

# IMPLICATIONS OF UNCERTAINTY FOR CANADA'S COMMERCIAL HUNT OF HARP SEALS (*PAGOPHILUS GROENLANDICUS*)

Russell Leaper<sup>1,2\*</sup> and Justin Matthews<sup>2</sup>

\* Author for correspondence

<sup>1</sup>School of Biological Sciences, Tillydrone Avenue, University of Aberdeen, AB24 2TZ, UK  
Email r.c.leaper@abdn.ac.uk

<sup>2</sup>International Fund for Animal Welfare, 87-90 Albert Embankment, London, SE1 7UD, UK.

## Abstract

The Canadian government's current management procedure for harp seals is described by Fisheries and Oceans Canada as using the Precautionary Approach. Employing a similar underlying population model, we simulated the effects of uncertainty involving bias in estimates of human induced mortality, natural mortality, and pup production estimates as a set of robustness trials. Our results indicated that for the range of annual total allowable catches (TAC) considered and set for Canada's commercial harp seal hunt (250,000 – 350,000), there were plausible circumstances under which the government's management procedures failed to meet their own conservation objectives. By contrast, a precautionary management regime should be robust to such levels of uncertainty. For some scenarios the current management strategy, although not fully specified, is likely to maintain a high TAC despite a declining population. In particular, once a high TAC has been set, the assessments are unlikely to provide the necessary evidence that the TAC should be reduced until the population is at a low level. Hence there is a substantial risk that the population may be depleted below the 'minimum' ( $N_{50}$ ) and 'critical' ( $N_{30}$ ) population reference points. There is a need for a management procedure based on risk analysis to be fully specified and tested. In the interim, reducing TACs to within limits calculated from a well-established precautionary procedure, such as Potential Biological Removal, would be a step towards more precautionary management.

**Key words:** management procedure; population dynamics; precautionary approach

## Introduction

The commercial exploitation of harp seals (*Pagophilus groenlandicus*) by Canada is the largest marine mammal hunt in the world with an average annual reported catch of 324,000 between 2003 and 2005 (Hammill and Stenson, 2007). Although conservation concerns have been expressed regarding this hunt (e.g. Johnston et al., 2000) the total allowable catch (TAC) in recent years has been set well in excess of estimated replacement yield (Hammill and Stenson, 2003).

The aim of this study was to investigate the conservation implications of uncertainty in the input data for the current Canadian management regime for harp seals. Simulations

were conducted using the same population modelling approach underlying the assessments by Department of Fisheries and Oceans (DFO, 2005). These were intended as a set of robustness trials to provide a basis for evaluating whether the TACs set for harp seals by Canada can be considered as following a precautionary approach.

DFO (2005) lists key aspects of the Objective Based Fisheries Management (OBFM) framework adopted in the last Canadian management plan for harp seals. If the population is above 70% of its highest estimated abundance ( $\hat{N}_{70}$ ) then the OBFM attempts to ensure at least an 80% probability that the population will remain above  $\hat{N}_{70}$ . If the population falls below  $\hat{N}_{70}$  then management measures are introduced with the intent of achieving an 80% chance of bringing the population back above that 70% level. More stringent management measures would be implemented in the event that the population falls below 50% of its highest estimated abundance ( $\hat{N}_{50}$ ) including closure of much, if not all, of the commercial seal hunt. If the population drops below the level of 30% of its highest estimated abundance ( $\hat{N}_{30}$ ) then all removals would be stopped.

The OBFM does not specify how catch levels will be set, nor the time periods within which certain objectives should be met. Thus it was not possible to simulate the full management decision process. Instead scenarios of constant TAC were assumed and the simulation results were used to describe the information that would likely be available to managers at the time when decisions would be made. The feedback mechanisms by which catch limits are adjusted on the basis of each assessment of the population are a critical component of management procedures (Butterworth, 2007). A key objective for this study was to compare predictions of the actual status of the population with how it would be assessed using the population model underlying the OBFM when some of the input parameters were subject to bias. These results allow comparison with other procedures and help identify issues that should be considered in any new management plan.

Other procedures for setting limits on takes of marine mammals include the Revised Management Procedure (RMP) of the International Whaling Commission (Cooke 1995; Punt and Donovan, 2007) and the calculation of Potential Biological Removal (PBR) levels (Wade 1998; Johnston et al., 2001). The RMP and PBR are both examples of a management procedure approach including a fully specified catch algorithm. This has allowed extensive simulation testing to demonstrate their robustness to errors in input data, such that management based on these procedures results in a low probability that human induced mortality will cause the stock to decline below a given level. These procedures are widely acknowledged as precautionary. In contrast to the management procedure approach of the RMP and PBR, the OBFM follows what is described by Butterworth (2007) as the “traditional approach” in which a TAC is set on the best assessment at the time taking into account stated reference points, but without any formal basis to make allowance for uncertainties.

Acknowledged areas of uncertainty in modelling harp seal populations include survey estimates of pup production (e.g. Stenson et al., 2003) and estimates of human induced

mortality including reporting errors and struck and lost (e.g. Bowen and Sergeant, 1983, Lavigne, 1999, Stenson, 2005). Estimates of pup production used in the model were generated by mark-recapture methods in 1978, 1979, 1980, 1983 and aerial surveys in 1990, 1994, 1999, 2004 (Hammill and Stenson, 2005). Thus there is potential for a trend in bias due to different methodologies. Finally, ice condition is a major factor known to affect harp seal pup mortality (Hammill and Stenson, 2005). Sudden changes or prolonged trends in mortality in this ice-breeding species are a real possibility (Johnston et al. 2005), but the extent of these changes is unknown. Given these uncertainties, the scenarios selected for the trials in this study included changes in natural mortality, bias in estimates of pup production and bias in human induced mortality.

## Methods

### Population dynamic model

The core population dynamic model was originally introduced by Roff and Bowen (1983) but has been modified and altered since in various ways. Major changes include incorporation of struck-and-lost rates (Stenson et al., 1999), bycatch (Healey and Stenson 2000) and additional mortality due to poor ice conditions (Hammill and Stenson 2003). In recent years the model has been treated explicitly as a two or three parameter model, with further fixed deterministic parameters (e.g. struck-and-lost rates) independently estimated. The variations and developments over time have led to a range of parameter estimates, as shown in Table 1. In particular, the estimate of instantaneous mortality  $m$  has varied, with most estimates in the range 0.05-0.1.

The population model is represented here as a Leslie matrix equation:

$$\underline{n}(t+1) = L_t(\underline{n}(t) - \underline{c}(t)) \quad (1)$$

where at time  $t$ ,

$\underline{n}(t) = (n_{0,t} \ n_{1,t} \ \dots \ n_{12,t})^T$ , the population vector of numbers in each age class where  $n_{a,t}$  is the number of animals of age-class  $a$  in year  $t$  and age 12 and greater is a plus age-class for which mortality and pregnancy rates are not age-dependent.  $T$  indicates the transpose.

$\underline{c}(t) = (c_{0,t} \ c_{1,t} \ \dots \ c_{12,t})^T$ , the vector of catches in each age class where  $c_{a,t}$  is the number of removals of age-class  $a$  in year  $t$ .

$$L_t \text{ is the Leslie matrix, } \begin{bmatrix} P_{0,t} & P_{1,t} & \cdot & \cdot & P_{12,t} \\ e^{-\gamma m} & 0 & \cdot & \cdot & 0 \\ 0 & e^{-m} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & e^{-m} & e^{-m} \end{bmatrix}$$

where  $P_{a,t}$  is the per-capita pregnancy rate for age-class  $a$  at time  $t$  from observational data. Data on per-capita pregnancy rates and their variances for the years 1960 to 1999 were taken from Hammill and Stenson (2003) based on data collected between 1954 and 1997. These vary over time but after 1999, values were assumed to be the same as the 1999 estimates. Biases in estimates of pregnancy rates were not considered specifically in this paper although this is potentially an issue that could be investigated further. The parameter  $\gamma$  allows for differential survival rates, and  $m$  is estimated using the model. Though in matrix form, our model is almost identical to that described by

Hammill and Stenson (2003). The main difference is that unreported mortality is included in our model. In each region (Front and Gulf, Canadian Arctic, and Greenland), total catch is estimated by region-specific scaling up of the reported landings to account for unreported mortality. Unreported mortality may be a result of non-reporting of catches and/or animals that are struck but lost to hunters. In our model, struck-and-lost-rates and reporting rates are included separately for pups and 1+ animals. Struck-and-lost rates are denoted by  $\phi_0$  and  $\phi_{1+}$ , and reporting rates by  $r_0$  and  $r_{1+}$ . Total catch is therefore estimated, separately for each region as:

$$\underline{c}(t) = \begin{bmatrix} \frac{k_0(t)}{r_0(1-\phi_0)} & \frac{k_1(t)}{r_{1+}(1-\phi_{1+})} & \frac{k_2(t)}{r_{1+}(1-\phi_{1+})} & \dots \end{bmatrix}^T \quad (2)$$

where  $k_i(t)$  is the reported catch for age-class  $a$  in year  $t$ .

