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 2011/011 **Document de recherche 2011/011**

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

Estimating abundance of Northwest Atlantic harp seals, examining the impact of density dependence

Estimation de l'abondance des phoques du Groenland de l'Atlantique nord-ouest, examen de l'impact de la dépendance envers la densité

M.O. Hammill[1] and G.B. Stenson[2]

[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

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

Canada

Correct citation for this publication:
La présente publication doit être citée comme suit :

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. iv + 27 p.

ABSTRACT

A population model was used to examine changes in the size of the Northwest Atlantic harp seal population between 1952 and 2010. 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 estimates of pup production beginning in 1952, including a revised estimate of 2008 pup production of 1.63 million animals. The unusually high 2008 estimate of pup production is due to high reproductive rates for the same year. This is in contrast to a general trend towards a decline in reproductive rates as pup production has increased suggesting that the dynamics of this population are being mediated by density-dependent changes. Under the assumption that the population is continuing to grow exponentially, the total population in 2008 was estimated to be 8.0 million (95% CI =6.8-9.3 million) animals, increasing to 9.1 million (95% CI=7.5 to 10.7 million) animals in 2010. Under the assumption that density-dependent population growth is occurring and the population is nearing carrying capacity (K=12 million), the population in 2008 was 8.1 million (95% CI=7.3-8.9 million animals) increasing to 8.6 million (95% CI=7.8 to 9.4 million) animals in 2010. Under both model formulations a harvest of 420,000 animals over the next three years would continue to respect the management plan to maintain an 80% probability that the population would remain above the precautionary reference level (N_{70}).

RÉSUMÉ

Un modèle de population a été utilisé pour étudier les changements dans la taille de la population de phoques du Groenland de l'Atlantique du nord-ouest entre 1952 et 2010. 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 de production de petits débutant en 1952, incluant une estimation révisée de la production de petits en 2008 de 1,63 millions d'animaux. L'estimation exceptionnellement élevé de production de petits en 2008 est due à des taux élevés de reproduction pour la même année. Ceci contraste avec une tendance générale vers une baisse des taux de reproduction alors que la production de petits a augmenté, ce qui suggère que la dynamique de cette population est régulée par les variations dépendantes de la densité. Dans l'hypothèse où la population continue de croître de façon exponentielle, la population totale en 2008 était estimée à 8,0 millions (95% IC = 6,8 à 9,300,000) d'animaux, augmentant à 9,1 millions (95% IC = 7,5 à 10,700,000) en 2010. Sous l'hypothèse que la croissance de la population dépend de la densité en cours et que la population est près de la capacité de support (K = 12 millions), la population en 2008, de 8,1 millions (95% CI = 7,3 à 8,900,000 animaux) a augmenté à 8,6 millions (95% CI = 7,8 à 9,400,000) animaux en 2010. Dans les deux formulations du modèle, une récolte de 420,000 animaux au cours des trois prochaines années permettra de respecter le plan de gestion pour maintenir une probabilité de 80 % que la population demeure au-dessus du niveau de référence de précaution (N_{70}).

INTRODUCTION

During March 2008, the harp seal herd was surveyed using a combination of visual and photographic surveys to obtain new estimates of pup production. The surveys consisted of extensive reconnaissance, flights to count the number of pups on the ice using both a visual counts and a digital camera (hereafter referred to as a photographic survey), as well as flights to determine the proportion of births that had occurred when the counting surveys have been completed. The results from these surveys were presented at the National Marine Mammal Peer Review in 2009. Although the results of repeated surveys of each whelping concentration were similar, the estimate obtained from a visual survey of the largest concentration located off Newfoundland (the 'Front) was significantly lower than that obtained from a photographic survey of the same group. Using visual and photographic survey estimates from the southern Gulf and a small group off Newfoundland, photographic surveys in the northern Gulf and the visual survey of the largest concentration at the 'Front', pup production was estimated to be 1,076,600 (SE=61,300) . Using the same surveys for the Gulf and the small group at the Front, but including the photographic survey of the large group resulted in a total pup production estimate was 1,648,800 (SE=118,000, Stenson et al 2009a)(Fig. 1). At the meeting it was not possible to reconcile the differences between these two estimates. Consequently, the lower estimate was accepted for the purposes of providing harvest advice in 2009. A second, low-density coverage survey had been flown on 12 March, 2008 at the Front, but the results were not available at the 2009 meeting. Subsequent analyses of the 12 March survey resulted in an estimated pup production extremely close to that of the photographic survey, indicating that the higher estimate was more likely. Combing these surveys resulted in an estimated pup production in 2008 of 1,630,300 (95% CI: 1,414,000 to 1,846,000; SE=110,400) animals (Stenson et al. 2010).

Total population size of harp seals is estimated using a model that incorporates data on reproductive rates and removals with independent, periodic estimates of pup production (Hammill and Stenson 2005, 2008). The model assumes a 1:1 sex ratio and uses annual estimates of age-specific reproductive rates obtained from seals collected during the last quarter of pregnancy (Stenson and Wells 2010). Four different sources of removals were incorporated into the model: 1) the Canadian commercial hunt, 2) the Greenland subsistence harvest, 3) the Arctic subsistence harvest, and 4) the bycatch in commercial fishing gear (Stenson 2009). The reported catch levels were corrected for seals killed, but not reported (referred to as 'struck and loss'). Annual estimates of removals are available beginning in 1952. Mortality of young seals due to poor ice conditions was also included in the model and incorporated as a proportion of animals surviving. This factor acts on the young of the year (YOY) only and occurs prior to the start of the commercial hunt (Hammill and Stenson 2008). The level of ice-related mortality varies among years and is based upon observations of the conditions encountered and reports of dead seals. In 2010, ice cover was the lowest since records had begun to be kept in 1969. Owing to poor market conditions only about 69,000 animals were taken in the Canadian commercial hunt.

Based upon the lower estimate of 2008 pup production available at the 2009 meeting of the NMMPRC, the total population was estimated to be 6.5 million (95% CI= 5.7 to 7.3 million) in 2008 (Hammill and Stenson 2009). Here, we incorporate the revised 2008 pup production estimate, as well as new information on removals and reproductive rates, into the population model to obtain an estimate of current population size. We also examine the effects if different model formulations are used to describe the dynamics of the population, specifically if the dynamics are described assuming exponential growth or if density-dependent changes in juvenile mortality are incorporated into the model.

MATERIALS AND METHODS

Modelling the dynamics of the Northwest Atlantic harp seal population occurs in two steps. In the first, the model is fitted to the estimates of pup production by adjusting initial population size (*α*) and adult (i.e. seals one year of age and older referred to as '1+') mortality rates (*M*)(Hammill et al. 2009). Referred to as the 'Fitting Model', multiple population matrices are created using Monte Carlo sampling and the parameters *M* and α are estimated. This is done from 1952 until the last year data are available. In the second part, referred to as the 'Projection Model', the population is projected into the future to examine the impacts of different management options on the population. The projection model is based on the same equations as the fitting model (Hammill and Stenson 2009)

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

- Reproductive rates (and variance) remain constant over the period of the projection
- Mortality from bycatch, the proportion of seals struck and loss, and catches in the Canadian Arctic remain constant
- Greenland catches may vary between 70,000 and 100,000 (uniform distribution), with an average of 85,000 animals
- In the past, ice-related mortality has varied from 0−30% of pup production (uniform distribution) with an average of 12%. For this assessment, ice-related mortality varied from 0-45%, with an average of 30%,
- Pup mortality is fixed at three times 1+ mortality (*M*) and remains unchanged.
- The dynamics of the population can be described assuming exponential growth i.e. excluding equations 5.
- The dynamics of the population can be described assuming density-dependent growth by replacing equation 1 with equation 5,

Model structure

The basic model has the form: $n_{a,t} =((n_{a-1,t-1*} w) - c_{a-1,t-1})\, e^{-(\gamma)m}$ (1)

for age *a* = 1

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

for 1 < *a* < *A*,

$$n_{A,t} = [(n_{a-1,t-1} + n_{A,t-1}) e^{-M/2} - c_{a-1,t-1}] e^{-M/2} \qquad (3)$$

for *a* = *A*, where *A*-1 is taken as ages *A*-1 and greater, and for *a* = 0;

$$n_{0,t} = \sum_{a=1}^{A} n_{a,t} P_{a,t} \qquad (4)$$

$n_{1,t} =((n_{a-1,t-1*} w) - c_{a-1,t-1})\, e^{-(\gamma)m} * [1-(N_t/K)^{\Theta}]$ (5)

where $n_{a,1}$ = 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. P is expressed as a Normally distributed variable, with mean and standard error taken from the reproductive data

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).

The model is adjusted using the weighted sum-of-square difference between the pup production estimated by the model and the observed production from the surveys. The two parameters (M and α) are optimized to minimize the weighted sum-of-square difference by iterative methods.

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. Both pregnancy rates and pup production data are resampled from normal distribution of known mean and standard error. For each Monte Carlo simulation, a new M and α were estimated and stored. The model functions within the programming language R.

Data Input

Pup production estimates

The model was fit to 11 independent estimates of pup production (Table 1) 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 inspection for concentrations seen, but not surveyed. Also, they did not correct for births occurring after the surveys. Although they are thought to provide some useful information, there is greater uncertainty surrounding these estimates. To reflect this, these surveys were assigned a coefficient of variation of 40%.

Table 1: 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%.*

Reproductive rates

The manner in which reproductive rates have been incorporated into the population model has evolved over time. All analyses have attempted to provide annual pregnancy rates from the available sampling data, but an approach was needed for years when no data were available. Also, the data exhibited a high degree of interannual variation that was considered to be due to sampling error and not to reflect inter-annual differences in reproductive rates. An analysis by Shelton et al. (1992) explored 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. During the 1990s, a contingency test approach was used to estimate pregnancy rates (Shelton et al. 1996; Warren et al. 1997). For each age, successive contingency table analysis tests successive pregnancy sample data for significant changes in pregnancy rates. This approach results 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.

