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on Canadian harp seal management.

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Summary

This study investigates the behaviour of the Canadian government's current management procedures for harp seals. These procedures are described by Fisheries and Oceans Canada as using both the Precautionary Approach and Objective Based Fisheries Management. Employing a similar underlying population modelling approach, we simulated the effects of uncertainty involving bias in estimates of human induced mortality, natural mortality and pup production estimates. These factors may combine such that the impact on the population of a certain level of take is much greater than would be predicted from assessments derived from the government model. Nevertheless, any precautionary management regime would be expected to be robust to reasonable levels of uncertainty. Our results indicate, however, that for the range of annual total allowable catches (TAC) considered and set for Canadian commercial catches of harp seals (250,000 – 350,000) there may be circumstances under which the government's management procedures fail to meet their own conservation objectives. Under some of the scenarios examined it appears 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 very low level. Hence the probabilities that the population may be depleted below the 'minimum' (N_{50}) and 'critical' (N_{30}) reference points are alarmingly high. In addition, when the TAC is reduced, the required cuts are likely to be drastic. Our results indicate that the Canadian government's approach to the management of harp seals results in a high level of risk that may, for example, not adequately account for changes in mortality related to poor ice conditions, such as are currently anticipated for spring 2006. There is a need for a fully specified management procedure based on risk analysis to be developed and tested. However, in the interim, setting TACs within limits calculated from a well-established precautionary procedure, such as Potential Biological Removal, would reduce the risks considerably.

Introduction

The aim of this study was to investigate the performance characteristics of the Canadian management plan for harp seals. We conducted some simulations for different scenarios including bias in abundance and mortality estimates, and changes in biological parameters, using the same population modelling approach underlying the current assessments. Based on the report of the Eminent Panel on Seal Management (McLaren *et al.*, 2001), it has been suggested that ‘the choice of any specific management action should be firmly based on a risk analysis approach. Before it can be implemented, its impact on the population and likelihood of reaching the intended objective must be evaluated in a manner that incorporates the uncertainties associated with the population estimates and predicated removals’ (DFO, 2005). This study is a step towards implementing these recommendations.

DFO (2005) describes the Objective Based Fisheries Management (OBFM) framework adopted in the last Canadian management plan for harp seals as follows:

- more flexible management measures to facilitate a market-based harvest that would ensure at least an 80% probability that the population would remain above the level of 70% of its highest known abundance (N_{70})
- more stringent management measures that would have at least a 80% chance of bringing the population back above that 70% level;
- very stringent management measures including a closure of much, if not all, of the commercial seal hunt in the event that the population falls below 50% of its highest known abundance; and
- closure to all seal hunting if the population drops to the level of 30% of its highest known abundance.

Other procedures for setting limits on takes of marine mammals include the Revised Management Procedure (RMP) of the International Whaling Commission (Cooke, 1995) and the calculation of Potential Biological Removal (PBR) levels (Wade, 1998; Johnston *et al.*, 2001). Both these approaches are widely acknowledged as precautionary and attempt to provide:

- (i) a fully specified catch algorithm
- (ii) a very low probability that the stock will decline below a given level
- (iii) robustness to errors in input data

The OBFM for harp seals in relation to these three characteristics is reviewed below:

(i) The OBFM does not provide a fully specified catch algorithm because it does not specify exactly how catch levels will be set nor the time periods for which certain objectives should be met. Being able to express objectives in terms of the probability of a certain situation occurring in a given amount of time is a key element of performance criteria for management procedures (Taylor *et al.*, 2000). Thus, in this study some assumptions need to be made regarding time periods in order to explore the characteristics of OBFM for harp seals through simulation of both harp seal population trajectories and related management decisions. It has been assumed that the goal of ensuring at least an 80% probability that the population will remain above the level of 70% of its highest known abundance applies to a 5 year catch limit block. If the population drops below N_{70} then the stated objective is to achieve at least an 80% chance of bringing it back above N_{70} . No timeframe is given within which this objective should be achieved and it might also be assumed that this would be within a single 5 year catch limit block. However, in many cases this may not be possible even with zero catches. If no time limit is assumed then this objective just equates to an 80% probability that the population growth rate is positive. The response to the population falling below N_{50} is less clear because it is not obvious what ‘much, if not all, of the commercial seal hunt’ actually means in terms of numbers. Thus we have not attempted to speculate what quantitative response might occur in situations where the population drops below N_{50} . Closure to all hunting at N_{30} is clearer, and in this case the remaining takes would presumably be just bycatch and catches outside of Canada by Greenland. Johnston *et al.* (2000) note the need for some form of bilateral agreement between Canada and Greenland

on harp seal management. It is also not clear whether the measures related to N_{50} and N_{30} refer to the point estimate of the population or the lower 20th percentile as appears to be used for comparison with N_{70} .

(ii) Neither the RMP or PBR have a ‘target’ level as a fundamental objective, rather the fundamental objective is a very low probability of depleting the population. In contrast, the OBFM would essentially appear to set N_{70} as a target. Hammill and Stenson (2003b) note this difference in philosophy: ‘Ideally, advice should be framed in terms of complying with precautionary reference points, rather than avoiding conservation (limit) reference points’.

(iii) In this study the OBFM was examined for robustness to certain levels of error in input data (such as survey estimates), errors in estimates of the numbers of animals killed (including struck and lost rates and unreported catches) and changes to the environment that may affect population dynamics. These are all acknowledged areas of uncertainty (e.g. Stenson *et al.* (2005) for survey estimates, Bowen and Segeant (1983), Lavigne (1999) and Stenson (2005) for human induced mortality including reporting errors and struck and lost). One of the major factors known to affect harp seal pup mortality is ice condition. For the poor ice years of 1998 and 2000, Hammill and Stenson (2003a) assume that only 92% of the pups that would otherwise have survived prior to harvesting actually survived. For the very poor ice year of 2002 this ratio was assumed to be 75%. Johnston *et al.* (2005) review the possible implications of climate change on future ice conditions and sudden changes or prolonged trends in mortality appear to be a real possibility.

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, pup production estimates have a number of different properties compared to direct surveys of the mature or 1+ population, with potentially important implications for management procedures. In the most simple 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. McLaren *et al.* (2001) note that the implications of such a delay must be accounted for in the management procedure. Changes in demographic parameters can also bias estimates of rates of population change (Berkson and DeMaster, 1985). Several studies demonstrate that management procedures utilising observational data directly perform better than those that rely on estimates of parameters derived from data by some process outside the management procedure (Cooke, 1995; Geremont *et al.*, 1999; Milner-Gulland *et al.*, 2001). DFO (2005) also suggests that ‘perhaps a more appropriate measure [than total population] may be to use pup production since it is the variable that is determined directly’. However, since the current management plan is based on estimates of total population, we have also used total population in this study.

Methods

The core population dynamic model was originally introduced by Roff and Bowen (1983) but has been modified and altered since in various ways. We have used the same approach as described by Hammill and Stenson (2003a) with some small modifications (full methods and model description are included in the Appendix). Data on all human induced mortality are taken from Stenson (2005) and the 2004 pup production estimate from Stenson *et al.* (2005). The model has been modified so that unreported mortality is now shown explicitly in the model, and a further age-dependence is introduced which allows for higher mortality in the plus age class (age 12 and older). We believe on biological grounds that this is a more reasonable model since increased mortality at advanced ages is a mammalian characteristic.