To date only struck-and-lost rates and bycatch have been considered as part of the unreported mortality parameters in the previous models, except for some adjustment for non-reporting of the Greenland statistics by Stenson (2005). Thus the introduction of the parameter  $r$  is new. The total catch is distributed amongst the age-classes using information from catch records (see Stenson, 2005).

#### *Likelihood-based estimation*

Estimation of parameters is based on the likelihood outlined in equations 3 and 4. In addition to  $\underline{n}(t)$  and  $\underline{c}(t)$  defined in equations 1 and 2, let

$t_0$  be the year at which pregnancy data first becomes available

$\underline{\theta} = [m, s, \gamma]$  be the vector of parameters to be estimated (these are assumed constant over time).

$t_1, t_2, \dots, t_d$  be the years where pup production estimates were obtained by survey

$n_0(t)$  be the number of pups at time  $t$

$p_1, \dots, p_d$  be the pup survey estimates (at  $t_1, t_2, \dots, t_d$ ) with variances  $\sigma^2_{t_1}, \dots, \sigma^2_{t_d}$

Pup survey estimates and their variances for the years 1978, 1979, 1980, 1983, 1990, 1994, 1999, 2004 were taken from Hammill and Stenson (2005).

The likelihood of the data, conditional on the initial population vector in the first year that pregnancy data are available,  $\underline{n}(t_0)$ , is then:

$$L(\underline{\theta} | \underline{n}(t_0)) = \Pr(p_1(t_1), p_2(t_2), \dots, p_d(t_d) | \underline{\theta}, \underline{n}(t_0)) \quad (3)$$

From the deterministic population dynamic model we obtain  $E(\underline{n}(t_i) | \underline{n}(t_0))$  by iterating equation (1) from  $t_0$  to  $t_i$ . This then also gives  $E(n_0(t_i) | \underline{n}(t_0))$ .

So if the pup production survey estimates are independent, unbiased and normally distributed:

$$L(\underline{\theta} | \underline{n}(t_0)) = \prod_{i=1}^d \frac{1}{\sqrt{2\pi}\sigma_i} \exp\left(-\frac{[p_i - E(n_0(t_i) | \underline{n}(t_0))]^2}{2\sigma_i^2}\right) \quad (4)$$

The likelihood specified above is conditional on  $\underline{n}(t_0)$  but this is unknown and therefore needs to be estimated. This is done via the ‘hunting selection parameter’,  $s$ . For years prior to  $t_0$  it is assumed that the catch of pups  $c_0(t)$  is related to pup production  $n_0(t)$  by:

$$sc_0(t) = n_0(t) \quad (5)$$

The  $c_0(t)$  prior to  $t_0$  are known (or at least assumed constant) and used with  $s$  to provide estimates of  $\underline{n}(t_0)$ . Further details are given by Cadigan and Shelton (1993).

### *Simulations*

The simulation process is shown as a flow diagram (Fig. 1). An important characteristic of the implementation is the distinction between what we have termed ‘reference’ trajectories generated in steps 1-3, and ‘estimated’ trajectories generated in steps 4-6 (steps described below). The estimated trajectories represent the information that would be used as the basis for management and setting a TAC, whereas the reference trajectories would represent the actual situation under the assumptions of the case study.

For each case study scenario a number of assumptions were made about biases in the input data. The input data were then corrected for these assumed biases to generate a set of 100 simulated reference trajectories based on the catch history (corrected for any assumed under-reporting or underestimated struck-and-lost rates), real pup production estimates (corrected for any assumed bias) and their variances. The reference trajectories were then projected forwards to generate simulated pup production estimates at 5 year intervals into the future. For each reference population trajectory a set of 100 estimated trajectories were generated using the time series of combined real pup production estimates from past surveys and simulated pup production estimates from future surveys. The input parameters for these estimated trajectories were *not* corrected for the biases that were assumed to occur in the particular scenario.

The fundamental steps were:

- (1) Generation of reference parameters ( $\underline{\theta}_0$ ) by Monte Carlo sampling of the pup survey distributions to date. This is similar to that approach taken by Warren et al. (1997). The estimation uses profile likelihood estimation and input values are corrected for the biases assumed in the scenario.
- (2) Alteration of reference parameters from  $\underline{\theta}_0$  to  $\underline{\theta}_I$  within a scenario, to examine the effects of sudden changes in mortality.
- (3) Projection of reference population trajectory forwards based on  $\underline{\theta}_0$  and  $\underline{\theta}_I$
- (4) Generation of new, simulated pup production estimates based on the reference population trajectory that was derived from steps 1 and 2.
- (5) Estimation of the parameters using the survey estimates but not correcting for any bias introduced into the scenario and assuming the same fixed ratio of pup mortality to adult mortality ( $\gamma=3$ ) as used by Hammill and Stenson (2003). The estimated parameter vector,  $\hat{\underline{\theta}}$  was estimated using maximum likelihood.
- (6) Projection of the population forwards based on  $\hat{\underline{\theta}}$  to give the estimated population trajectory.
- (7) Step 4-6 were repeated to obtain 100 estimated trajectories for each reference trajectory to establish the variance and shape of the distribution

Profile likelihood estimation was used to generate reference parameter vectors based on real survey estimates and their variances. The vector  $\underline{\theta}$  was divided into the parameters of interest ( $m, s$ ) and the nuisance parameter  $\gamma$ . The likelihood was maximised over the nuisance parameter (within limits) for a range of fixed values of the parameters of interest. In this way the potential variation in  $\gamma$  is incorporated in the population modelling.

An additional issue is that reference points based on maximum population size, such as the  $\hat{N}_{70}, \hat{N}_{50}, \hat{N}_{30}$  of the OBFM, will change each time the model is fitted to new data. This is because the complete historical population trajectory, including the estimate of maximum total population size, is revised each time new pup survey estimates are incorporated into the model (Hammill and Stenson, 2005). The notation used is that  $N_{Max}$  refers to the peak of the median observed population size from the reference model up until the time of assessment, and  $\hat{N}_{Max}$  the equivalent from the estimated trajectories. Results are also given for the 20<sup>th</sup> percentile of population estimates. This percentile was chosen because it has been used in the OBFM for the goal of maintaining an 80% probability of the population remaining above  $\hat{N}_{70}$  (DFO, 2005).

#### *Case study scenarios*

In the absence of a fully specified catch algorithm it was not possible to simulate the management decision process fully. Instead, the estimated trajectories under constant catch were compared with those from the reference model to examine the available information on which management decisions would be based.

The 18 scenarios reported in this paper are specified in Table 2. In each case projections were made to 2019 with  $t_0$  as 1960. These scenarios were chosen as the most informative robustness trials from a conservation perspective. Total reported historical removals by age class were taken from Stenson (2005), with the addition of a Canadian reported commercial catch of 329,829 for 2005. Projections for future reported landings from Greenland were taken from a uniform distribution of 70,000 to 100,000 (Hammill and Stenson, 2005). Projections for future reported Canadian commercial landings were in the range 250,000 to 325,000 and assumed to be 90% young of the year with catch proportions at other ages taken from Stenson (2005). The minimum value of 250,000 was chosen because this was the lowest number mentioned in DFO (2005). Struck and lost and reporting error adjustments are shown in tables 3 and 4. These are the same as given by Stenson (2005) except that a struck and lost of 10% and reporting rate of 85% for Canadian commercial catches was used in the reference model. A new pup-production estimate was generated every 5 years with an assumed CV of 0.08, which is the mean CV from the aerial surveys in years 1990, 1994, 1999, 2004 (Stenson et al., 2005). It was also assumed that future pup surveys would be conducted every 5 years in 2008, 2013 and 2018 leading to assessments in the year following each survey.

Changes in mortality (i.e.  $\underline{\theta}_0$  to  $\underline{\theta}_t$ , see Figure 1) were modelled as follows. For all animals the change in mortality was modelled by multiplying the estimated  $m$  by a

factor  $m_{future}/m_{past}$ . For pups, the change in mortality was modelled by an additional factor  $\gamma_{future}/\gamma_{past}$ . This then gives modified annual survival rates for 1+ animals of :

$$\exp(-m(m_{future} / m_{past})) \quad (6)$$

and for pups of :

$$\exp(-m(m_{future} / m_{past})\gamma(\gamma_{future} / \gamma_{past})) \quad (7)$$

Although  $m$  is estimated for each scenario, typical values of  $m$  were around 0.06 with  $\gamma$  around 3. Thus these equations can be used to obtain approximate estimates of how the annual survival probabilities of pups and 1+ animals change with the multipliers used to simulate changes in mortality.

