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Assessing Harp Seals and Providing Advice in a Multiyear Framework

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The commercial harvest of harp seals in Atlantic Canada is managed under the Atlantic Seal Management Strategy (ASMS) using renewable 5 year management plans. The ASMS identifies two approaches to providing advice depending upon our understanding of the population dynamics of the population. Harp seals are classified as being 'Data Rich' and advice can be provided through an appropriate population model. Therefore, scientific advice on catch levels that will meet the management objectives are provided using a population model that incorporates data on annual reproductive rates, age specific removals (reported catches in Canada and Greenland, bycatch and estimates of the numbers of seals killed but not landed or reported), ice associated mortality of young and periodic estimates of pup production. Reproductive rates are obtained every year but major assessments are only carried out every 4-5 years when new pup production estimates are available. Under the ASMS, if the most recent estimates of pup production or reproductive rates are more than 5 years old, the population would be considered 'Data Poor' and a more conservative approach adopted for providing catch advice.

Because the assessments are carried at 4-5 year intervals, it is important that the uncertainty associated with multi-year assessments is incorporated in the provision of advice. The vast majority of seal are killed as young while the main indicator of population trends is pup production. Since seals are not sexually mature until, on average, 6 years of age, any proposed harvest must continue to respect the precautionary reference level over a period of at least 15 years. The projection period is extend to allow the impact of taking primarily (>95%) young of the year to be propagated through the population structure. Also, the precautionary reference level (N70) must be set to ensure that probability that the population will remain above the limit reference level remains high (~95%). To account for an increase in uncertainty in our population projections as the time since the last survey increases, proposed harvest levels are required to maintain an 80% probability that the population would remain above precautionary reference level, rather than the mean or medium of the runs. A multiyear Total Allowable Catch (TAC) was successfully used for harp seal in the past. Simulation studies show that up to 20% of the average quota can be transferred to other years as long as the total removals over the time of the management plan remain the same.

Évaluation du phoque du Groenland et présentation d'avis dans un cadre pluriannuel

RÉSUMÉ

La récolte commerciale des phoques du Groenland au Canada atlantique est gérée conformément à la Stratégie de gestion du phoque de l'Atlantique (SGPA) à l'aide de plans de gestion de 5 ans renouvelables. La SGPA identifie deux approches pour fournir des avis en fonction de notre compréhension de la dynamique des populations de la population. Les phoques du Groenland sont classés comme étant « riches en données » et les avis peuvent être fournis par un modèle de population approprié. Par conséquent, un avis scientifique sur les niveaux de capture qui vont répondre aux objectifs de gestion sont fournies à l'aide d'un modèle de population qui intègre des données sur les taux de reproduction annuelle, les prélèvements à l'âge spécifique (captures déclarées au Canada et au Groenland, les prises accessoires et les estimations du nombre de phoques tués, mais non débarqués ou déclarés), la mortalité des jeunes associée à la glace et une estimation périodique de la production de petits. Les taux de reproduction sont obtenus à chaque année, mais les grandes évaluations ne sont effectuées qu'à tous les 4 à 5 ans, lorsque de nouvelles estimations de la production de petits sont disponibles. Selon la SGPA, si les estimations les plus récentes de la production de petits ou les taux de reproduction sont plus vieilles que 5 ans, la population devrait être considérée comme « pauvre en données » et une approche plus conservatrice devrait être adoptée pour donner des avis sur les prélèvements.

Parce que les évaluations sont réalisées à des intervalles de 4 à 5 ans, il est important que l'incertitude associée aux évaluations pluriannuelles soit incorporée dans la prestation de l'avis. La grande majorité des phoques sont tués lorsqu'ils sont jeunes alors que le principal indicateur de l'évolution de la population est la production de petits. Comme les phoques ne sont pas sexuellement matures, en moyenne, avant l'âge de 6 ans, tous les prélèvements proposés doivent continuer de respecter le niveau de référence de l'approche de précaution pour une période d'au moins 15 ans. La période de projection est étendue afin de permettre à l'impact de la récolte de jeunes de l'année principalement (> 95 %) de se propager à travers la structure de la population. En outre, le niveau de référence de précaution (N_{70}) doit être réglé afin d'assurer que la probabilité que la population restera au-dessus du niveau de référence limite reste élevé (~ 95 %). Pour tenir compte de l'augmentation de l'incertitude dans nos projections de la population alors que le temps écoulé depuis le dernier relevé augmente, les niveaux de récolte proposés doivent maintenir une probabilité de 80 % que la population resterait au-dessus du niveau de référence de précaution, plutôt que la moyenne ou la médiane des itérations. Un total autorisé des captures (TAC) pluriannuel a été utilisée avec succès pour le phoque du Groenland dans le passé. Des études de simulation montrent que jusqu'à 20 % du quota moyen peut être transféré à d'autres années, tant que les prélèvements totaux sur la durée du plan de gestion demeurent les mêmes.

INTRODUCTION

Harp seals (*Pagophilus groenlandicus*) are an abundant, migratory pinniped that are hunted throughout their range. Although they are taken by unregulated, subsistence hunters in the Canadian Arctic and Greenland, harp seals are also the focus of the annual commercial seal hunt that takes place in Atlantic Canada. This hunt is managed under the Atlantic Seal Management Strategy which uses an annual TAC that is divided among sealers in the Gulf of St. Lawrence (Maritimes, Magdalen Islands, Quebec north shore, west coast of Newfoundland) and at the Front (northeast Newfoundland and southern Labrador). Scientific advice is provided based upon an assessment of population obtained from an age-structured population model that incorporates information on annual age-specific reproductive rates, removals, environmentally induced mortality and periodic estimates of pup production. Although annual estimates of sustainable TACs have been provided based upon updated reproductive data and catches, full assessments of the status of harp seals are only carried out when new pup production estimates are available. As a result, the management approach has developed to incorporate multi-year assessments and to provide multi-year advice.

POPULATION ASSESSMENT

Harp seal abundance and population trajectories are estimated by fitting a population model to independent estimates of pup production obtained from periodic aerial surveys and mark-recapture studies by adjusting the initial population size and adult mortality rates (e.g. Hammill and Stenson 2003, 2011; Hammill et al. 2011). The basic model was first developed in the early 1980's (Roff and Bowen 1983), but has since undergone a series of improvements (e.g. Shelton et al. 1992, Sjare and Stenson 2002) (Table 1). One of the first was to identify additional sources of removals including the proportion of seals killed but not recovered or reported (i.e. struck and loss) and bycatch in commercial fishing gear. Because the model estimates mortality, the addition of specified removals does not change the population estimates significantly but does result in a change in the estimate of the remaining mortality (Stenson et al. 1999). The incorporation of unusual mortality of young seals associated with poor ice conditions was also an important change that acknowledged the impact of climate change on this ice breeding seal (Hammill and Stenson 2003). More recently, 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 reproductive rates and young of the year mortality. Also, improvements were made in the way in which the reproductive rate data were smoothed to interpolate data for years when samples were not available. Finally, the model was modified so that it fit to both the reproductive rates and the pup production data, by estimating environmental carry capacity (K), as well as the mortality rate of animals aged 1+ years (M) and initial population (α) (Hammill et al. 2012). 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.