An important characteristic of the implementation of the model used here is that it generates what we have called ‘true’ and ‘estimated’ trajectories. This allows the implications of bias in the input parameters (catch history, pup production estimates) or changes in population parameters (mortality or pregnancy rates) to be examined. In this case a simulated set of ‘true’ trajectories are generated based on the catch history and real survey estimates and their variances, corrected for any assumed bias. The ‘true’ trajectories can then be projected forwards to generate simulated pup surveys. The ‘estimated’ trajectories are derived by fitting the model to these data by maximum likelihood without correcting for bias and assuming the same fixed ratio of pup mortality to adult mortality as used by Hammill and Stenson (2003a). It is these estimated trajectories that would be used as the basis for management and setting a Total Allowable Catch (TAC).

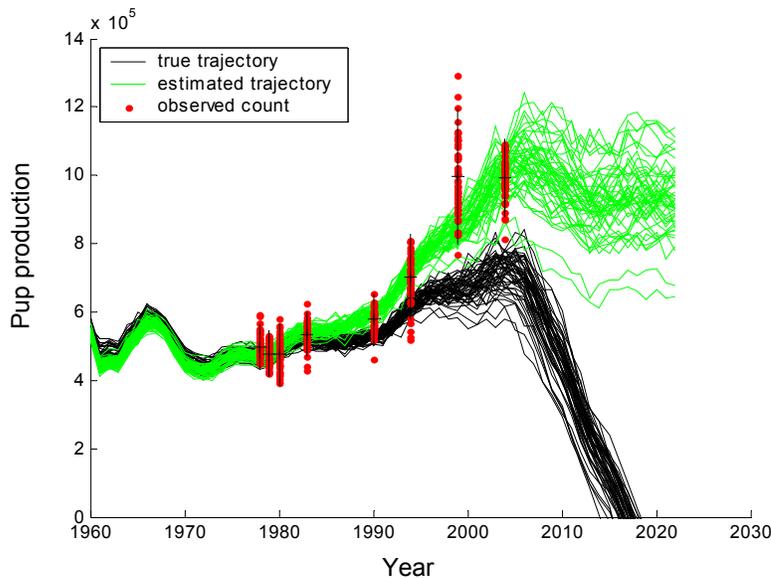


Figure 1. Example of simulated ‘true’ (black lines) and ‘estimated’ (green lines) trajectories of pup production. Red dots indicate estimates of pup production sampled from the survey estimates.

The modelling process is illustrated in Figure 1. In this case it was assumed that the Canadian commercial catch was set to estimated replacement yield (such that the total population in the following year was expected to be the same as the current year) every 5 years and that there were no further pup surveys after 2004. It was also assumed that aerial surveys were positively biased by 30%, no bias in the mark-recapture surveys, 10% struck and lost rates for the Front and Gulf and 85% of takes in the Front and Gulf being reported. The pup survey estimates are illustrated by the red dots with the spread indicating the sampled values taken from the distribution of the estimates each time the simulation is run.

In addition to illustrating the characteristics of the model, Figure 1 highlights the need for new data to provide feedback in the management procedure, currently obtained by regular pup surveys. Some procedures such as the RMP require catch limits to be reduced by a certain annual percentage after a certain time has lapsed without new survey data. In this example, the population drops to around N_{50} within about 10 years after the last survey. Thus at this point the Canadian commercial TAC would be expected to be set to zero suggesting that reducing catches by 20% for each year beyond 5 years when there are no new survey data might have allowed management objectives to be met. However, this is just one example and further simulation testing of possible phase-out rules would be necessary if a management procedure was to be fully specified and tested.

An additional factor when using reference points, which are a certain proportion of an estimate of the maximum observed population size, is that the estimate of maximum total population size is revised each time a new pup survey is undertaken. Thus reference points based on maximum population size such as the N_{70} , N_{50} and N_{30} of the OBFM will change each time the model is fitted to new data. In this study we

consider the maximum of the mean estimates up until the year 2004 as the reference for maximum observed population size (N_{Max}). The notation used is that N_{Max} refers to the ‘true’ trajectories and N_{Max}^* to the ‘estimated’ trajectories. Results are also given for the lower 20th 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 N_{70} .

Case study scenarios

Management procedures such as PBR and RMP have been subjected to extensive simulation testing to investigate their robustness. It is not possible to fully reproduce these approaches for the Canadian harp seal plan because it does not have a fully specified catch algorithm. Instead we have examined some scenarios where changes in population parameters or bias in input values result in a less favourable conservation status than perceived at the time. For each scenario it is then possible to compare the estimated and true trajectories and the results of some likely management action based on the estimates.

The scenarios that have been run (A-G) are given in Table 1. In each case the total reported historical removals by age class are taken from Stenson (2005), with the addition of an assumed Canadian reported commercial catch of 323,826 for 2005. Projections for future reported landings from Greenland are taken from a uniform distribution of 70,000 to 100,000. Projections for future reported Canadian commercial landings are in the range 250,000 to 350,000 and assumed to be 90% young of the year. The minimum figure of 250,000 was chosen because this was the minimum figure mentioned in DFO (2005). These runs are all subject to the struck and lost and reporting error adjustments shown in Tables 2 and 3. It is assumed that historical mark-recapture estimates of pup production were unbiased (this assumption is unlikely to have a large impact on the results, nevertheless the implications of both positive and negative bias could be investigated further). In each of these scenarios, a new pup production estimate is 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 is also assumed that pup surveys are conducted every 5 years i.e. 2004, 2009, 2014 and 2019.

Changes in mortality are modelled according to equation (4) of the Appendix. For 1+ animals the change in mortality is modelled by multiplying the estimated m by a factor m_{future}/m_{past} . In the absence of catches, if the number of 1+ animals surviving at the end of the year is (N_{t+1}) and the number of pups (P_{t+1}) then these can be expressed as a proportion of the numbers of 1+ and pups, N_t and P_t respectively, at the beginning of the year;

$$N_{t+1} = N_t e^{-m(m_{future}/m_{past})}$$

For pups, the change in mortality is modelled by an additional factor $\gamma_{future}/\gamma_{past}$ giving:

$$P_{t+1} = P_t e^{-m(m_{future}/m_{past})\gamma_1(\gamma_{future}/\gamma_{past})}$$

Although m is estimated for each model run, typical values of m were around 0.06 with γ_1 around 3. Thus these equations can be used to obtain approximate estimates of how the ratios N_{t+1}/N_t and P_{t+1}/P_t change with the multipliers used to simulate changes in mortality.

Hammill and Stenson (2003a) consider that for the very poor ice year of 2002, only 75% of the pups that would have survived in a normal year actually survived. For the moderately poor years of 1998 and 2000, they assumed that this ratio was 92%. As of end of January 2006, predictions from the Canadian Ice Service (<http://ice-glaces.ec.gc.ca>) are for above average temperatures persisting through February and freeze up in the Gulf of St. Lawrence delayed by about a month. These ice conditions could potentially result in 2006 also being a year of very high pup mortality.

For our mean estimates of m of 0.0524 (for the F scenarios) an increase in m of a factor of 1.2 results in each 1+ animal having a 93.9% chance of being alive at the end of the year compared to 94.9% without a change in m i.e. approximately 1% decrease in survival. For our mean estimate of γ_1 of 2.68 (for the F scenarios), the combined change in γ by a factor 3 and m by a factor of 1.2 approximates to a change from around 87% of pups being alive at the end of the year to about 61% (i.e. 70% of what would otherwise have survived). The less severe case of a change in γ by a factor of 1.5 and m by factor of 1.2 approximates to

78% of pups being alive at the end of the year (i.e. about 90% of what would otherwise have survived). Thus these changes are roughly equivalent in terms of pup mortality to the assumptions made by Hammill and Stenson (2003a) for either a single very poor year or a single moderately poor year respectively, but are assumed to be ongoing in our simulations.

