Fisheries and Oceans Canada | Pêches et Océans Canada
Science | Sciences

C S A S | S C C S

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

Research Document 2012/148

Document de recherche 2012/148

Quebec and Newfoundland and Labrador Regions

Régions du Québec et de Terre-Neuve et Labrador

Estimating carrying capacity and population trends of Northwest Atlantic harp seals, 1952-2012

Évaluation de la capacité de support et des tendances de la population de phoques du Groenland de l'Atlantique Nord-Ouest, 1952-2012

M.O. Hammill[1], G.B. Stenson[2], T. Doniol-Valcroze[1], A. Mosnier[1]

[1] Science Branch, Department of Fisheries and Oceans
Institute Maurice Lamontagne, P.O. Box 1000
Mont-Joli, QC. G5H 3Z4

[2] Science Branch, Department of Fisheries and Oceans
Northwest Atlantic Fisheries Centre, PO Box 5667
St. John's, NL A1C 5X1

***Erratum*: July 2013**

***Erratum*: juillet 2013**

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

Canada

Correct citation for this publication:

Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T., and Mosnier, A. 2013. Estimating carrying capacity and population trends of Northwest Atlantic harp seals, 1952-2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/148. iii + 31 p. (Erratum: July 2013)

ABSTRACT

A population model was used to examine changes in the size of the Northwest Atlantic harp seal population between 1952 and 2012. The model incorporated information on reproductive rates, reported removals, estimates of non-reported removals and losses through bycatch in other fisheries to determine the population trajectory. The model was fit to eleven periodic estimates of pup production from 1952 to 2008, and to annual pregnancy rate data collected between 1954 and 2012. Pup production declined throughout the 1960s reaching a minimum in 1971, and then increased to a maximum in 2008. Estimated pup production in 2012 was 1.5 million animals (95% CI=1.0-2.1million); the total estimated population size in 2012 was 7.1 million (95% CI=5.9 to 8.3 million). Fitting the model to both the aerial survey data and the reproductive rate data (age classes 8+ only), resulted in estimates of K=10.0 million. Different formulations were used to describe future population trends. If the harvest rates in Greenland and future reproductive rates are fixed, then an annual harvest of 300,000 animals would respect the management objective. If future catches in Greenland, future reproductive rates and juvenile survival are linked to changes in population size then annual harvests of up to 400,000 animals would respect the management objectives. The effect of variable harvest levels was also examined. Ice conditions, reproductive rates and removals from the Greenland harvest continue to be important factors affecting the dynamics of this population. Modifications to the assessment model have provided a means of estimating environmental carrying capacity assuming a certain functional relationship between total population size and juvenile survival, and between population size and reproductive rates.

RÉSUMÉ

Un modèle de population a été utilisé pour examiner les changements dans la taille de la population de phoques du Groenland entre 1952 et 2012. Le modèle intègre des informations sur les taux de reproduction, les prélèvements déclarés, les estimations des prélèvements non déclarés et les pertes dans les prises accessoires dans d'autres pêcheries pour déterminer la trajectoire de la population. Le modèle a été ajusté à onze estimations périodiques de la production de petits de 1952 à 2008, et les données annuelles récoltées sur les taux de gestation entre 1954 et 2012. La production de petits a diminué pendant les années 1960, pour atteindre un minimum en 1971, et a ensuite augmenté à un maximum en 2008. La production estimée de petits en 2012 était de 1 500 000 d'animaux (95 % IC = 1 000 000 à 2 100 000); la taille de la population totale estimée était de 7 100 000 (95 % IC = 5 900 000 à 8 300 000). L'ajustement du modèle aux données des relevés aériens et aux données du taux de reproduction (classes d'âge 8+ seulement), a abouti à des estimations de K = 10,0 millions. Différentes formulations ont été utilisées pour décrire les tendances démographiques à venir. Si les taux de récolte au Groenland et l'évolution des taux de reproduction sont fixés, alors une récolte annuelle de 300 000 animaux respecterait l'objectif de gestion. Si les futures captures au Groenland, les futurs taux de reproduction et de survie des juvéniles sont liés aux changements de la taille de la population, alors une récolte annuelle jusqu'à 400 000 animaux respecterait les objectifs de gestion. L'effet de niveaux de récolte variables a également été examiné. Les conditions de glace, les taux de reproduction et les prélèvements dans la récolte au Groenland demeurent des facteurs importants qui influent sur la dynamique de cette population. Les modifications apportées au modèle d'évaluation ont fourni un moyen d'estimer la capacité de support environnementale en supposant une certaine relation fonctionnelle entre la taille de la population totale et la survie des juvéniles, et entre la taille de la population et les taux de reproduction.

INTRODUCTION

Information on abundance of natural resources is required for setting appropriate harvest limits, building ecosystem models and/or evaluating the impacts of environmental change or industrial activities upon a resource. Phocid life–histories are characterized by foraging at sea, with a requirement to return to a solid substrate for reproduction (Kovacs 1995). Throughout much of the year, animals are dispersed widely at sea where they are often below the surface and hence difficult to count. During the breeding season, mature animals aggregate, and although adults may not always be hauled-out, the young are available to be counted using visual or photographic surveys (Bowen et al. 1987; Stenson et al. 1993, 2002, 2003). An estimate of total population size is then obtained by incorporating the estimates of young of the year (YOY) into a population model along with information on reproductive and/or mortality rates (Roff and Bowen 1986; Skaug et al. 2007).

The harp seal (*Pagophilus groenlandicus*) assessment incorporates information on annual age-specific reproductive rates, reported harvests, struck and loss, and ice-related mortality of young of the year (YOY), into an age-structured model to estimate total population size. The model is fitted to estimates of pup production obtained from aerial surveys and mark-recapture studies by adjusting the initial population size in 1952 and adult mortality rates (Hammill et al. 2011a). The basic model was first developed in the early 1980’s (Roff and Bowen 1983), but has since undergone a series of improvements (eg Shelton et al. 1992), including consideration of struck and loss, and incorporating unusual mortality related to poor ice conditions (Sjare and Stenson 2002; Hammill and Stenson 2003) (Table 1).

Two significant changes occurred in recent years (Table 1). First, the model formulation was changed from describing the dynamics of the population assuming exponential growth to a model describing the dynamics of the population assuming density-dependent changes in young of the year mortality. In 2010 and 2011, environmental carrying capacity was set (rather than estimated from the data) and was assumed to be 12 million animals (Hammill et al. 2011b). Secondly, unusually high reproductive rates were observed in 2007 and 2008, resulting in much higher than expected pup production (Stenson and Wells 2010; Stenson et al. 2010), in spite of an overall declining trend in reproductive rates among animals aged 8 years and older. Consequently, the manner in which the reproductive data were incorporated into the model was changed (Hammill and Stenson 2011; Hammill et al. 2011a). Until then, it was assumed that the pregnancy rates did not vary widely between years, and therefore averaged or smoothed values were used. In the 2010 formulation, the annual proportion of pregnant females aged 8+ years was incorporated into the model for years with sufficient data in order to capture the high interannual variability.

At the National Marine Mammal Peer review meeting in Mont-Joli, it was suggested to fit the model to observed changes in the annual reproductive rate data, in addition to the existing fitting to estimates of pup production obtained from the aerial surveys. This approach appeared promising because whereas there are only 11 aerial survey estimates available since 1950, there are 30+ years of reproductive rate data available since 1952. In this paper, we fit the model to both the reproductive rate data and to the aerial survey estimates. The model does this by adjusting estimates of adult mortality rates (M), initial population size (α), and environmental carrying capacity (K) to minimize the sum of squares differences between observed reproductive rates and survey estimates and model predictions for these estimates. These estimates of α, K and M are then incorporated into a projection model to evaluate whether different harvest scenarios respected the management objective, over the duration of a management plan that runs for 1,2,3 and 4 years.

For the harp seal assessment a major difficulty is to predict how reproductive rates may change in the future as well as how the unregulated Greenland subsistence harvest may also change. In this paper, in addition to changes in how the model is fitted to the aerial survey and reproductive rate data, we also use a density dependent relationship to predict how reproductive rates may vary in the future as the overall population size changes. Since changes in the environment may also explain some of the variability in observed reproductive rates (Stenson and Wells 2010), we apply an environmental factor to modify these rates. Also, we assume that the harvest in Greenland will change as the size of the Northwest Atlantic harp seal population changes.

MATERIALS AND METHODS

Modelling the dynamics of the Northwest Atlantic harp seal population occurs in two steps. In the first, using Monte Carlo resampling, the model is fitted to independent estimates of the total pup production, and the pregnancy rates observed for seals 8 years old and older (referred to as 8+) by adjusting initial population size (α), adult (i.e. one year old and older, referred to as 1+) mortality rates (M) and the carrying capacity (K). The model integrates data on removals and ice-related mortality. It is considered that the dynamics of the population can be described by assuming density dependent mortality acting on both juvenile survival and pregnancy rates of the 8+ individuals. It is also assumed that the sex ratio is 1:1.

A second component of the model, referred to as the 'Projection Model', projects the population into the future to examine the impacts of different management options on the population. The projection model is based mainly on the same equations as the fitting model.

Model structure

Initial population

$$P = \sum_{i=1}^{26} (\alpha \times l_i)$$

Survival

For age 1:

$$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1}) \times e^{-M_1} \times (1 - (N_t / K)^{\theta})$$

with $M_1 = \gamma \times M$

For age a, with 1<a<A:

$$n_{a,t} = (n_{a-1,t-1} \times e^{-M/2} - c_{a-1,t-1}) \times e^{-M/2}$$

For age A

$$n_{A,t} = [(n_{A-1,t-1} + n_{A,t-1}) \times e^{-M/2} - (c_{A-1,t-1} + c_{A,t-1})] \times e^{-M/2}$$

Reproduction

$$n_{0,t} = \sum_{a=1}^{A} n_{a,t} \times P_{a,t}$$

For age a, with 1<a<8

$$P_{a,t} \sim CorBin(n_{a.reprod,t}, p_{a.preg,t})$$

For age a, with a ≥ 8 (i.e. 8+)

$$P_{a,t} = P_{8,t} \sim CorBin(n_{8+.reprod,t}, p_{8+.preg,t})$$

also $Psim_{8+,t} = 0.88 \times (1 - N_t / K)^{\theta}$

where

P_{init}	= size of the total initial population,
α	= multiplying factor,
l_i	= initial population size for the i[th] age class,
$n_{a,t}$	= population numbers-at-age *a* in year *t*,
$c_{a,t}$	= the numbers caught at age *a* in year *t*,
$P_{a,t}$	= per capita pregnancy rate of age *a* parents in year *t*, assuming a 1:1 sex ratio,
$CorBin$	= multivariate distribution composed of binomial distributions which degree of correlation is controlled via an 8-dimension Gaussian copula (Sklar 1959; Joe 1997; Trivedi and Zimmer 2005). Note: this function is used during the fitting to establish a correlation between age-classes in pregnancy rates, assuming that if the mature animals (8+ years) have a better year, then younger age classes will also have better years.
$n_{a.reprod,t}$	= sample size used to obtain the observed pregnancy rate in year t,
$p_{a.reprod,t}$	= proportion of pregnancy in the observed group in year t,

$Psim_{8+,t}$ = per capita pregnancy rate of age 8+ parents estimated by its relation with the carrying capacity. The value of 0.88 corresponds to the maximum pregnancy rate observed when the population was low (i.e. far from the carrying capacity). This estimation is used to fit the model with observed pregnancy rates obtained during the same period.