For example, from the mean estimates of  $m$  of 0.055 from Scenario A0 an increase in  $m$  of a factor of 1.2 results in each 1+ animal having a 93.7% chance of being alive at the end of the year compared to 94.7% without a change in  $m$  i.e. an approximately 1% decrease in annual survival. The change in  $\gamma$  by a factor of 1.5 and  $m$  by factor of 1.2 approximates to 75% of pups being alive at the end of the year (i.e. about 90% of what would otherwise have survived). These changes are roughly equivalent in terms of pup mortality to the assumptions made by Hammill and Stenson (2005) who chose a random value for additional annual pup mortality from the set (0, 0, 10%, 20%, 20%) for future projections.

The combined effect of a struck and lost rate of 0.1, and a reporting rate of 0.85 for Canadian commercial catches (giving reported landings = 0.77 true landings), are within the range of the estimates by Lavigne (1999) of the proportion of the total removals that are reported (0.61 to 0.84). Stenson (2005) also notes that further work to estimate probable levels of misreporting is needed. In respect to mortality, both PBR and RMP were tested for biases in annual mortality rates of a factor of two (IWC, 1992; Wade, 1998).

The majority of scenarios examined in this study had survey biases of 0 - 20% in magnitude, but three included a positive aerial survey bias of 30%. Since these were robustness trials, only combinations of mark-recapture and aerial survey bias where the direction of change in bias over time generated the greatest problems from a conservation perspective are presented. A negative bias in mark-recapture estimates could well arise as a consequence of heterogeneity in capture probabilities, which "is expected in almost all natural populations" (Chao and Huggins 2005). There has also been considerable discussion of these mark-recapture estimates (e.g. Warren 1991) and modellers have sometimes had to make rather subjective decisions on which estimates to use (Warren et al., 1997).

## Results

Results from the 18 different scenarios are listed in table 5 with parameter estimates in table 6. In each case, the simulations were projected forwards until 2019 to include three new pup survey estimates. Estimates of  $N$  and  $\hat{N}$  are median values but mean values were also calculated and these were close to the median in all cases. The

estimated trajectories, and hence estimates of  $\hat{N}_{Max}$ , were revised each time a new pup production estimate is available whereas the reference trajectories do not change with the year of assessment.

The reference model used in Scenario A0 is the closest to the assumptions made by Hammill and Stenson (2005) regarding pup mortality and showed broadly similar results with the mean reference population trajectory approximately level under a catch of 250,000 (Figure 2). The CV of the reference population estimate for this scenario (0.12 in 2009 and 0.17 in 2014) was rather less than that of Hammill and Stenson (2005), but this is likely due to our assumption of a constant change in mortality compared to allowing for random variability in  $m$ . In this case (Figure 2), the estimated population trajectory shows what would be predicted if additional mortality had not been included.

Scenario A3 involved a combination of modest bias in several factors: underestimation of true catches, decreased annual survival from 2005 onwards, 10% negative bias in mark recapture estimates and 10% positive bias in aerial surveys. Figure 3 shows the projected situation assessed in 2009. The median of the estimated population trajectories showed positive growth despite the reference trajectory being in decline. Assessments at subsequent 5 year intervals, 2014 and 2019 are shown in Figures 4 and 5 respectively. These illustrate a general characteristic that with more survey data, the reference and estimated population trajectories eventually converge as the model is fitted to the new data.

The conservation implications of all the scenarios are illustrated in Figures 6 and 7. In these figures the size of the symbol indicates catch, the symbol shape the combination of survey bias, and shading indicates increased mortality (see symbol list in Table 2). The plots show the predicted levels of depletion from the estimated population trajectories against the situation for the reference case using the results given in table 5. The dotted lines indicate the population level zones,  $\hat{N}_{70}$ ,  $\hat{N}_{50}$  and  $\hat{N}_{30}$  at which different management responses might take place (Hammill and Stenson, 2007). These management responses may depend on either the median estimate or 20<sup>th</sup> percentile (shown by the error bars). It can be seen from Figure 6 that for all the scenarios, the 20<sup>th</sup> percentile of the predictions for 2014 made in 2009 is greater than  $\hat{N}_{70}$ . However, the reference model indicates that two scenarios would be below  $N_{50}$  and six between  $N_{50}$  and  $N_{70}$ . Predictions for 2019 made in 2014 under continued constant catch are shown in Figure 7. Although the predictions have moved closer to the reference model, in the majority of cases the 20<sup>th</sup> percentile of the estimates is still above the line  $y = x$  (*i.e.* the predicted 20<sup>th</sup> percentile is still greater than the reference model). Not surprisingly, the scenarios with a 30% positive bias in aerial surveys (Scenarios, A5, C5, D5) provided the most severe tests. In all three cases, populations were reduced to below  $N_{30}$  by 2019 under constant catch.

The implications of a change in bias over time from -10% to 10% (Scenarios A3, C3, D3) was rather more severe than a -20% bias only in mark-recapture estimates (Scenarios A1, C1, D1). However, the latter cases had more serious implications than a 10% positive aerial survey bias (Scenarios A4, C4, D4), and results for either -10%

mark recapture (Scenarios A2, C2, D2) and 10% aerial survey bias were similar. These results show that if surveys at different ends of the time period are subject to different bias then biased estimates of natural mortality will also affect future predictions.

Although for comparable scenarios the lower catch of 250,000 resulted in lower depletion compared to a catch of 325,000 ( $A_i$  Scenarios compared to  $C_i$  Scenarios), the performance under a combination of increased mortality and change in bias of 20% (Scenarios A1 and A3) would still give rise to concern since these cases showed a large difference between predicted depletions and the reference cases.

### ***Discussion***

For a management regime to be considered precautionary, it must be sufficiently robust both to errors due to uncertainty in input parameters, and to potential changes in population dynamics, such that there is a low probability that exploitation will result in undesirable outcomes (FAO, 1995). The definition of ‘undesirable outcomes’ such as unintended depletion and whether these are considered unacceptable is a value judgement. Nevertheless, the OBFM for harp seals does include reference levels  $\hat{N}_{50}$  and  $\hat{N}_{30}$  that relate to conservation status and this study has shown that under scenarios with modest errors in input parameters there is a substantial risk of depleting the population below these levels. Based on these results, the management of Canada’s commercial harp seal hunt cannot be considered precautionary. DFO (2005) notes that “use of replacement yield is a high risk approach” a sentiment echoed by Holt (2006) specifically in the case of the Canadian harp seal hunt. Catches in excess of replacement yield will only increase the risks. Even in situations where the Canadian management plan for harp seals meets its own conservation objectives, it is likely to require large changes in TAC at the first signs that the TAC has been set too high. By contrast when the RMP was developed in the early 1990s, stability of catch-limits was one of the key objectives. Decisions to reduce TAC may be difficult for those responsible for management (MacCall, 1996). In particular, for some scenarios the mean estimates might give little cause for concern and the only indication of a problem requiring a reduction in the TAC may be related to the estimated variance of future predictions. Under these circumstances it may be difficult to communicate the need for a reduction in TAC purely on the basis of a poor model fit and uncertain predictions. The model itself is also rather sensitive to its parameterisation and slightly different formulations of the same basic modelling approach will give different variances under different circumstances even if the means are similar. These concerns could most effectively be addressed by moving towards a management procedure approach bearing in mind some of the following considerations.

As with many pinnipeds, surveys of harp seal pups on the whelping grounds are much more practical than attempting to survey the widely dispersed population at sea. However, the differences between estimates of total population based on pup production (as used for the OBFM) and direct surveys of the mature or 1+ population have potentially important implications for management procedures. In the simplest case, there will be a delay of some 5-7 years (the time taken for pups to be fully recruited into the breeding population) before any overexploitation of pups will be reflected in reduced pup production. This delay must be accounted for in the management

procedure (McLaren et al., 2001). Changes in demographic parameters can also affect estimates of rates of population change based on pup counts (Berkson and DeMaster 1985). Studies have also demonstrated that management procedures that use data-based estimates of quantities of interest (e.g. population size) perform better than procedures that rely on estimates derived from complex population models (Cooke 1995, Geremont et al., 1999, Milner-Gulland et al., 2001). An additional advantage of specifying procedures and objectives is that management algorithms can be tuned through an iterative process of testing and development to provide the desired trade off between competing performance goals (Cooke, 1999).

This study gives some indications of how the population model might perform but should not be considered to be exhaustive. The timing of events relative to pup surveys may also have a substantial influence. For example, the changes in biological parameters were always assumed to occur in the year immediately following a pup survey. This meant that little or no effect from increased pup mortality would be seen in the subsequent assessment (in this case 2009) but the next assessment (2014) has maximum chance of detecting the change. Further simulations involving other timings in relation to management time periods, and episodic rather than constant changes, could also be undertaken. The constant changes to key parameters such as mortality in this study are useful for investigating the performance of the model but will have the effect that the variance of the estimates of total numbers tends to be underestimated. Any changes in reporting or struck and lost rates will also have implications for the model especially if these involve a trend over time. The individual factors used for the difference in total mortality compared to reported landings and bias in aerial and mark-recapture surveys are all within plausible ranges and are much less severe than factors used to test other management procedures such as PBR (Wade, 1998) and RMP (Punt and Donovan, 2007).