Table 1. Parameters of simulation runs

	ϕ^*	ϕ	r^*	r	Aerial survey bias	$\gamma_{\text{future}}/\gamma_{\text{past}}$ (2005 onwards)	$m_{\text{future}}/m_{\text{past}}$ (2005 onwards)	Canadian commercial reported landings
Scenario A	0.1	0.1	0.85	0.85	1.3	1	1.2	250000
Scenario B1	0.1	0.1	0.85	0.85	1.1	3	1.2	250000
Scenario B2	0.1	0.1	0.85	0.85	1.1	3	1.2	300000
Scenario C1	0.1	0.1	0.85	0.85	1.1	1.5	1.2	250000
Scenario C2	0.1	0.1	0.85	0.85	1.1	1.5	1.2	300000
Scenario C3	0.1	0.1	0.85	0.85	1.1	1.5	1.2	320000
Scenario C4	0.1	0.1	0.85	0.85	1.1	1.5	1.2	350000
Scenario D	0.1	0.1	0.85	0.85	1.1	1.5	1	300000
Scenario E	0.1	0.1	0.85	0.85	1.1	1.7	1	300000
Scenario F1	0.05	0.1	1	0.85	1.1	1.5	1.2	250000
Scenario F2	0.05	0.1	1	0.85	1.1	1.5	1.2	300000
Scenario F3	0.05	0.1	1	0.85	1.1	1.5	1.2	320000
Scenario G	0.05	0.1	1	0.85	1	1.5	1.2	320000

ϕ and ϕ^* refer to struck and lost rates for Canadian commercial catches for true and estimated trajectories respectively

r and r^* refer to the proportion of landings reported for true and estimated trajectories respectively

For pup surveys (true value = estimate/aerial survey bias)

Table 2. Assumed struck and lost rates

	Front and Gulf		Canadian Arctic		Greenland	
	0	1+	0	1+	0	1+
1952-1982	0.01	0.5	0.5	0.5	0.5	0.5
1983-	ϕ	0.5	0.5	0.5	0.5	0.5

Table 3. Assumed reporting rates.

	Front and Gulf		Canadian Arctic		Greenland	
	0	1+	0	1+	0	1+
1952-1982	r	r	1	1	1	1
1983-	r	r	1	1	1	1

Note: Canadian Arctic reporting rate is 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 is assumed to be already incorporated into catch figures (Stenson, 2005)

Results

Results of model runs are listed in Tables 4 and 5. Table 5 gives the maximum values of the mean true (N_{Max}) and estimated (N^*_{Max}) trajectories up until 2004 from 100 runs. These are used as the basis of the relative proportions of N_{Max} and N^*_{Max} given in Table 4.

The results of scenario F2 are illustrated in Figures 2a-2c. The 'F' scenarios involve a combination of modest changes (10-15%) but to several factors: underestimation of true catches, decreased annual survival from 2005 onwards and positive aerial survey bias. The reported Canadian commercial catch is 250,000 for F1, 300,000 for F2 and 320,000 for F3. For F2, Figure 2a shows the projected situation assessed in 2010. In this case the mean and the lower 20th percentile of the estimated trajectories show positive growth and little change respectively, despite the true trajectory being in decline. The situations assessed at subsequent 5 year intervals, 2015 and 2020 are shown in Figures 2b and 2c respectively. These illustrate a general characteristic that with more survey data, the true and estimated trajectories eventually converge as the parameter estimates from the estimated trajectories are fitted to the new data.

The estimates as a proportion of the true maximum (N_{Max}) and estimated maximum (N^*_{Max}) are given in Table 4. Mean estimates of N_{Max} and N^*_{Max} are given in Table 5. In this case when the situation is assessed in 2010 the estimated population is very close to its maximum value (108%) and its lower 20th percentile is at 92% of N^*_{Max} . Thus managers might be expected to consider that there are no problems and continue with the same, or even increase, the TAC. By 2015 the estimated trajectory has flattened out (Figure 2b) but the lower 20th percentile of the estimated is still just above N_{70} at 70% of N^*_{max} . At this point, the true population is at only 71% of its maximum with the lower 20th percentile at 56%. If the TAC remained the same then by 2020 it would be apparent that the population was declining. At this point however, the mean true population would already be below N_{50} with the lower 20th percentile below N_{30} . This lower 20th percentile represents a total population of 1.4 million seals, 63% of the previous estimated minimum mean total population from the same trajectory of 2.24 million in 1973 (Figure 2). It is also likely that even setting all Canadian commercial catches to zero might not result in positive population growth because of the combined ongoing catches in Greenland, Canadian Arctic and bycatch. In addition, even though the assessment in 2020 would raise some concerns it is still not clear whether the Canadian commercial catch would actually be set to zero given the mean estimate of total population at 0.66 of N^*_{Max} .

Reducing the TAC for 2016-2020 might result in a slightly less serious situation, but it is not clear that the TAC would be reduced given the mean projection for 2020 made in 2015 was for a steady population i.e. the ongoing TAC would be estimated to be the short-term sustainable yield. Scenario F1 uses the same parameters except with a constant Canadian commercial reported catch of 250,000 animals a year. In this case all of the assessments prior to 2020 indicate a stable or increasing population with lower 20th percentiles above N^*_{70} . By contrast the true trajectories show that if no change were made to the TAC then the mean population would be at 65% of N_{Max} in 2020 with the lower 20th percentile at 45%. For scenario F3 with the same parameters but with a constant Canadian commercial reported catch of 320,000 animals a year, the mean prediction based on the 2015 assessment would still be for the population to be at 81% of N^*_{Max} in 2020. The lower 20th percentile in 2015 would, however, indicate that the TAC should be reduced. If this action were not taken however then the true trajectories show a mean population at 41% of N_{Max} in 2020 with a lower 20th percentile of 19%.

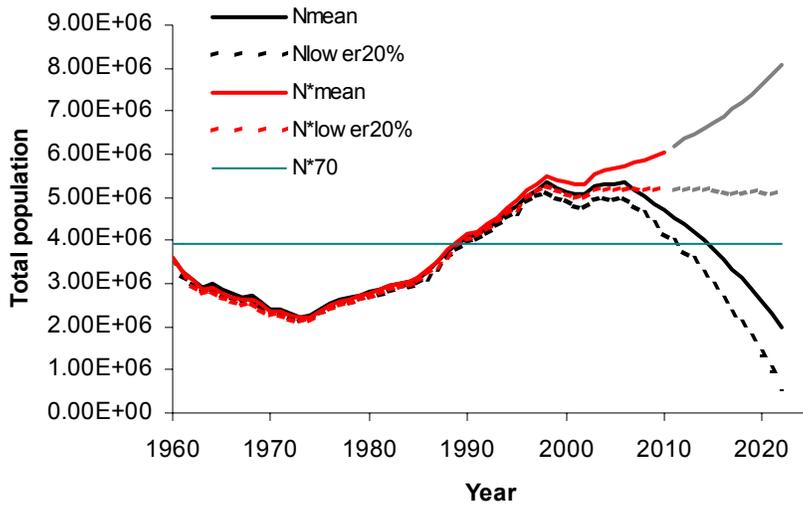


Figure 2a. Scenario F2 assessed in 2010. Grey lines indicate future projections.