There are no reproductive data for many year-age combinations, and in some years the samples are quite small. To fill in data gaps, we assumed that the population pregnancy rates did not vary widely between years, so we used a non-parametric regression estimator to estimate the expected pregnancy rates. The method used is described in Stenson et al (2009a). Uncertainty in the smoothed rates was estimated by assuming the numbers pregnant in the samples were binomially distributed and refitting the smoothed line to random samples for each data point drawn from this distribution. Reproductive rate data were updated to include data up to 2008 (Stenson and Wells 2010). Seals 4 years old and younger were considered immature while seals 8 years and older were considered to be fully recruited into the population. The smoothed reproductive rates were extrapolated backwards from 1954 to 1952 and forward from 2008 to 2011 (Fig. 2)

As an alternate approach, the annual proportion of pregnant females aged 8+ years was incorporated into the model, for years where we had sufficient data, while the smoothed rates were used if no data were available, or if fewer than 5 samples were available for that year. The smoothed rates were used for animals aged seven years or less (Fig. 2). The variance in the estimates were assumed to be the same as estimated for the smoothed data.

Catches

Recent catches were taken from Stenson (2009). Data were updated to include the most recent data on the Canadian commercial harvest. The 2009 Canadian commercial catch was revised to 76,668 while the 2010 harvest was 69,101 seals (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 (Stenson 2009; Sjare and Stenson 2002). The levels of struck and loss applied were the same as previously, i.e., since 1983, 95% of the YOY and 50% of the animals aged 1+ years in the Canadian commercial hunt (Front and Gulf) were recovered while 50% of all animals killed in Greenland and the Canadian Arctic were assumed to be recovered and reported (Stenson 2009).

Poor ice conditions result in increased mortality (M_{ice}) that affects animals prior to the hunt (Hammill et al. 2009). This is incorporated into the model as a survival term. In most years M_{ice} was set to 0, but in years where particularly poor conditions were noted or observed, and reports of large numbers of carcasses or animals disappearing were received, this factor was adjusted. In 2010, there was almost no ice in the Gulf. Frequent reconnaissance flights using helicopter and fixed wing aircraft failed to find large seal concentrations on what ice was present. A significant concentration was observed near Anticosti Island, which may have had 10's of thousands of animals, but this ice disappeared within a week of animals being located (Hammill pers. obs.). The impression was that many animals had moved elsewhere to pup, nevertheless, it was assumed that 90% of the animals born in the Gulf died. Poor ice conditions were also encountered at the Front, and some animals were located approximately 180 km north of where they normally occur. Mortality of pups along beaches in the northern Gulf and Strait of Belle Isle was high (Stenson, pers. obs.). It was felt that approximately 25% of the Front herd also died due to poor ice conditions, resulting in an overall mortality rate of 45%, assuming that 30% of the animals are born in the Gulf and 70% are born at the Front (Table 2).

Table 2. Years when unusual ice mortality is assumed to have occurred, and values input to the model to account for this mortality. The data are input as proportions of animals surviving (i.e., 1-mortality).

Year	Survival
1969	0.75
1981	0.75
1998	0.94
2000	0.88
2002	0.75
2005	0.75
2006	0.90
2007	0.78
2010	0.55

The model was re-run several times to provide a more complete series of outputs under different assumptions. The objective was to examine the impact on the population trajectory of using annual and smoothed reproductive rates and exponential vs a density-dependent growth model. Under the assumption of density-dependent population growth, juvenile mortality was assumed to increase as population size increased under different assumptions of carrying capacity (K) , where K= 10, 12, 14, 16, 18 or 20 million . For these simulations it was assumed that all future harvests were 325,000 animals.

RESULTS

The fit to of the non-parametric model to the reproductive data for animals aged 4 years old was very poor, but overall the model fitted the data reasonably well for the remaining age classes using years with sample sizes greater than 5 (Fig. 2). For most ages, pregnancy rates appeared to be more variable in recent years.

Assuming that the population continues to grow in an exponential manner (Table 3, Fig 3, 4), the model that used the smoothed reproductive rate data was unable to fit to the 2008 survey point, while the model using the annual reproductive estimates for 8+ animals fit both the 2004 and 2008 survey estimates closely. Overall the population estimates from the model using the annual reproductive rates were higher, with lower adult mortality rates than the estimates obtained using the smoothed reproductive rates. Under the assumption of exponential growth, revised estimates from the 2004 survey would be 874,600 or 1,113,300 pups and a total population of 7,357,300 or 7,985,700 animals depending on whether smoothed or annual reproductive rates were used. For 2008, pup production is 1,277,400 or 1,684,600 animals with a total population of 8,040,700 to 9,497,400 animals depending on which reproductive rates were used (Table 3).

The model was also run under the assumption of density-dependent growth, with different carrying capacity levels (K), of 10, 12, 14, 16, 18 and 20 million animals, and using annual or smoothed reproductive rate data (Tables 5-10, Fig 5-8). The models incorporating annual reproductive rates provided a better fit to the aerial survey data and had lower estimates of adult mortality than models that incorporated the smoothed reproductive rates (Table 4). Under all simulations, little difference was observed between projected pup production and population estimates under different carrying capacity assumptions up to 2010. After 2010, the different trajectories began to diverge depending on values of K (Tables 5-10, Fig 5-8). The lowest estimates were obtained assuming a K of 10 million (Table 5, Fig. 5-8).Assuming smoothed reproductive rates, pup production increased from 1,081,600 in 2004 to 1,156,900 in 2008 while total population increased only slightly from 6,393,100 to 6,476,400. Using the annual reproductive estimates resulted in pup production estimates of 843,800 in 2004 and 1,542,000 in 2008. Total population was estimated to have increased from 6,810,700 in 2004 to 7,519,100 in 2008. Both models predicted only slight increases in population between 2008 and 2010 (6,905,400 and 7,811,400).

The highest estimates were obtained assuming a K of 20 million, while assuming K=12, 14, 16 or 18 million animals provided intermediate estimates (Tables 6-10, Fig 5-8). For K=20 million animals, pup production in 2004 was estimated to be 1,105,500 or 869,800,000, with a total population of 7,117,200 or 7,747,900, depending on whether the model used smoothed or annual reproductive rates (Table 10). In 2008, at K=20 million, pup production was estimated to be either 1,239,400 or 1,656,900 with a total population of 7,978,600 or 9,011,600 depending on whether smoothed or annual reproductive rates are applied.

The impact of different harvest levels on the population were examined assuming : that young of the year comprised 95% of the harvest; the Greenland harvest followed a uniform distribution with mean=85,000 (range: 70,000 to 100,000); no change was observed in by-catch and Canadian Arctic catches and future ice-related mortality prior to the start of the hunt, the ice-related survival (=1-mortality) factor (*w* in equations 1 and 5) was set to a mean of 70% (range: 0.55 to 1). The impact of different harvest levels on a population growing exponentially as well as a population regulated by density-dependent growth were examined. The management objective is to have an 80% probability that the population remains above N_{70}. N_{70} was adjusted based upon the most recent survey (2008) and the model assumptions related to population growth. Assuming that the population continues to grow exponentially, and with smoothed reproductive rates, N70 was set at 5.6 million. Assuming density dependence and annual reproductive rates, was set, for example, at 5.7 million and 6.1 million for assumed K of 12 million and 16 million, respectively.

Harvest levels that respected the management objective varied from as low as 350,000 animals assuming K=10 million, to as high as 540,000 animals assuming K=20 million animals (Fig. 9). If poor ice conditions occur in 2011, then assuming 50% mortality and a harvest of 100,000 animals, then a harvest of 400,000 animals in subsequent years (2012, 2013, 2014) would continue to respect the management plan (Fig.10).

DISCUSSION

Two estimates of Northwest Atlantic pup production were presented in Stenson et al (2009b). One estimate was lower and in line with expectations from previous modelling with an estimated pup production in 2008 of around 1,000,000 animals (Hammill and Stenson 2008). The second estimate, based upon the photographic estimates, was much higher at around 1.6 million animals (Table 1). The traditional modelling approach fit well to the low estimate, while the fit to the high estimate was very poor (Hammill and Stenson 2009). During the 2009 meeting, it was suggested that unusually high reproductive rates could account for the sudden increase in pup production observed in 2008. Annual reproductive rate for 2008 were not available at the time, but were available for the 2010 meeting. Incorporating the annual data up to, and including 2008, into the population model improved the fit to the survey data. It showed that the pup production observed in 2004 was due to lower than expected reproductive rates in that year, whereas the significantly higher estimate observed in 2008 resulted from higher than average reproductive rates in 2008 (Stenson and Wells 2010).

Although incorporating the annual rates into the model helped us to understand what might be happening in this population ecologically, there are temporal gaps in the reproductive data requiring interpolation in order to estimate rates in all years. Using annual rates also results in undue importance being assigned to the last reproductive rate/survey point, when this point serves as a starting point to evaluate the impacts of future harvests on the population. Evaluating the impact of future harvests based on estimates from the very low annual reproductive rates and the 2004 surveys would have provided quite a different impression of the population trajectory, than would be the case using the 2008 survey/reproductive rate data. In resource management, undue weight is often given to the last survey point if it is high, or it is rapidly downgraded if it is unusually low. Incorporating the smoothed reproductive rates into the model provides an appropriate method to fill in data gaps. Projecting the smoothed rates into the future and capturing the uncertainty around these rates also provides an approach to evaluating the impacts of harvests on predicted population changes that accounts for the uncertainty in future reproductive rates.