PUP PRODUCTION ESTIMATES

Major assessments of the harp seal population occur when new pup production estimates are available. Prior to 1990 pup production estimates were only available sporadically; incomplete aerial surveys were attempted in 1950 and 1960 while mark-recapture experiments provided estimates in 1978, 1979, 1980 and 1983 (Fig 1). Since 1990, visual and photographic aerial surveys have been carried out every 4 – 5 years to estimate pup production off Newfoundland and in the Gulf of St. Lawrence (e.g. Stenson et al. 1993, 2002, 2003, 2010, 2014a). These surveys are time consuming, logistically complex and expensive and could not be carried out

annually or biennially. The most recent survey (2012) resulted in over 20,000 photographs that had to be examined, taking over 1 year to analyze (Stenson et al 2014a).

Although surveys have been carried out regularly since 1990 and the management plan assumes a maximum interval of 5 years, the actual timing of surveys is not confirmed. The Department of Fisheries and Oceans, through its virtual Centre of Excellence for Marine Mammalogy has developed a rotational schedule for marine mammal surveys that identifies the need to carry out harp seal surveys every 4 years. Although this schedule has been approved in principle, funding has not been obtained. Under the Atlantic Seal Management Strategy survey intervals greater than 5 years would result in a population being classified as Data Poor and more conservative catches identified (see below). Therefore, it is unlikely that the current survey interval will change in the near future.

REPRODUCTIVE RATES

The population model incorporates annual estimates of age specific late term pregnancy rates obtained from annual sampling programs maintained by the Department of Fisheries and Oceans since 1954 (Sjare and Stenson 2010, Stenson and Wells 2010; Stenson et al 2014b). However, there are gaps in the time series of the data, and in some years sample sizes are small. For this reason, various methods have been used to smooth the data to provide estimates for all years and age classes (Fig. 2). In the most recent assessment, the data were smoothed by applying a local logistic regression (Loader 1999; Tibshirani and Hastie 1987) to the binary data (pregnant or non-pregnant) (Appendix 1).

The reproductive data have high inter-annual variability. This variability was assumed to be primarily due to sampling error and therefore the smoothed values were used in the population model (e.g. Hammill and Stenson 2003, Stenson et al. 2009). Annual reproductive samples were not considered necessary as the smoothed values could be used. However, 2008 the aerial survey resulted in very high estimates of pup production, which the model was unable to fit to using smoothed reproductive data. This led to the realization that the variation in observed reproductive rates reflected actual changes and the population model was modified to incorporate the observed rates whenever possible (Hammill and Stenson 2011, Fig. 3). Therefore it is important that annual data on reproductive rates be obtained in order to track changes in fecundity in this population.

REMOVALS

Annual catch data are available since 1952 (Stenson 2009, 2014). There are a number of sources of data: 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, and the Greenland subsistence hunt (Fig. 4). Reported catch levels from the Canadian and Greenland hunts are divided into numbers of animals aged 0 and numbers of animals aged 1+ years. All harvests are corrected for seals killed, but not landed or reported (i.e. struck and lost). 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 are assumed to have been lost.

Although annual removals are used in the assessment, only the Canadian commercial catches are available each year. The total number of seals reported killed in Greenland are available with a 2 year lag. Therefore, the average catch taken over the past decade is assumed and a range of catches used in the forward projections. This increases the uncertainty associated with the estimates and projections that must be accounted for in the management approach.

ICE-RELATED MORTALITY OF YOY

Poor ice conditions result in increased mortality (M_{ice}) that affects the number of animals surviving from birth to the start of the hunt (Stenson and Hammill 2011). This is incorporated into the model as a survival term that varies annually and is based upon the ice cover as determined by Canadian Ice Service. (Hammill and Stenson 2014).

MANAGEMENT FRAMEWORK

McLaren et al. (2001) identified a need to manage seals under a framework that incorporated benchmarks and harvest control rules. In 2003, the Department implemented a management approach, referred to as the Atlantic Seal Management Strategy (ASMS), which incorporated the precautionary approach into the management of Atlantic seals. ASMS provides a framework that stipulates objectives for the management of Atlantic seal populations, and identifies precautionary and critical reference points, along with management actions that are triggered when thresholds are exceeded to reduce potential damage to the resource (Hammill and Stenson 2007, 2009)

The amount of information available for resource management varies among populations. Therefore, the ASMS distinguishes between two categories; “data rich” and “data poor” (Fig 5). Data-rich populations are those for which we think we have a reasonable understanding of their recent abundance and population dynamics. Currently, data-rich species are defined as having three or more abundance estimates over a 15-year period, with the last estimate obtained within the last five years, and current information (within the last five years) on fecundity and/or mortality to determine sustainable levels of exploitation. If these data are not available, the species would be considered as data-poor.

For species not satisfying the data-rich criteria, the uncertainty associated with resource status and with the effects of particular management actions increases. Therefore, a risk-adverse approach is needed. A highly conservative approach, referred to as Potential Biological Removals (PBR), has been developed in response to the United States Marine Mammal Protection Act (Wade 1998). The management objective is to prevent populations from becoming depleted, where depletion is considered to have occurred if a population falls below its maximum net productivity level (defined as being between 50% and 85% of carrying capacity)(Taylor and DeMaster 1993). The PBR approach has been subjected to extensive simulation testing to examine how it behaves under different scenarios, with the objective that the population must have a 95% probability that it will not become depleted.

PBR is calculated as:

$$PBR = 0.5 \cdot R_{max} \cdot f \cdot N_{min}, \quad (1)$$

where R_{max} is the maximum rate of population increase, f is a recovery factor (between 0.1 and 1.0) and N_{min} is the estimated population size using the 20-percentile of the log-normal distribution of the most recent population estimate (Wade and Angliss 1997, Wade 1998). Within the ASMS, f is set at 1.0, unless there is an obvious serious conservation concern. In the absence of data, R_{max} is assumed to be 12% for pinnipeds (Wade and Angliss 1997).

Under the criteria for data rich species, reducing the frequency of harp seal surveys to be less often than 5 years would result in the species being classified as data poor and the PBR being used to provide advice for allowable catches. This would result in a significant reduction of the catch levels considered acceptable to the management objectives.

Harp seals are currently classified as being 'Data Rich'. For such species, the framework identifies a precautionary reference level at 70% of the largest population size. A secondary reference level is set at 50% while the critical reference limit has been identified at 30% of the largest estimated population (Hammill and Stenson 2007). These thresholds were used to identify when certain management actions are to occur. The primary goal of these management actions is to ensure that the population remains, or returns, to a 'healthy' level which is defined as being above the precautionary reference level. If the population falls below N_{70} , then the TAC was to be reduced to ensure an 80% likelihood that the population would recover above N_{70} within 10 years. If the population was estimated to be below N_{30} , then commercial harvesting was to end until recovery of the population was observed (Hammill and Stenson 2007).