The results highlight the need to ensure that future aerial survey estimates are not subject to bias. Although the maximum bias of 30% considered for the aerial surveys may seem large, it is not beyond the plausible range given the reliance on visual counting and that comparison of photo and visual techniques can produce large differences (Stenson et al., 2005). The RMP (IWC, 1992) and PBR (Wade, 1998) were tested and required to be robust to positive biases in survey estimates of 50% and 100% respectively. Any aerial survey technique that relies on visual estimates of strip width that cannot be confirmed by further analysis on the ground raises the possibility of undetected sources of bias (Ottichilo and Khaemba, 2001). Thus efforts should be made during surveys to obtain data that provide a permanent record that enables strip width and detection probability to be measured at the analysis stage. Other sources of potential bias are corrections applied to counts for pups not available at the time of the survey and corrections for misidentified pups on photographs. For example, Stenson et al. (2003) note that the estimate of pup production from the 1990 survey would decrease by 10% if a different model for the proportion of pups present at the time of the survey was used. Corrections for reader errors in photographic surveys involved regression lines for multiple readings of the same photograph. The slopes on these regressions varied from 0.86 to 4.09 for the 2004 survey (Stenson et al., 2005). This indicates that readers both over and under estimate the number of pups on photographs to an extent much greater than reported from previous studies such as Myers and Bowen (1989). It

would not be surprising if similar effects occurred on visual surveys but there is no means to check such counts. Some of these issues are highlighted in Stenson et al. (2005). For example it was only at the analysis stage that it became apparent that one photographic pup survey in 2004 was “severely biased and should be discarded”.

The sensitivity of the management model to time-dependent bias in surveys is an important consideration. Due to the estimation of natural mortality from the model, a trend in survey bias may cause more problems than the bias itself. This problem is potentially exacerbated by having two different methods of abundance estimation (mark recapture and line transect), each with its own characteristic bias potential, at either end of the timeline. Although these effects will decline in future as aerial surveys (presumably) continue, our results show that assessments over the next decade will still be highly sensitive to any biased results from surveys conducted 20-30 years ago. Hammill and Stenson (2005) also note the sensitivity of the model to small changes in estimates of adult mortality rates and the lack of any independent information on mortality rates. The dependency of  $m$  on model assumptions and input data is demonstrated by the range of estimates shown in Table 1.

Management of Canada’s commercial seal hunt to date has been conducted assuming all harp seals in the northwest Atlantic to be a single unit. This is the least precautionary assumption regarding population structure and any concerns over the effects on the total population would be exacerbated in the presence of population sub-structure. Although we have not considered population structure in this study the conclusion reported by Simon (2005) that “it would be precautionary to consider the northern Gulf seal as a separate management unit” should also be taken into account.

### **Conclusions**

Although the prior probability of the scenarios presented here actually occurring cannot be quantified, it seems clear that even for the minimum TAC of 250,000 considered in DFO (2005), there is a risk of failing to meet conservation objectives. Any TAC higher than this will only increase these risks. The most pressing management requirement is thus to reduce the current TAC. At the same time, there is a need to develop a fully specified management procedure and agree appropriate robustness criteria against which this is tested. Reducing TACs to within limits calculated from a well-established precautionary procedure such as PBR, would be a step towards more precautionary management. However, any calculated PBR limits should take into account the complications arising from model-based estimates of total population based on pup surveys, rather than direct estimates of the total population.

### **Acknowledgments**

Funding for this study was provided by IFAW. We thank David Lavigne for comments on an earlier draft.

### **References**

- Berkson J, DeMaster D. 1985. Use of pup counts in indexing population changes in pinnipeds. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 873-879.

- Bowen W, Sergeant D. 1983. Mark-recapture estimates of harp seal pup (*Phoca groenlandica*) production in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 728-742.
- Butterworth DS. 2007. Why a management procedure approach? Some positives and negatives. *ICES Journal of Marine Science* **64**: 613–617.
- Cadigan N, Shelton P. 1993. SAS programs for fitting a seal population dynamics model. Canadian Technical Report of Fisheries and Aquatic Sciences 1927.
- Chao A, Huggins R. 2005. Modern closed population capture-recapture models. In: Amstrup, S., McDonald, T., Manly, B. (Eds.), *Handbook of Capture-Recapture Analysis*. Princeton University Press.
- Cooke JG. 1995. The International Whaling Commission's Revised Management Procedure as an example of a new approach to fishery management. In: Blix, A.S., Walløe, L., Ulltang, O. (Eds.), *Whales, Seals, Fish and Man*. Elsevier Science, London, pp 647-657
- Cooke JG. 1999. Improvement of fishery-management advice through simulation testing of harvest algorithms. *ICES Journal of Marine Science* **56**: 797–810.
- Department of Fisheries and Oceans. 2005. 2005 Seal Forum Workbook. [http://www.dfo-mpo.gc.ca/seal-phoque/reports-rapports/2005-forum/2005-forum\\_e.htm](http://www.dfo-mpo.gc.ca/seal-phoque/reports-rapports/2005-forum/2005-forum_e.htm).
- FAO. 1995. Precautionary approach to fisheries. Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fisheries Technical Paper, 350, Part 1. 52 pp.
- Geremont H, De Oliveira J, Johnston S, Cunningham C. 1999. Development and application of management procedures for fisheries in southern Africa. *ICES Journal of Marine Science* **56**: 952-966.
- Hammill MO, Stenson GB. 2003. Harvest simulations for 2003-2006 harp seal management plan. Canadian Science Advisory Secretariat Research Document 2003/068.
- Hammill MO, Stenson GB. 2005. Abundance of Northwest Atlantic harp seals (1960 – 2005). Canadian Science Advisory Secretariat Research Document 2005/090.
- Hammill MO, Stenson GB. 2007. Application of the precautionary approach and conservation reference points to management of Atlantic seals. *ICES Journal of Marine Science* **64**: 702–706.
- Healey B, Stenson, GB. 2000. Estimating pup production and population size of the Northwest Atlantic harp seal (*Phoca groenlandica*). Canadian Science Advisory Secretariat Research Document. 2000/081.

- Holt SJ. 2006. The notion of sustainability. pp. 43-81. In D.M. Lavigne (ed.). *Gaining Ground: In Pursuit of Ecological Sustainability*. International Fund for Animal Welfare, Guelph, Canada, and University of Limerick, Limerick, Ireland.
- IWC. 1992. Report of the Third Comprehensive Assessment Workshop on Management Procedures, Oslo, 1–8 February 1990. *Reports of the International Whaling Commission* **42**: 271–304.
- Johnston DW, Meisenheimer P, Lavigne DM. 2000. An evaluation of management objectives for Canada's commercial harp seal hunt, 1996-1998. *Conservation Biology* **14**: 729-737.
- Johnston DW, Friedlaender AS, Torres LG, Lavigne D.M. 2005. Variation in sea ice cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. *Climate Research* **29**: 209-222.
- Lavigne DM. 1999. Estimating total kill of Northwest Atlantic harp seals, 1994-1998. *Marine Mammal Science* **15**(3): 871-878.
- MacCall AD. 1996. Too little, too late: treating the problem of inaction. *Ecological Applications* **6**: 368–369.
- McLaren IA, Brault S, Harwood J, Vardy D. 2001. Report of the Eminent Panel on seal management. [http://www.dfo-mpo.gc.ca/seal-phoque/reports-rapports/expert/rep-sm-rgegp\\_e.htm](http://www.dfo-mpo.gc.ca/seal-phoque/reports-rapports/expert/rep-sm-rgegp_e.htm)
- Milner-Gulland EJ, Shea K, Possingham H, Coulson T, Wilcox C. 2001. Competing harvest strategies in a simulated population under uncertainty. *Animal Conservation* **4**: 157-167.
- Myers R. Bowen D. 1989. Estimating bias in aerial surveys of harp seal pup production. *Journal of Wildlife Management* **53**(2): 361-372
- Ottichilo WK, Khaemba WM. 2001. Validation of observer and aircraft calibration for aerial surveys of animals. *African Journal of Ecology* **39**: 45-50
- Punt AE, Donovan GP. 2007. Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission. *ICES Journal of Marine Science* **64**: 603–612.
- Roff D, Bowen W. 1983. Population dynamics and management of the Northwest Atlantic harp seal. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 919-932.
- Shelton PA, Cadigan NG, Stenson GB. 1992. Model estimates of harp seal trajectories in the northwest Atlantic. Canadian Atlantic Fisheries Scientific Advisory Committee, CAFSAC Research Document Research Document. 92/89.