Eberhardt (1977, 2002) outlined a paradigm for density-dependent regulation which has received support in the literature (Fowler 1987; Gaillard et al. 1998). This framework proposes that the density-dependent changes that would occur as a population approaches environmental carrying-capacity (K) would be manifested as changes in growth (Eberhardt and Siniff 1977), followed by an increase in juvenile mortality, then a decline in reproductive rates and finally an increase in adult mortality. However, large long-lived mammals, showing delayed maturity and low productivity require long-term monitoring in order to measure these attributes. Furthermore, population regulation involves a complex interaction between environmental and habitat attributes, density-dependent mediated changes in recruitment and mortality, including predation, and time-lagged effects (Owen-Smith 2006; Bradshaw et al. 2006; Hadley et al. 2007; Chamaillé-Jammes et al. 2008).

If the paradigm proposed by Eberhardt (1977) is correct, then in addition to the decline observed in reproductive rates, there has likely also been an increase in juvenile mortality rates, and possibly adult mortality rates. At some point there will be a change in the ratio of pup mortality to adult (γ) such that the exponential model is no longer suitable for describing the dynamics of this population. Changes observed over the last 60 years in size at age (Chabot and Stenson unpublished) 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. Similar changes reflecting the interaction between density-dependent mediated changes in population dynamics and environmental factors have been observed among other pinniped (Rotella et al. 2009; McMahon et al. 2009; Hadley et al. 2007; Pistorius et al. 2008) and ungulate populations (Owen-Smith 2006; Owen-Smith and Mills 2006). Consequently, it would be more appropriate to include annual reproductive rates and a density-dependent function in the model formulation. 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 complicates 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). To understand potential effects of density dependence on the population trajectory, density-dependent changes in juvenile mortality were assumed and several levels of carrying-capacity (K) were examined (10-20 million). Values of K=10 to 12 million are within the range of estimates of pristine population size (Hammill and Stenson unplublished data), while a K=20 million resulted in only slightly slower growth rates of the population compared to that observed in an exponential model over a projection period of 15-20 years. Given the uncertainties surrounding the level of K, a consensus was adopted to run projections and assess harvest scenarios using 3 model formulations:

1) Annual pregnancy rates with K=12 million
2) Annual pregnancy rates with K=16 million
3) Smoothed pregnancy rates with exponential growth.

K=10 million was not retained because it currently appears to be inconsistent with the continued observed increase in population. Setting K at 12 million provided a better fit to the pup survey data than did the model with K=10 million, resulted in significant density-dependent changes occurring quite early in the projected dynamics of the population and represents a reasonable lower level to evaluate the impacts of different harvest levels on the population. At K=16 million, the model imposes minimal density dependence at current population levels yet avoids unrestrained growth in future projections. Continued use of the exponential growth model with smoothed reproductive rates provide some consistency with previous assessments. However, it was recognized that these values of K would likely be revised as new information becomes available.

In the previous assessment the 2004 population was estimated to be 5.74 million (95% CI= 4.19-7.35 million). After the 2008 survey, the 2004 population was revised to 7.36 million (95% CI 6.48 to 8.08 million), using the exponential growth model. This change resulted from the combination of several factors and is a reminder that estimates are heavily influenced by the most recent estimate. Although the two estimates are not significantly different, it is important to remember that with a point estimate, there is a 50% probability that the true population size is actually lower, or in this case higher than the mean. Prior to this, the population appeared to be leveling off at a level between 5.5 and 6.0 million (Hammill and Stenson 2008). However, results from the 2008 survey suggest that the population continues to grow albeit at a very low rate, or the differences observed between the 2004 and 2008 assessment may also reflect natural fluctuations in abundance that would be expected for a population nearing carrying capacity.

The Northwest Atlantic harp seal population is currently at the highest levels observed since monitoring began almost 60 years ago. Pup production in 2008 was on the order of 1.63 million animals with a total population size of around 8.0 to 8.7 million animals in 2008 increasing to a range of 8.6 to 9.6 million animals in 2010. The likelihood that the population is no longer growing exponentially needs to be considered further, particularly within the context of levels of K. An additional survey and continued collection of reproductive rate material are critical to understanding the dynamics of this population. Assuming exponential growth or density dependent growth of the population with K values of 12 or 16 million, a harvest of up to 400,000 animals per year would continue to respect the management plan over the next three years.

LITERATURE CITED

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.

Bradshaw, C.J.A., Fukuda, Y., Letnicand, M. and Brook, B.W. 2006. Incorporating known sources of uncertainty to determine precautionary harvests of saltwater crocodiles. Ecol. App. 16:1436-1448.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. and Clobert, J. 2008. Having your water and drinking it too: resource limitation modifies density regulation. J. An. Ecol. 77:1-4.

Eberhardt, L.L. 1977. Optimal policies for the conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205-212.

Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Eberhardt, L. L. and Siniff, D. B. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada **34**:183–190.

Fowler, C.W. 1987. A review of density-dependence in populations of large mammals. Pages 401-441, in Current Mammalogy, Edited by H.H. Genoways. Plenum press.

Gaillard, J.-M, Festa-Bianchet, M. and Yoccoz, N. G. 1998. Population dynamics of large herbivores:variable recruitment with constant adult survival. Tree 13:58-63.

Hadley, G.L., Rotella, J. and Garrott, R.A. 2007. Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. Oikos 116:601-613.

Hammill, M.O. and Stenson, G.B. 2005. Abundance of Northwest Atlantic harp seals (1960-2005). DFO Can. Sci. Advis. Sec. Res. Doc. 2005/090. 38 p.

Hammill, M.O. and Stenson, G.B. 2008. Abundance of Northwest Atlantic harp seals (1960 – 2008). DFO Can. Sci. Advis. Sec. Res. Doc. 2008/077.

Hammill, M.O., Ferland-Raymond, B., Rivest, L.-P. and Stenson, G.B. 2009. Modelling Northwest harp seal populations: modifying an Excel model to R. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/108.

Hammill, M. O. and Stenson, G. B. 2009. A preliminary evaluation of the performance of the Canadian management approach for harp seals using simulation studies. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/093.

McMahon, C.R., Bester, M.N., Hindell, M.A., Brook, B.W. and Bradshaw, C.J.A. 2009. Shifting trends:detecting environmentally mediated regulation in long-lived marine vertebrates using time-series data. Oecologia 159:69-82.

Owen-Smith, N. 2006. Demographic determination of the shape of density dependence for three African ungulate populations Ecol. Mon. 76:93-109.

Owen-Smith, N. and Mills, M.G.L. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecol. Mon. 76:73-92.

Pistorius, P.A., Taylor, F.E., Bester, M.N., Hofmeyr, G.J.G. and Kirkman, S.P. 2008. African zoology 43:75-80.

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.

Rotella, J.J., Link, W.A., Nichols, J.D., Hadley, G.L., Garrott, R.A. and Proffitt, K.M. 2009. An evaluation of density-dependent and density independent influences on population growth rates in Weddell seals. Ecology 90:975-984.

Sergeant, D.E. and Fisher, H.D. 1960. Harp seal population sin 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.

Stenson, G.B. 2009. Recent catches of harp seals in the Northwest Atlantic. CSAS Res. Doc. 2009/112

Stenson, G.B., Hammill, M.O. and Lawson, J.W. 2011. How many harp seal pups are there? Additional results from the 2008 surveys. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/137 iv + 22 p. Available at http://www.dfo-mpo.gc.ca/csas

Stenson, G.B and Wells, N.J. 2011. Current reproductive and maturity rates of Northwest Atlantic Harp Seals, *Pagophilus groenlandicus*. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/136 iv + 15 p. Available at http://www.dfo-mpo.gc.ca/csas

Stenson, G.B., Hammill, M.O. and Healey, B. 2009a. 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. 2009b. Estimating pup production of northwest Atlantic harp seals, Pagophilus groenlandicus: results of the 2008 surveys. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/103.

Stenson, G. B., 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., Hammill, M.O., Lawson, J.W., Gosselin, J.-F. and 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., 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., 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.

Trzcinski,M.K., Mohn, R. and Bowen, W.D. 2006. Continued Decline Of An Atlantic Cod Population: How Important Is Gray Seal Predation? Ecological Applications, 16(6), 2006, Pp. 2276–2292

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 3. Estimated pup production and total population size from 2004-2010 assuming exponential growth and incorporating annual or smoothed reproductive rates into the model.

			Smoothed reproductive rates					
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,113,300	52,600	1,011,800	1,213,500	7,357,300	420,200	6,478,400	8,076,909
2005	1,150,200	90,600	990,600	1,357,200	7,587,800	477,700	6,616,364	8,454,542
2006	1,179,000	1,04,600	988,300	1,393,900	7,589,500	527,000	6,518,383	8,685,116
2007	1,237,600	1,20,900	996,900	1,451,800	7,813,300	592,100	6,595,173	8,992,400
2008	1,277,400	1,07,600	1,056,400	1,486,300	8,040,700	631,600	6,768,914	9,260,294
2009	1,301,300	1,32,800	1,074,300	1,568,000	8,503,700	712,700	7,045,337	9,864,763
2010	1,341,300	1,50,200	1,066,900	1,671,800	9,114,000	807,300	7,486,117	10,671,260
				Annual reproductive rates				
2004	874,600	55,500	766,300	977,400	7,985,700	382,100	7,180,200	8,805,200
2005	1,312,000	97,800	1,113,500	1,498,500	8,391,300	444,400	7,572,600	9,402,000
2006	1,229,100	94,600	1,027,700	1,407,500	8,380,600	483,900	7,447,600	9,381,800
2007	1,646,300	136,500	1,388,500	1,924,500	8,994,900	572,300	7,892,600	10,068,500
2008	1,684,600	102,000	1,498,000	1,896,700	9,497,400	612,400	8,389,700	10,743,800
2009	1,495,000	129,200	1,279,700	1,784,900	10,084,900	700,000	8,732,100	11,349,200
2010	1,569,900	147,900	1,316,500	1,885,200	10,868,700	807,600	9,388,700	12,495,100

Table 4. Estimates of adult mortality and standard errors obtained under different model assumptions of population growth with different assumption for carrying capacity and ways to incorporate the reproductive data into the model.

