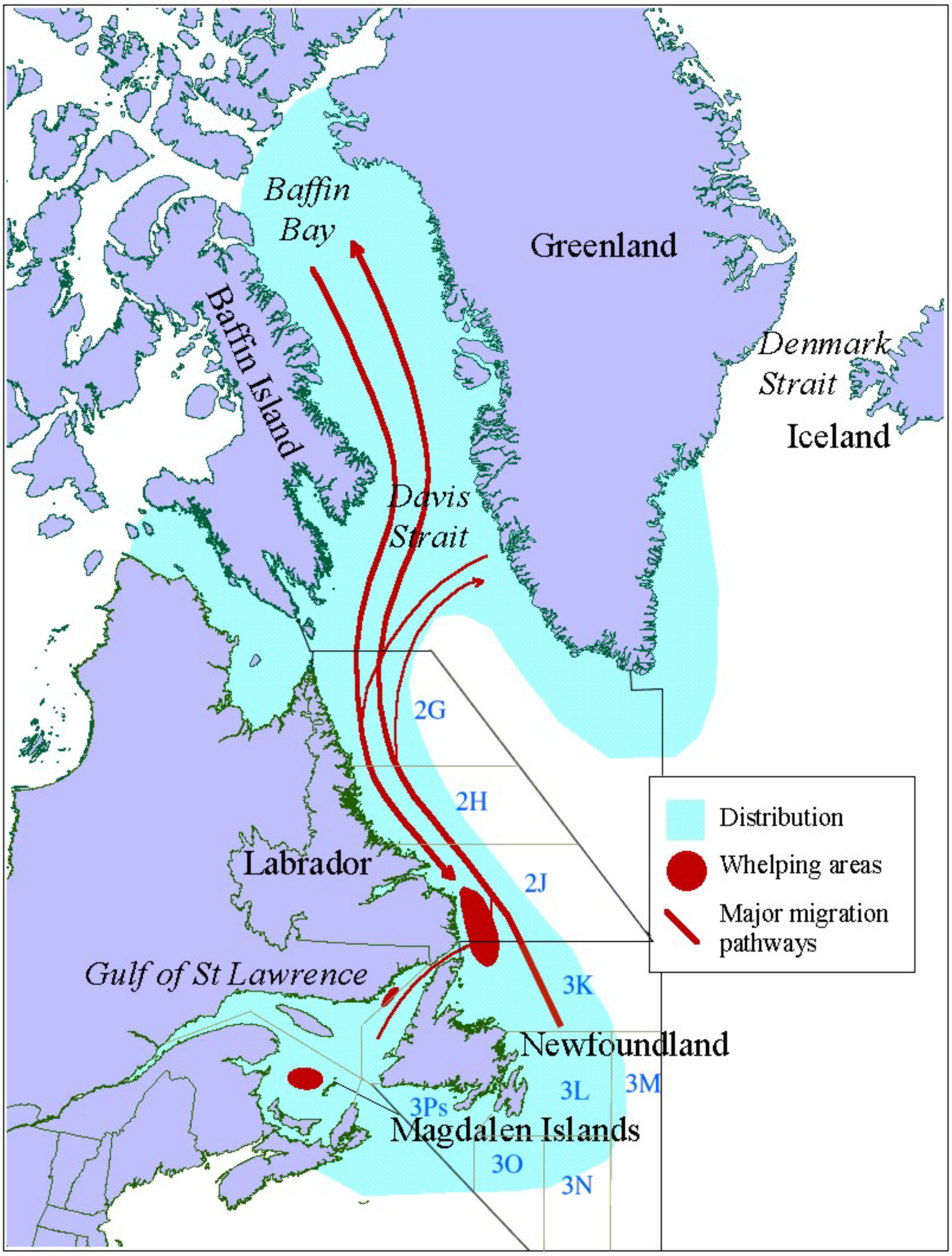

Figure 1. Distribution, generalized migration pathways and breeding (whelping) areas of Northwest Atlantic harp seals.