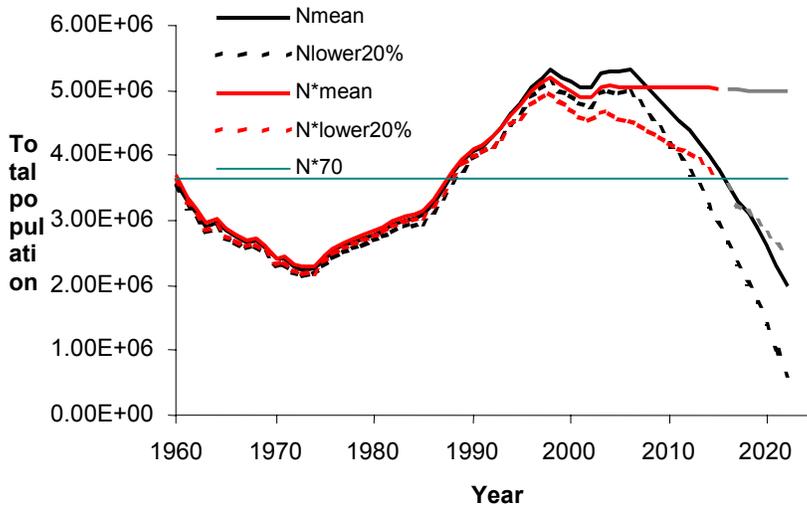


Figure 2b. Scenario F2 assessed in 2015. Grey lines indicate future projections.

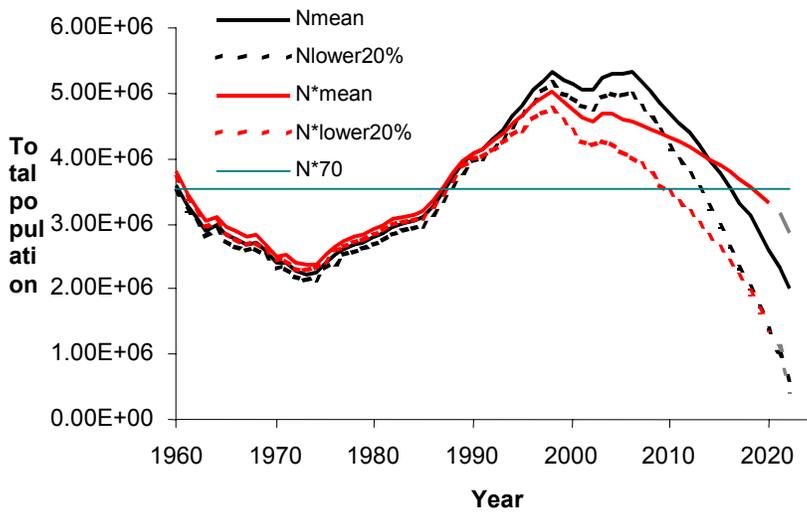


Figure 2c. Scenario F2 assessed in 2020. Grey lines indicate future projections.

Table 4. Simulation results relative to N_{Max} and N^*_{Max} . N_{mean} and N^*_{mean} refer to mean values from 100 simulation runs.

Scenario A	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.71		0.47		0.16
$N_{lower20\%}/N_{Max}$	0.63		0.36		-0.01
N^*_{mean}/N^*_{Max}	0.99	1.00	0.66	0.43	0.18
$N^*_{lower20\%}/N^*_{Max}$	0.83	0.73	0.40	0.02	-0.16
Scenario B1	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.86		0.68		0.44
$N_{lower20\%}/N_{Max}$	0.79		0.56		0.28
N^*_{mean}/N^*_{Max}	1.08	1.20	0.93	0.90	0.60
$N^*_{lower20\%}/N^*_{Max}$	0.91	0.94	0.71	0.56	0.27
Scenario B2	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.83		0.60		0.31
$N_{lower20\%}/N_{Max}$	0.74		0.48		0.15
N^*_{mean}/N^*_{Max}	1.04	1.09	0.78	0.60	0.37
$N^*_{lower20\%}/N^*_{Max}$	0.92	0.86	0.57	0.24	0.05
Scenario C1	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.92		0.81		0.66
$N_{lower20\%}/N_{Max}$	0.84		0.67		0.41
N^*_{mean}/N^*_{Max}	1.08	1.20	1.02	1.05	0.81
$N^*_{lower20\%}/N^*_{Max}$	0.92	0.93	0.76	0.66	0.44
Scenario C2	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.87		0.68		0.43
$N_{lower20\%}/N_{Max}$	0.77		0.55		0.22
N^*_{mean}/N^*_{Max}	1.02	1.03	0.82	0.67	0.49
$N^*_{lower20\%}/N^*_{Max}$	0.87	0.79	0.59	0.30	0.10
Scenario C3	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
N_{mean}/N_{Max}	0.86		0.67		0.41
$N_{lower20\%}/N_{Max}$	0.77		0.50		0.17
N^*_{mean}/N^*_{Max}	1.02	1.02	0.80	0.62	0.45
$N^*_{lower20\%}/N^*_{Max}$	0.87	0.77	0.53	0.18	0.05

Scenario C4	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.84		0.61		0.31
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.75		0.47		0.11
$N^*_{\text{mean}}/N^*_{\text{Max}}$	0.99	0.95	0.71	0.44	0.29
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.83	0.68	0.46	0.03	-0.04
Scenario D	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.94		0.86		0.74
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.85		0.70		0.50
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.06	1.15	1.01	1.02	0.86
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.94	0.91	0.79	0.64	0.52
Scenario E	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.93		0.84		0.70
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.84		0.70		0.46
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.05	1.13	0.99	0.97	0.81
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.95	0.94	0.73	0.56	0.46
Scenario F1	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.92		0.81		0.65
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.83		0.68		0.45
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.11	1.30	1.08	1.20	0.90
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.96	1.05	0.87	0.83	0.56
Scenario F2	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.88		0.71		0.49
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.78		0.56		0.26
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.08	1.20	0.96	0.96	0.66
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.92	0.92	0.70	0.53	0.28
Scenario F3	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.87		0.67		0.41
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.77		0.53		0.19
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.06	1.15	0.89	0.81	0.56
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	0.94	0.91	0.64	0.41	0.19
Scenario G	2010		2015		2020
	Assessment	Prediction for 2015	Assessment	Prediction for 2020	Assessment
$N_{\text{mean}}/N_{\text{Max}}$	0.97		0.90		0.79
$N_{\text{lower20\%}}/N_{\text{Max}}$	0.87		0.74		0.52
$N^*_{\text{mean}}/N^*_{\text{Max}}$	1.11	1.28	1.13	1.27	1.06
$N^*_{\text{lower20\%}}/N^*_{\text{Max}}$	1.01	1.07	0.88	0.84	0.64

Table 5 Values of N_{Max} and N^*_{Max} . These are taken as the maximum value of the mean trajectory for the total population up until 2004. Values of N_{Max} do not change at each assessment.

Scenario A	2010	2015	2020
N_{Max}	4.66E+06		
N^*_{Max}	5.24E+06	4.87E+06	4.64E+06
Scenario B1	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.66E+06	5.19E+06	4.99E+06
Scenario B2	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.67E+06	5.16E+06	4.97E+06
Scenario C1	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.67E+06	5.29E+06	5.15E+06
Scenario C2	2010	2015	2020
N_{Max}	5.31E+06		
N^*_{Max}	5.56E+06	5.20E+06	5.05E+06
Scenario C3	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.64E+06	5.22E+06	5.08E+06
Scenario C4	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.63E+06	5.19E+06	5.05E+06
Scenario D	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.84E+06	5.50E+06	5.33E+06
Scenario E	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.84E+06	5.44E+06	5.29E+06
Scenario F1	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.64E+06	5.25E+06	5.08E+06
Scenario F2	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.63E+06	5.22E+06	5.03E+06
Scenario F3	2010	2015	2020
N_{Max}	5.33E+06		
N^*_{Max}	5.62E+06	5.17E+06	4.98E+06
Scenario G	2010	2015	2020
N_{Max}	6.15E+06		
N^*_{Max}	6.02E+06	5.65E+06	5.39E+06

The 'C' scenarios are similar to the 'F' scenarios except that it is assumed that the 10% struck and lost rate and 85% reporting rate are used in the model to generate the estimated trajectories i.e. there is no bias in catch history or projections. These runs illustrate that the need for a reduction in TAC would be apparent earlier than for the 'F' scenarios.