M = the instantaneous rate of natural mortality,

γ = a multiplier to allow for higher mortality of first year seals. Assumed to equal 3, for consistency with previous studies,

w = 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),

N_t = total population size,

K = carrying capacity

θ = theta, set at 2.4 (*Trczinski et al 2006*).

Monte Carlo resampling and parameter estimation

The model creates a population matrix with 26 age classes from 1952 until the current year. The initial population vector (26 × 1) was created as an initial population age structure which size is adjusted by a multiplying factor (α). We included the uncertainty in the pregnancy rates and the pup production estimates in the fitting model by resampling the parameters using Monte Carlo techniques. At each iteration of the model, pregnancy rates are resampled for each year assuming a binomial distribution (correlated among age classes), and pup production estimates are resampled assuming a normal distribution (with variance based on estimates of the survey errors). For each iteration, the model then minimizes (1) the weighted sum-of-square differences between the pup production estimated by the model ($n_{0,t}$) and the resampled production estimates from the surveys, (2) the weighted sum-of-square differences between the 8+ pregnancy rate estimated ($P_{sim8+,t}$) and the resampled pregnancy rates, by estimating three parameters; the initial population factor (α), the instantaneous mortality rate (*M*), and the carrying capacity (*K*). The three parameters (α, *M* and *K)* are optimized by iterative methods. For each Monte Carlo iteration, new *M, K* and α are estimated and stored. The model runs in the programming language R.

Data Input

Pup production estimates

The model was fitted to 11 independent estimates of pup production (Table 2) obtained in 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 surveys did not cover the entire area and included estimates of pupping based upon visual estimates for concentrations seen, but not surveyed. Also, they did not correct for births occurring after the surveys. These two surveys are thought to provide useful information, but there is greater uncertainty surrounding their estimates. To reflect this, these surveys were assigned a coefficient of variation of 40%.

Reproductive rates

Estimates of late term pregnancy rates are available from sampling programs maintained by the Department of Fisheries and Oceans since 1954 (Sjare and Stenson 2010, Stenson and Wells 2010). Samples represent late-term pregnancy rates since they are collected only a few months (October to February) prior to pupping in March. It is assumed that there would have been no mortality after the samples were taken and animals are incorporated into the model at the age they would have had at the time of pupping. Data included in the model were available from 1954 to 2012 (Table 3). Seals 3 years old and younger were considered immature while seals 8 years and older were considered to be fully recruited into the population.

There are gaps in the time series of the data, and in some years sample sizes are small (Table 3). For this reason, we smoothed the data by applying local logistic regression (Loader 1999) to the binary data (pregnant or non-pregnant) (Tibshirani and Hastie 1987). This smoother yields errors around predictions and allows weighting by sample size to take into account the local density of data. Thus, there is no need to reject data points for which sample size is below an arbitrary threshold. Smoothing was performed using the R package LocFit (Loader 2010). Since we expected substantial curvature in the trajectory of pregnancy rates, we used a 2^{nd} degree polynomial to further reduce bias (Sun and Loader 1994). The degree of smoothing was controlled with an adaptive bandwidth: for each fitting point, the bandwidth was chosen so that the local neighbourhood always contained a specified proportion (β) of the dataset. We determined β for each age class by testing a range of values and selecting the β that yielded the best fit (lowest AIC, Loader 1999). To compute confidence intervals, variance in the smoothed data was estimated using log-likelihood in the framework of normal approximations (Loader 1999). Using the binomial family kept pregnancy rates in the [0,1] interval and resulted in non symmetric errors around the mean.

The smoothed reproductive rates were extrapolated backwards from 1954 to 1952. In previous assessments, the smoothed rates were used if less than 5 samples were available in a given age class for a given year; otherwise the observed rate was used. The impact of the number of samples on model estimates of pup production and total population size was examined by repeatedly fitting the model using different criteria for choosing between actual and smoothed rates. Runs examined thresholds of 5, 10, 20, 25 and 75, where if the number of samples in a given year was greater than the threshold, then the model used the actual data when fitting to the estimates of pup production. If the sample for a given year was below the threshold, then the model replaced the actual observed value with a smoothed value derived from the smoothing model for that year and age class. When the smoothed rates were used, uncertainty was incorporated by resampling pregnancy rates from a normal distribution in logit space, with a mean equal to the smoothed value and the standard error equal to the square root of the estimated variance.

Catches

Catch data are available since 1952 and have been summarized by Stenson (2009). Briefly, there are five different types of catch input: the Canadian commercial harvest (Department of Fisheries and Oceans Statistics Branch); the Canadian Arctic subsistence hunt; animals caught incidentally in Canadian and American commercial fisheries (Sjare et al. 2005; Waring et al. 2005, 2007); and the Greenland subsistence hunt. Data were updated to include the most recent data to 2012 (Table 4). Reported catch levels from the Canadian and Greenland hunts were divided into numbers of animals aged 0 and numbers of animals aged 1+ years. For example, the Canadian hunt consists of 97% of young of the year while the Greenland hunt is limited to 14% young of the year (Stenson 2009). Consequently, 3% of the Canadian commercial harvest and 86% of the Greenland harvest are considered to be 1+ seals, which are distributed proportionally among the 1+ age classes. All harvests were corrected for 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). Since 1983, it was assumed that 95% of the YOY and 50% of the 1+ animals in the Canadian commercial hunt (Front and Gulf) were recovered while 50% of all animals killed in Greenland and the Canadian Arctic were assumed not to have been recovered and/or reported (Stenson 2009).

Ice-related mortality of YOY

Poor ice conditions result in increased mortality (M_{ice}) that affects animals prior to the hunt. This is incorporated into the model as a survival term. Currently, M_{ice} is a qualitative measure based upon ice conditions, storm frequency and reports of mortality and/or dead seals washing ashore. In this assessment, M_{ice} was recalculated for the Gulf and the Front herds separately, with M_{ice} for the total herd being estimated based on a ratio of 0.7 Front to 0.3 Gulf . The estimates for ice mortality for the combined herds are presented in Table 5.

Projection model

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

1. mortality from bycatch, the proportion of seals struck and loss, and catches in the Canadian Arctic remain constant;
2. Greenland catches: for the forward projections, two approaches were used. As in previous assessments it was assumed that the levels, and age structure, and proportion of struck and lost and bycatch were the same as used in the last year of the fitting model. Greenland harvest was assumed to vary uniformly between 70,000 and 100,000. For this assessment, a second approach was also used to project future catches from Greenland. It was assumed that Greenland catches are dependent on the harp seal population size (Fig. 1). A piecewise regression, considering observed catches and the corresponding seals population size estimated in the simulation part of the model, allowed determining a break point between two parts of the data. In the first part, Greenland catches can be described by a linear relation with the seal population size (-1.4e+04 + 1.36e-02 * population size) and a 95% prediction interval can be estimated around the estimated mean assuming normal distribution of the error. In the second part of the relation (i.e. when population size is larger than ~ 7.1 million individuals) the catches were assumed to follow a uniform distribution centered on the mean Greenland catch estimated at the break point (~ 82,500 animals) with a range equal to the observed values (69,400 – 95,500);
3. Ice-related mortality (actually, expressed as survival in model), was assumed to vary with values of 0.94, 0.59, 0.21, ,0.9, or 1 based on estimate mortality over the last 5 years. Each value had an equal opportunity of being randomly selected;
4. In previous assessments, reproductive rates for 8+ animals were assumed to be fixed in the projection model to the values of the last 5 years, with each year having an equal probability of being selected (r=0.75, 0.22, 0.3, 0.55, 0.74). Reproductive rates for all other age classes were fixed at the value for the last year of the fitting model. For this

assessment an alternative approach was also used to predict how reproductive rates might change in the future. Reproductive rates are assumed to be related primarily to the population size by the density-dependence equation (r=0.88 * $(1-(N/K)^{2.4})$. Thus, pregnancy rates within ages (4 to 8+) were described by a logistic curve fitted on the observed rates, with the rate for animals aged 8+ years being the asymptote. This was done for the projection model under the assumption that if the 8+ pregnancy rates can be predicted using a density-dependent relationship, then it is possible to evaluate pregnancy rates for other ages while keeping the correlation among values of each age class. Moreover, taking into account the error around the other parameters of the logistic curve allows for consideration of some "natural" variability around each pregnancy rate that is estimated;

5. An environmental effect on pregnancy rates exists (Sjare and Stenson 2010, Stenson and Wells 2010). The impact of changes in food or some other resource availability was represented by increasing/decreasing mean pregnancy rate by a multiplier. For the moment, the multiplier was equivalent to the proportional difference observed between reproductive rates predicted by the density-dependent relationship and the observed rate over the last five years. This is incorporated into the model as discrete values (1.4, 1.5, 1, 0.7, 0.6), with each multiplier having an equal probability of being selected.
6. The basic pup mortality is fixed at three times 1+ mortality (M) and remains unchanged; the dynamics of the population can be described assuming density-dependent mortality acting on juvenile survival and pregnancy rates of the 8+ individuals by the relationship:

$$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1}) \times e^{-M_1} \times (1 - (N_t / K)^{\theta})$$

The model is projected forward to determine what level of catches will respect the management plan (i.e. 80% likelihood of population remaining above the Precautionary Reference Level) for the next 15 years.