	Annual Estimate	se	Smoothed Estimate	Se
K=10	0.030	0.005	0.036	0.003
K=12	0.034	0.003	0.039	0.003
K=14	0.037	0.003	0.041	0.003
K=16	0.039	0.003	0.042	0.003
K=18	0.040	0.003	0.043	0.003
K=20	0.041	0.003	0.044	0.003
Exponential	0.043	0.003	0.046	0.003

Table 5. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=10 million animals and incorporating annual or smoothed reproductive rates into the model.

		K=10 million		Smoothed reproductive rates				
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,079,400	49,500	984,400	1,170,400	6,439,300	253,900	5,963,100	6,875,600
2005	1,099,000	77,500	962,400	1,258,400	6,517,600	284,600	5,972,100	7,014,800
2006	1,113,700	80,600	947,000	1,275,200	6,432,200	303,700	5,871,800	6,993,100
2007	1,136,200	88,200	974,400	1,303,300	6,473,800	328,200	5,826,700	7,047,900
2008	1,155,100	83,200	993,100	1,307,100	6,525,200	337,700	5,862,200	7,143,700
2009	1,155,500	95,000	999,200	1,346,500	6,702,000	354,800	6,024,000	7,331,600
2010	1,175,200	101,700	1,001,200	1,378,800	6,954,600	365,100	6,227,100	7,581,500
				Annual reproductive rate				
2004	840,400	81,600	730,700	939,300	6,774,700	551,900	6,261,800	7,271,100
2005	1,272,400	128,400	1,109,000	1,458,500	7,127,600	604,600	6,498,800	7,721,000
2006	1,149,100	123,600	955,300	1,304,700	6,956,800	600,500	6,327,000	7,594,800
2007	1,540,800	166,200	1,323,100	1,817,500	7,364,400	654,900	6,634,000	8,092,300
2008	1,528,900	148,300	1,314,800	1,720,100	7,481,000	649,200	6,755,400	8,158,000
2009	1,336,300	145,100	1,161,600	1,574,700	7,538,300	650,300	6,856,000	8,228,700
2010	1,354,300	145,200	1,170,500	1,566,600	7,768,200	659,600	7,121,300	8,435,200

Table 6. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=12 million animals and incorporating annual or smoothed reproductive rates into the model.

			K=12 million		Smoothed reproductive rates			
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,085,500	92,400	982,100	1,194,200	6,658,700	566,500	6,112,100	7,342,900
2005	1,097,900	113,100	944,600	1,265,600	6,766,500	596,900	6,110,300	7,592,900
2006	1,123,400	122,500	956,300	1,325,400	6,703,700	612,600	5,934,800	7,565,700
2007	1,151,400	127,600	976,100	1,340,500	6,783,100	635,500	6,011,600	7,701,500
2008	1,180,700	127,000	1,002,600	1,393,000	6,875,200	653,400	6,000,900	7,767,600
2009	1,187,700	140,000	994,900	1,421,300	7,114,200	689,800	6,268,700	8,044,700
2010	1,206,500	148,600	993,200	1,451,100	7,434,100	724,300	6,496,100	8,479,900
				Annual reproductive rates				
2004	857,500	59,800	737,000	967,600	7,212,300	311,700	6,674,700	7,831,100
2005	1,286,300	95,500	1,131,400	1,492,000	7,566,000	373,700	6,915,100	8,311,800
2006	1,188,200	100,200	1,015,200	1,375,500	7,441,400	390,200	6,751,700	8,187,900
2007	1,587,100	123,400	1,369,900	1,811,700	7,896,000	440,400	7,067,900	8,751,200
2008	1,598,100	94,300	1,404,900	1,746,800	8,110,300	416,800	7,335,500	8,895,100
2009	1,399,200	125,700	1,190,100	1,661,200	8,274,400	443,600	7,476,200	9,076,000
2010	1,434,100	118,400	1,235,200	1,651,400	8,608,200	444,800	7,798,100	9,427,900

Table 7. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=14 million animals and incorporating annual or smoothed reproductive rates into the model.

		K=14 million		Smoothed reproductive rates				
	Pup Mean	SE	L_{pup}95	U_{pup}95	Total Mean	SE	L_{total}95	U_{total}95
2004	1,097,155	52,219	997,110	1,200,389	6,870,725	334,484	6,225,410	7,432,097
2005	1,122,702	88,974	942,836	1,284,343	7,015,989	377,704	6,298,072	7,638,468
2006	1,141,573	86,260	963,680	1,296,785	6,962,547	405,211	6,175,897	7,688,127
2007	1,169,307	103,725	984,021	1,378,615	7,066,923	448,245	6,189,492	7,840,816
2008	1,210,261	96,252	1,025,876	1,401,901	7,192,446	470,736	6,279,453	8,005,291
2009	1,223,814	108,302	1,034,621	1,456,980	7,483,557	506,428	6,489,821	8,401,982
2010	1,257,088	133,739	1,026,049	1,520,940	7,876,828	555,300	6,812,867	8,832,374
				Annual reproductive rates				
2004	874,736	56,529	753,424	979,013	7,476,368	358,672	6,855,621	8,143,511
2005	1,303,777	107,295	1,091,460	1,512,591	7,846,357	430,125	7,119,395	8,627,209
2006	1,197,649	103,736	970,806	1,391,336	7,739,442	451,391	6,901,633	8,629,280
2007	1,612,067	127,835	1,403,159	1,888,031	8,237,783	503,873	7,332,738	9,214,343
2008	1,632,333	99,514	1,455,364	1,839,699	8,522,158	494,872	7,646,976	9,424,024
2009	1,449,194	145,300	1,197,837	1,770,499	8,793,156	537,308	7,846,191	9,789,913
2010	1,477,704	126,965	1,243,785	1,716,659	9,207,253	543,168	8,189,588	10,150,074

Table 8. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=16 million animals and incorporating annual or smoothed reproductive rates into the model.

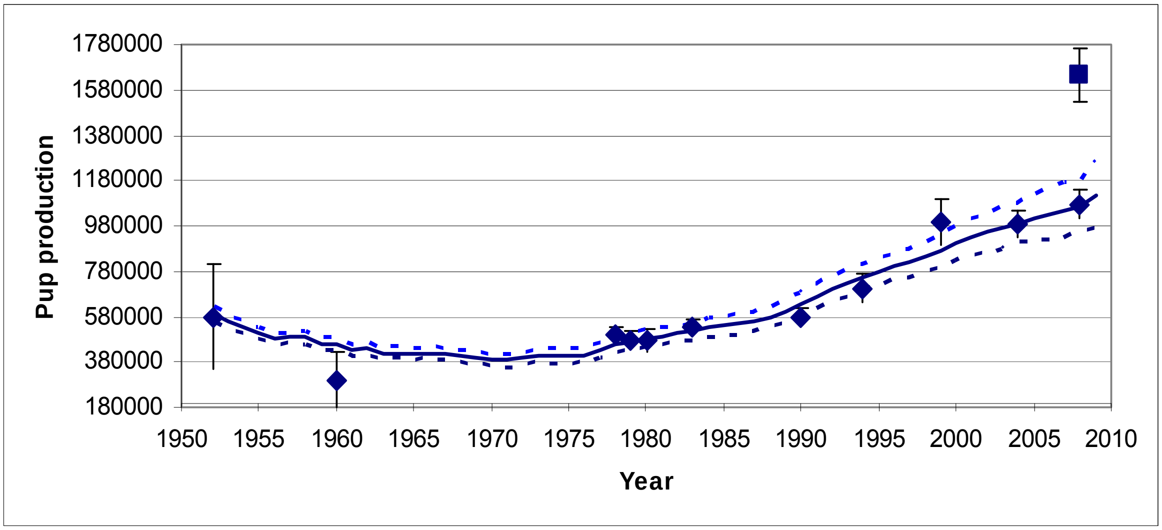
		K=16 million			Smoothed reproductive rates			
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,105,385	52,863	1,014,699	1,219,595	7,047,144	349,907	6,400,105	7,786,870
2005	1,137,114	84,534	1,003,226	1,328,658	7,215,711	395,519	6,510,518	8,127,505
2006	1,164,352	94,205	1,010,750	1,366,716	7,181,709	425,813	6,440,610	8,258,729
2007	1,199,082	105,146	1,025,187	1,394,004	7,318,324	467,870	6,495,715	8,422,504
2008	1,237,932	95,982	1,087,904	1,429,506	7,467,030	488,392	6,591,991	8,566,991
2009	1,255,240	117,017	1,061,473	1,506,977	7,799,044	531,582	6,904,704	8,976,077
2010	1,281,214	126,805	1,068,052	1,582,658	8,230,701	576,052	7,229,705	9,505,957
				Annual reproductive rates				
2004	874,250	54,834	769,132	982,321	7,589,185	332,219	7,004,509	8,286,663
2005	1,293,592	97,924	1,125,490	1,491,820	7,954,503	395,611	7,251,958	8,748,539
2006	1,199,556	93,840	1,012,388	1,396,634	7,870,188	417,724	7,070,955	8,797,496
2007	1,621,746	137,780	1,386,529	1,925,717	8,398,052	495,059	7,544,433	9,430,498
2008	1,641,672	102,850	1,461,033	1,851,047	8,728,366	496,302	7,817,805	9,827,116
2009	1,451,967	128,430	1,256,497	1,708,116	9,061,406	536,149	8,117,923	10,155,711
2010	1,497,049	127,885	1,280,979	1,753,862	9,554,203	567,373	8,509,553	10,795,408

Table 9. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=18 million animals and incorporating annual or smoothed reproductive rates into the model.