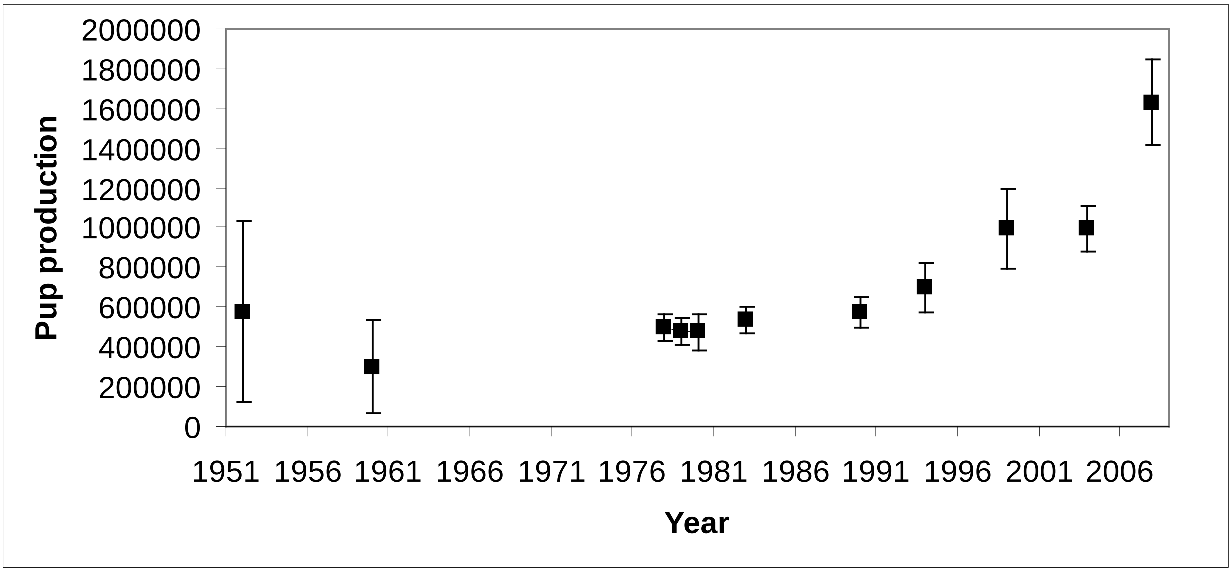

Figure 2 . Estimates of pup production of Northwest Atlantic harp seals from 1952 to 2008. The 1952 and 1960 aerial surveys were incomplete and a CV of 40% has been assigned. The 1977 to 1983 estimates are mark-recapture. Estimates since 1990 are from aerial surveys.

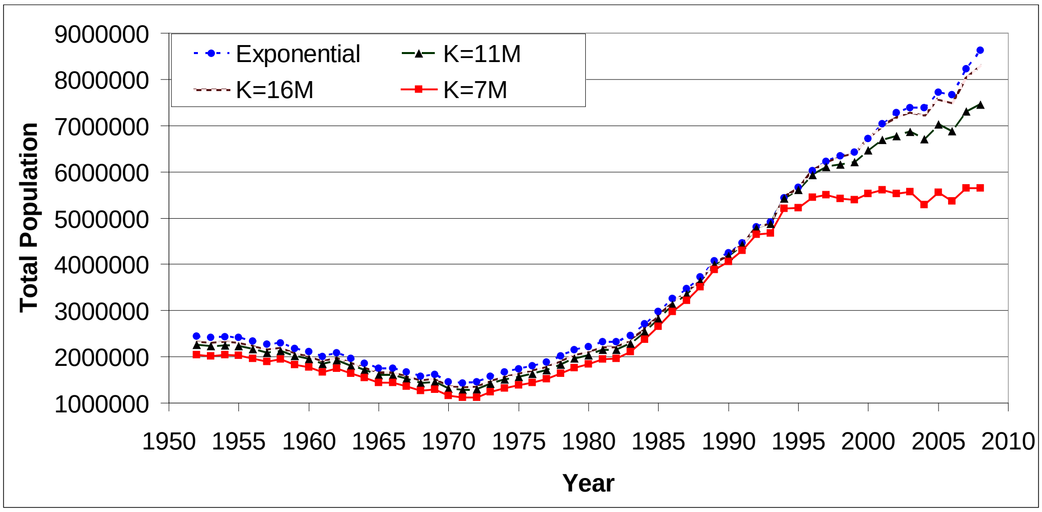

Figure 3. Changes in estimated population size of Northwest Atlantic harp seals between 1952-2008 obtained from an age structured model (Hammill and Stenson, in prep), under different assumptions of population growth and maximum population size (K)..