RESULTS

Sampling for reproductive rate data was not undertaken prior to 1954, from 1955 to 1963, 1971 to 1977, 1983 and 1984. There are additional years where data are not available for specific age classes or sample sizes are very small (<5) (Table 3) The smoother fitted to the reproductive data provide a means of interpolating for missing years and captured the variability in the data fairly well over the years from 1952 – 2012 (Fig. 2). For the age classes 4-6 years, age specific pregnancy rates were relatively low during the 1960s, increased during the 1970s to reach a peak value in the 1980s and then generally declined. For the 7 years old age class, a similar pattern was observed, but the increase during the 1970s was less evident than for the younger animals. The greatest number of samples was available for the 8+ year class (Table 3). For this group, reproductive rates remained high from the 1950s to the 1980s and then declined throughout the 1990s and 2000s. This trend has continued over the last two years, although the 2012 sample suggests an increase (r=0.75). However, the sample size for 2012 is small (n=20) (Fig. 2).

There is considerable inter-annual variability in the reproductive data (Table 3, Fig. 2). Some of the variability in observed rates is associated with small sample sizes, particularly among the age classes that are less than 8 years old, but sample sizes do not account for all of the interannual variability (Table 3). For the 8+ year age class, which accounts for most of the pup production in this population, where adequate sample sizes indicate that reproductive rates have varied considerably over the last 5 years (Fig. 3). For the 8+ year age class, reproductive rates have ranged from a high of 0.78 in 2007-08 to a low 0.23 in 2011, then increasing again to 0.75 in 2012 (Table 3, Fig. 2).

Different model runs were completed by varying the minimal sample size necessary for the model to use either the raw reproductive data or the predicted smoothed value. The different runs tracked closely the changes in pup production determined from the surveys and produced similar estimates of pup population size, with the exception of the runs that used a threshold of 75 samples in the age or year class (i.e. the model primarily used smoothed values), which estimated a higher K=11 million, and predicted that the population continued to rise throughout the 1990s, until 2008, when it leveled off. This is in sharp contrast to the other runs that estimated K=10 million and predicted that the rate of population growth had been slowing since the early 1990s (Fig. 4). The run that used a threshold of 75 samples did not fit the 1977-1985, 1998 and 2008 data as well as the other model runs, but provided better fits to the 1994, and 2004 survey estimates. Runs where the model used the original reproductive rate data only if the number of samples was greater than 75, 25, and 10 provided better fits to the 1990 survey data. It would appear that year/age class combinations with at least 10 samples provide reasonable fits to the pup production survey data. In the estimates presented below, actual reproductive rate data was used if the year/age class combinations had at least 10 samples; otherwise the smoothed estimate of reproductive rates was used.

Fitting the model used in the 2011 assessment (old model), to the aerial survey data resulted in M=0.038 (SE=0.011) for an assumed K= 12 million (SE=240000). Fitting the model to both the aerial survey data and the reproductive rate data (age classes 8+ only), resulted in estimates of M=0.036 (SE=0.005) and K=10.0 million (SE=700,000) (Fig. 3).

Little difference was observed between the 'old' and the 'new' models up until the early 1990s, which approximates when the effects of different values of K began to influence the dynamics of the population. Generally, the old model resulted in a slightly higher population, owing to the higher 'K', (Fig. 5, 6) with the old model, estimating current (2012) pup production and total population size at 1.7 million (95% CI =1.4-2.1 million) and 8.3 million (95% CI=7.4 to 9.3 million), respectively. With the new model, estimates for current pup production and total population size are: 1.5 million (95% CI =1.0-2.1 million) and 7.1 million (95% CI=5.9 to 8.3 million), respectively. The differences were not statistically significant, due to the wider confidence limits associated with the new formulation of the model.

Scenarios where the hunt consists of 97% beaters were examined. Using the old model with K=12 million, an annual harvest of up to 300,000 annually for 4 years would continue to respect the management plan (Fig. 7-9). Such a harvest could be allocated as 400,000 animals in year 1, followed by 200,000 animals in year 2. Using the new model, an annual harvest of up to 400,000 animals would continue to respect the objectives for a 4 year management plan. This could be allocated as 600,000 in years 1 and 3, and 200,000 in years 2 and 4 (Fig. 7-9).

DISCUSSION

Previous analyses have attempted to provide annual pregnancy rates from the available sampling data. Bowen et al. (1981) used annual smoothing (as opposed to smoothing by age used in this analysis) to ensure that for any given year the proportion mature increased with age in the event that the sampling predicted otherwise. An analysis by Shelton et al. (1992)

attempted multi-linear regression, analysis of covariance, analysis of variance, and auto-regression models, and discovered that all methods were inadequate to predict the unknown pregnancy rates. More recent efforts to estimate pregnancy rates were based upon the method described in Shelton et al. (1996) (presented with some modifications in Warren et al. (1997)). For each age, successive contingency table analysis tested successive pregnancy rate data for significant changes in pregnancy rates (referred to as `harmonized' rates.). However, this approach resulted in significant jumps in pregnancy rates, and if pregnancy data are 'pooled' over an extended time period in the contingency analysis, an extreme change in sampled rates is needed before the change is considered statistically significant.

Some of the variability in observed reproductive rates was attributed to sampling error. Therefore, some form of smoothing on the available data allowed for the inter-annual variability to be captured and allowed for some interpolation for years where data were missing. In recent assessments, a non-parametric smoother was applied to the reproductive rate data (Stenson et al. 2009). However, this smoother, which estimated variance based upon refitting to the samples assuming a normal distribution, appears to have underestimated the uncertainty associated with the reproductive rate data. Since the 2011 assessment, the data have been considered to be binomially distributed and a new smoother has been applied to the data. This smoother appears to better account for the uncertainty in the data, as well as changes occurring in reproductive rates (Fig. 2). In this study we tested the effects of using the actual reproductive rate data and sample size to fit to the survey. In other words, if the number of reproductive rates did not exceed certain thresholds, then the model automatically used the smoothed reproductive rate estimate when fitting to the pup production data. Using only year/age class combinations with less than 5 samples yielded highly variable pup production estimates, whereas combinations with 10 or more samples appeared to provide better fits to the survey data. Limiting the model to using only year/age class combinations with a very large number of samples (≥75), resulted in a poorer fit to the survey data.

Changes observed in size at age (Chabot and Stenson unpublished data) and in reproductive rates (fecundity and mean age of sexual maturity; Sjare and Stenson 2010, Stenson and Wells 2010), have roughly mirrored changes in pup production (i.e. increasing pup production, declining reproductive rates) in a manner that is consistent with density-dependent changes in the dynamics of the population. However, the impacts of highly variable harvests as individual cohorts work their way through the population, an absence of data on mortality rates and the fact that surveys are only flown every 4-5 years complicate attempts to determine the underlying density-dependent mechanisms required to incorporate a density-dependent function into the model fitting and reliably estimate the environmental carrying capacity (K). Hammill et al. (2011b) attempted to reconstruct the population back to the 18th century to obtain an estimate of K. They obtained an estimated K of approximately 11,000,000 (10.8 million, range = 7.6-15.4 million). In 2011, a K of 12 million was assumed, which was slightly higher, but within the range of possible values. Following the recommendations from the 2010 NMMPR meeting, we fitted the model to both the aerial survey estimates and the reproductive rates to estimate K (rather than setting the value). This resulted in an estimated K of 10.0 million (SE=700,000) which is very close to the historical estimate from Hammill et al. (2011b).

Harp seals require stable pack ice for pupping and early development of the young. The mid-1980's until the late 1990s were characterized by a period of heavier than normal ice conditions, which would have favoured pup survival (Bajzak et al. 2011, Johnston et al. 2005). This has been followed by a period of lighter than normal ice-conditions, and the winters of 2010 and 2011 are notable as the poorest winters on record for ice cover in the Atlantic. Mortality among young of the year (YOY) was high in both years, particularly in 2011, when good ice started to form, providing a platform for animals to pup on, but rapidly disintegrated resulting in high mortality (Stenson and Hammill 2011). Reproductive rates in 2011 were the lowest on record (fecundity < 25%), resulting in an estimated pup production of only 600,000 animals or only 38% of the 2008 pup production (1.6 million). If only 21% of these animals survived due to poor ice conditions, this would have left only 120,000 animals available to harvesters. The commercial hunt removed 40,000 animals leaving approximately 80,000 YOY (excluding struck & loss) to migrate north during the spring. We would expect very few animals from this cohort to have survived, which will have an important impact on future population trajectories

At the 2010 assessment, reproductive data up to 2008 were incorporated into the model and used to provide harvest advice. Reproductive rates were high in 2008 (~70% of 8+ being pregnant) and were used to project the population forward and to evaluate impacts of different harvest levels. The addition of lower reproductive rates from 2009 – 2011 in the last assessment, reduced the outlook. For this assessment, we updated the reproductive data with samples obtained in 2012. Although the sample is small, 15 of 20 mature females were pregnant indicating some increase in reproductive rates, which is consistent with the assumption of density-dependence or favourable environmental conditions. The reproductive data are an important input into the population model and drive the future predictions; slight changes in assumed fecundity have significant implications for the population trajectory. For example, the new model assumes that reproductive rates change in a manner consistent with density-dependent factors, therefore as the population declines, reproductive rates will increase. Although we feel that this is a more realistic approach than the fixed rate used in previous assessments, there is also considerable uncertainty associated with this relationship. The current model does allow for some variability, and we have augmented this variability by multiplying the reproductive rates by an additional factor to account for additional environmental stochasticity. For the moment, this multiplier is simplistic, it assumes that the variation is random and not indicative of a trend (e.g. climate change), but can be easily modified as more information becomes available.

In the current version of the model, we also consider how environmental factors affect YOY survival in the first 2 months of life, beyond that, we assume that first year mortality also varies in a density-dependent manner, and we assume that this mortality follows the same relationship as that used to describe the density-dependent effects on reproductive rates. In other words, we are assuming that density-dependent changes in both demographic parameters can be described using a common value for carrying capacity (K) and a theta value of 2.4. In addition to the density-dependent relationships, interannual variability in environmental factors may lead to both improved or reduced reproduction, beyond the population effects outlined above, as well as improved or reduced first-year survival of YOY. This could be explored in future developments of the model.