		K=18 million		Smoothed reproductive rates				
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,101,633	51,528	998,677	1,195,115	7,077,826	362,020	6,402,916	7,862,586
2005	1,133,708	81,496	991,233	1,302,412	7,256,049	401,793	6,550,956	8,111,632
2006	1,150,830	94,540	964,394	1,348,549	7,216,556	440,863	6,412,014	8,151,592
2007	1,189,552	113,683	993,879	1,420,433	7,359,971	500,804	6,421,756	8,425,938
2008	1,236,207	99,831	1,046,766	1,448,299	7,523,474	521,924	6,509,926	8,653,585
2009	1,255,473	130,367	1,029,111	1,483,463	7,878,311	585,755	6,851,592	9,049,726
2010	1,276,096	132,069	1,059,966	1,542,165	8,333,994	637,908	7,152,739	9,584,523
				Annual reproductive rates				
2004	873,529	60,885	760,470	986,464	7,753,063	387,036	7,005,401	8,477,330
2005	1,311,504	98,993	1,123,587	1,532,740	8,138,277	448,513	7,234,124	9,006,272
2006	1,219,771	106,926	1,036,928	1,437,778	8,073,927	479,685	7,133,790	8,958,541
2007	1,645,524	131,214	1,410,675	1,893,615	8,629,760	546,025	7,530,632	9,612,410
2008	1,659,276	110,379	1,454,959	1,881,491	8,991,224	559,089	7,974,573	10,033,775
2009	1,476,220	127,348	1,264,204	1,701,549	9,380,644	600,272	8,339,131	10,399,996
2010	1,542,182	136,561	1,279,149	1,815,582	9,946,957	644,248	8,815,887	11,133,277

Table 10. Changes in pup production and total population size from 2004-2010 assuming density-dependent growth with K=20 million animals and incorporating annual or smoothed reproductive rates into the model.

		K=20 million		Smoothed reproductive rates				
	Pup Mean	SE	$L_{pup}95$	$U_{pup}95$	Total Mean	SE	$L_{total}95$	$U_{total}95$
2004	1,105,500	50,400	1,019,800	1,204,500	7,117,200	351,700	6,433,400	7,776,800
2005	1,120,300	91,400	933,400	1,296,900	7,288,800	407,000	6,492,600	8,047,600
2006	1,162,800	93,300	985,800	1,332,300	7,270,300	442,800	6,418,000	8,084,900
2007	1,203,400	106,500	1,023,000	1,410,800	7,432,300	493,100	6,559,400	8,341,200
2008	1,239,400	98,400	1,046,200	1,440,800	7,601,400	522,900	6,591,600	8,533,500
2009	1,265,500	116,500	1,039,700	1,493,300	7,978,600	577,900	6,884,800	9,034,700
2010	1,292,000	127,900	1,082,300	1,546,000	8,466,600	635,900	7,285,800	9,630,500
				Annual reproductive rates				
2004	869,800	53,200	771,500	980,200	7,747,900	410,300	6,976,400	8,475,300
2005	1,302,600	104,200	1,120,800	1,525,800	8,129,100	482,400	7,259,400	8,967,300
2006	1,206,600	103,100	1,034,200	1,408,700	8,065,000	514,400	7,168,600	8,973,100
2007	1,627,600	141,200	1,386,600	1,930,600	8,619,500	600,900	7,581,000	9,776,200
2008	1,656,900	113,700	1,448,700	1,904,000	9,011,600	621,000	7,937,300	10,175,800
2009	1,477,300	151,200	1,205,500	1,783,900	9,442,400	692,700	8,226,500	10,800,900
2010	1,513,700	139,600	1,251,100	1,794,100	10,019,100	741,100	8,752,500	11,296,600



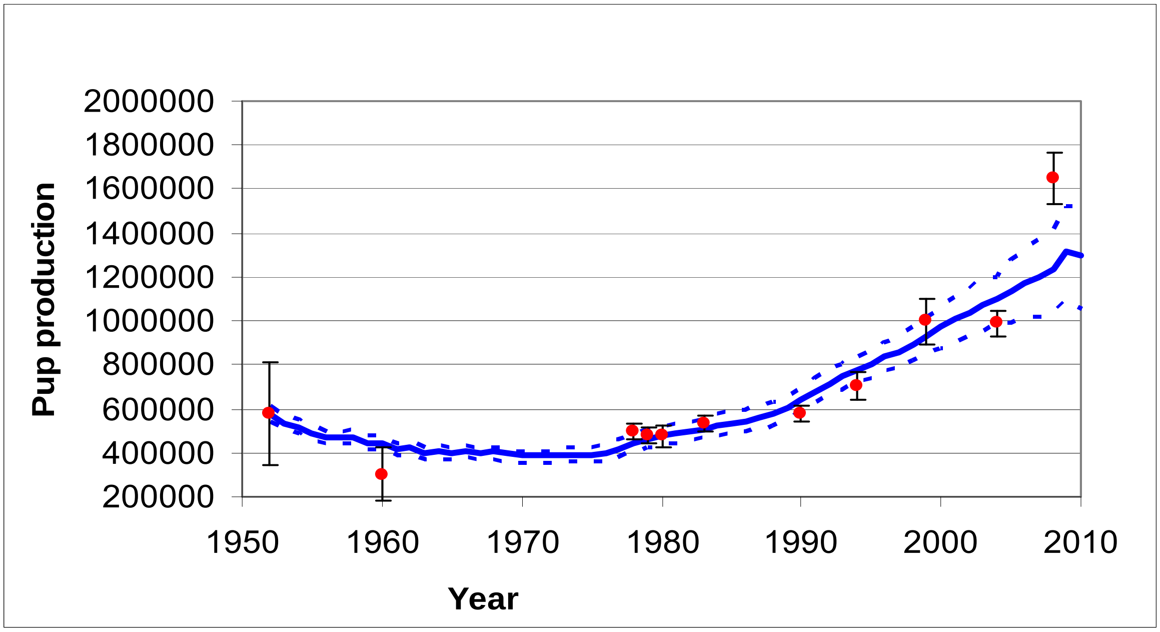


Figure 1. Changes in estimated pup production (mean±95% C.I.) and survey estimates (mean±95% C.I.) (top) when the model was fitted to the low estimate of pup production from the 2008 survey and when the model is fit to the high pup production estimate (bottom). In both cases, exponential growth is assumed and smoothed reproductive rates are used. The high estimate is also shown (mean±se) from Hammill and Stenson (2009).