Because the assessments are carried at 4-5 year intervals, it is important that the uncertainty associated with multi-year assessments is incorporated. One component is the setting of the precautionary reference level (N_{70}). The second component of the uncertainty is to require that harvest levels maintain an 80% probability that the population would remain above N_{70} . By using the lower 20th percentile of the abundance estimates, the management advice acknowledges there is an increase in uncertainty as the time since the last survey increases. Taken together, these two factors contribute to ensuring that the probability that the population will remain above the limit reference level remains high (~95%) given nature of a hunt that focus on young of the year seals, the use of pup production surveys to monitor the population and the frequency of the assessments (Hammill and Stenson 2009).

The third very important aspect of the ASMS, which contributes to ensuring that the probability of staying above the critical reference level remains high (~95%) is that the Harvest Control Rule requires that proposed harvest must continue to respect the precautionary reference level over a period of at least 15 years. In the past decade, over 95% of the seals caught in the Canadian commercial harvest have been between 1 and 3 months old. Therefore, the impact of a given harvest is not discernible in the pup production surveys for at least 5 years and more likely 10-20 years. Therefore the projection period must be extended to allow the impact of taking primarily (>95) young of the year to be propagated through the population structure.

PROVISION OF ADVICE

The first component of the modelling procedure is to estimate the current abundance of harp seals. The 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 on the same equations as the fitting model, but uses the parameter values estimated for M and K in the projections. The advice provided is the probability of the population remaining above the reference level for a period of 15 years (Fig 6). Details on model structure are included in Appendix 1.

A major difficulty in determining the impact of future catches is to predict how reproductive rates may change in the future, as well as how the unregulated Greenland subsistence harvest may change. Future reproductive rates are assumed to follow pattern seen in the recent past. The model selects from a sample of reproductive rates observed during the last 5 or 10 years. As for Greenland catches, future harvests were assumed to followed a uniform distribution with a minimum of 70,000 and a maximum of 100,000 animals (average=85,000). Uncertainty in these assumptions is incorporated into the population projections and as a result, influence the confidence intervals used as the metric to determine the impact of harvests.

Based upon a pup production survey carried out in 2012 (Stenson et al. 2014a), the most recent assessment estimates that $M=0.025$ (SE=0.007), $K=10.8$ million (SE=564,000), a 2012 estimated pup production of 929,000 (SE=148,000), and a total population of 7,400,000 (SE=698,000) (Fig. 7). N_{\max} was estimated to be 7.8 million (SE=850,000) and was observed in 2008 (Hammill et al. 2014).

Using these estimates, we ran a simulation to illustrate the importance of the harvest control rule that takes account of the nature of the exploitation, biology of the species and assessment metric. In the first runs we assume that the harvest respects the management objectives for the length of the 5 year management plan only. If our management objective is to maintain an 80% probability that the herd will remain above the Precautionary Reference Limit (PRL) ($N_{70} = 5.4$ million) and if future reproductive rates are similar to what has been observed over the last decade (mean reproductive rate of 0.5 for mature animals), then an annual harvest of 1.1 million animals (95% Young of the Year) would maintain the population above the PRL for the next 5 years (i.e the life of the management plan). During that period (2014 to 2018), the population would drop from 7.4 to 6.2 million, but this decline would not be reflected in the surveys of pup production. In fact, the next survey (5 years later) would indicate that pup production had actually increased slightly from 900,000 to 1.2 million animals (Fig. 8). Because it takes, on average 5-8 years before seals are recruited to the breeding population, the decline in the population would not be detected by the pup production surveys until 2024. By then, catches would have to decline to 130,000 animals to respect the management framework over the next 5 year (2019-2023) management period. The significant reduction in the new TAC, reflects the effects of the harvest as the harvested cohorts are recruited to the breeding population. If the actual reproductive rates were much lower than we predicted, (e.g. resembled rates observed over the last 5 years, with mean productivity of 0.3), then we would not see much change in pup production at the time of the next survey, even though the population would be declining and approaching the Critical Reference Limit (CRL) (Fig. 8).

Projecting the impact of a harvest over a longer time period results in a lower TAC but it contributes to maintaining an adequate buffer between the PRL and CRL to help deal with uncertain negative events. It has other benefits as well. Assuming that future productivity resembles conditions that have been observed over the last 10 years, then a TAC of 300,000 animals per year would respect the management objective over the next 20 years also results in a more stable catch, and the total harvest over the 20 year period would be greater (Fig. 9).

MULTI- YEAR ADVICE

Because of the way in which the forward projections are made, the advice is, by definition, multi-year. Currently, catches are modelled as being constant over the time period but some flexibility is possible. A multi-year TACs for harp seals was implemented in 2003. At that time, the annual harvest that would respect the management objectives was estimated to be 325,000 seals (Hammill and Stenson 2003). Simulation studies indicated that up to 20% of the average annual quota could be transferred among years as long as the total harvest over the life of the management plan remained the same (Hammill and Stenson 2003, 2009, Fig. 10). Based upon these studies, a three year quota of 975,000 was set for the period 2003 -2005. A maximum of 350,000 could be taken in any one year as long as the total did not exceed 975,000. The approach was quite successful with annual catches of 289,512, 365,971 and 329,829 for a total of 985,312. However, the industry did not support continuation of the multi-year TAC because of the public perception that the quota was very high (~1 million) when the allowable catch over the entire management plan was announced.

TRIGGERS POINTS FOR RE-EVALUATION

Several factors should be monitored to determine if a multiyear TAC should be re-evaluated. In general, significant changes in any of the major assumptions used in the projections would trigger a new analysis. The most important of these assumptions is associated with annual monitoring of reproductive rates; changes in reproductive rates either leading to an increase in productivity, or to a decrease, will have an important impact on the trajectory of the population. In addition to changes in abundance, reproductive rates are affected by environmental conditions (e.g. ice) and food availability which can change rapidly. A significant decline in average reproductive rates, or multiple years with rates below the average rates used in the projections should trigger a re-assessment to ensure that the TACs will not adversely harm the population.

Catches of harp seals in Greenland appear to be relatively stable, but this harvest is not regulated. Significant changes in the level of Greenland harvest or a major unusual mortality event would also result in a need to re-evaluate the TAC. Given the importance of ice conditions for pup survival, a series of years (e.g. three consecutive winters) with significantly below average ice conditions, particularly at the Front where approximately 70% of pup production occurs, could indicate a need to reassess the population and re-evaluate a multiyear TAC.

Finally, changes in age composition of the harvest will have a major impact on the population and should trigger a re-examination of TAC levels. Harvests with higher proportions of adults will have a more rapid and serious impact on the population than harvests dominated by YOY (Fig. 6).