- Shelton P, Stenson GB, Sjare B, Warren WG. 1996. Model estimates of harp seal numbers-at-age for the Northwest Atlantic. *NAFO Science Council Studies* **26**: 1-14.
- Simon P. 2005. Proceedings of the meeting on scientific advice for the Atlantic seal management (September 7-8, 2005). Canadian Science Advisory Secretariat, Proceedings Series 2005/017
- Stenson GB, Healey B, Shelton PA, Sjare B. 1999. Recent trends in the Population of Northwest Atlantic Harp Seals, *Phoca groenlandica*. Canadian Science Advisory Secretariat Research Document 1999/107.
- Stenson GB, Rivest L, Hammill MO, Gosselin J, Sjare B. 2003. Estimating pup production of harp seals, *Phoca groenlandicus*, in the northwest Atlantic. *Marine Mammal Science* **19**(1):141-160
- Stenson GB, Hammill MO, Lawson J, Gosselin JF, Haug T. 2005. 2004 Pup Production of Harp Seals, *Pagophilus groenlandicus*, in the Northwest Atlantic. Canadian Science Advisory Secretariat Research Document 2005/037.
- Stenson GB. 2005. Estimates of human induced mortality in Northwest Atlantic Harp Seals, 1952-2004. Canadian Science Advisory Secretariat Research Document 2005/050.
- Wade P. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*. **14**:1-37.
- Warren WG. 1991. A critical review of mark-recapture estimation of Northwest Atlantic harp seal production 1977–1983. Canadian Atlantic Fisheries Scientific Advisory Committee, CAFSAC Research Document 1991/059.
- Warren WG, Shelton P, Stenson GB. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption part 1: uncertainty in the estimates of harp seal population size. *Journal of Northwest Atlantic Fisheries Science*. **22**: 289-302

## Tables

Table 1. Previous estimates of parameters  $m$  (natural mortality) and  $s$  (the ‘hunting selection parameter’ used to construct the initial population vector) as the parameter  $\gamma$  (a multiplicative factor to allow for higher mortality of pups compared to adults) is varied.

	$\gamma = 1$		$\gamma = 3$		$\gamma = 5$	
	$m$	$s$	$m$	$s$	$m$	$s$
Roff and Bowen (1983)	0.075	- <sup>a</sup>	0.0725	-	-	-
Shelton et al. (1992) <sup>c</sup>	0.136	- <sup>a</sup>	-	-	-	-
Shelton et al. (1996)	0.107	2.912	0.0898	2.928	-	-
Warren et al. (1997)	0.107 0.107 <sup>b</sup>	2.91 2.93 <sup>b</sup>	-	-	-	-
Stenson et al. (1999)	0.085	-	0.073	-	-	-
Healey and Stenson (2000)	0.0701	2.151	0.0584	2.227	0.0502	-
Hammill and Stenson (2003)	-	-	0.058	- <sup>d</sup>	-	-
Hammill and Stenson (2005)	-	-	0.057	- <sup>e</sup>	-	-

<sup>a</sup>  $s$  not estimated, but further process used to estimate initial population vector; see source

<sup>b</sup> these estimates from model which included variation in pregnancy rate

<sup>c</sup> results with  $s$  not estimated, but  $n_0(1960)$  estimated as 493,000; see source

<sup>d</sup>  $s$  not estimated, but  $n_0(1960)$  estimated as 488,000

<sup>e</sup>  $s$  not estimated, but  $n_0(1960)$  estimated as 493,000

Table 2. Input parameters to the simulation for different scenarios. Symbols refer to plots in Figures 6 and 7 grouped according to characteristics of scenarios (size relates to catch, shading to mortality and shape to survey bias).  $m_{\text{future}}/m_{\text{past}}$  and  $\gamma_{\text{future}}/\gamma_{\text{past}}$  indicate changes in mortality from 2004 onwards.

Scenario	Canadian commercial catch	$m_{\text{future}}/m_{\text{past}}$	$\gamma_{\text{future}}/\gamma_{\text{past}}$	Mark recapture bias	Aerial survey bias	Symbol group in plot
A0	250000	1.2	1.5	0	0	●
A1	250000	1.2	1.5	-0.2	0	▲
A2	250000	1.2	1.5	-0.1	0	●
A3	250000	1.2	1.5	-0.1	0.1	▲
A4	250000	1.2	1.5	0	0.1	●
A5	250000	1.2	1.5	0	0.3	■
C0	325000	1.2	1.5	0	0	●
C1	325000	1.2	1.5	-0.2	0	▲
C2	325000	1.2	1.5	-0.1	0	●
C3	325000	1.2	1.5	-0.1	0.1	▲
C4	325000	1.2	1.5	0	0.1	▲
C5	325000	1.2	1.5	0	0.3	■
D0	325000	1	1	0	0	○
D1	325000	1	1	-0.2	0	△
D2	325000	1	1	-0.1	0	○
D3	325000	1	1	-0.1	0.1	△
D4	325000	1	1	0	0.1	○
D5	325000	1	1	0	0.3	□

Table 3. Assumed struck and lost rates

	Front and Gulf		Canadian Arctic		Greenland	
	Pups	1+	Pups	1+	Pups	1+
Reference trajectory						
1952-1982	0.01	0.5	0.5	0.5	0.5	0.5
1983-	$\phi = 0.1$	0.5	0.5	0.5	0.5	0.5
Estimated trajectory						
1952-1982	0.01	0.5	0.5	0.5	0.5	0.5
1983-	$\hat{\phi} = 0.05$	0.5	0.5	0.5	0.5	0.5

Table 4. Assumed reporting rates.

	Front and Gulf		Canadian Arctic		Greenland	
	Pups	1+	Pups	1+	Pups	1+
Reference trajectory						
1952-1982	$r = 0.85$	$r = 0.85$	1	1	1	1
1983-	$r = 0.85$	$r = 0.85$	1	1	1	1
Estimated trajectory						
1952-1982	$\hat{r} = 1$	$\hat{r} = 1$	1	1	1	1
1983-	$\hat{r} = 1$	$\hat{r} = 1$	1	1	1	1

Note: Canadian Arctic reporting assumed to be 1 in absence of data (catches are also sufficiently small that this assumption will not have a major impact). Greenland non-reporting assumed already incorporated into catch figures (Stenson, 2005).

Table 5. Results of simulations. Values of  $\hat{N}$  and  $N$  are medians. The value of  $N_{Max}$  is constant for any given scenario whereas  $\hat{N}_{Max}$  changes with each assessment. Values in parentheses indicate the 20<sup>th</sup> percentiles. For  $N$  percentiles are taken from 100 replicates, for  $\hat{N}$  percentiles are taken from 10,000 replicates.