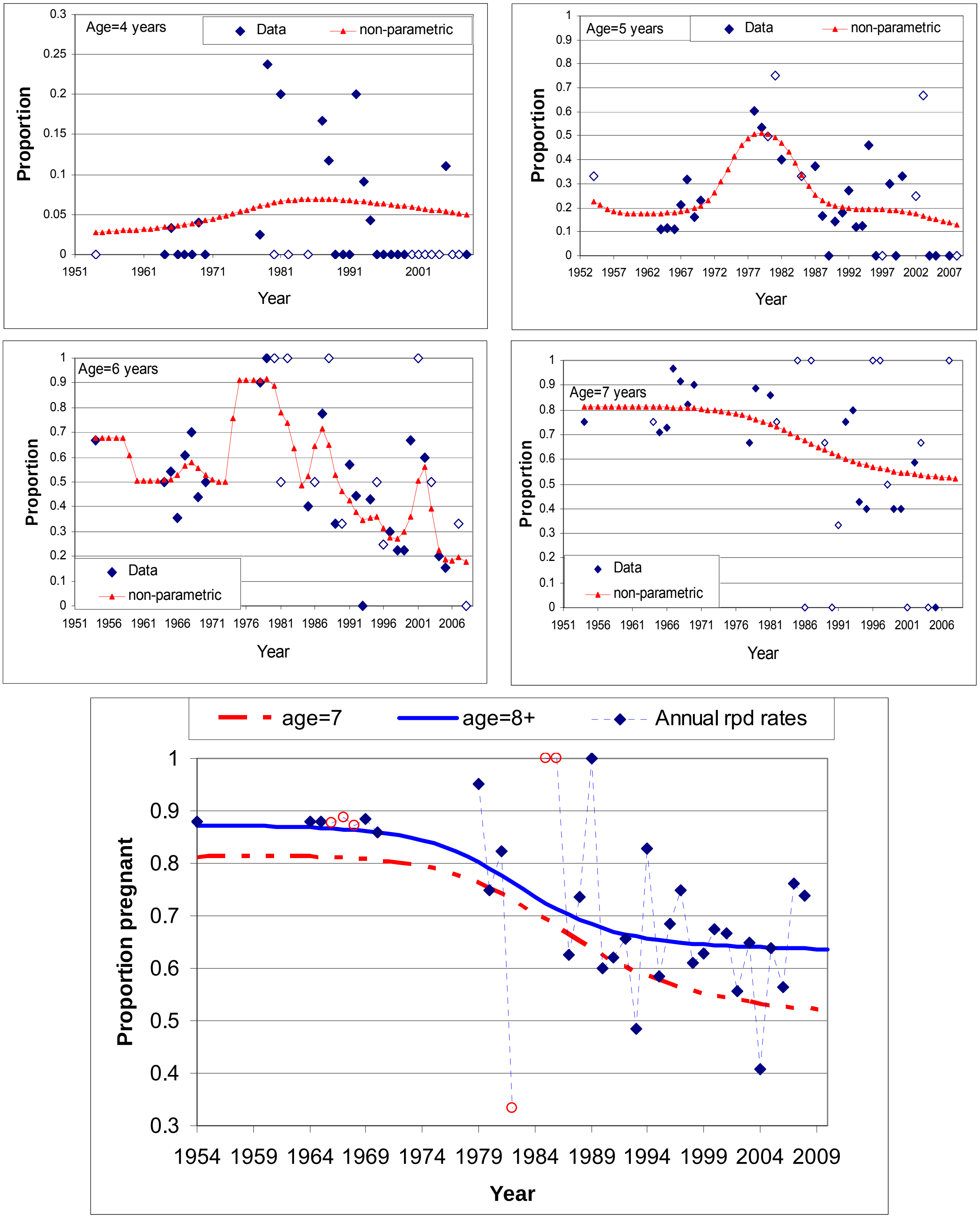
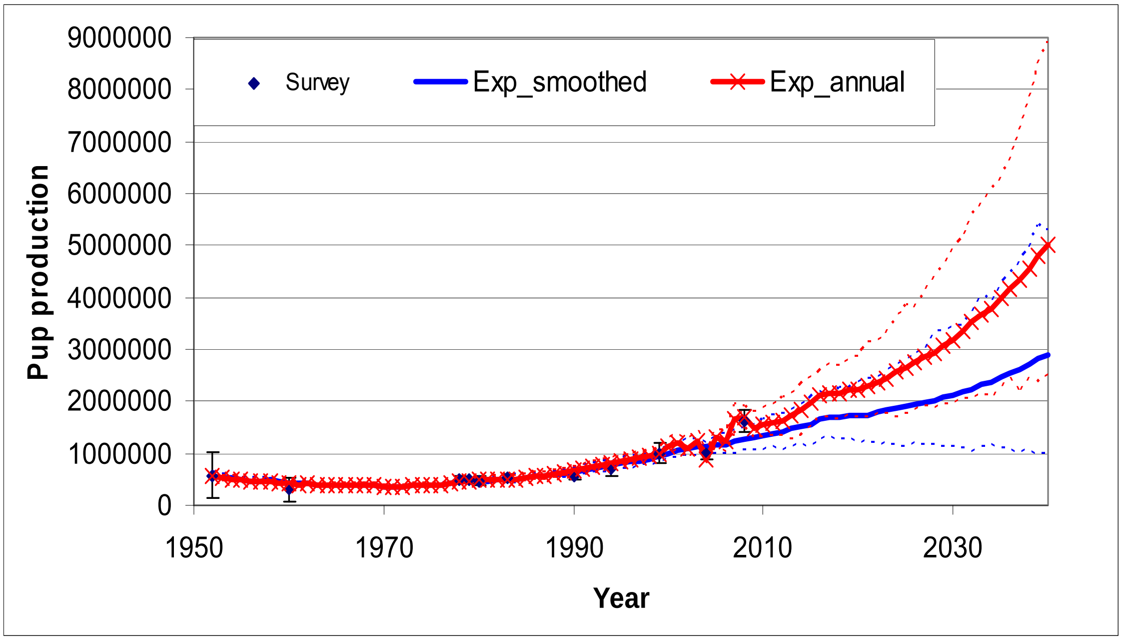


Figure 2. Age specific reproductive rates and non-parametric smoothed rates. Open symbols represents N<5 samples.



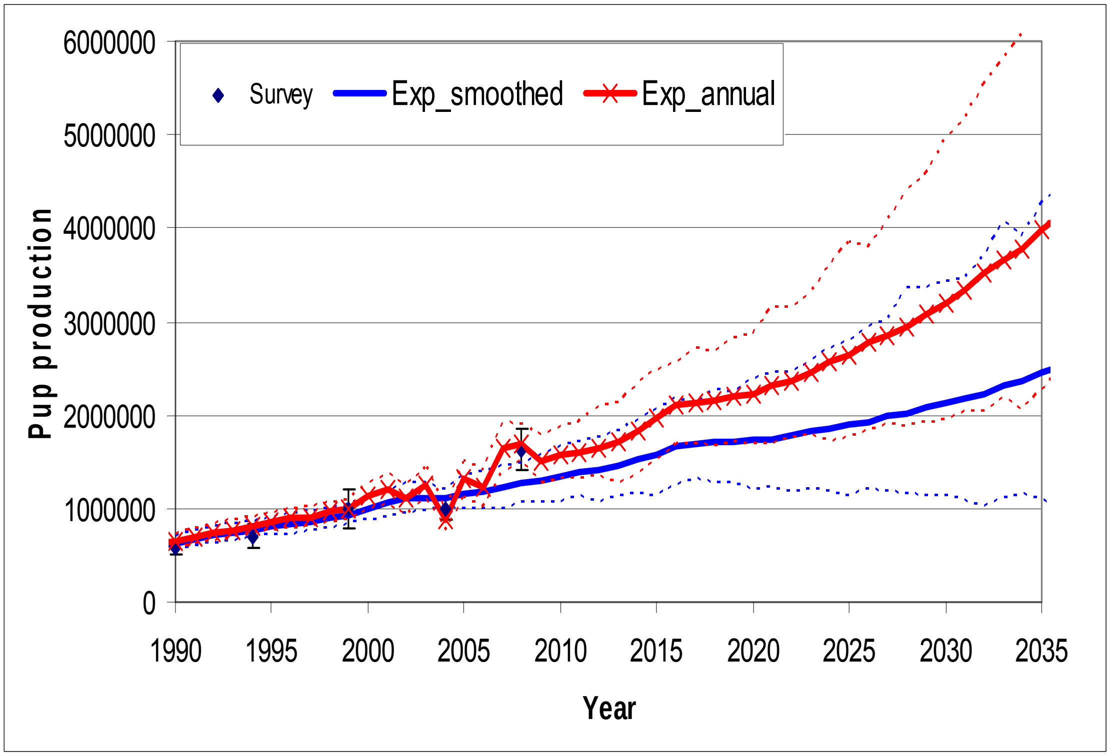
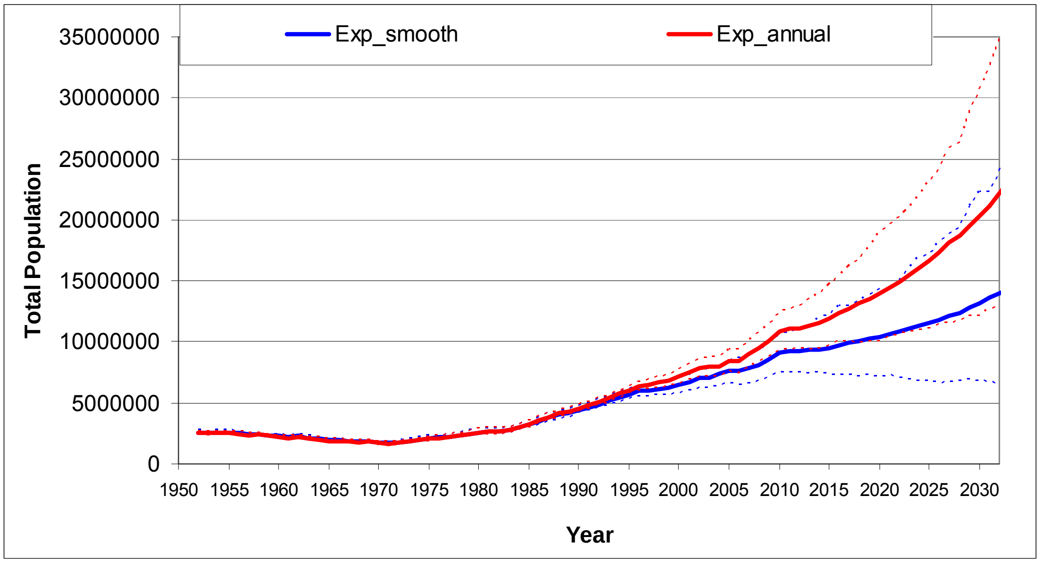


Figure 3. survey estimates (±95% CI) Trend in pup production assuming an exponential model and using annual reproductive rates up to 2008, then smoothed rates beginning in 2009 or smoothed reproductive rates throughout the time series. Dotted lines are 95% confidence intervals. Future harvests used in projections are 325,000 per year.



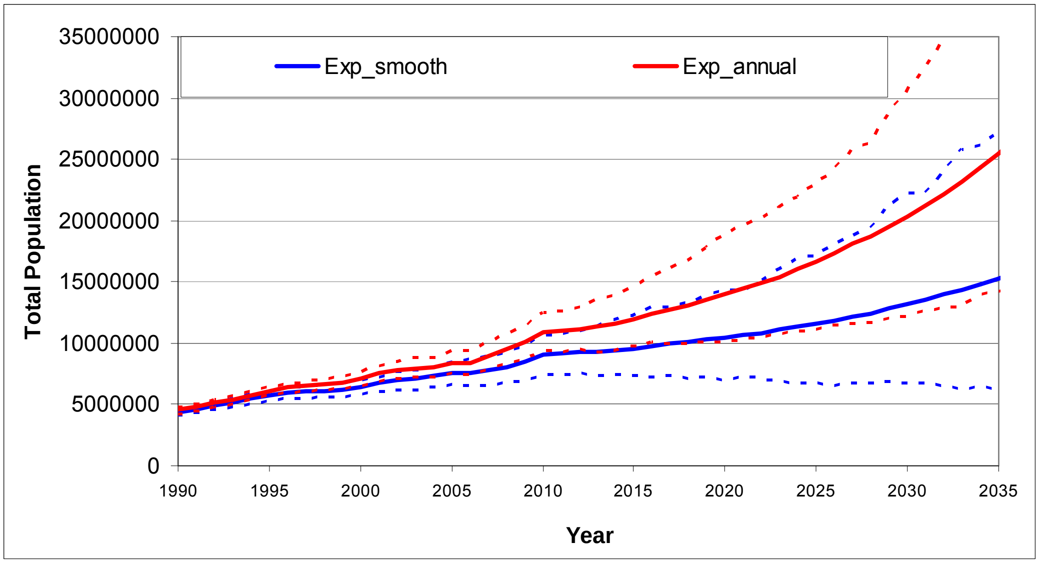


Figure 4. Trends in total population size (+ 95% CI) assuming exponential population growth model and incorporating annual or smoothed reproductive rates into the model. Future harvests used in projections are 325,000 per year.