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FIGURES

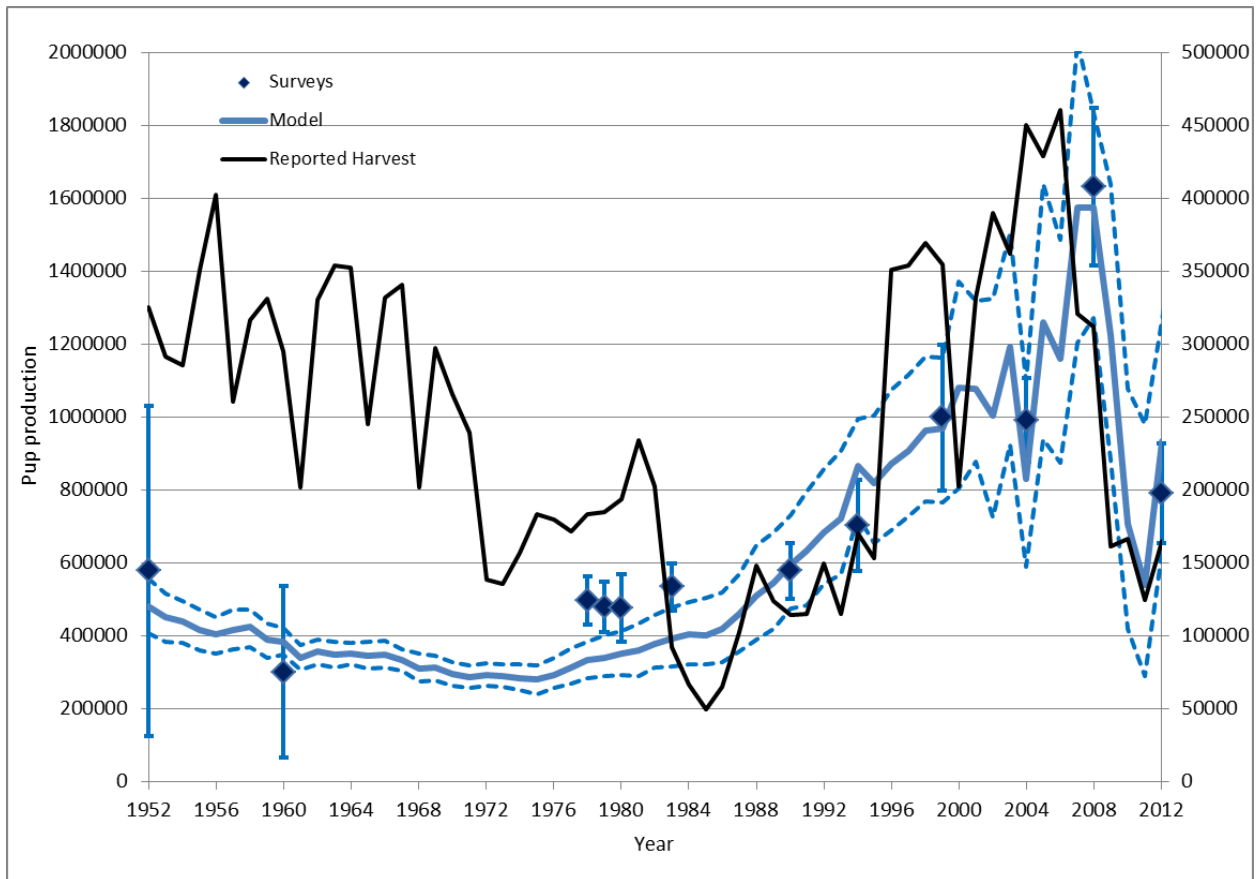


Figure 1. Estimated pup production from the model fitted to pup survey estimates (mean \pm 95%CI) and reported catches from 1952 to 2012, when the last pup survey was completed.

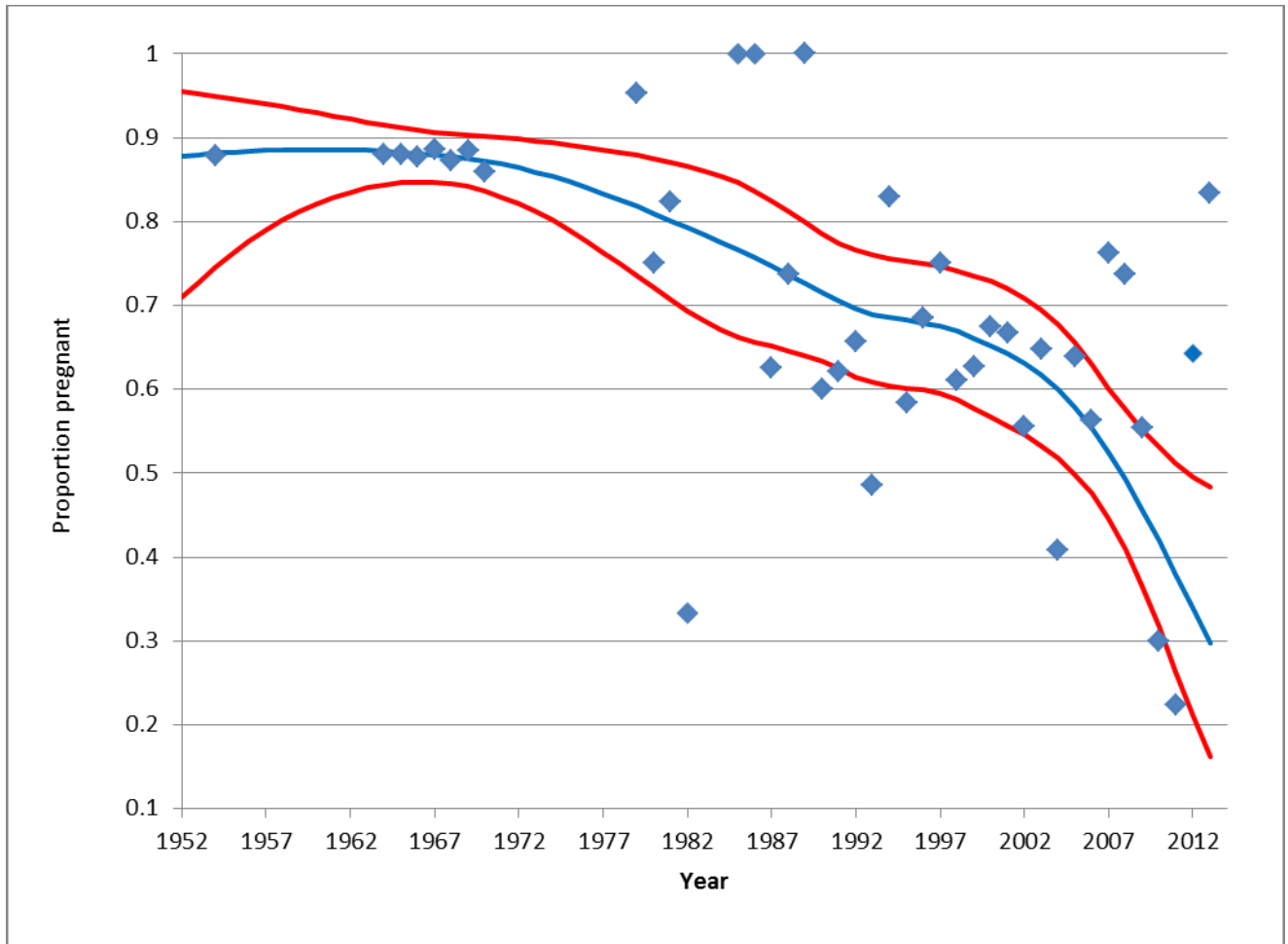


Figure 2. Reproductive rates, and smoothed rates ($\pm 95\%$ CI) of female harp seals age 8 years and older from 1952 to 2013. This component of the population accounts for at least 60% of the annual pup production.