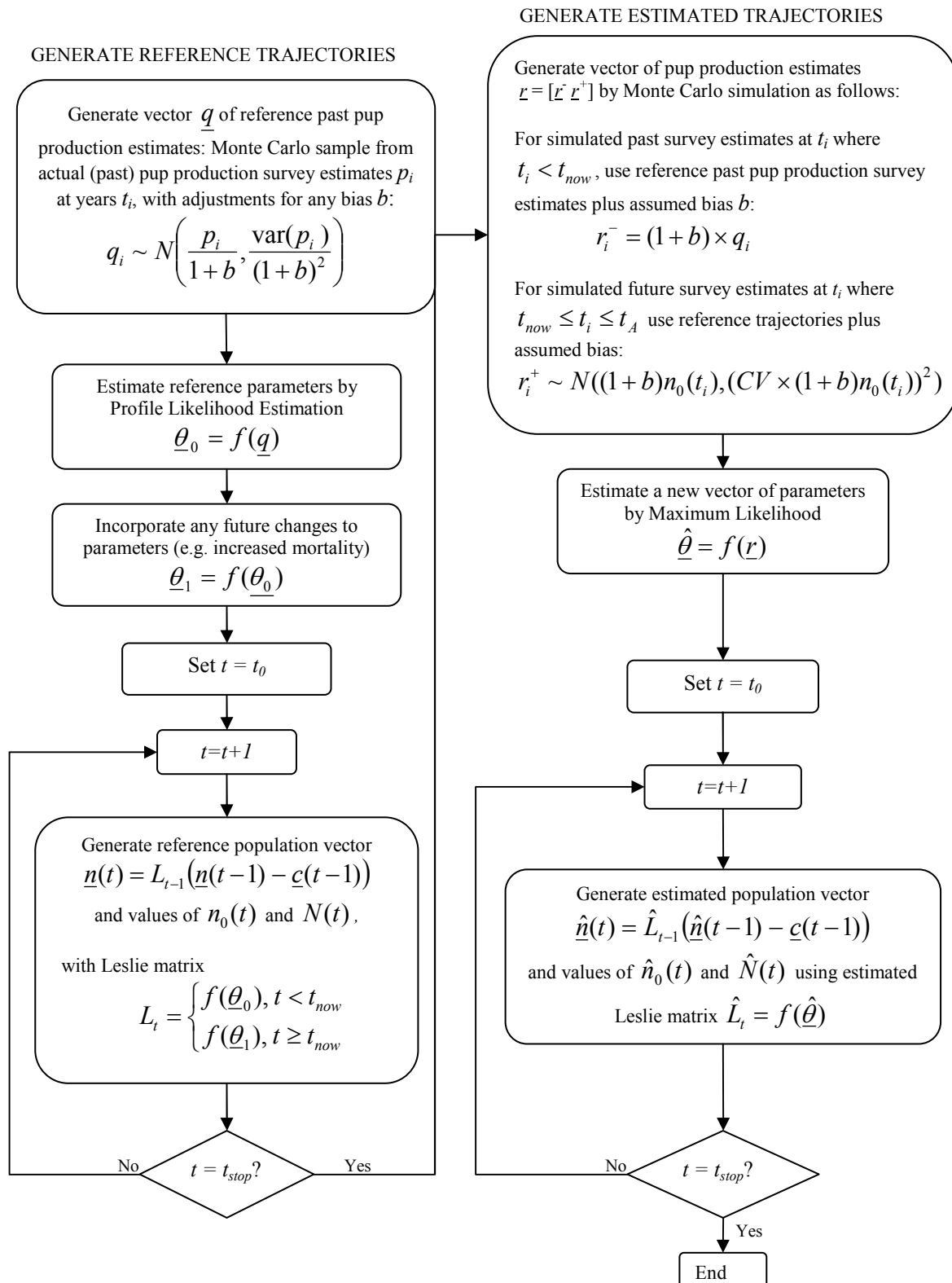
Scenario		2009			Prediction for 2014 made in 2009	2014			Prediction for 2019 made in 2014	2019		
		Estimates				Estimates				Estimates		
	$N_{Max}$ $\times 10^6$	$\hat{N}_{Max}$ $\times 10^6$	$\frac{N}{N_{Max}}$	$\frac{\hat{N}}{\hat{N}_{Max}}$	$\frac{\hat{N}}{\hat{N}_{Max}}$	$\hat{N}_{Max}$ $\times 10^6$	$\frac{N}{N_{Max}}$	$\frac{\hat{N}}{\hat{N}_{Max}}$	$\frac{\hat{N}}{\hat{N}_{Max}}$	$\hat{N}_{Max}$ $\times 10^6$	$\frac{N}{N_{Max}}$	$\frac{\hat{N}}{\hat{N}_{Max}}$
A0	6.21	6.71	0.99 (0.91)	1.00 (0.92)	1.14 (1.01)	7.16	0.98 (0.89)	1.00 (0.85)	1.14 (0.92)	7.44	0.96 (0.84)	0.99 (0.78)
A1	5.87	5.92	0.85 (0.74)	1.00 (0.85)	1.07 (0.84)	5.27	0.69 (0.55)	0.96 (0.74)	0.94 (0.63)	4.92	0.51 (0.31)	0.69 (0.46)
A2	5.98	6.39	0.94 (0.81)	1.00 (0.88)	1.12 (0.91)	6.28	0.87 (0.67)	1.00 (0.75)	1.06 (0.71)	6.14	0.76 (0.51)	0.90 (0.58)
A3	5.29	5.80	0.80 (0.71)	1.00 (0.87)	1.07 (0.86)	5.43	0.61 (0.50)	0.88 (0.65)	0.83 (0.52)	5.06	0.37 (0.23)	0.65 (0.31)
A4	5.42	6.55	0.95 (0.86)	1.00 (0.90)	1.12 (0.97)	6.30	0.88 (0.76)	1.00 (0.84)	1.09 (0.85)	5.90	0.78 (0.62)	0.94 (0.75)
A5	4.59	5.78	0.77 (0.62)	1.00 (0.83)	1.06 (0.80)	5.08	0.56 (0.38)	0.87 (0.56)	0.79 (0.36)	4.66	0.29 (0.04)	0.47 (0.11)
C0	6.17	6.40	0.95 (0.86)	1.00 (0.91)	1.08 (0.93)	6.42	0.87 (0.77)	1.00 (0.82)	1.04 (0.78)	6.30	0.76 (0.63)	0.92 (0.67)
C1	5.87	5.69	0.80 (0.69)	0.98 (0.83)	0.98 (0.75)	5.09	0.58 (0.44)	0.81 (0.60)	0.67 (0.38)	4.81	0.32 (0.13)	0.41 (0.16)
C2	5.98	6.08	0.89 (0.76)	1.00 (0.87)	1.06 (0.84)	5.81	0.75 (0.56)	0.94 (0.66)	0.88 (0.52)	5.51	0.56 (0.30)	0.72 (0.37)
C3	5.29	5.56	0.75 (0.65)	0.98 (0.81)	0.97 (0.72)	5.13	0.49 (0.39)	0.71 (0.52)	0.51 (0.27)	4.74	0.15 (0.03)	0.36 (0.01)
C4	5.42	6.11	0.89 (0.81)	1.00 (0.92)	1.06 (0.93)	5.70	0.73 (0.62)	0.97 (0.75)	0.94 (0.63)	5.37	0.53 (0.34)	0.71 (0.47)
C5	4.59	5.55	0.70 (0.57)	0.98 (0.80)	0.96 (0.70)	4.81	0.40 (0.24)	0.68 (0.37)	0.46 (0.02)	4.45	0.00 (-0.23)	0.10 (-0.14)
D0	6.36	6.75	1.00 (0.91)	1.00 (0.89)	1.10 (0.93)	7.34	1.07 (0.93)	1.00 (0.84)	1.12 (0.88)	8.05	1.16 (0.93)	0.99 (0.76)
D1	5.87	5.89	0.88 (0.78)	0.99 (0.87)	1.02 (0.83)	5.56	0.76 (0.63)	0.94 (0.75)	0.88 (0.62)	5.36	0.61 (0.41)	0.74 (0.50)
D2	5.98	6.36	0.97 (0.85)	1.00 (0.87)	1.07 (0.87)	6.53	0.93 (0.75)	1.00 (0.72)	1.05 (0.64)	6.73	0.85 (0.59)	0.90 (0.54)
D3	5.29	5.78	0.82 (0.72)	0.99 (0.85)	1.00 (0.80)	5.64	0.66 (0.52)	0.85 (0.61)	0.73 (0.43)	5.43	0.42 (0.23)	0.65 (0.30)
D4	5.42	6.54	0.97 (0.88)	1.00 (0.89)	1.08 (0.91)	6.39	0.93 (0.80)	1.00 (0.82)	1.05 (0.79)	6.36	0.87 (0.66)	0.93 (0.69)
D5	4.59	5.79	0.76 (0.62)	1.00 (0.80)	1.01 (0.72)	5.14	0.55 (0.32)	0.81 (0.51)	0.68 (0.24)	4.78	0.21 (-0.11)	0.35 (-0.03)

Table 6. Estimates of parameters  $m$ ,  $s$  and  $\gamma$  (for reference cases) from simulations. Scenario number refers to Scenarios listed in table 2 and values given are means, i.e. for Scenario number 1 the value given is the mean result from A1, C1 and D1. Note that  $m$  and  $s$  are not independent.

Scenario number	Reference trajectories			Estimated trajectories ( $\gamma=3.00$ )					
	$(\gamma \text{ estimated})$			2009		2014		2019	
	$m$	$s$	$\gamma$	$m$	$s$	$m$	$s$	$m$	$s$
0	0.055	2.81	2.96	0.060	2.96	0.061	2.99	0.062	3.04
1	0.070	3.22	2.86	0.062	3.04	0.066	3.13	0.067	3.18
2	0.062	2.98	2.87	0.061	3.00	0.063	3.06	0.064	3.10
3	0.064	3.05	2.88	0.063	3.05	0.066	3.14	*	*
4	0.056	2.83	2.93	0.060	2.98	0.063	3.05	0.065	3.12
5	0.058	2.90	2.96	0.063	3.05	0.068	3.20	*	*

\* No estimate due to population becoming extinct for some simulations

Figure 1. Flowchart of process to generate reference and estimated trajectories. The values used were: first year of data  $t_0 = 1960$ , most recent assessment year  $t_{now} = 2004$ , future assessment years,  $t_A = 2009, 2014, 2019$ , with  $t_{stop} = 2019$  as the last assessment year.  $f(x)$  indicates ‘some function of’  $x$ .