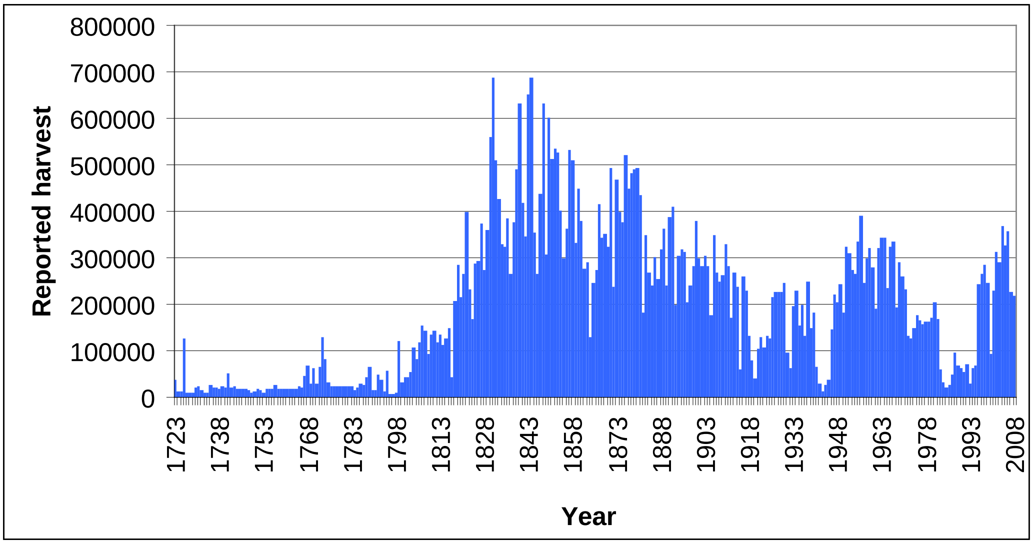

Figure 4. Reported catches of Northwest Atlantic harp seals in Newfoundland and Canada between 1723 and 2008.

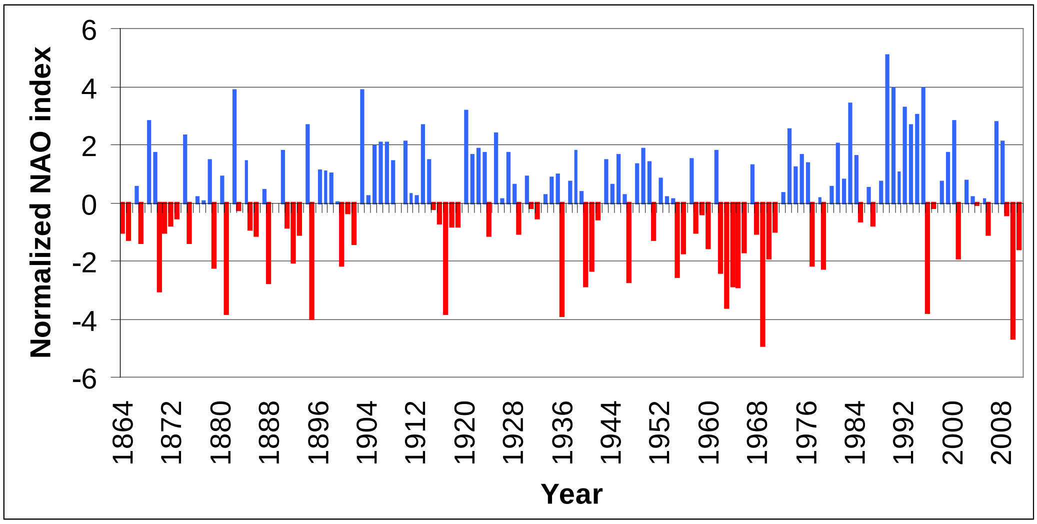

Figure 5. Winter Normalized NorthAtlantic Oscillation index for the period 1864 to 2011. (http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html).