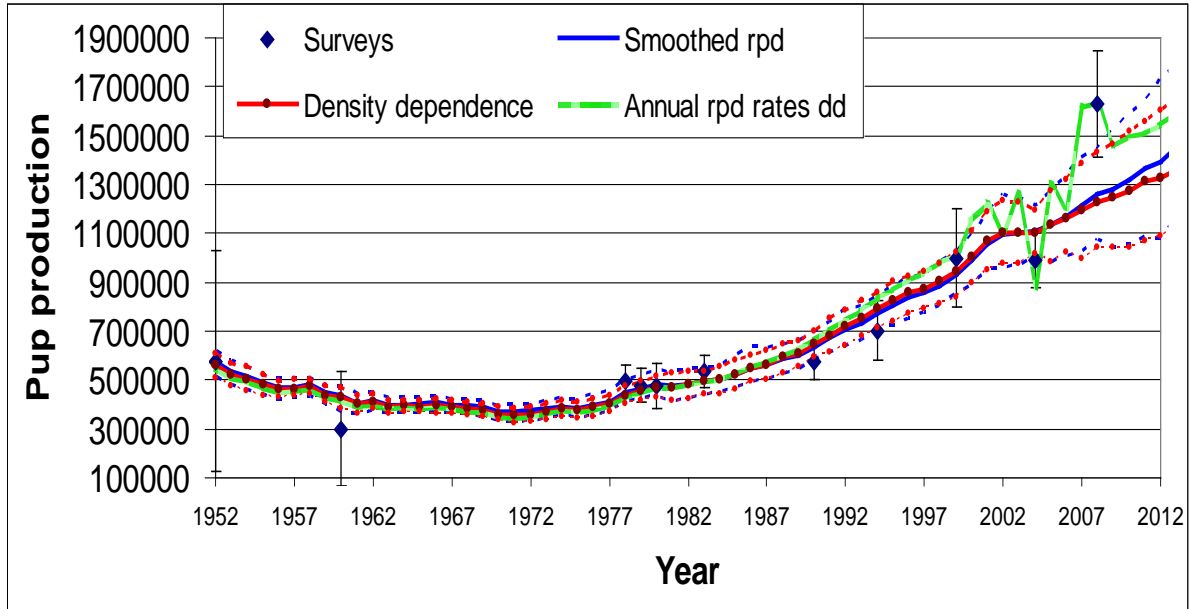


Figure 3. Comparison of estimated pup production when using only smoothed annual reproductive rates or using observed estimates of reproductive rates (data from Hammill and Stenson 2011). Note the poor fit to the 2004 and 2008 pup production estimates using the smoothed data.

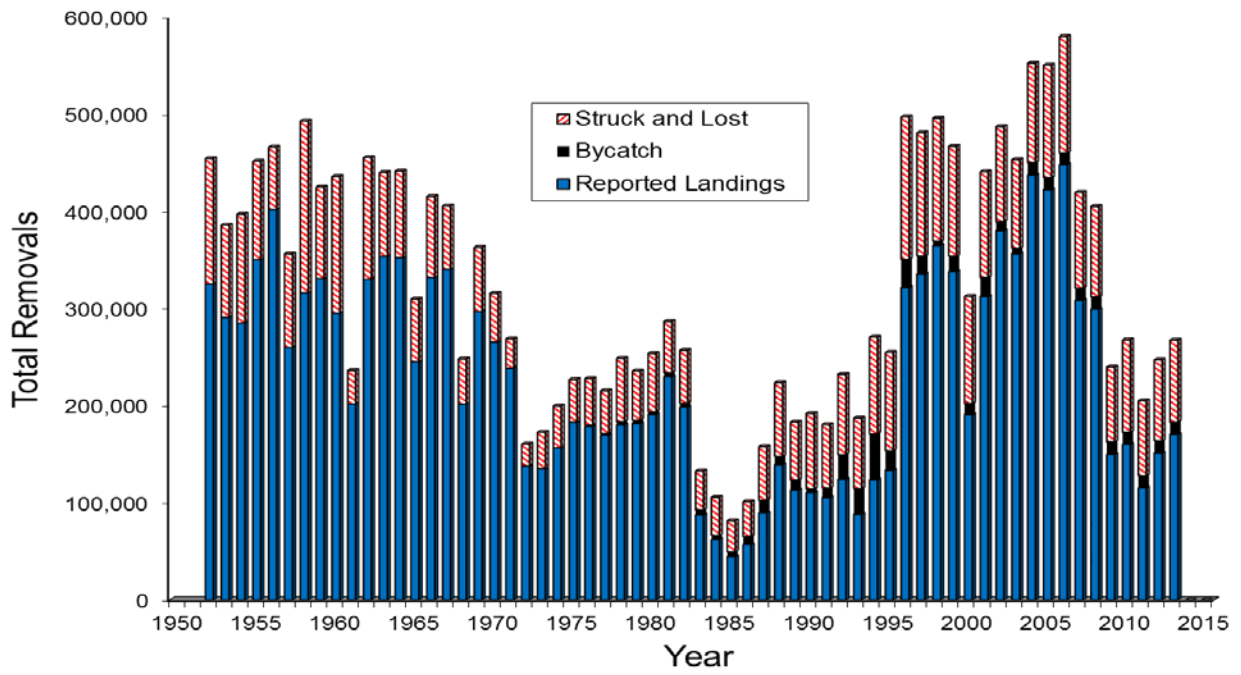


Figure 4. Total removals of Northwest Atlantic harp seals, 1952-2013 (from Stenson 2014).