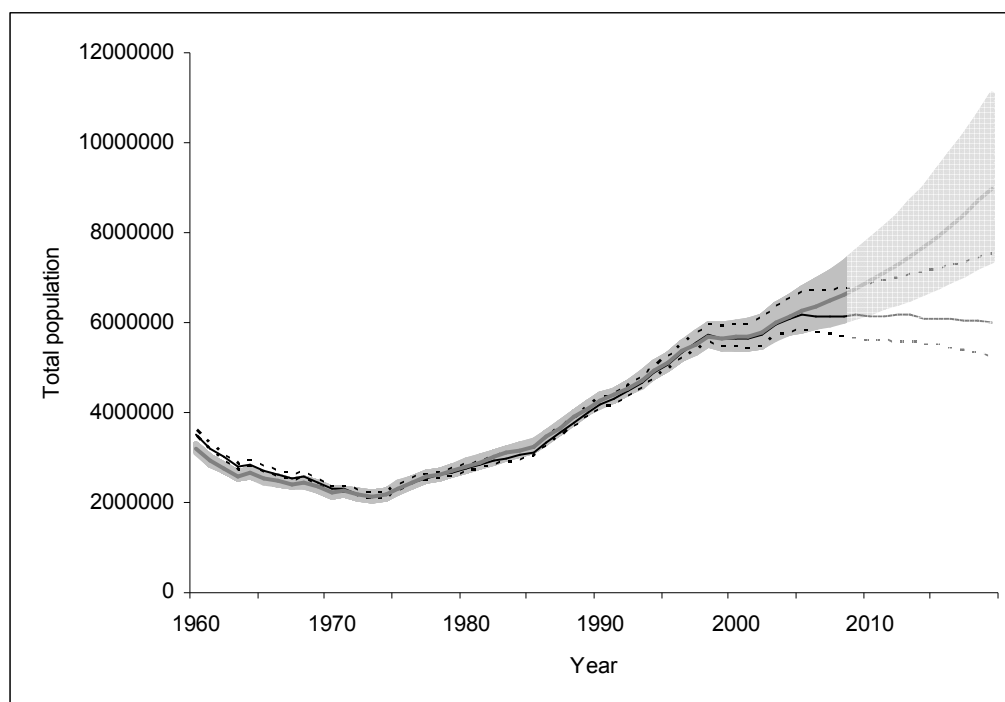


Figure 2. Scenario A0 assessed in 2009. Shaded area in Figures 2- 5 shows 20-80 percentiles of estimated trajectory with heavier line showing median. Paler shading from 2009 onwards indicates predictions. Solid black line represents median of reference model trajectory and dotted black lines the 20<sup>th</sup> and 80<sup>th</sup> percentiles.

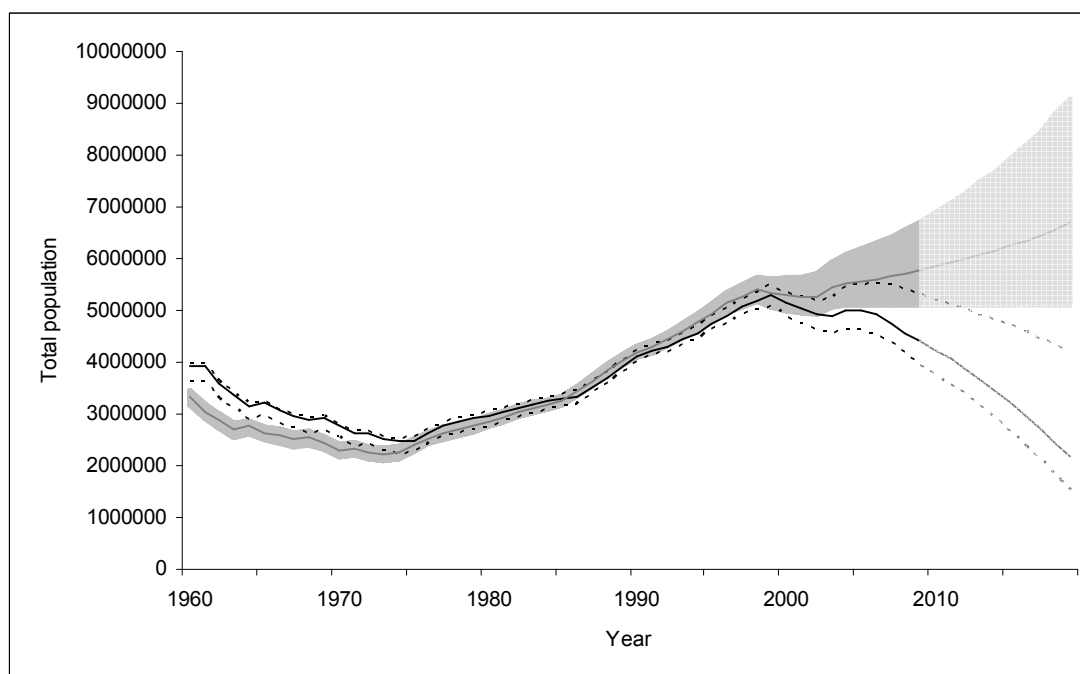


Figure 3. Scenario A3 assessed in 2009.

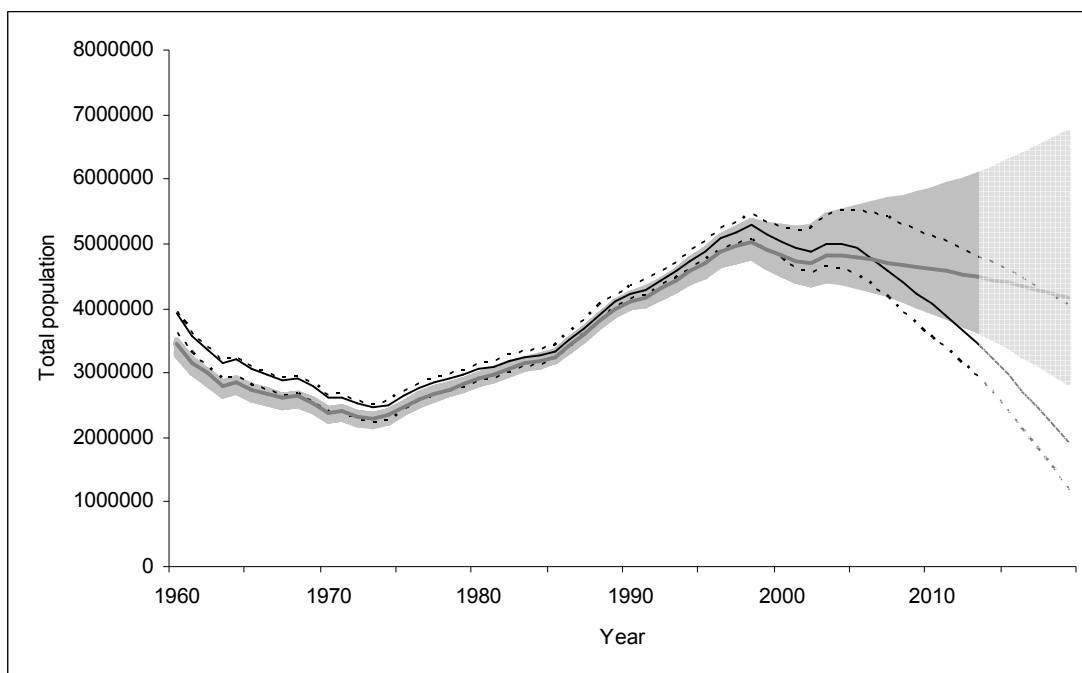


Figure 4. Scenario A3 assessed in 2014.

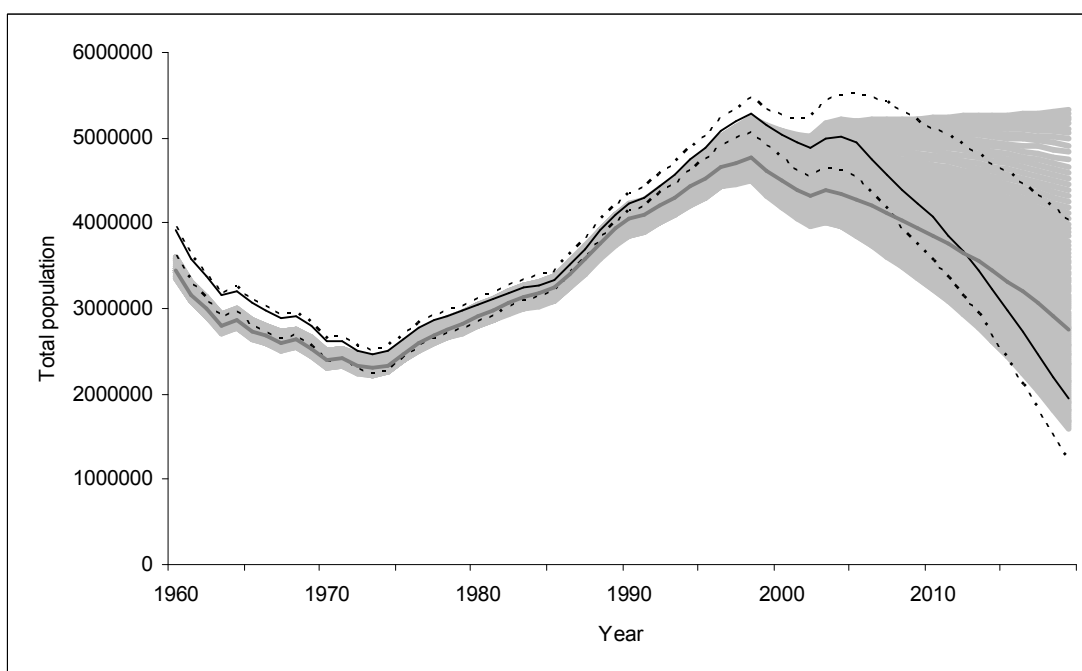


Figure 5. Scenario A3 assessed in 2019.