Under the formulation of the model used in 2011 (the ‘old model’), a constant four year harvest of up to 300,000 per year would continue to respect the management plan. The amount harvested in a single season could be higher, as long as the total removal over the four year period of the management plan did not exceed 1.2 million. We examined removals of 400,000 alternating with 200,000 in the second year. Some preliminary runs suggested that larger differentials could still respect the management plan, but these were not examined further. One factor that needs to be considered is the possibility that a high harvest coincides with an extremely poor year due to unusually high ice mortality or low reproductive rates resulting in the removal of most, if not all of a single year class. To date, hunters appear to have difficulty in removing large numbers of animals in years where ice conditions are poor, so there may be some cancelling out of effects. However, if significant harvests were to occur, in years when YOY survival is low, this would have an important effect on the population, especially if pairing of these factors continued over several years.

Assuming that reproductive rates tracked changes in the population size in a density-dependent manner, the population could support a constant harvest of 400,000 animals per year and still respect the management plan over a four year period. As in the previous scenario, variable TACs could be allocated, and still respect the management objective, as long as total removals did not exceed 1.6 million animals over the duration of the 4 year plan.

The old model with fixed K=12 million, the fixed reproductive rates, and fixed high Greenland catch showed a sharper decline in pup production and total population size compared to the new density dependent model with K=10 million when projected out to 2030. The higher allowable catch under the new model formulation is likely due to two factors. The first is the assumed density-dependent relationship that as the population size declines, reproductive rates and first-year survival are now assumed to increase. The second factor is the change in how the Greenland harvest is predicted to change as the total population changes. Under the old formulation, the unregulated subsistence harvest was assumed to remain unchanged, with an average reported removal of 85,000 animals. However, the catch data suggest that, if the harp seal population falls below a threshold of about 7.1 million animals, removals from the Greenland harvest appear to be linked to total population size (Fig. 1). This relationship has been incorporated into the new formulation of the model which reduces the relative impact of this hunt on the harp seal population.

The Northwest Atlantic harp seal population is currently near the highest levels observed since monitoring began almost 60 years ago. The main factors affecting the trajectory of the herd appear to be the response of animals to changes in ice conditions, the impacts of environmental variability on reproductive rates and harvest levels in Greenland. Modifications to the current assessment model provide a means of estimating environmental carrying capacity assuming a certain functional relationship between total population size and juvenile survival and between population size and reproductive rates. As more information is obtained, our understanding of this functional relationship may also change which could result in changes to estimates of total population size and trends.

LITERATURE CITED

Bajzak, C.E., Hammill, M.O., Stenson G.B. and Prinsenberg. S. 2011. Drifting away: Implications of changes in ice conditions for a pack-ice breeding phocid, the harp seal (*Pagophilus groenlandicus*). Can. J. Zool. 89:1050-1062.

Bowen, W.D. and Sergeant, D.E. 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 Sergeant, D.E. 1985. A mark-recapture estimate of 1983 harp seal pup production in the northwest Atlantic. Northwest Atl. Fish. Organ. SCR Doc. 85/I/1, Ser., N935. 14p.

Bowen, W. D., Capstick, C. K., and Sergeant, D. E. 1981. Temporal changes in the reproductive potential of female harp seal, Pagophilus groenlandicus. Can. J. Fish. Aquat. Sci. 38: 495–503.

Hammill, M.O. and Stenson, G.B. 2003. Harvest Simulations for 2003-2006 Harp Seal Management Plan. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/068. 29 p.

Hammill, M.O. and Stenson, G.B. 2011. Estimating abundance of Northwest Atlantic harp seals, examining the impact of density dependence. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/011.

Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T. and Mosnier, A. 2011a. Northwest Atlantic Harp Seals Population Trends, 1952-2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/99. iv + 28 p. Available at http://www.dfo-mpo.gc.ca/csas

Hammill, M.O., Stenson, G.B. and Kingsley, M.C.S. 2011b. 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.

Johnston, D.W. Friedlaender, A.S. Torres, L.G. and Lavigne, D. M. 2005. Vartiation in sea ie cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. Climate Research 29:209-222.

Healey, B.P., Stenson, G.B. and Cadigan, N. G. 2003. Modelling the Population Dynamics of the Northwest Atlantic Harp Seal (*Phoca groenlandica*). Unpublished manuscript. 40p

Joe, H. 1997. Multivariate Models and Dependence Concepts. Chapman and Hall, London

Kovacs K.M., 1995. Harp and hooded seals-a case study in the determinants of mating systems in pinnipeds. Pages 329-333, In.A.S. Blix, L. WallØe and Ø. Ulltang (eds). Whales, seals, fish and man. Elsevier, New York. 720p.

Loader, C. 1999. Local Regression and Likelihood. New York: Springer, 1999. 290 pp

Loader C. 2010. locfit: Local Regression, Likelihood and Density Estimation. R package version 1.5-6. Available at http://CRAN.R-project.org/package=locfit

Roff, D. A., and Bowen, W. D. 1983. Population dynamics and management of the northwest Atlantic harp seal (Phoca grcaeniacrlzdica). Can. J. Fish. Aquat. Sci. 40: 914 - 932.

Roff, D.A. and Bowen, W. D. 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 Fisher, H.D. 1960. Harp seal populations in the western North Atlantic from 1950 to 1960 Fisheries Research Board of Canada, Arctic Unit. Circular No. 5.

Shelton, P. A., Cadigan, N. G. and Stenson, G. B. 1992. Model estimates of harp seal trajectories in the northwest Atlantic. Can. Atl. Fish. Stock Assess. Comm. Res. Doc., No. 89, 23 p.

Shelton, P. A., Stenson, G. B., Sjare, B. and Warren, W. G. 1996. Model estimates of harp seal numbers-at-age for the Northwest Atlantic. NAFO Sci. Coun. Studies. 26: 1-14.

Sjare, B. and Stenson, G. B. 2002. Estimating struck and loss rates for harp seals (Pagophilus groenlandicus) in the Northwest Atlantic. Mar. Mamm. Sci. 18:710-720.

Sjare, B. and Stenson, G. B. 2010. Changes in the Reproductive Parameters of Female Harp Seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. ICES J. Mar. Sci. 67:304-315.

Sjare, B., Walsh, D., Benjamins, S., and Stenson, G.B. 2005. An update of estimated harp seal by-catch in the Newfoundland lumpfish fishery. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/049.

Skaug, H. J., Frimannslund, L., and Øien, N. I. 2007. Historical population assessment of Barents Sea harp seals (Pagophilus groenlandicus). – ICES Journal of Marine Science, 64: 1356–1365.

Sklar, A. 1959. Fonctions de répartition à n dimensions et leurs marges, Publ. Inst. Statist. Univ. Paris 8: 229–231

Stenson, G.B. 2005. Estimates of human induced mortality in Northwest Atlantic harp seals, 1952-2004. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/050.

Stenson, G.B. 2009. Recent catches of harp seals in the Northwest Atlantic. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/112

Stenson, G.B. and Hammill, M.O. 2011. Living on the edge: Observations of Northwest Atlantic harp seals in 2010 and 2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/108 iv + 12p. Available at http://www.dfo-mpo.gc.ca/csas

Stenson, G.B. and Wells, N. 2010. Current reproductive and maturity rates of northwest Atlantic harp seals. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/136.

Stenson, G.B., Myers, R.A. Hammill, M.O., Ni, I-H. Warren, W.G. and Kingsley, M.C.S. 1993. Pup production of harp seals, Phoca groenlandica, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 50:2429-2439.

Stenson, G. B., Hammill, M.O., Kingsley, M.C.S., Sjare, B., Warren, W.G. and Myers, R.A. 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., Rivest, L.-P., Hammill, M.O., Gosselin, J.-F. and Sjare, B. 2003. Estimating Pup Production of Harp Seals, *Pagophilus groenlandicus*, in the Northwest Atlantic. Mar. Mammal. Sci. 19:141-160.

Stenson, G.B., Hammill, M.O., Lawson, J., Gosselin, J.F., Haug, T. 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., Hammill, M.O., and Healey, B. 2009. Reproductive rates of Northwest Atlantic harp seals, 1954-2007. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/113

Stenson, G.B., Hammill, M.O. and Lawson, J.W. 2010. How many harp seal pups are there? Additional results from the 2008 surveys. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/137.

Sun J. and Loader, C. 1994. Simultaneous confidence bands for linear regression and smoothing. The Annals of Statistics. 22(3), 1328-1345.

Tibshirani, R. J. and Hastie, T. J. 1987. Local likelihood estimation. Journal of the American Statistical Association 82, 559–567.

Trivedi, P. and Zimmer, D. 2005. “Copula Modeling: An Introduction for Practitioners”, Foundations and Trends in Econometrics, vol 1, 1-111.

Waring, G.T., Pace, R.M., Quintal, J.M., Fairfield, C.P., and Maze-Foley, K. 2005. Draft U.S. Atlantic and Gulf of Mexico marine mammal stock assessments-2004. NOAA Tech. Mem. NMFS-NE

Waring, G.T., Josephson, E., Fairfield, C.P., and Maze-Foley, K. (eds). 2007. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments-2006. NOAA Tech. Mem. NMFSNE-201.

Warren, W. G., Shelton, P. A. and Stenson, G. B. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part II: Uncertainty in the estimates of harp seal population size. J. Northw. Atl. Fish. Sci. 22:289-302.

Table 1: Summary of changes to harp seal model . Exponential model=exp, density dependent model=dd, carrying capacity in millions=K, mortality =M.

Year	Population Model type	Reproductive rates	Population (million)	Significant changes
2000	Exp	Contingency table harmonized rates		90% beater
2003	Exp	Healey smoother non-parametric (Healey et al. 2003) , Extended 1997 rates to 2003 and future	2002 = 5.5 2003 = 5.3	92% beater, ice related M approximately 15% EXCEL model ,
2005	Exp	Healey smoother non-parametric , (Healey et al. 2003) Extended 1997 rates to 2005 and future	2004=5.7 2005=5.8	95% beater, ice M=0.1 in projections
2008	Exp	Healey smoother non-parametric , (Healey et al. 2003), to 1999, averaged 2000-2005 and extrapolated forward	2005=5.7 2008=5.6 2009=5.6	95% beater, Model reprogrammed from EXCEL to R, projected ice M=average 12%
2009	Exp	Healey smoother non-parametric , (Healey et al. 2003) Rpd rates updated to 2007, projected	2008 (lo)=6.9 2008 (hi)=8.2	Uncertainty in pup survey estimate (low count accepted), smoothed rates until 2007. poor fit to data in 2008 using high pup count
2010	DD K=12 set, Exp examined	Annual reproductive rates for 8+ ages, average last 5 years used in projections, Reproductive rates were correlated so if one year class had a poor year, other year classes also had poor years.	2004=7.4 2008 (exp)=8.7 2010 (exp) =9.6 2008 (dd)=8.1 2010 (dd)=8.6	ice mortality updated to average 30%, transition from exponential growth to density-dependent (DD) growth of population. K was set.
2011	DD, K=12, estimated/set	updated to 2010, new binomial smoother, annual rpd rates for 8+, projection used uniform distribution for reproduction from last 5 years in projections	2008=8.4 2010=7.8	
current	DD, K=10, estimated	updated to 2011, binomial smoother, annual rpd rates for 8+, correlation in rpd rates re-established. Projection can be DD prediction for rpd rates or some other function eg uniform distribution among observed rates from last 5 years	2008=7.2† 2010=6.8† 2012=7.1†	Model fitted to reproductive rates (in addition to existing fitting to pup production estimates) Future Greenland harvest expressed as a function of population size

† Erratum May 2013
2008= 7.5, 2010=7.1, 2012=6.9 was replaced with 2008=7.2, 2010=6.8, 2012=7.1

Table 2: Pup production estimates used as input into the population model.