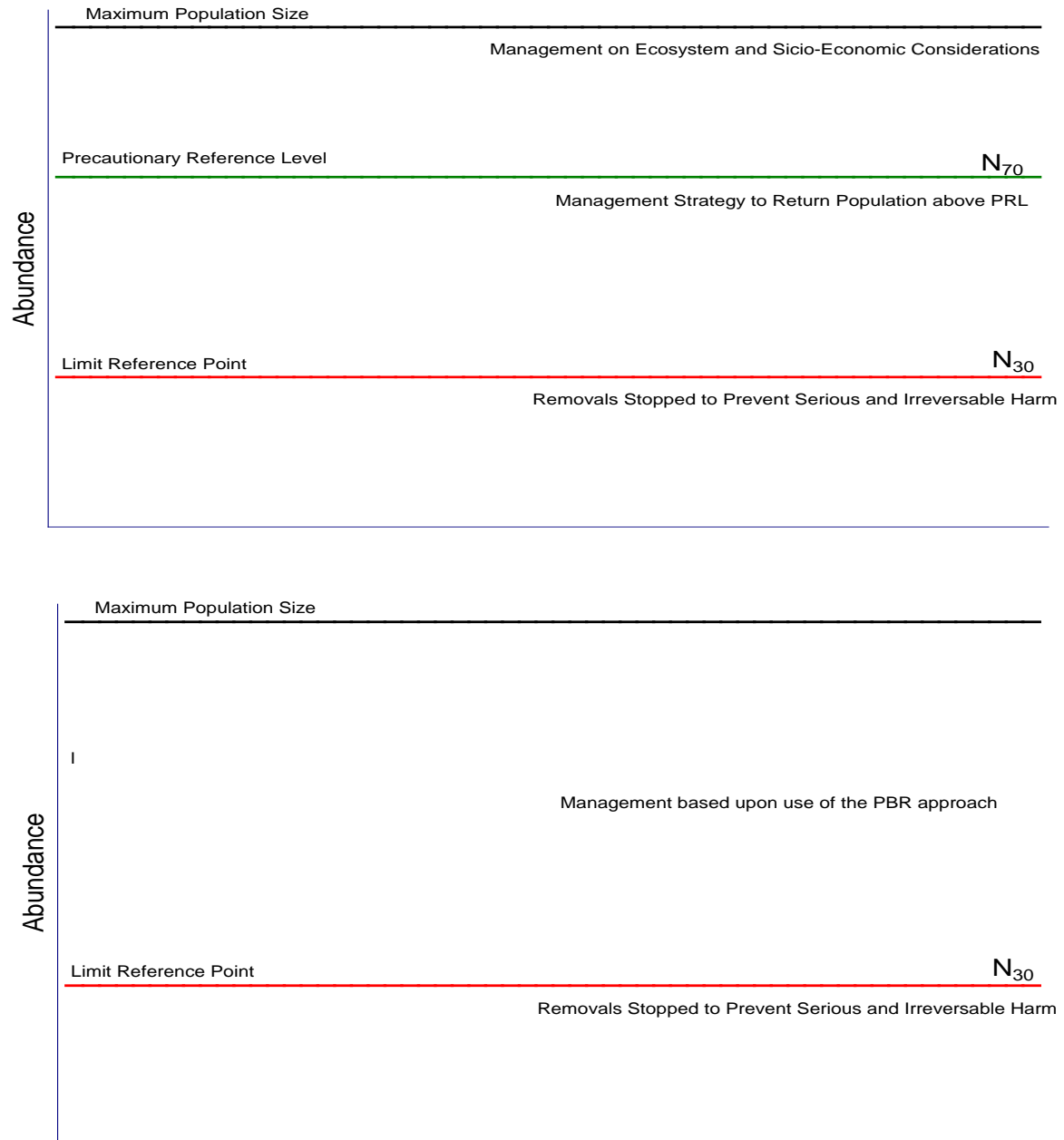


Figure 5. Atlantic Seal Management Strategy framework outlining precautionary (N_{70}) and limit (N_{30}) reference levels developed to manage data rich (top) and data poor (bottom) seals Atlantic Canada. A secondary precautionary level at 50% of maximum indicates a change in the harvest control rule. Both frameworks are self adjusting in response to changes in understanding of maximum population size observed or environmental carrying capacity and maximum sustainable yield.

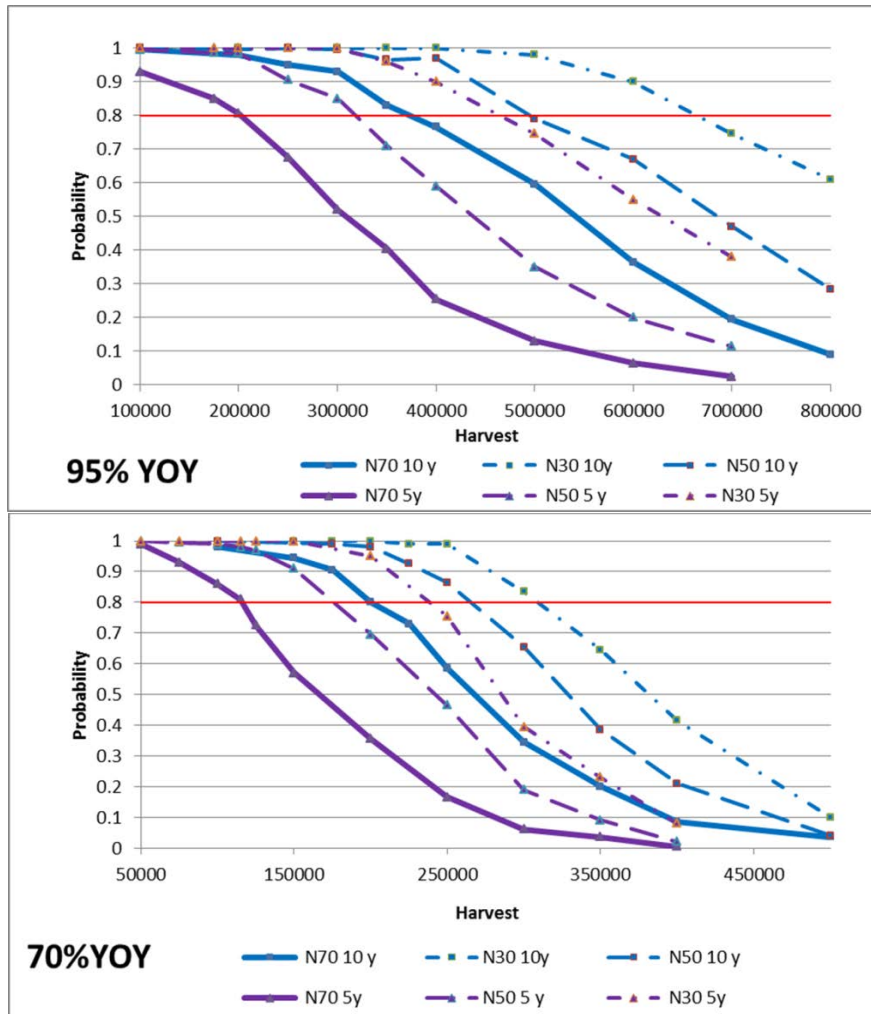


Figure 6. Changes in harvest rates resulting from changes in herd productivity and age composition of the harvest. The 10 year scenario represents a period of higher herd productivity than does the 5 year scenario.

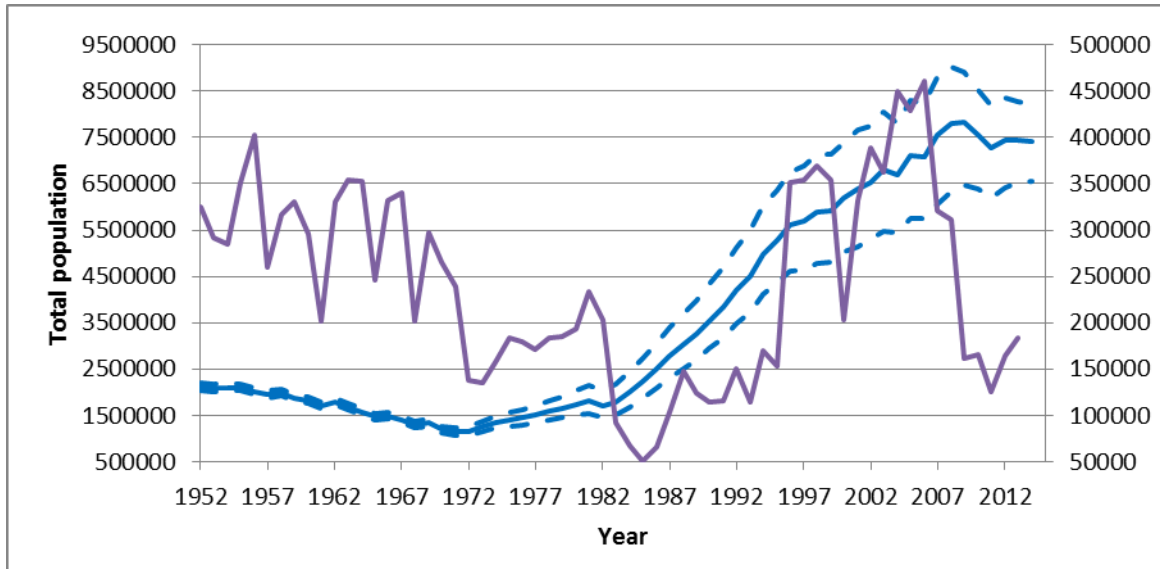


Figure 7. Estimated population trajectory for model fitted to pup survey estimates (mean \pm 95%CI) (including the 2012 estimate) and reproductive data up to and including 2013 (left Y-axis). Annual reported catches are also included (right Y-axis) (Hammill et al. 2014).