Scenario B1 and B2 also assume no bias in the catches used in the model, but the increase in natural pup mortality from 2005 is assumed to be greater than for the 'F' scenarios.

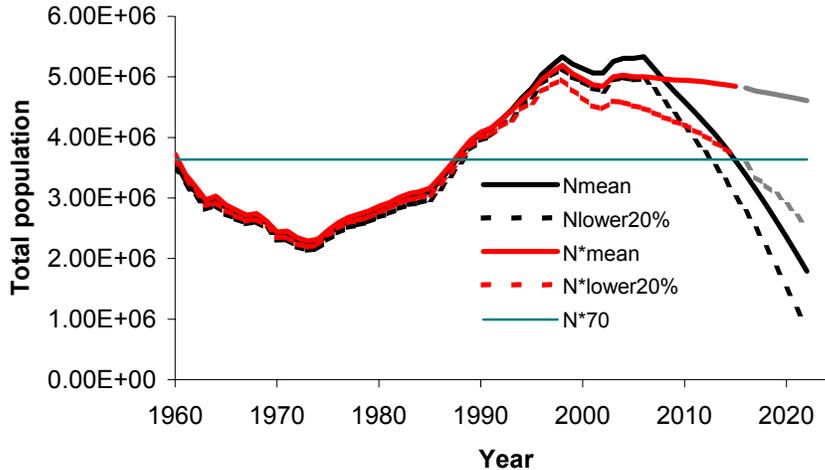


Figure 3. Scenario B1 assessed in 2015. Grey lines indicate future projections.

In the case of Scenario B1, the 2015 assessment still has the lower 20th percentile above N^*_{70} with the mean projected population for 2020 still at 90% of N^* (Figure 3). However if the TAC were not reduced then the mean population in 2020 would be at only 44% of N with the lower 20th percentile below N_{30} (Table 4). Based on the assessment in 2015 it may be difficult to identify the need for a large reduction in TAC based purely on uncertainty in future projections when the mean values might appear to support a continuation of the current TAC. The large spread of modelled trajectories basically indicates a poor model fit in this instance and the significance of this may not be easy to interpret in real situations.

Scenario G assumed no bias in survey results, so the difference between estimated and true is just due to bias in estimates of the total take of pups (due to non-reporting and struck and lost) and a change in mortality. Despite three surveys and 15 years since the change in mortality, the model still shows an increasing estimated trajectory in 2020 (Figure 4). This is in sharp contrast to the downward gradient of the true trajectory. One general feature illustrated by this example is that the lower percentiles of the true and estimated trajectories tend to converge more quickly than the mean values. This is also apparent in the sequence of Scenario F2 (Figures 2a-c).

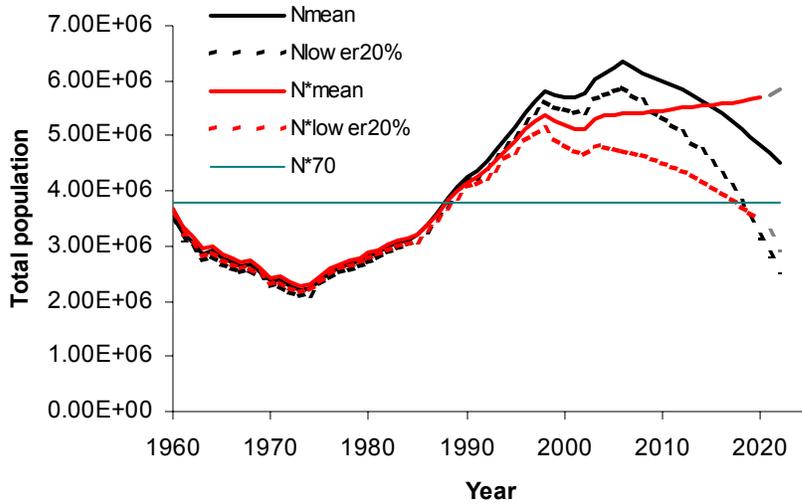


Figure 4. Scenario G assessed in 2020. Grey lines indicate future projections.

Scenario A assumes a 30% bias in survey results. Of the scenarios considered, this one would result in the most serious levels of depletion by 2015 (Table 4) despite a reported Canadian commercial catch of only 250,000. This is partly due to the fact that N_{Max} evaluated in 2010 is considerably higher than N^*_{Max} . Another point of concern with this scenario is that the lower 20th percentile of the estimates is also much greater than the mean of the true trajectories (Figure 5).

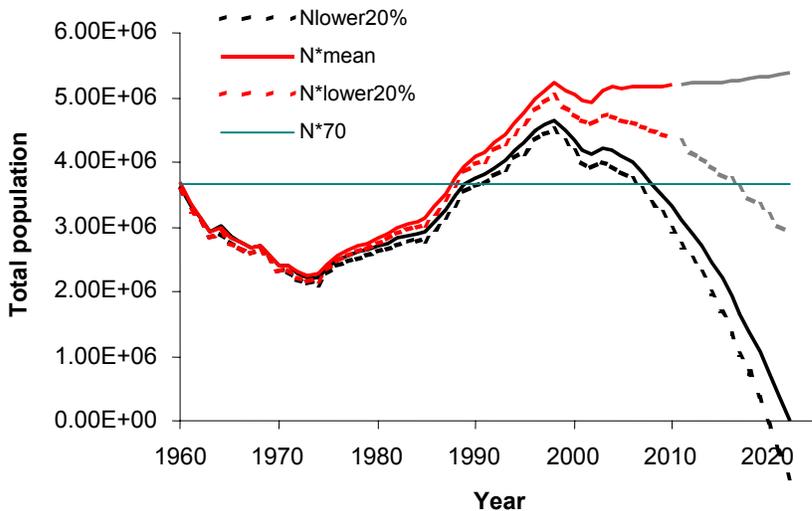


Figure 5. Scenario A assessed in 2010. Grey lines indicate future projections.

Discussion

All of the simulation runs described relate to situations where factors combine such that the impact of takes on the population is greater than would be anticipated. Thus in a situation where the TAC for Canadian commercial catches is initially set close to replacement yield, this TAC ought to be reduced to meet conservation objectives. The results of these runs use the likely information that would be available at the time of making such decisions and indicate the implications if the interpretation of that information is that there is no need to reduce the TAC.

For a management procedure 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 poor conservation status. The definition of 'poor conservation status' and the probability that is considered 'unacceptable' are value judgements. However, in the absence of fully specified objectives and an agreed procedure with catch limit rules, this judgement falls on politicians. The OBFM for harp seals does include reference levels N_{50} and N_{30} that relate to conservation status, but no precise catch limit algorithm has been provided. This contrasts with both RMP and PBR that provide precise limits on the maximum level of take according to a strictly defined procedure that once adopted would remove the need for discussion about how to set a TAC following each assessment.

The scenarios examined in detail here are examples of cases where a number of factors combine together. They give some indication of how the population model might perform but should not be considered as exhaustive tests. In particular, the timing of events relative to pup surveys may 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 in most cases little or no effect from increased pup mortality would be seen in the following assessment (in this case 2010) but the next assessment (2015) has maximum chance of detecting the change. Further simulations involving all possible combinations of time periods and episodic rather than constant changes could also be undertaken. This study did not attempt to assess the performance of the general population modelling approach used as a basis for management. To do this would require the development of alternative modelling approaches for comparison.