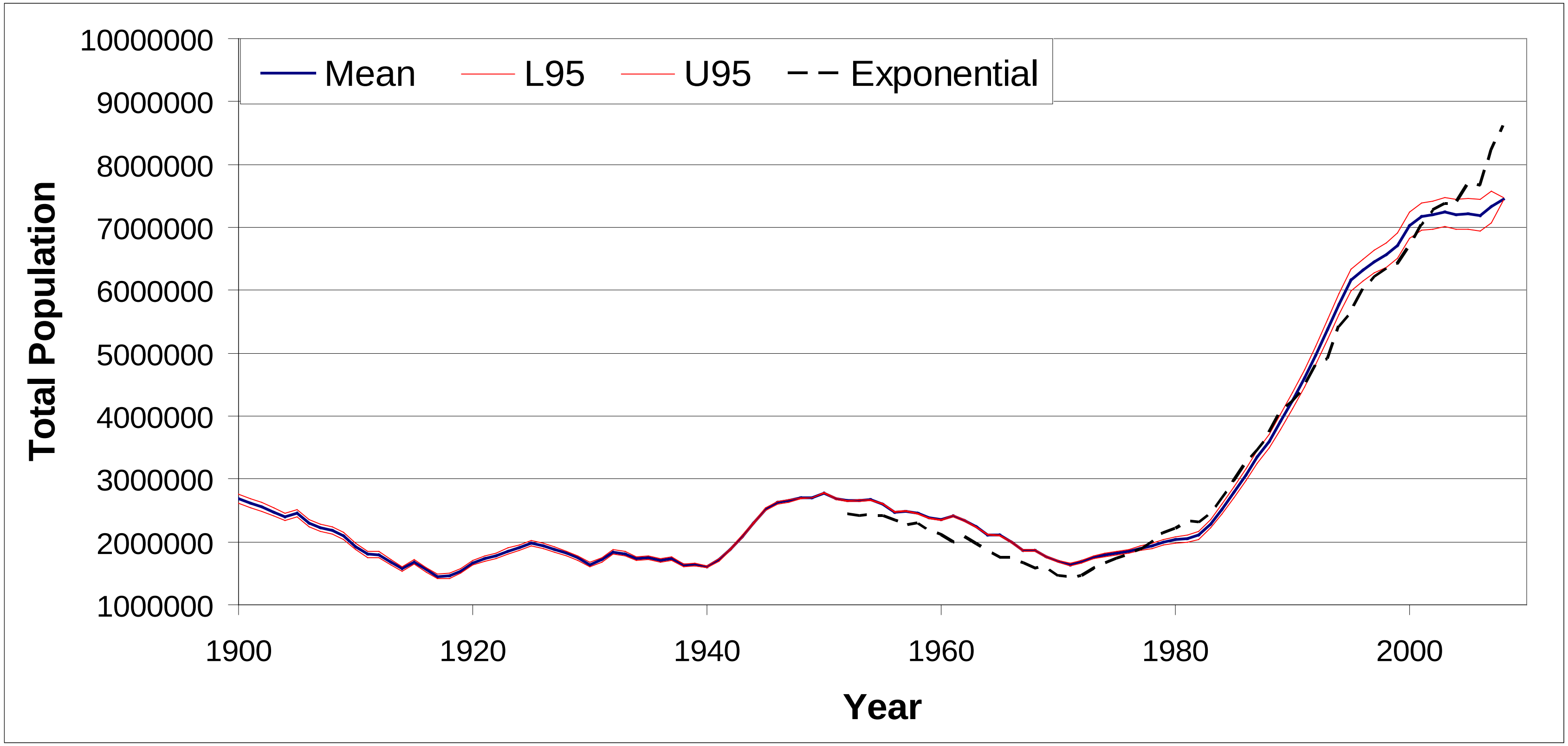

Figure 6a. Estimated abundance (95% CI) of Northwest Atlantic harp seals. The population shows signs of increasing during the early portion because of the low initial population size introduced into the model.