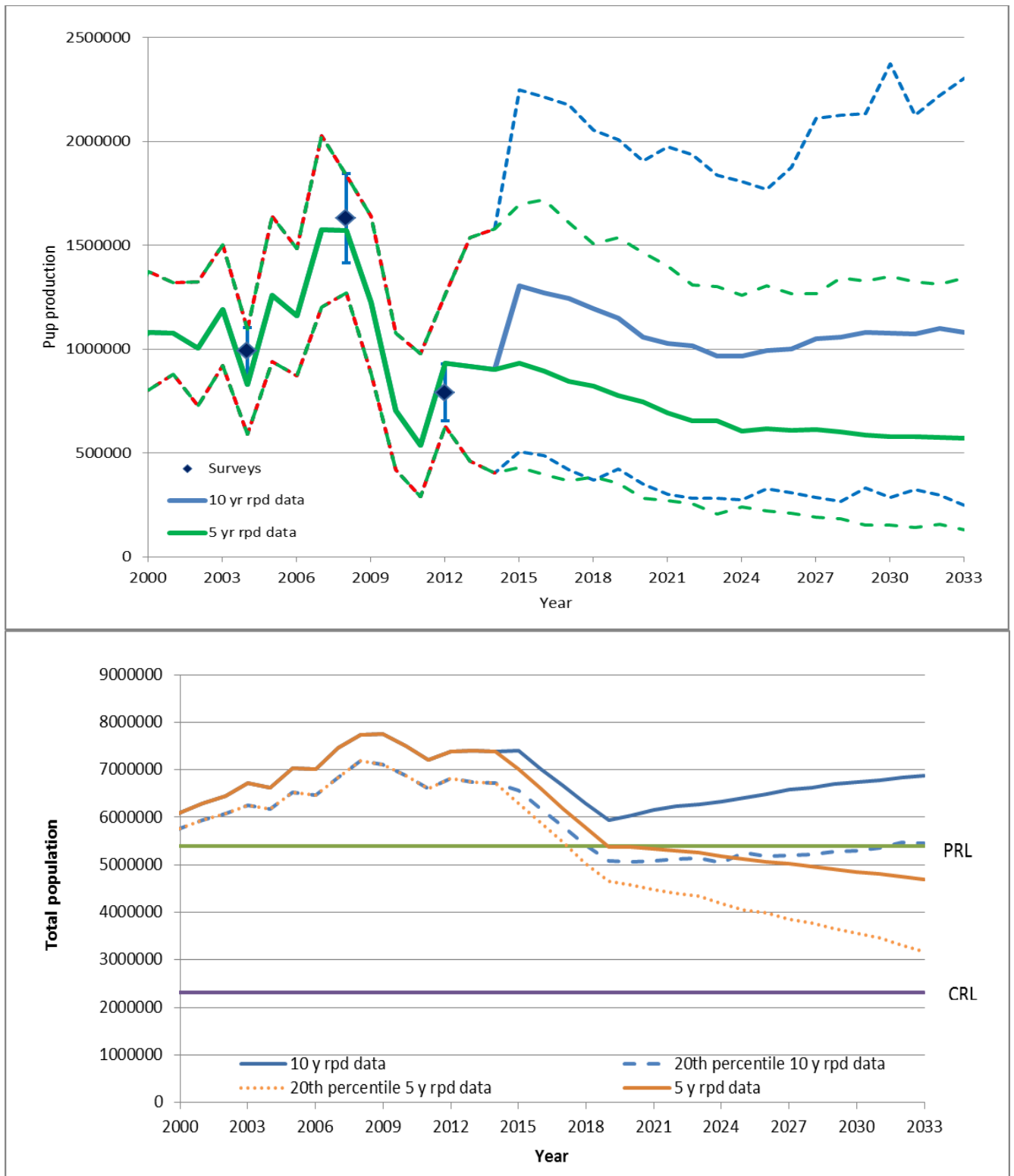


Figure 8. Impacts of one harvest scenario (5 years with a harvest of 1.1 million seals, followed by 15 years with harvests of 130,000 animals) on pup production and population trends under two herd productivity regimes. The CRL is the Critical Reference Limit and the PRL is the Precautionary Reference Limit.