The individual factors for the difference in total mortality compared to reported landings and bias in aerial 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 (IWC, 1994). Although a bias of 30% on the aerial survey may seem large, it is not beyond the plausible range given the reliance on visual counting and the data from comparison of photo and visual techniques that can produce differences of much larger than 30% (Stenson *et al.*, 2005). It is also worth noting that both the RMP and PBR were tested, and required to be robust to, biases of 50% in survey estimates. The simulation (scenario A) assuming a positive bias of 30% in the aerial survey estimates does highlight the need to ensure that estimates cannot be subject to bias. Any 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. Thus all possible efforts should be made during surveys to obtain data which provide a permanent record that enables strip width and detection probability to be measured at the analysis stage. 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 combined effect of a struck and lost rate of 10%, and a reporting rate of 85% for Canadian commercial catches (giving reported landings = 0.77 true landings), are also 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 mortality rates of a factor of 2. The changes in pup survival considered are of a similar magnitude to that estimated by Hammill and Stenson (2003a) for either poor ice years or very poor ice years, but in this study were assumed to be ongoing rather than sporadic.

The results presented here raise both conservation concerns and operational concerns for the sealing industry. Management procedures that rely on sudden, drastic, changes in catch limits are not good for the industry or conservation. Even in situations where the Canadian management plan for harp seals meets its own conservation objectives, it is likely to require drastic changes in TAC at the first signs that the TAC has been set too high, in order to meet these objectives. Such decisions will be very difficult and politically unpopular for those responsible for management. 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 the estimated variance of future trajectories. 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 or large variance in predicted trajectories. The model itself is also rather sensitive to parameters and slightly different formulations of the same basic modelling approach may give different variances under different circumstances even if the means are similar.

DFO (2005) notes that 'Use of Replacement yield is a high risk approach'. This observation has also been made by Holt (2006) specifically in the case of harp seal management by Canada. Although we have not specifically used replacement yield in these simulations, our results confirm this conclusion and suggest 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 likelihood of the scenarios presented here actually happening cannot be quantified. However, it seems clear that the current management options under consideration would fail under the scenarios considered. By contrast a truly precautionary management regime would be expected to be robust to a combination of plausible factors leading to lower population numbers than anticipated. As an interim measure, while a fully specified management procedure can be developed and tested, setting catches according to PBR would be less of a high risk strategy both from a conservation perspective and for the stability of the industry. 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. The model runs presented here suggest that at least for this implementation of the population model and the scenarios considered, the lower 20th percentiles of the estimated and true trajectories converge much more quickly than the mean values. Thus the use of N_{MIN} (which is defined as the lower 20th percentile of the abundance estimate in the PBR calculations) may adequately account for the lack of direct estimates of abundance. However, some further simulation runs should be conducted based on PBR calculations to further investigate this.

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Appendix

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. In recent years it has been treated explicitly as a three parameter model (γ , m , s ; see below). Further implicit, deterministic parameters relating to unreported mortality have been independently guessed. The variations and developments over time, and the role of the parameters, are summarised in Table A1. These changes have led to a range of estimates, as shown in Table A2. In particular, the estimate of instantaneous mortality m has mostly varied between about 0.05-0.1.

Table A1. Models and data used for harp seal population dynamic model based on pup counts.

Study	Survey years					Other parameters varied deterministic	Sources of unreported mortality			Algorithm	Notes
	78-80	83	90	94	99		Struck and lost	Bycatch	Unreported catch		
Roff and Bowen 1983						γ^a				-	<ul style="list-style-type: none"> first use of likelihood method
Shelton <i>et al</i> 1992										SAS PROC NLIN	
Shelton <i>et al</i> 1996						γ^a				SAS PROC NLIN	<ul style="list-style-type: none"> 'harmonized' pregnancy rates introduced parameter s
Warren <i>et al</i> 1997						γ^a				SAS PROC NLIN	
Stenson <i>et al</i> 1999						γ^a $\Phi_{J,K}$ β			^c	SAS PROC NLIN	<ul style="list-style-type: none"> revised Greenland catch estimates first accounting for struck and lost animals
Healey and Stenson 2000						γ β		^b	^c	SAS PROC IML	<ul style="list-style-type: none"> explicit use of γ first accounting for bycatch nonparametric smoothing of pregnancy rates
Hammill and Stenson 2003a	?	?	?	?	?			^b	^c	Genetic algorithm minimising MMS	<ul style="list-style-type: none"> applied natural mortality after catch introduced additional mortality due to poor ice conditions
											<ul style="list-style-type: none">

ANNOTATIONS:

a: implicit use of γ

b: Newfoundland lump fishery; eastern US fishery

c: adjustment for unreported catch in Greenland only

SYMBOLS:

γ : for differential mortality of pups

m : instantaneous mortality

s : hunting selection parameter

$\Phi_{J,K}$: unreported mortality rates for age class J ($0 / 1+$) in area K (Front and Gulf / Canadian Arctic and Greenland)

β : proportion of pups in catch

Table A2. Previous estimates of parameters s and m as the parameter γ_1 is varied.

Study	γ_1					
	1		3		5	
	m	s	m	s	m	s
Roff and Bowen 1983	0.075	- ^a	0.0725	-	-	-
Shelton <i>et al</i> 1992 ^c	0.136	- ^a	-	-	-	-
Shelton <i>et al</i> 1996	0.107	2.912	0.0898	2.928	-	-
Warren <i>et al</i> 1997	0.107 0.107 ^b	2.91 2.93 ^b	-	-	-	-
Stenson <i>et al</i> 1999	0.085	-	0.073	-	-	-
Healey and Stenson 2000	0.0701	2.151	0.0584	2.227	0.0502	-
Hammil and Stenson 2003a	-	-	0.058	- ^d	-	-

a : s not estimated, but further process used to estimate initial population vector; see source

b : with variation in pregnancy rate

c : results for model *e* given here; see source

d : s not estimated, but $n_0(1960)$ estimated as 488,000

The following is a matrix representation of the population dynamics. Though presented here in matrix form, it is for the most part identical to the model described by Hammil and Stenson (2003a). It has been modified so that unreported mortality is now shown explicitly in the model, and a further age-dependence is introduced through the parameter γ_2 , which allows for higher mortality in the plus (>12) age class. Therefore, from here on we alter the notation for the pup mortality parameter from γ to γ_1 . We also believe on biological grounds that this is a more reasonable model; mortality increases at advanced ages are a mammalian characteristic.

Leslie equation for population dynamics

The population model is represented as a Leslie matrix equation, the simple, familiar form of which:

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

where at time t ,

$$\underline{n}(t) = [n_{0,t} \quad n_{1,t} \quad n_{2,t} \quad n_{3,t} \quad \dots \quad n_{A,t}]^T$$
 is the population vector at time t

and L_t is the Leslie matrix at time t .

The more elaborate form of this equation used in the harp seal model is now described. The Leslie equation can be decomposed using the time-dependent matrix Λ_t to represent births and transitions, and time-independent matrix S to represents (natural) survival:

$$\Lambda_t = \begin{bmatrix} f_{0,t} & f_{1,t} & f_{2,t} & \dots & f_{A-1,t} & f_{A,t} \\ 1 & 0 & 0 & & 0 & 0 \\ 0 & 1 & 0 & & 0 & 0 \\ \vdots & & \ddots & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 \end{bmatrix} \quad (2)$$

where $f_{i,t}$ is the per-capita pregnancy rate of age class i at time t

$$S = \text{diag}([S_0 \quad S_1 \quad S_1 \quad \dots \quad S_1 \quad S_2]) \quad (3)$$

where S_0, S_1, S_2 are the annual survival rates of the 0, 1+ and ‘plus’ age classes respectively.