Year	Estimate	Standard Error	Reference
1951	645,000	322,500[1]	Sergeant and Fisher 1960
1960	235,000	117,500[1]	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	1,630,000	110,400	Stenson et al. 2010

[1] Assumed a coefficient of variation of 40%.

Table 3. Year , sample size (n), number pregnant (#preg) and late term age-specific reproductive rates of Northwest Atlantic harp seals.

Year	Age = 4			Age = 5			Age = 6			Age = 7			Age=8+		
	n	#Preg	rate	n	#Preg	rate	n	#Preg	rate	n	#Preg	rate	n	#Preg	rate
1954	4	0	0.00	3	1	0.33	3	2	0.67	16	12	0.75	33	29	0.88
1964	11	0	0.00	9	1	0.11	2	1	0.50	4	3	0.75	25	22	0.88
1965	30	1	0.03	44	5	0.11	37	20	0.54	38	27	0.71	109	96	0.88
1966	7	0	0.00	9	1	0.11	17	6	0.35	11	8	0.73	49	43	0.88
1967	10	0	0.00	19	4	0.21	33	20	0.61	29	28	0.97	123	109	0.89
1968	27	0	0.00	19	6	0.32	20	14	0.70	12	11	0.92	55	48	0.87
1969	25	1	0.04	25	4	0.16	16	7	0.44	28	23	0.82	165	146	0.88
1970	13	0	0.00	13	3	0.23	12	6	0.50	10	9	0.90	107	92	0.86
1978	40	1	0.03	38	23	0.61	20	18	0.90	9	6	0.67			
1979	21	5	0.24	15	8	0.53	5	5	1.00	9	8	0.89	21	20	0.95
1980	2	0	0.00	2	1	0.50	1	1	1.00	0			12	9	0.75
1981	5	1	0.20	4	3	0.75	2	1	0.50	7	6	0.86	17	14	0.82
1982	4	0	0.00	5	2	0.40	1	1	1.00	4	3	0.75	3	1	0.33
1985	4	0	0.00	3	1	0.33	5	2	0.40	3	3	1.00	1	1	1.00
1986	1	1	1.00	0			2	1	0.50	1	0	0.00	7	7	1.00
1987	12	2	0.17	8	3	0.38	9	7	0.78	4	4	1.00	24	15	0.63
1988	17	2	0.12	6	1	0.17	3	3	1.00	0			19	14	0.74
1989	8	0	0.00	9	0	0.00	6	2	0.33	3	2	0.67	22	22	1.00
1990	8	0	0.00	7	1	0.14	3	1	0.33	1	0	0.00	10	6	0.60
1991	10	0	0.00	11	2	0.18	7	4	0.57	3	1	0.33	29	18	0.62
1992	10	2	0.20	11	3	0.27	9	4	0.44	8	6	0.75	32	21	0.66
1993	11	1	0.09	17	2	0.12	7	0	0.00	5	4	0.80	35	17	0.49

1994	23	1	0.04	16	2	0.13	14	6	0.43	7	3	0.43	41	34	0.83
1995	10	0	0.00	13	6	0.46	4	2	0.50	5	2	0.40	24	14	0.58
1996	8	0	0.00	6	0	0.00	4	1	0.25	1	1	1.00	35	24	0.69
1997	6	0	0.00	4	0	0.00	10	3	0.30	2	2	1.00	36	27	0.75
1998	6	0	0.00	10	3	0.30	9	2	0.22	4	2	0.50	36	22	0.61
1999	6	0	0.00	7	0	0.00	18	4	0.22	15	6	0.40	59	37	0.63
2000	1	0	0.00	9	3	0.33	6	4	0.67	5	2	0.40	43	29	0.67
2001	2	0	0.00	0			2	2	1.00	3	0	0.00	39	26	0.67
2002	2	0	0.00	4	1	0.25	5	3	0.60	17	10	0.59	72	40	0.56
2003	1	0	0.00	3	2	0.67	2	1	0.50	3	2	0.67	91	59	0.65
2004	2	0	0.00	5	0	0.00	5	1	0.20	1	0	0.00	76	31	0.41
2005	9	1	0.11	9	0	0.00	13	2	0.15	7	0	0.00	86	55	0.64
2006	2	0	0.00	0			0			0			119	67	0.56
2007	1	0	0.00	5	0	0.00	3	1	0.33	2	2	1.00	84	64	0.76
2008	6	0	0.00	3	0	0.00	2	0	0.00	0			61	45	.74
2009	1	0	0.00	1	1	0.20	1	0	0.00	1	1	1.00	103	57	0.55
2010	-	-		-	-		-	-		-	-		117	35	0.30
2011	-	-		-	-		-	-		-	-		94	21	0.22
2012	3	0	0	3	0	0	2	0	0				20	15	0.75

Table 4. Catches of Northwest Atlantic harp seals from different sources updated from Stenson 2009.

Year	Arctic	Greenland	Commercial (Age =0)	Commercial (Age=1+)	Bycatch (Age=1+)	Bycatch (Age=0)
1952	1,784	16,400	198,063	109,045	0	0
1953	1,784	16,400	197,975	74,911	0	0
1954	1,784	19,150	175,034	89,382	0	0
1955	1,784	15,534	252,297	81,072	0	0
1956	1,784	10,973	341,397	48,013	0	0
1957	1,784	12,884	165,438	80,042	0	0
1958	1,784	16,885	140,996	156,790	0	0
1959	1,784	8,928	238,832	81,302	0	0
1960	1,784	16,154	156,168	121,182	0	0
1961	1,784	11,996	168,819	19,047	0	0
1962	1,784	8,500	207,088	112,901	0	0
1963	1,784	10,111	270,419	71,623	0	0
1964	1,784	9,203	266,382	75,281	0	0
1965	1,784	9,289	182,758	51,495	0	0
1966	1,784	7,057	251,135	72,004	0	0
1967	1,784	4,242	277,750	56,606	0	0
1968	1,784	7,116	156,458	36,238	0	0
1969	1,784	6,438	233,340	55,472	0	0
1970	1,784	6,269	217,431	40,064	15	53
1971	1,784	5,572	210,579	20,387	99	391
1972	1,784	5,994	116,810	13,073	141	480
1973	1,784	9,212	98,335	25,497	107	358
1974	1,784	7,145	114,825	32,810	41	141
1975	1,784	6,752	140,638	33,725	66	219
1976	1,784	1,1956	132,085	32,917	169	923
1977	1,784	1,2866	126,982	28,161	296	1,281
1978	2,129	1,6638	116,190	45,533	538	2,381
1979	3,620	17,544	132,458	28,083	511	2,799
1980	6,350	15,255	132,421	37,105	263	2,454
1981	4,672	22,974	178,394	23,775	382	3,539
1982	4,881	26,926	145,274	21,465	343	3,442
1983	4,881	24,784	50,058	7,831	458	4,504
1984	4,881	25,828	23,922	7,622	425	3,683
1985	4,881	20,785	13,334	5,701	632	4,225
1986	4,881	26,098	21,888	4,046	1,042	7,136
1987	4,881	37,859	36,350	10,446	1,978	11,118
1988	4,881	40,415	66,972	27,074	1,391	7,154
1989	4,881	42,970	56,346	8,958	799	9,457
1990	4,881	45,526	34,402	25,760	921	2,700
1991	4,881	48,082	42,382	10,206	615	9,074
1992	4,881	50,638	43,866	24,802	6,507	18,969
1993	4,881	56,319	16,401	10,602	7,596	18,876
1994	4,881	57,373	25,223	36,156	10,513	35,881
1995	4,881	62,749	34,106	31,661	6,060	13,641
1996	4,881	73,947	184,856	58,050	18,347	10,765
1997	2,500	68,815	220,476	43,734	5,059	13,541
1998	1,000	81,272	251,403	31,221	975	3,571

1999	500	93,117	237,644	6,908	6,280	9,750
2000	400	98,458	85,035	7,020	1,608	9,715
2001	600	85,427	214,754	11,739	4,828	14,572
2002	1,000	66,734	297,764	14,603	3,837	5,492
2003	1,000	66,149	280,174	9,338	1,881	3,486
2004	1,000	70,585	353,553	12,418	3,796	8,494
2005	1,000	91,695	319,127	4,699	3,796	8,494
2006	1,000	92,210	346,426	8,441	3,796	8,494
2007	1,000	82,836	221,488	3,257	3,796	8,494
2008	1,000	80,554	217,565	285	3,796	8,494
2009	1,000	71,046	76,688	0	3,796	8,494
2010	1,000	83,669	68,654	447	3,796	8,494
2011	1,000	71,000	40,238	132	3,796	8,494
2012	1,000	77,800[1]	69,048	141	3,796	8,494

[1] average of last 5 years.

Table 5. Years when unusual ice mortality is assumed to have occurred, and values input to the model to account for this mortality. Survival was assumed to be normal (i.e. 1.0) in all other years.