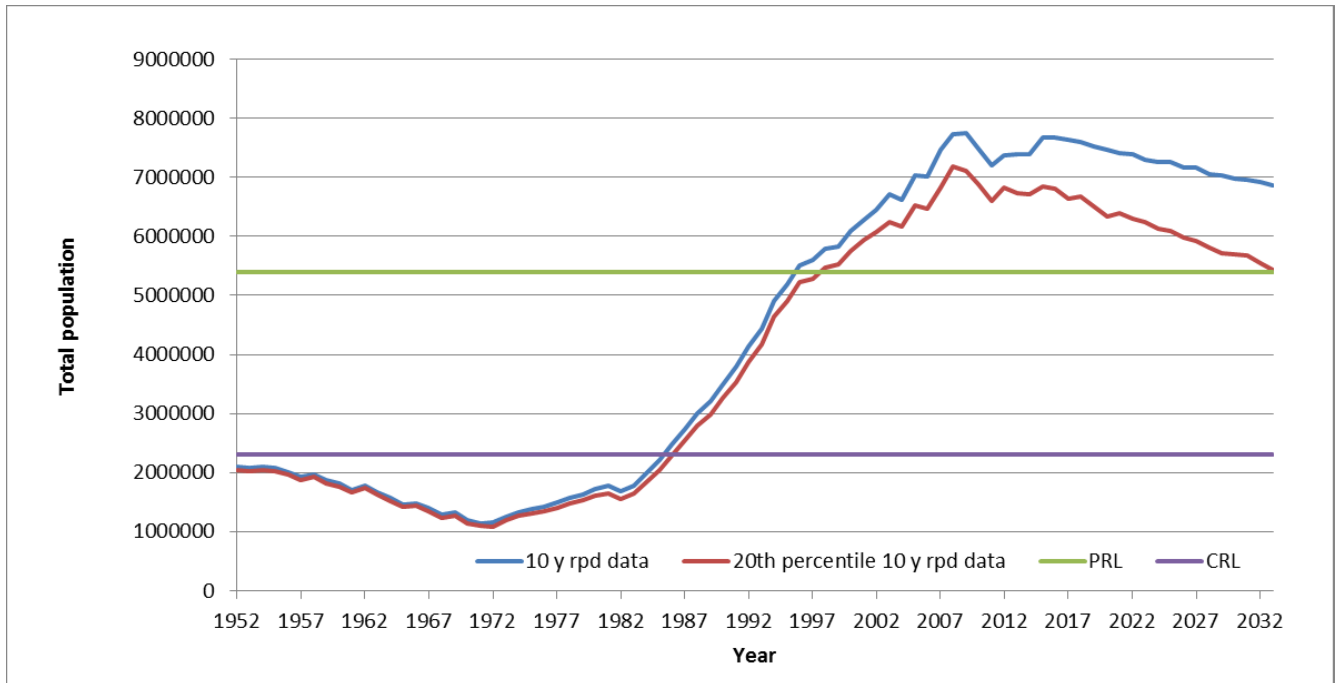


Figure 9. Impacts of one harvest scenario (20 years with a harvest of 300,000 seals) on population trends assuming that future reproductive rates resemble rates encountered over the last decade. The CRL is the Critical Reference Limit and the PRL is the Precautionary Reference Limit.

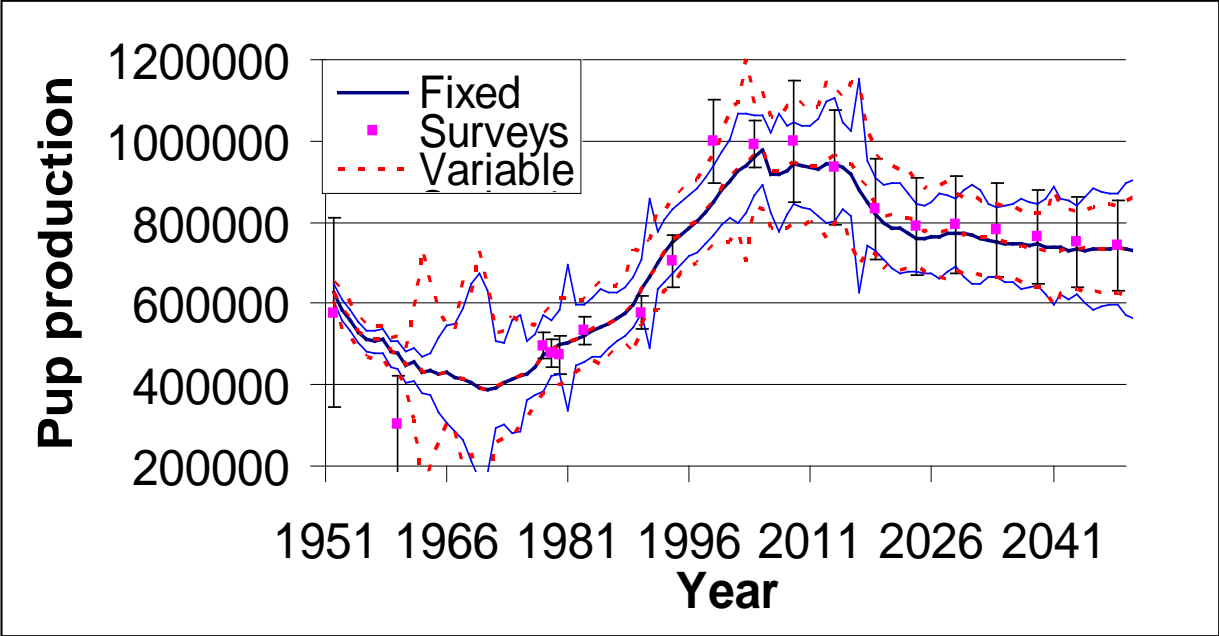


Figure 10. Comparison of pup production and total population subjected to a constant harvest and a variable harvest. From Hammill and Stenson (2009)

APPENDIX 1

Age structured model used to describe the dynamics of the Northwest Atlantic harp seal population and to evaluate the impacts of different harvest scenarios on the population. Essentially the same model is also used to describe the dynamics of grey seals and hooded seals as well.

MODEL STRUCTURE

Initial population

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

Survival

For age 1:

$$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1}) \times e^{-M_0} \times (1 - (N_t / K)^\theta) \quad (2)$$

with $M_0 = \gamma \times M$

For age a, with $1 < a < A$:

$$n_{a,t} = (n_{a-1,t-1} \times e^{-M/2} - c_{a-1,t-1}) \times e^{-M/2} \quad (3)$$

For age A

$$n_{A,t} = [(n_{A-1,t-1} + n_{A,t-1}) \times e^{-M/2} - (c_{A-1,t-1} + c_{A,t-1})] \times e^{-M/2} \quad (4)$$

Reproduction

$$n_{0,t} = \sum_{a=1}^A n_{a,t} \times P_{a,t} \quad (5)$$

For age a, with $1 < a < 8$

$$P_{a,t} \sim \text{CorBin}(n_{a.reprod,t}, P_{a.preg,t}) \quad (6)$$

For age a, with $a \geq 8$ (i.e. 8+)

$$P_{a,t} = P_{8,t} \sim \text{CorBin}(n_{8+.reprod,t}, P_{8+.preg,t}) \quad (7)$$

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

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,
<i>CorBin</i>	= 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 of animals aged 1+ years,
M_0	= the instantaneous rate of natural mortality of animals in their first year,
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 (Trczynski 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 ($P_{\text{sim}8+,t}$) 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.

Reproductive rates

There are gaps in the time series of the data, and in some years sample sizes are very small, especially for the year classes of animals aged 4 to 7 years (Table 3). The data are smoothed by applying a 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 is performed using the R package LocFit (Loader 2010). Since we expected substantial curvature in the trajectory of pregnancy rates, we used a 2nd degree polynomial to further reduce bias (Sun and Loader 1994). The degree of smoothing is controlled with an adaptive bandwidth: for each fitting point, the bandwidth is chosen so that the local neighbourhood always contains a specified proportion (β) of the dataset. We determine β for each age class by testing a range of values and selecting the β that yields the best fit (lowest AIC, Loader 1999). To compute confidence intervals, variance in the smoothed data is estimated using log-likelihood in the framework of normal approximations (Loader 1999). Using the binomial family keeps pregnancy rates in the $[0, 1]$ interval and results in non-symmetric errors around the mean.

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 it was assumed that the levels, and age structure, and proportion of struck and lost and bycatch were the same as used in the fitting model. We also assume that the Greenland catch can be described by a uniform distribution with a minimum catch of 66,000 (from 2003) and a maximum catch of 92,000 (from 2006), which results in an average of 79,000 animals.

Ice-related mortality (actually, expressed as survival in model), is assumed to vary with values of 0.94, 0.59, 0.21, ,0.9, or 1 based on estimate mortality over the last 4 years, with one year where there was no ice related mortality (average=0.73, SE=.16). Each value has an equal opportunity of being randomly selected.

Reproductive rates vary considerably over time and between years. In the projections reproductive rates animals are assumed to be fixed in the projection model to the values of the last 5 years, or an alternative scenario is provided, with the model drawing from a sample of reproductive rates observed over the last 10 years, with each year having an equal probability of being selected.

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.