In the Canadian harp seal model these individual survival rates are given by:

$$\begin{aligned} S_0 &= \exp(-\gamma_1 m / 2) \\ S_1 &= \exp(-m / 2) \\ S_2 &= \exp(-\gamma_2 m / 2) \end{aligned} \quad (4)$$

where m is the instantaneous mortality
 γ_1 and γ_2 are parameters ≥ 1 which control the mortality of the 0 and plus age classes respectively.

In addition to the effects of natural mortality, a catch vector $\underline{c}(t)$ is also incorporated. The Leslie matrix equations are then:

$$\underline{n}(t+1) = \Lambda_t S(\underline{n}(t) - \underline{c}(t)) \quad (5)$$

when catches were applied midway through the season (most previous studies), or

$$\underline{n}(t+1) = \Lambda_t S^2(\underline{n}(t) - \underline{c}(t)) \quad (6)$$

when catches were applied at the beginning of the season (Hammill and Stenson, 2003a).

For simplicity we use simpler notation for equation (6) in the remaining text:

$$\underline{n}(t+1) = L_t(\underline{n}(t) - \underline{c}(t)) \quad (7)$$

Catches

The reported landings are represented in each of the three regions (Front and Gulf; Canadian Arctic; and Greenland) as:

$$\underline{k}(t) = [k_{0,t} \quad k_{1,t} \quad k_{2,t} \quad \dots \quad k_{A,t}]^T$$

The total catch is distributed amongst the age-classes using sampling information (see Stenson, 2005).

In each region, 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. Under the current model, struck-and-lost-rates and reporting rates are estimated separately for pups and 1+ animals. Struck-and-lost rates are denoted by Φ_0 and Φ_{1+} , and reporting rates by r_0 and r_{1+} . Total catch is therefore estimated, separately for each region, as:

$$\underline{c}(t) = \left[\frac{k_{0,t}}{r_0(1-\phi_0)} \quad \frac{k_{1,t}}{r_{1+}(1-\phi_{1+})} \quad \frac{k_{2,t}}{r_{1+}(1-\phi_{1+})} \dots \right] \quad (8)$$

To date only struck-and-lost rates and bycatch have been considered as part of the unreported mortality parameters in the Canadian modelling, so the introduction of the parameter r is new¹.

Likelihood

Estimation of parameters is based on the likelihood now outlined.

Let

- $\underline{g}(t)$ be the catch vector at time t
- t_0 be the time at which fertility data first becomes available
- $\underline{\theta}=[m,s,\gamma_1,\gamma_2]$ be the vector of parameters to be estimated.
- a_1, a_2, \dots, a_d be the years where pup production estimates were obtained by survey
- $\underline{n}(t)$ be the age structure at time t
- $n_0(t)$ be the number of pups at time t
- p_{a_1}, \dots, p_{a_d} be the pup survey estimates for years a_1, \dots, a_d with variances $\sigma_{a_1}^2, \dots, \sigma_{a_d}^2$

The likelihood of the data, conditional on $\underline{n}(t_0)$, is then:

$$L(\underline{\theta} | \underline{n}(t_0)) = \Pr(p_{a_1}, p_{a_2}, \dots, p_{a_d} | \underline{\theta}, \underline{n}(t_0)) \quad (9)$$

From the deterministic population dynamic model we obtain $E(\underline{n}(t_a) | \underline{n}(t_0))$ by iterating equation (7) from t_0 to t_a . This then also gives $E(n_0(t_a) | \underline{n}(t_0))$.

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

$$L(\underline{\theta} | \underline{n}(t_0)) = \prod_{i=1}^d \frac{1}{\sqrt{2\pi}\sigma_{a_i}} \exp\left(\frac{[p_{a_i} - E(n_0(t_{a_i}) | \underline{n}(t_0))]^2}{-2\sigma_{a_i}^2}\right) \quad (10)$$

The likelihood specified above is conditional on $\underline{n}(t_0)$ but this is unknown and therefore itself 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:

$$sc_0(t) = n_0(t) \quad (11)$$

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

Simulations

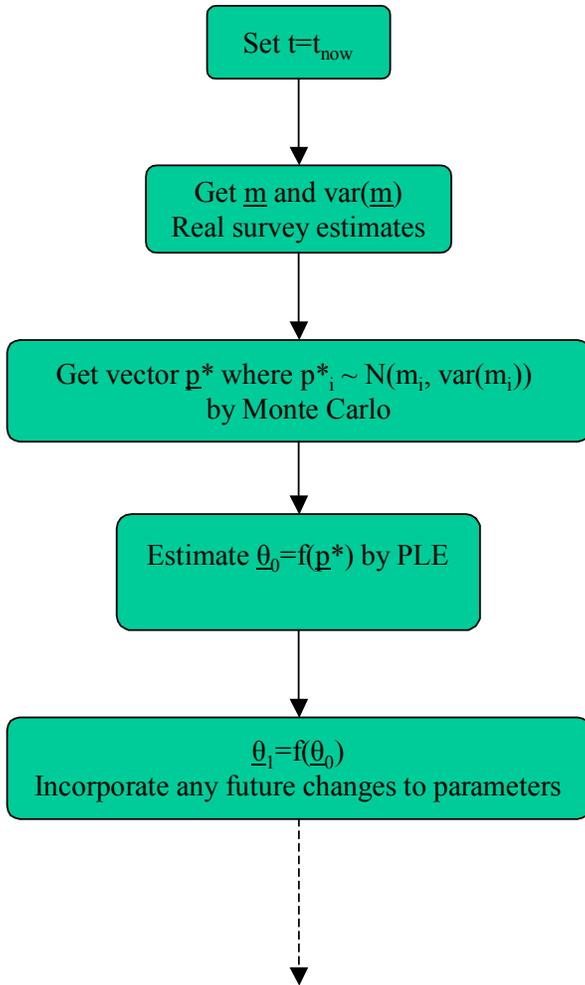
The simulation process is shown as a flow diagram below.

The fundamental steps are:

- (1) Generation of ‘true’ parameter estimates ($\underline{\theta}_0$) by Monte Carlo sampling of the pup survey distributions to date. This is similar to that approach taken by Warren (1997). As explained below, the estimation at this stage uses profile likelihood estimation (PLE).
- (2) Projection of true population trajectory forwards based on $\underline{\theta}_0$ or known modifications of it (giving $\underline{\theta}_1$). These alterations of $\underline{\theta}_0$ to $\underline{\theta}_1$ are to examine the effect of unknown changes to the population parameters e.g. higher mortality.
- (3) Generation of new, projected survey estimates based on the known true trajectory.
- (4) Estimation of the parameters using the survey estimates (giving $\underline{\theta}^*$) using maximum likelihood estimation (MLE).
- (5) Projection of the population forwards based on $\underline{\theta}^*$ to give the estimated population trajectory.