Year	Survival (previous assessments)	Updated survival estimates
1969	0.75	0.60
1981	0.75	0.43
1998	0.94	0.94
2000	0.88	0.91
2002	0.75	0.88
2005	0.75	0.83
2006	0.90	0.99
2007	0.78	0.94
2010	0.55	0.59
2011		0.21
2012		0.90

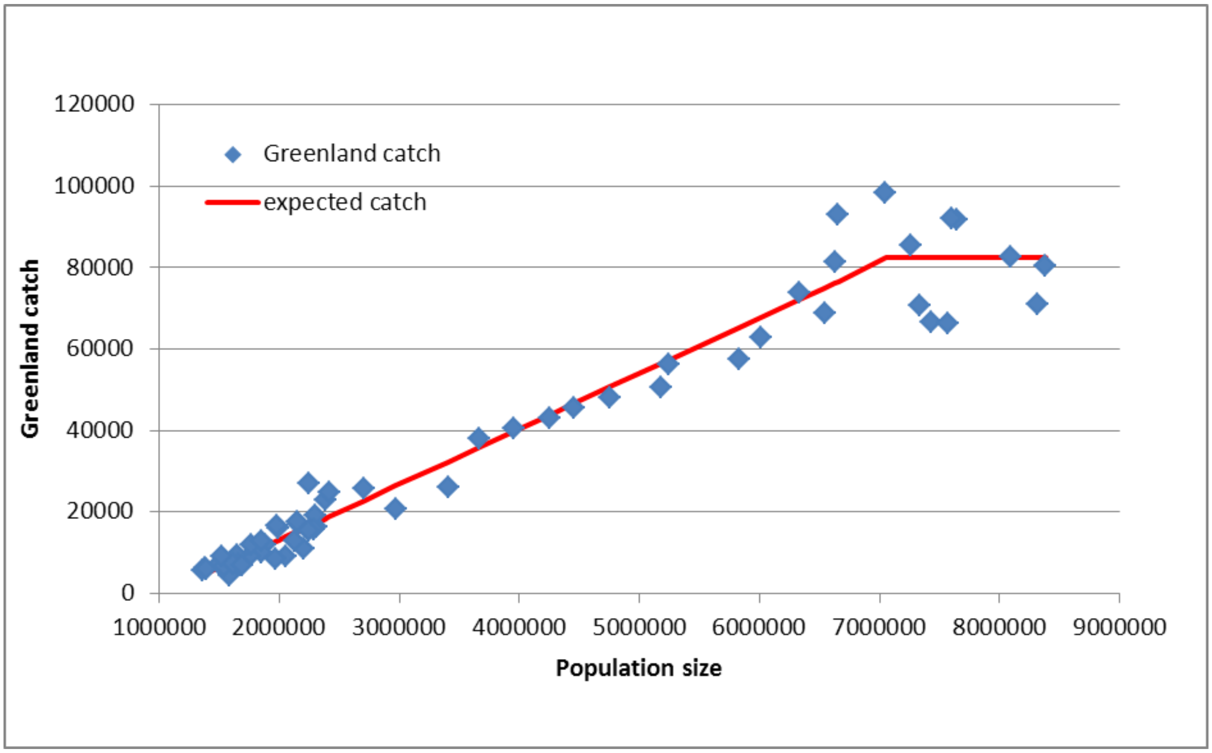


Figure 1. Relationship between population size and reported Greenland catches

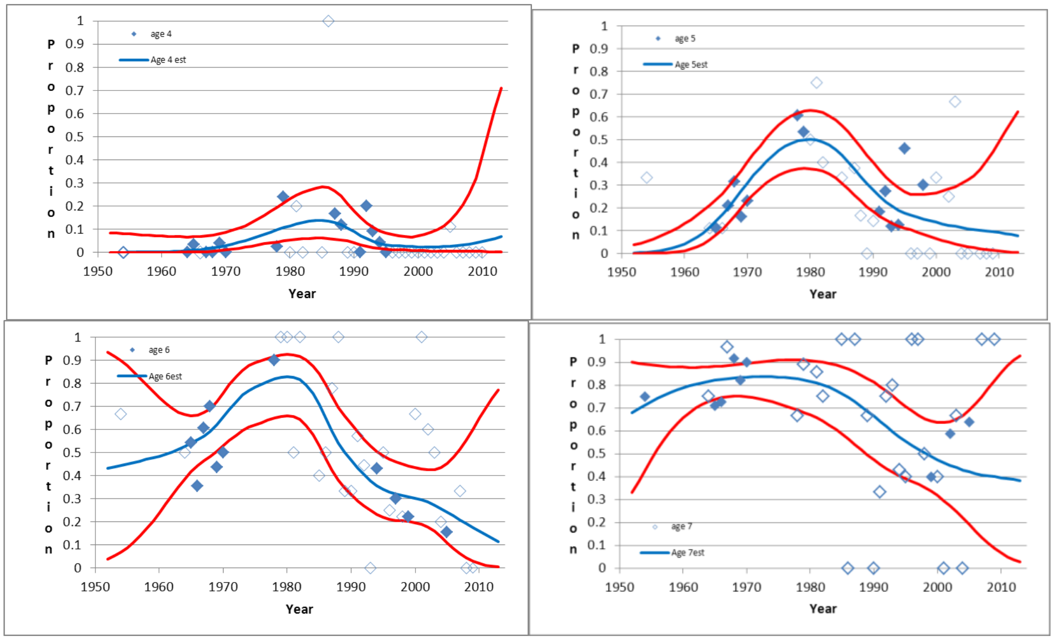


Figure 2. Age specific reproductive rates and non-parametric smoothed rates. Solid symbols represent data points based on 10 or more samples, open symbols represent less than 10 samples.

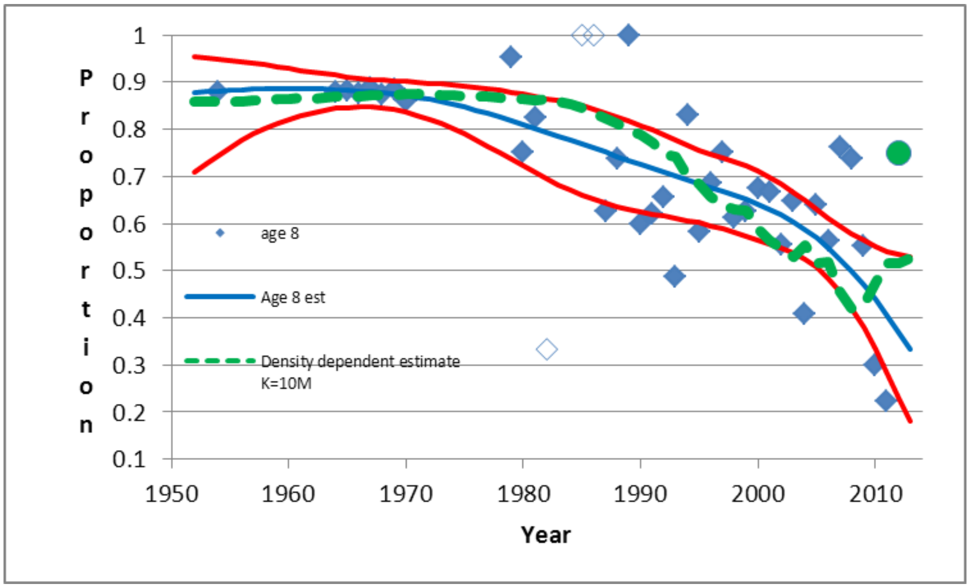


Figure 2 (continued). Age specific reproductive rates and non-parametric smoothed rates. The dashed line represents the expected density-dependend decline in reproductive rates as population size declines. The large solid dot represents the 2012 reproductive rate. Open symbols represent data points with less than 10 symbols. Solid symbols represent 10 or more samples.

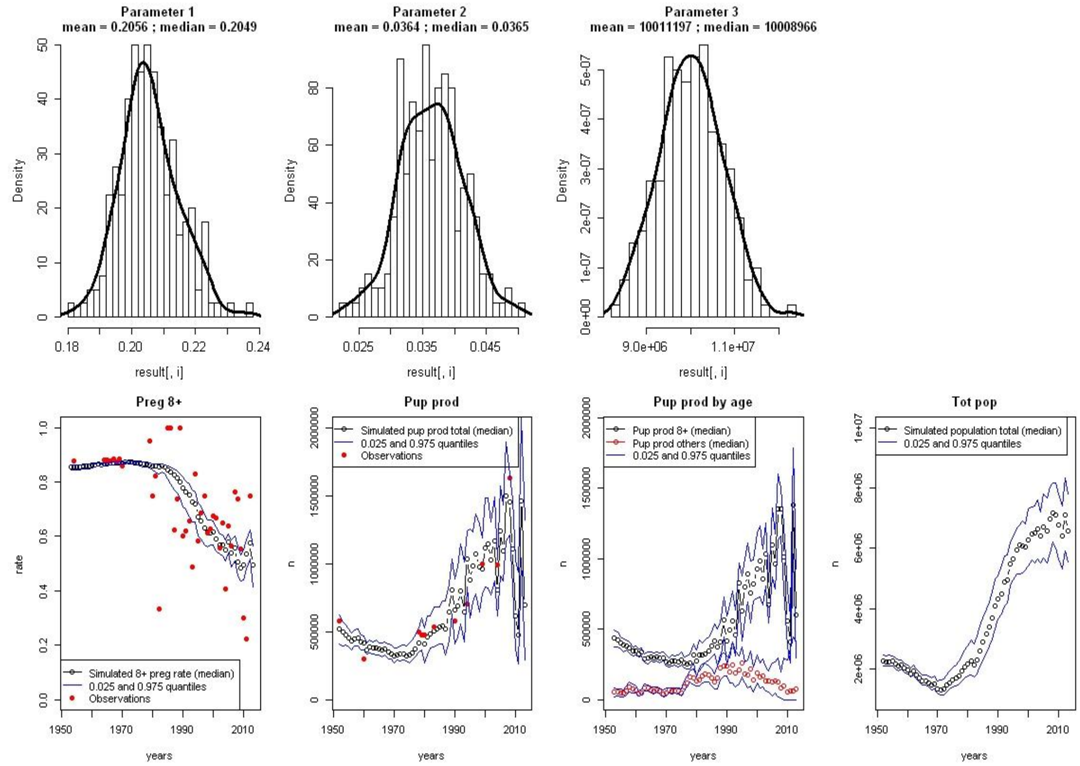


Figure 3. Output parameters from population model: alpha, the multiplier to set the initial population size, M=adult mortality rate (mean and median) and K=carrying capacity (mean and median). The bottom row of figures illustrates the smoothed reproductive rates for animals aged 8+ years, pup production, and pup production that can be attributed to animals 8 years and older, and less than 8 years and total population size.