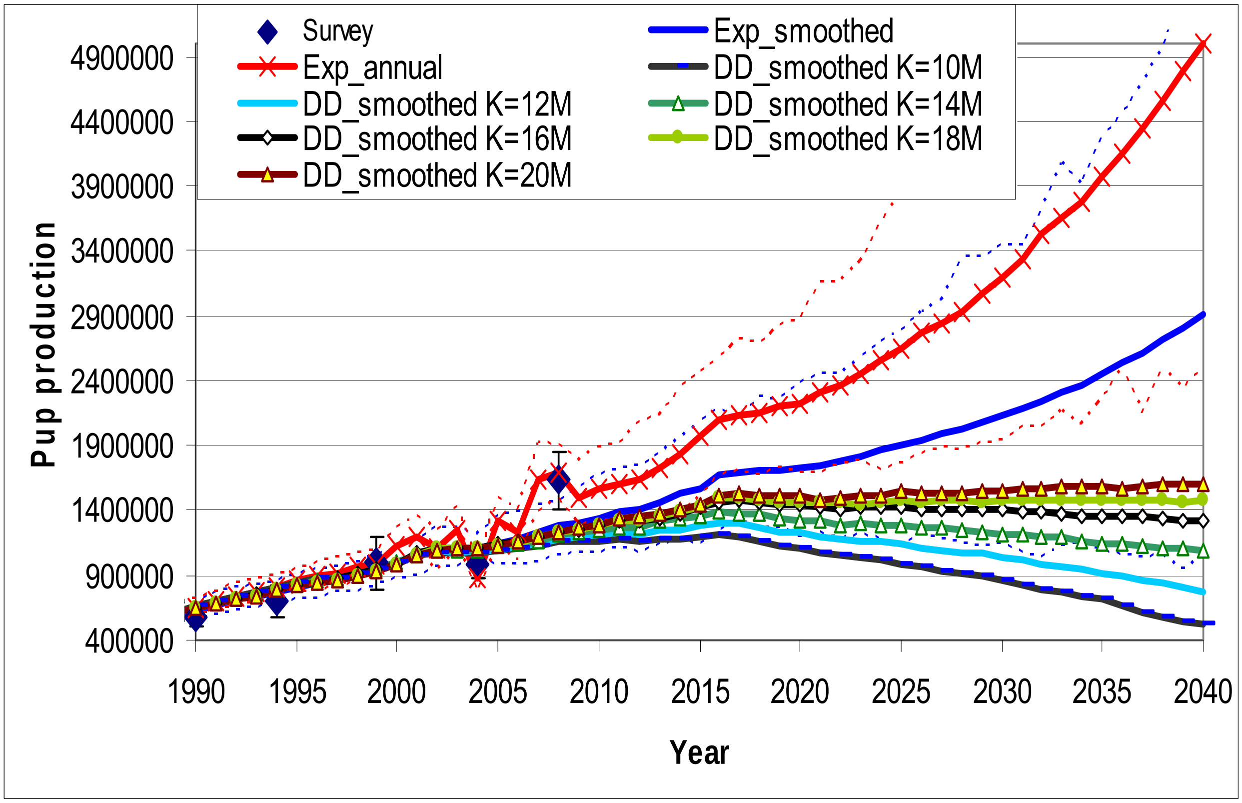


Figure 5. Changes in pup production assuming the population is growing exponential with annual or smoothed rates (with 95% CI), or the population is growing under different carrying capacity assumption using the smoothed reproductive rate data. The survey data include 95% CI. Future harvests used in projections are 325,000 per year.

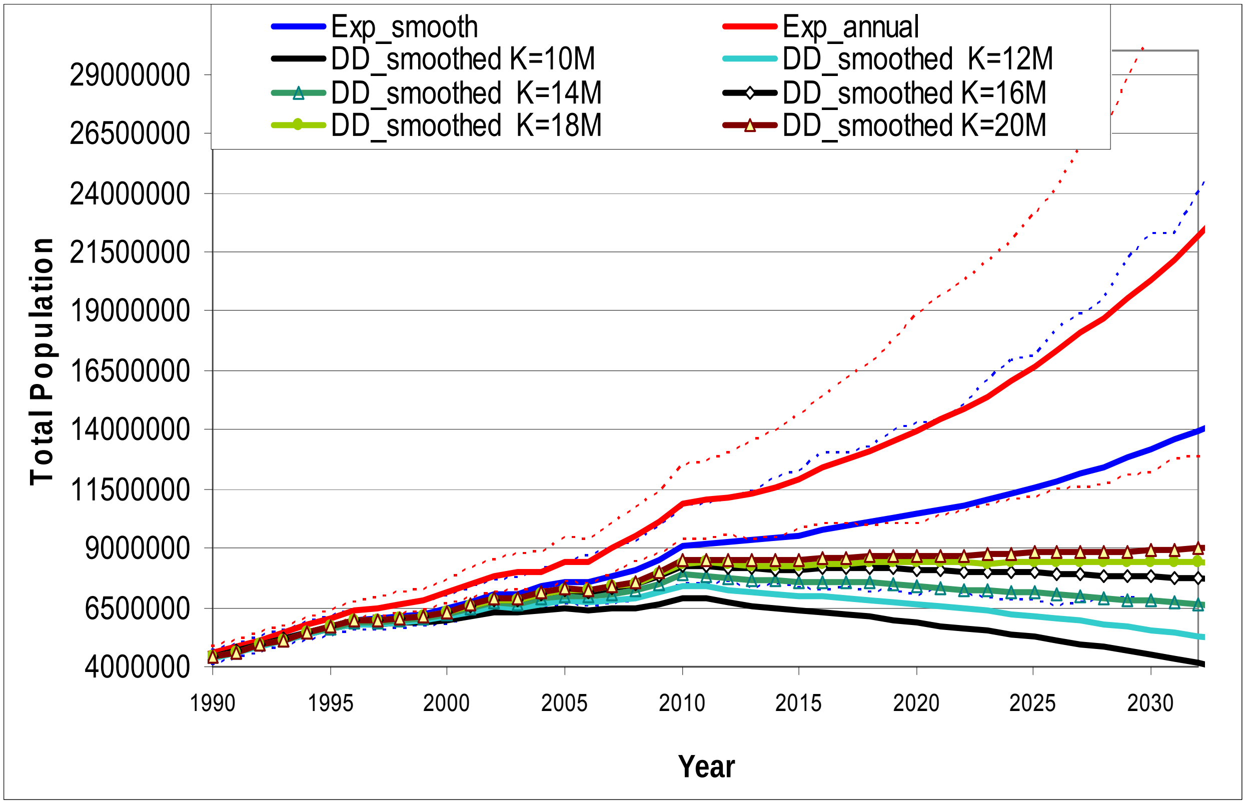


Figure 6. Changes in total population size, assuming the population is growing exponential with annual or smoothed rates (with 95% CI), or the population is growing under different carrying capacity assumptions using the smoothed reproductive rate data. Future harvests used in projections are 325,000 per year.

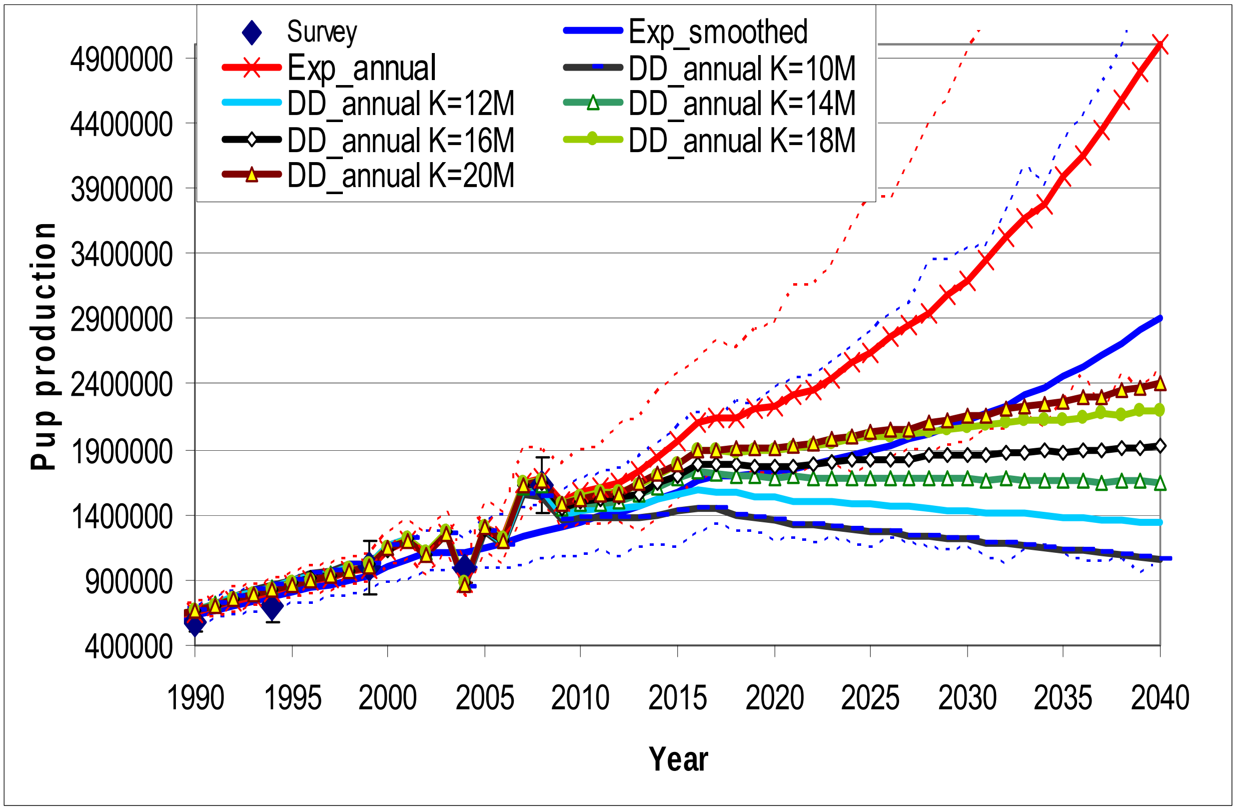


Figure 7. Changes in pup production assuming the population is growing exponential with annual or smoothed rates (with 95% CI), or the population is growing under different carrying capacity assumption using the annual reproductive rate data. Future harvests used in projections are 325,000 per year.