¹ Some adjustment for non-reporting were made directly to the Greenland kill statistics by Stenson. (2005)

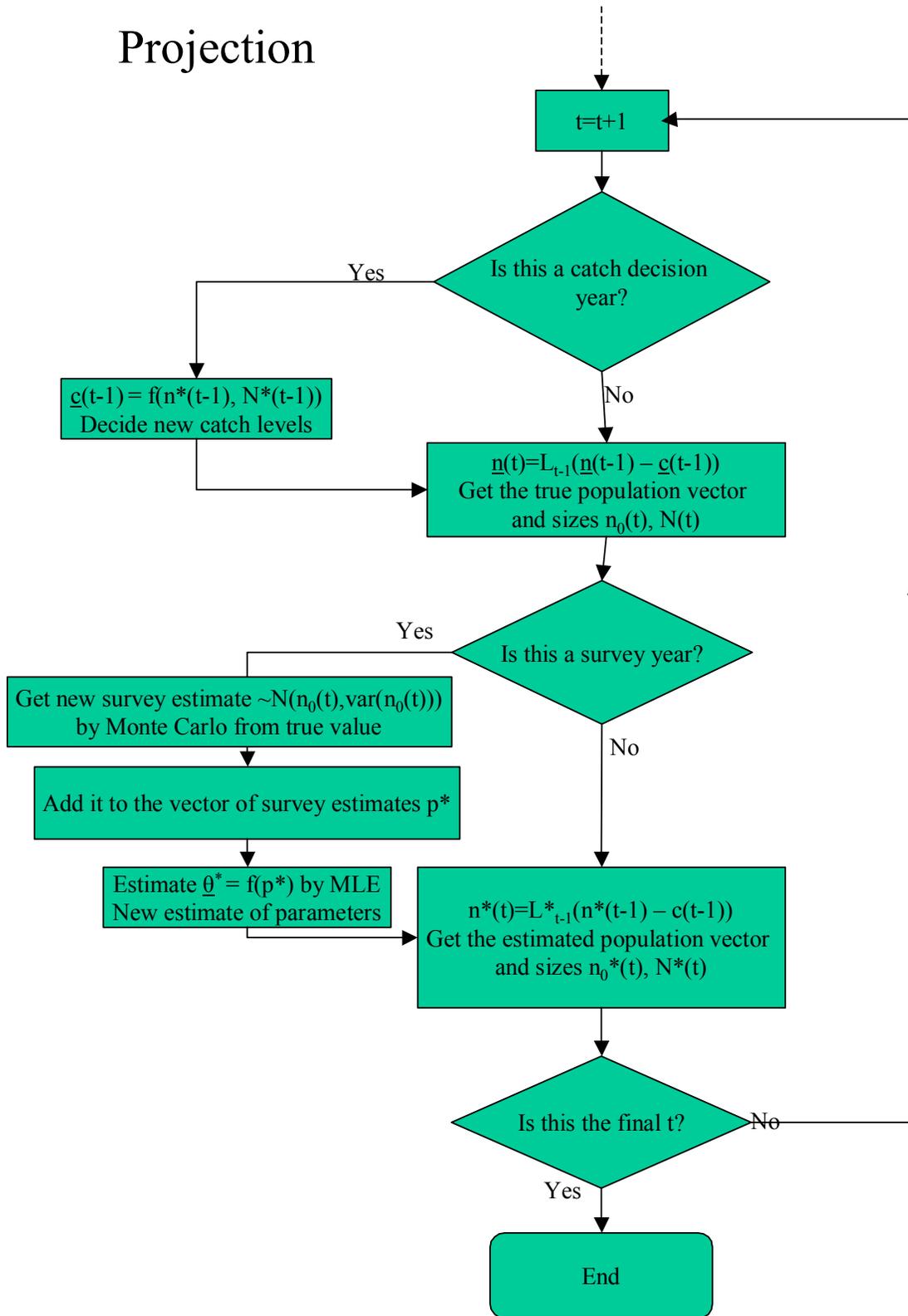
Initialisation



Notation:

t_{now}	time of most recent survey
$f(\)$	'function of'
\underline{m}	vector of survey estimates from previous years
\underline{p}^*	vector of Monte Carlo pup survey estimates
MLE	maximum likelihood estimation
PLE	profile likelihood estimation
$\underline{\theta}_0$	true parameter values up to t_{now}
$\underline{\theta}_1$	true parameter values from t_{now}
$\underline{\theta}^*$	estimated parameter values
$\underline{n}(t)$ and $\underline{n}^*(t)$	true and estimated population vectors
$N(t)$ and $N^*(t)$	true and estimated total population sizes
$n_0(t)$ and $n_0^*(t)$	true and estimated pup population sizes
$\underline{c}(t)$	catch vector at time t
$L(\underline{\theta}_1)$	true Leslie matrix
$L^*(\underline{\theta}^*)$	estimated Leslie matrix

Projection



An illustration of this process is given in Figure A1. The black line is the true population trajectory (for this simulation event) based on $\underline{\theta}_0$ and $\underline{\theta}_1$. The blue line is the estimated trajectory assuming $\underline{\theta}^*$ which is based on the survey data (red dots). The survey data is based on real pup surveys (red dots with confidence limits) and simulated future pup surveys (red dots) from the true trajectory (black line).

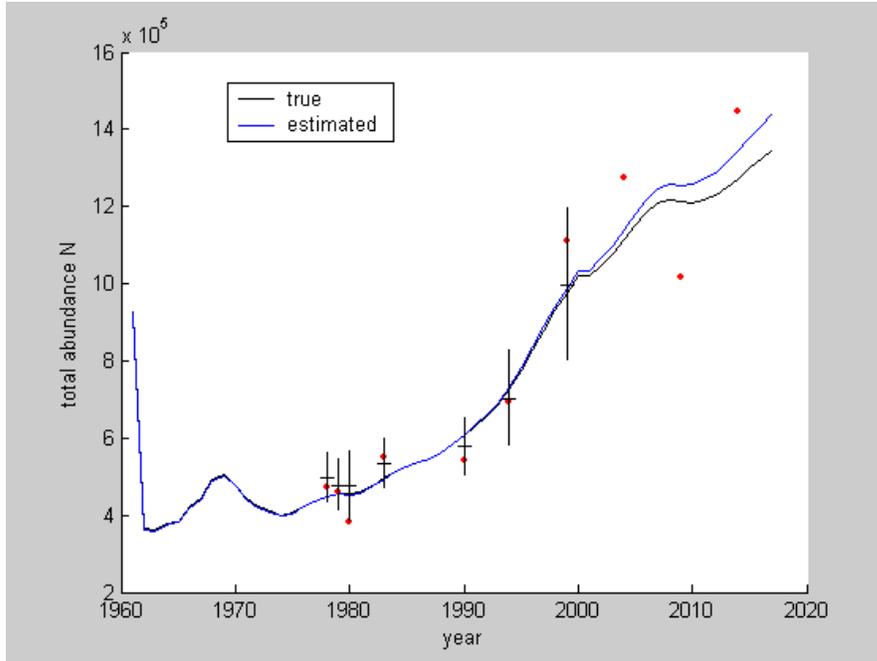


Figure A1. Illustration of simulated population trajectories.

An important point to note about this process is the linkage between the true and estimated trajectories. The estimated population sizes $N^*(t)$ determine the catch levels. The levels of these catches determine the true population $N(t)$ the following year. Survey estimates (and estimated population sizes) are based on the true pup population sizes. This cycle then begins again at the next iteration.

Likelihood-based estimation

Two methods are used: profile likelihood estimation and maximum likelihood estimation.

Profile likelihood estimation is used to generate ‘true’ parameter vectors based on real survey estimates and their variances. The vector $\underline{\theta}$ is divided into the parameters of interest $\underline{\rho}=(m,s)$ and the nuisance parameters $\underline{\eta}=(\gamma_1,\gamma_2)$. The nuisance parameters are not estimated directly but are allowed to vary (within limits). The use of profile likelihood has two advantages. Firstly, the potential variation in $\underline{\eta}$ is incorporated in the population modelling. Secondly, there were numerical difficulties in optimising a near-collinear system using standard methods, which are circumvented.

Maximum likelihood estimation is used to estimate the parameter vector based on survey data (real and projected). Estimates are made of $\underline{\rho}$ given *fixed* values of $\underline{\eta}$. This approach is used because it has been taken by DFO. Hammill and Stenson (2003a) use $\gamma_1=3$ and effectively use $\gamma_2=1$ (the latter is not a free parameter in their models).