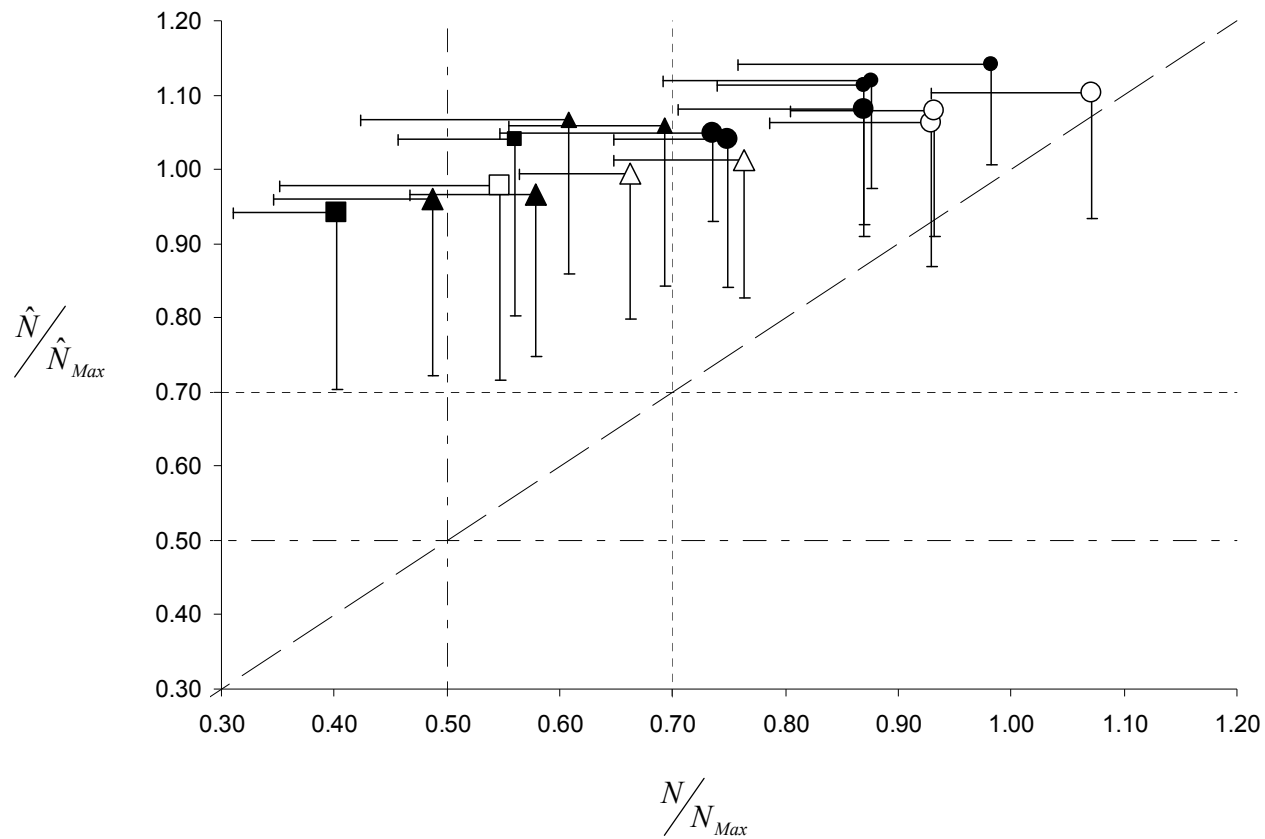


Figure 6. Predicted estimates for all 18 scenarios made in 2009 for the ratio  $\hat{N}/\hat{N}_{Max}$  in 2014 against the ratio  $N/N_{Max}$  in 2014 for the reference model. Error bars show 20<sup>th</sup> percentiles. Scenarios are grouped by symbols listed in Table 2. Dotted lines indicate reference points at 50% and 70% of maximum population size.

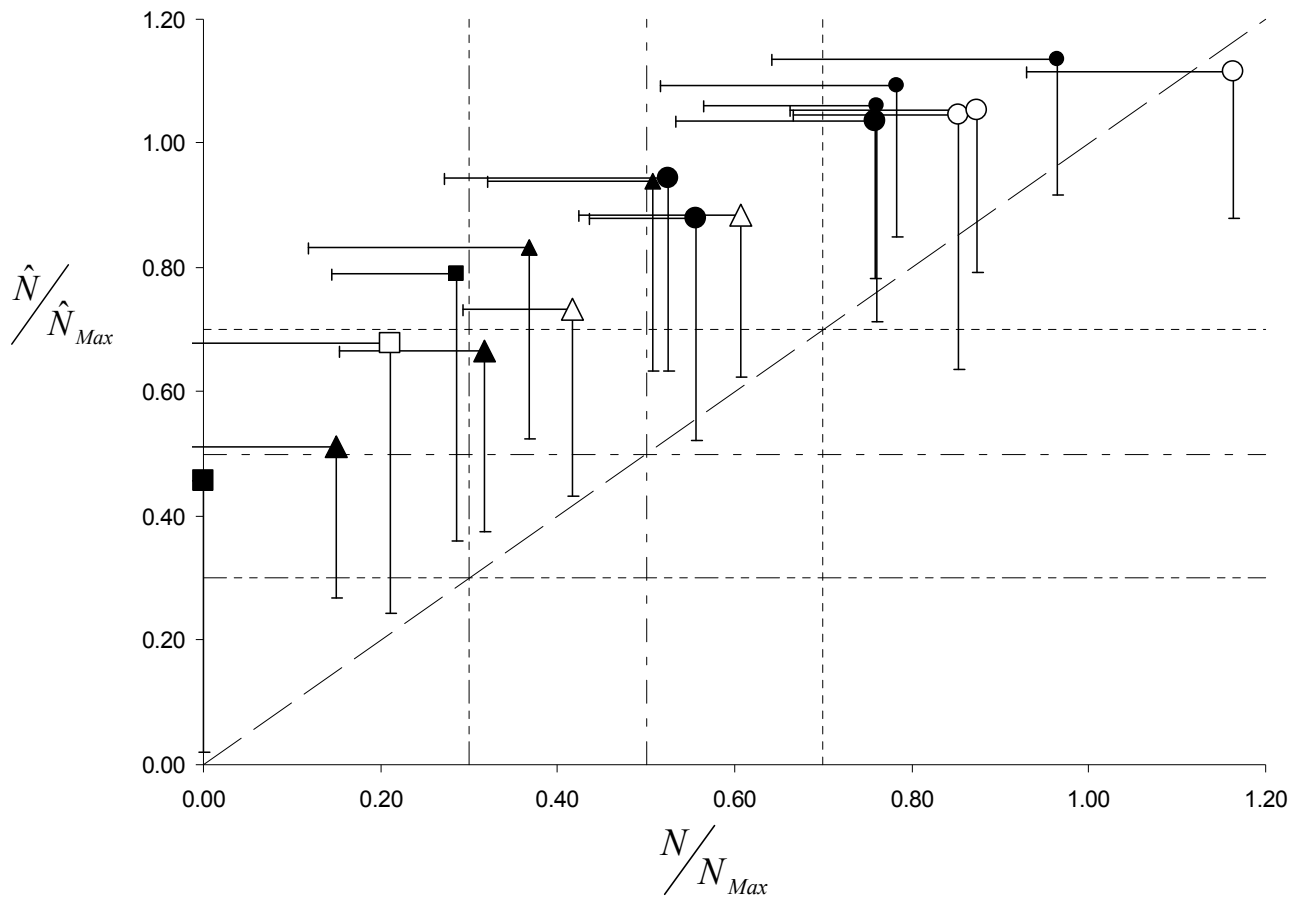


Figure 7. Predicted estimates for all 18 scenarios made in 2014 for the ratio  $\hat{N}/\hat{N}_{Max}$  in 2019 against the ratio  $N/N_{Max}$  in 2019 for the reference model. Error bars show 20<sup>th</sup> percentiles. Scenarios are grouped by symbols listed in Table 2. Dotted lines indicate reference points at 30%, 50% and 70% of maximum population size.