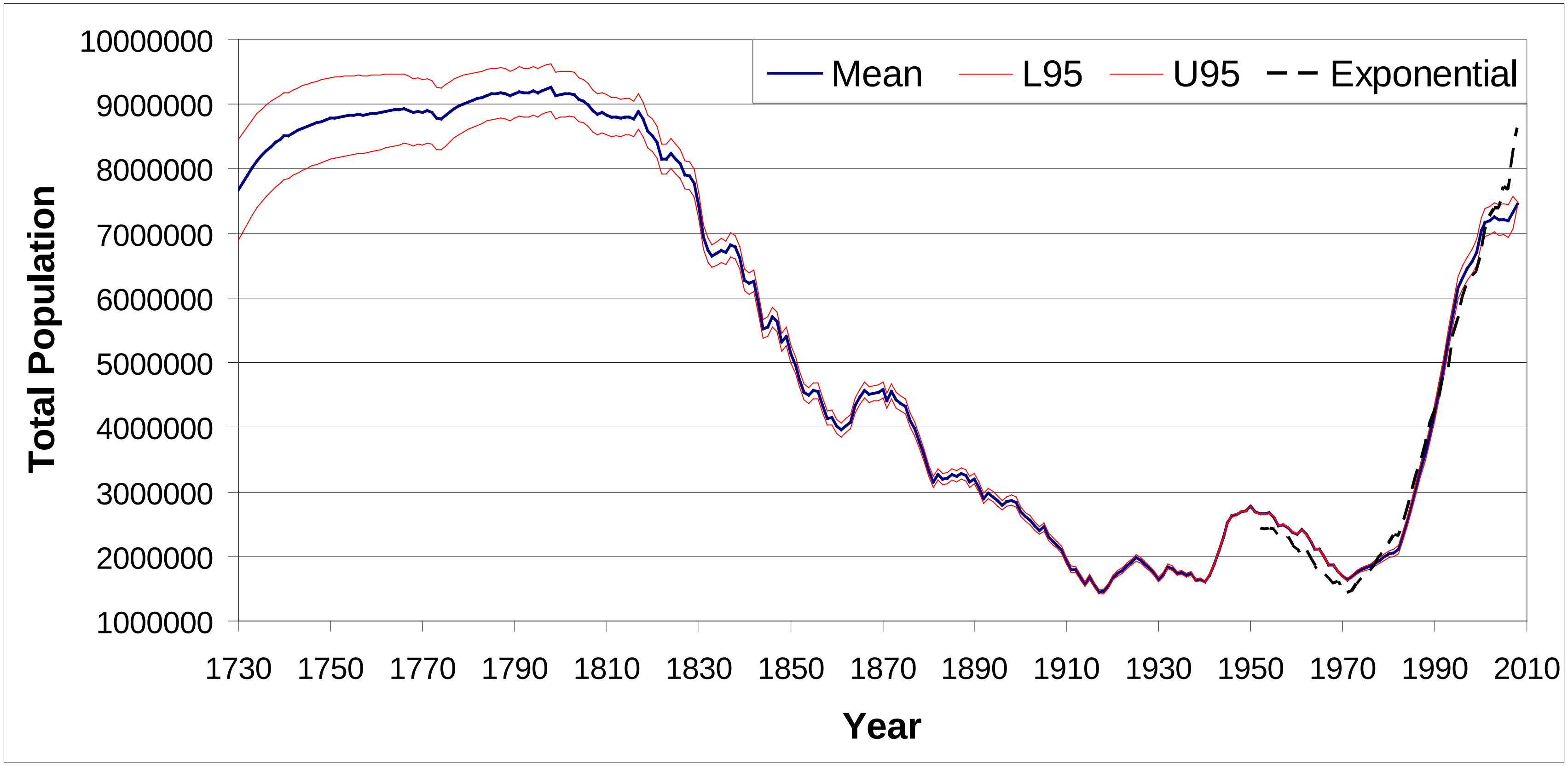

Figure 6b. Estimated abundance (95% CI) of Northwest Atlantic harp seals. The population shows signs of increasing during the early portion because of the low initial population size introduced into the model.