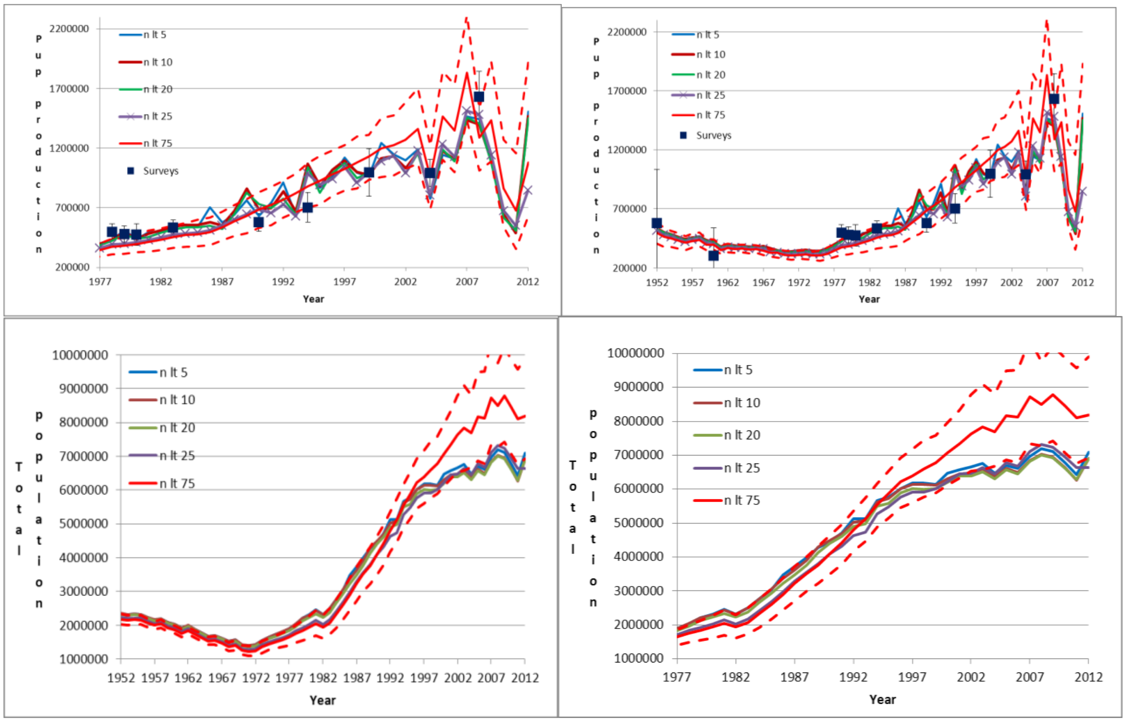


Figure 4. Survey and model estimates of pup production (top), and total population size (bottom), obtained by fitting the model using different reproductive rate values. Different runs were completed by varying the minimal sample size necessary for the model to use either the raw reproductive data or the predicted smoothed value estimated from the smoothing model. For example in the run where the sample size for a given year and age class was less than 5 (n lt 5), the model used the smoothed reproductive rate, otherwise it used the actual reproductive data if sample sizes were greater than 5. The dotted lines are the 95% confidence limits around the run considering actual reproductive data only if sample sizes were greater than 75. Since few age classes except for the animals aged 8+, had more than 75 samples, this resulted in the reproductive rate values provided by the smoother being substituted for most years and age classes including the 8+ year class in some years (Table 3).

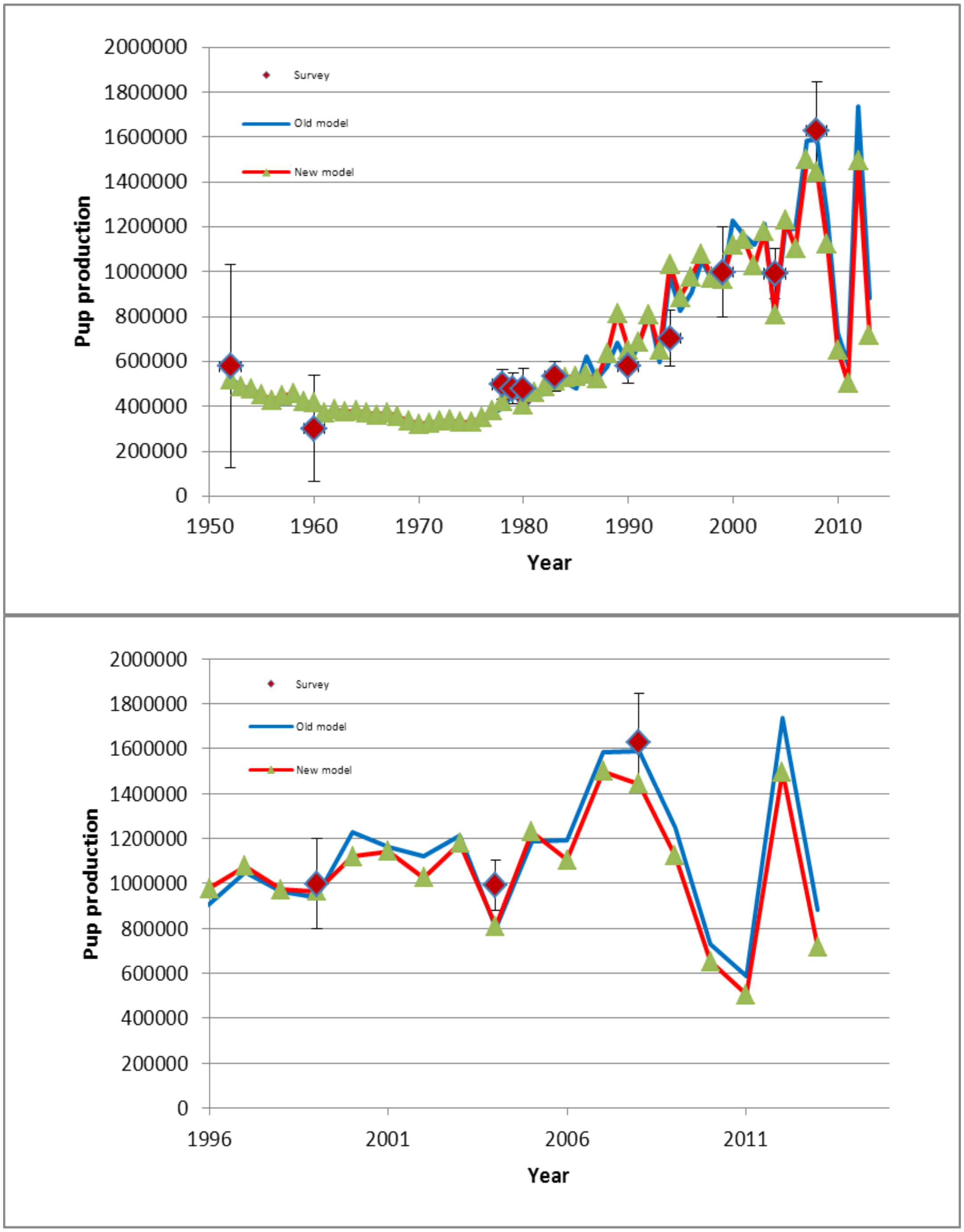


Figure 5. Changes in estimated pup production and survey estimates (mean±95% C.I.) from 1952 to 2013, using the old model with K=12 million, and the new density-dependent model with K=10 million.

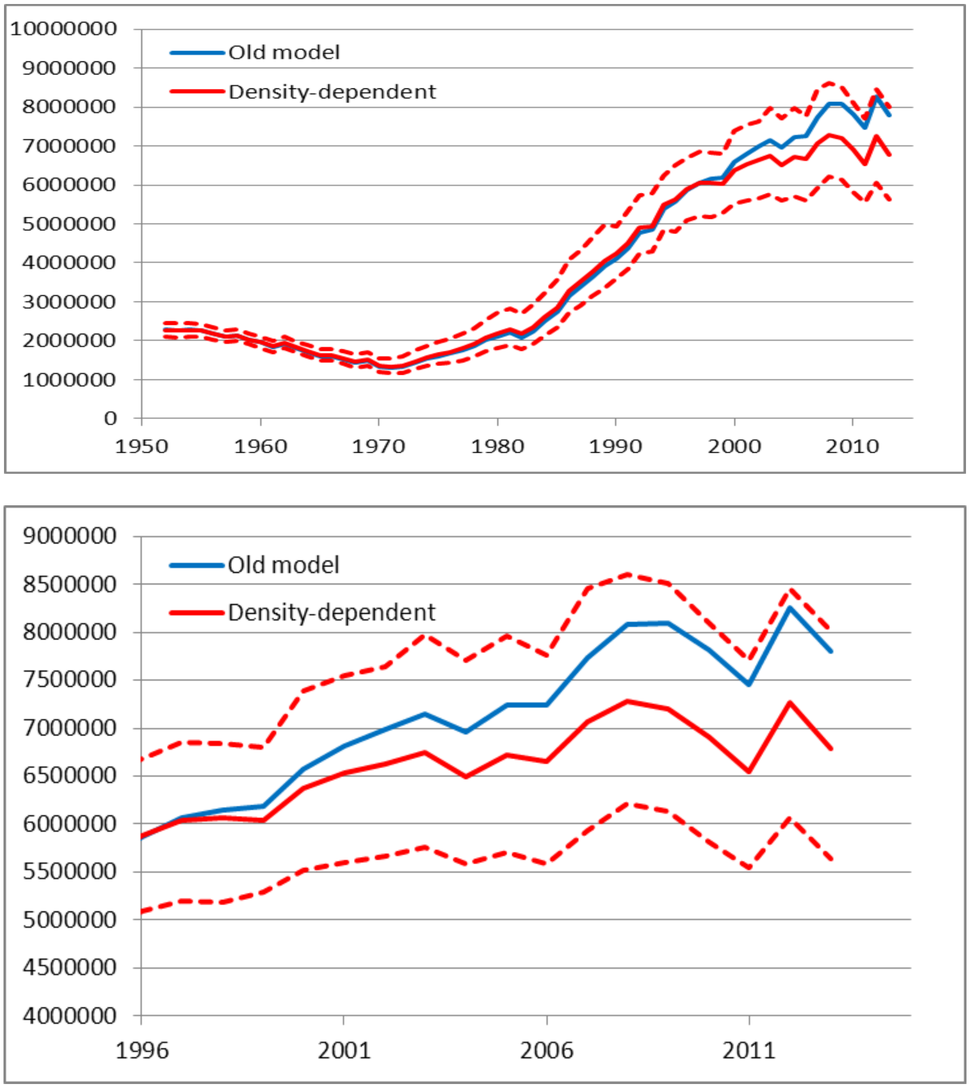


Figure 6. Changes in estimated population size (mean±95% C.I.) from 1952 to 2013, using the old model with K=12 million, and the new density-dependent model with K=10 million.