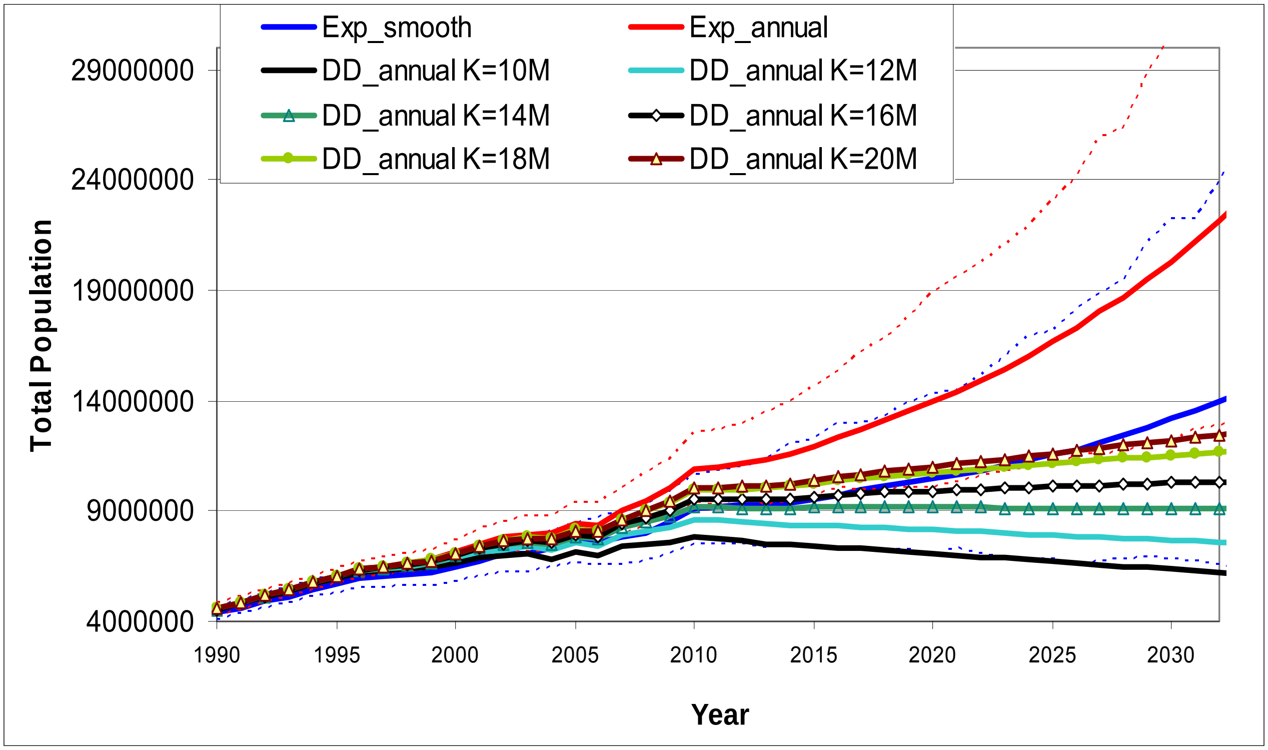


Figure 8. Changes in total population size, assuming the population is growing exponential with annual or smoothed rates (with 95% CI), or the population is growing under different carrying capacity assumptions using the annual reproductive rate data. Future harvests used in projections are 325,000 per year.

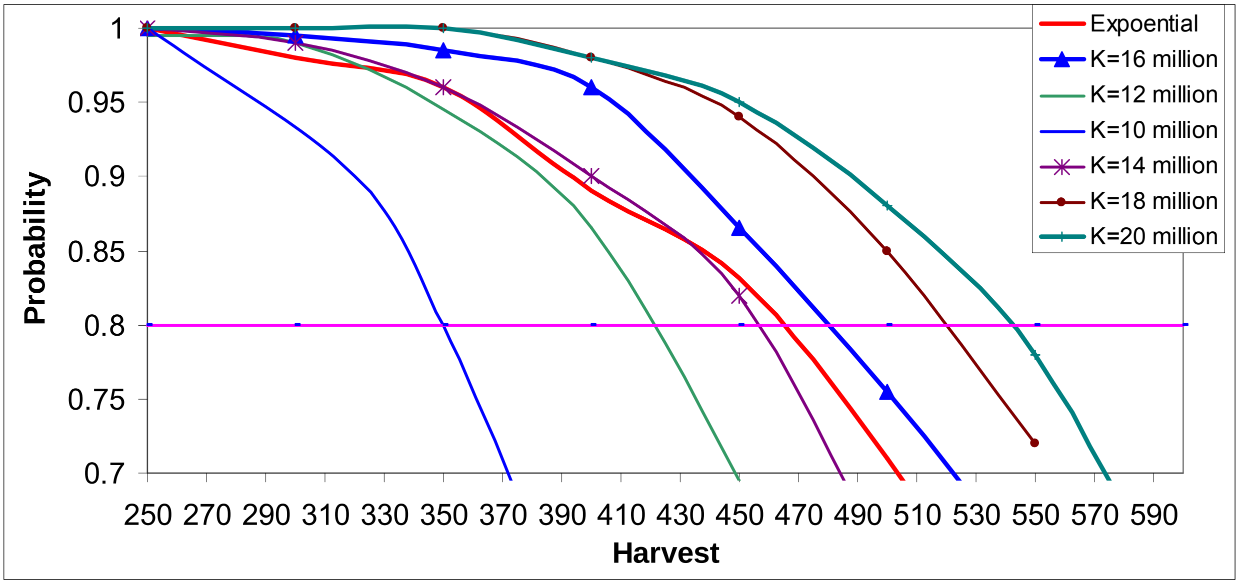


Figure 9. Probability of the population remaining above N_{70} (straight line), under different harvest levels. Model runs assumed exponential population growth and smoothed reproductive rates or assumed density-dependent population growth under different values of K and using annual reproductive rates.

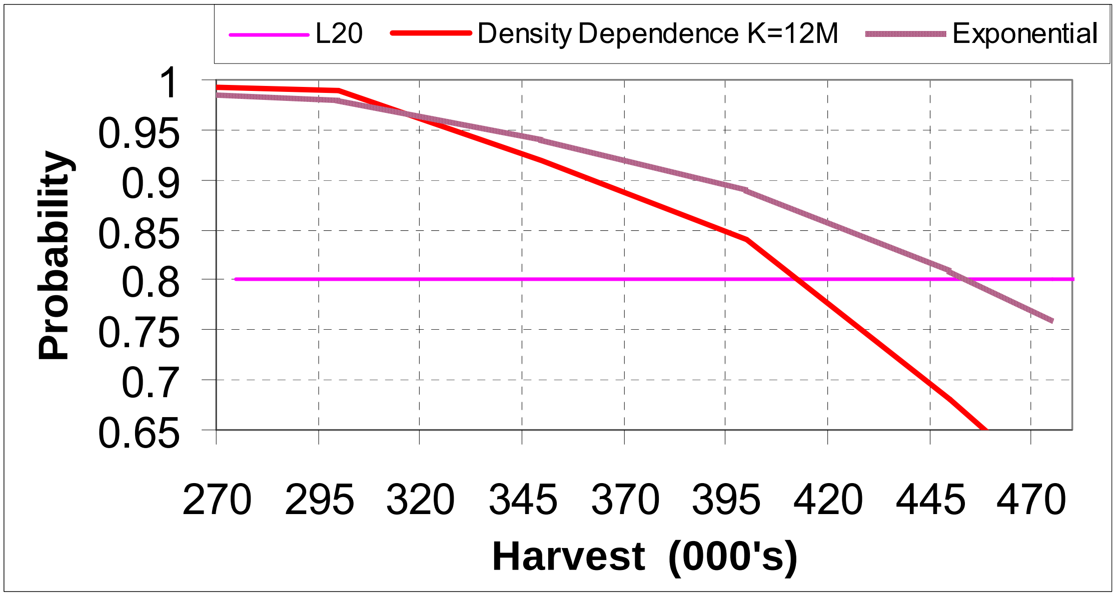


Figure 10. Probability of the population remaining above N_{70} (straight line), under different harvest levels in 2012, 2013 and 2014, if ice conditions in 2011 result in pup mortality of 50% prior to the hunt starting and 100,000 animals are taken in 2011. Model runs assumed exponential population growth and smoothed reproductive rates or assumed density-dependent population growth with K=12 million.