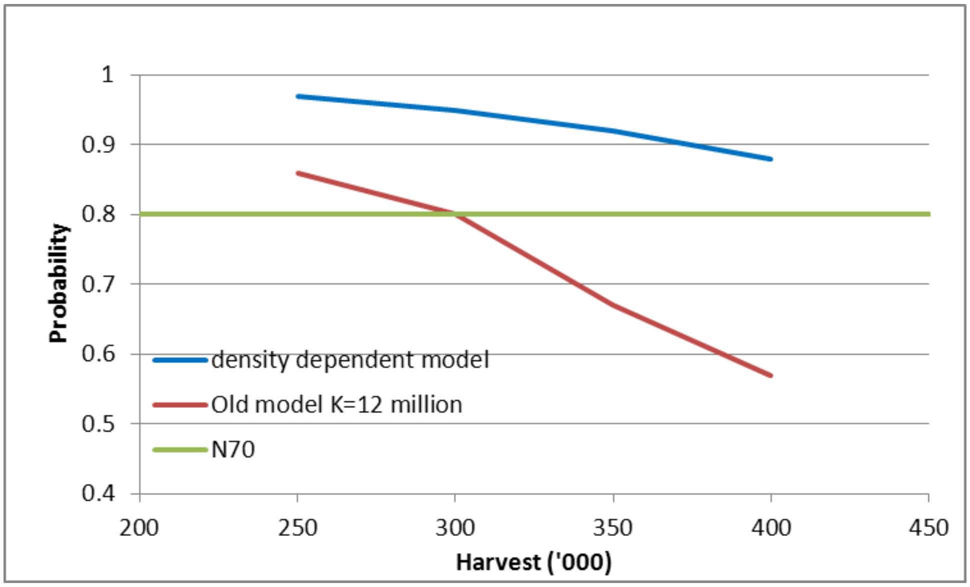
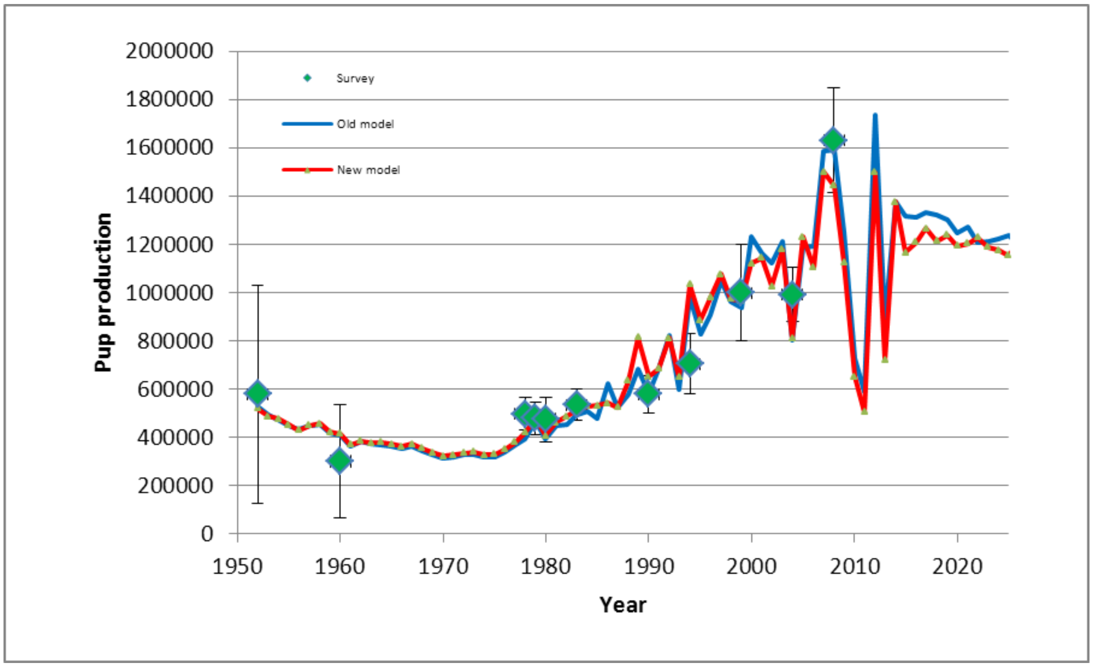


Figure 7. Probability of different harvest scenarios under a 4 year management plan respecting the management objective to maintain an 80% probability of staying above N70. This ensures a 95% probability of remaining above N30



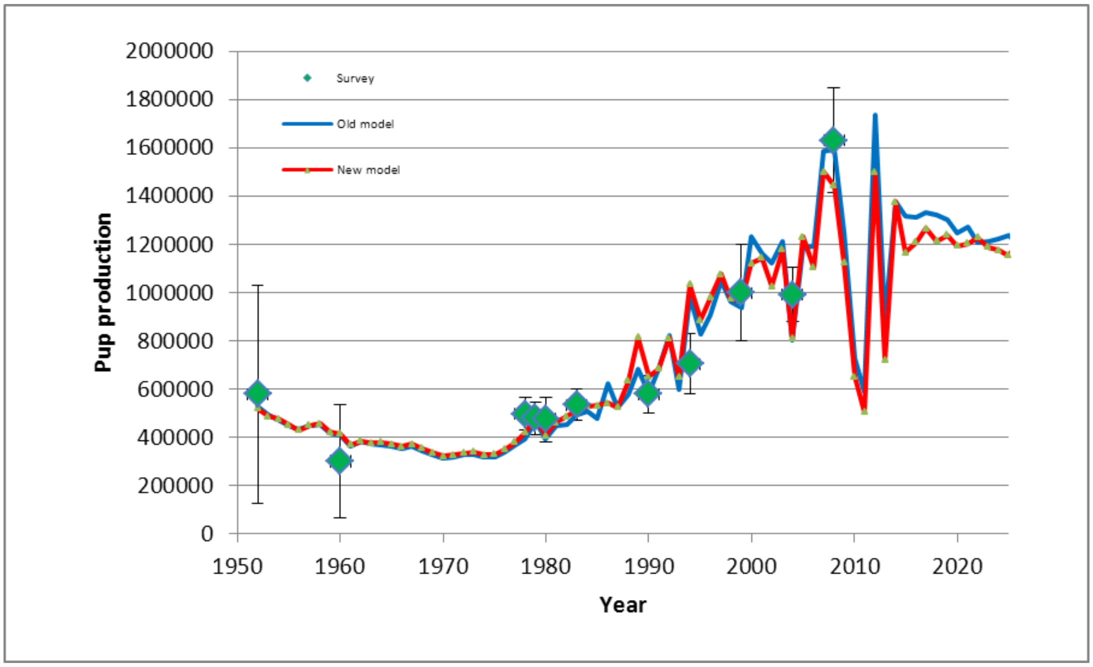


Figure 8. Expected trajectory of the northwest Atlantic harp seal pup production subject to a harvest of 300,000 animals annually and assuming that 97% of the harvest is comprised of YOY. Points with error bars represent survey estimates

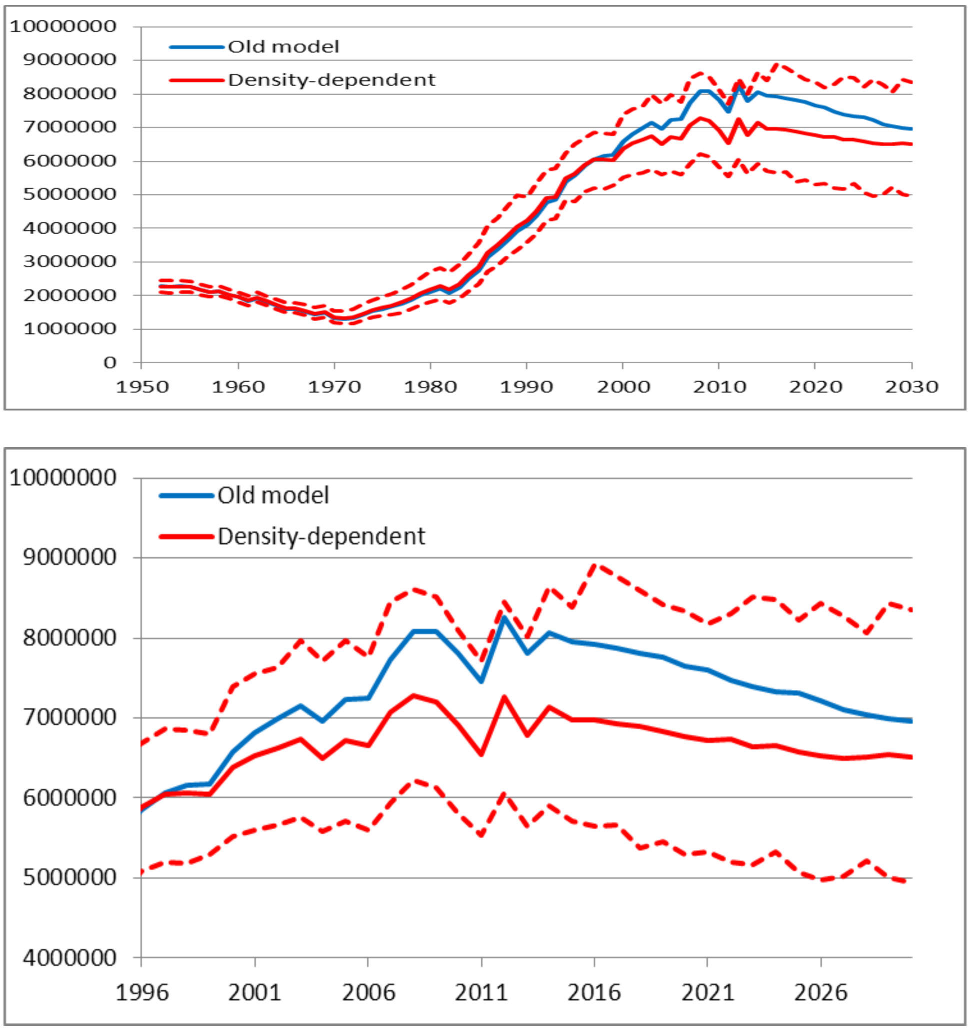


Figure 9 Expected trajectory (± 95% C.I.) of the northwest Atlantic harp seal population subject to a harvest of 300,000 animals annually and assuming that 97% of the harvest is comprised of YOY.