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A review of the analysis to evaluate the recovery of bowhead whales, *Balaena mysticetus*, in the eastern Canadian Arctic

Examen de l'analyse visant à évaluer le rétablissement des baleines boréales, *Balaena mysticetus*, dans l'est de l'Arctique canadien

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ABSTRACT

The present investigation calculates possible times to recovery of the bowhead whale population of the eastern Canadian Arctic Ocean, based on the limited knowledge currently available. Recovery was defined as the population growing up to 70% of the assumed pre-exploitation abundance. The simulation used a stochastic generalized logistic model and considered alternative assumptions about parameter values; current status and possible future catch levels. One single stock was assumed to constitute the bowhead whale population in the eastern Canadian Arctic, including Prince Regent Inlet, Baffin Bay, Davis Strait, Hudson Bay and Foxe Basin. The uncertainty associated with the current level of knowledge about the population dynamics and status of the bowhead whale population in the eastern Canadian Arctic leads to a wide range in the possible times to recovery. Results indicate that improvements in the estimate of the current population size would considerably narrow the range in times to recovery. Of all harvest levels explored, a removal of 50 animals caused the greatest delay in the time to recovery. Removing 15 animals per year can cause a considerable delay under some parameter assumptions, but if the catch is below 10 animals, there is virtually no delay in the time to recovery. This result will hold under the assumptions that this population is appropriately described by a logistic model with parameter values within the range used in the present analysis; that current environmental conditions won't change beyond the limits imposed by the model (including the occurrence of catastrophic events); and that there are no other significant sources of mortality. Finally, the behaviour of the component of process error in the population model indicated that values of $\sigma_{process}$ 0.015 and higher lead to annual growth values that may be unrealistic for the population of bowhead whales in the eastern Canadian Arctic. On the other hand, all tested values of $\sigma_{process}$ allow negative growth when the population is approaching carrying capacity, but only if set to 0.2 or higher, can the population present negative growth at lower population levels. Although this can be considered a caveat of this component of the model, it was considered to be acceptable to represent natural variability. Fluctuations in the annual growth due to process error are expected to be smaller than the observed fluctuations in the eastern stock of gray whales and a choice of $\sigma_{process}$ of 0.01 and ρ of 0.8 was made for the analysis.

RÉSUMÉ

Le présent examen vise à calculer le délai de rétablissement possible de la population de baleines boréales de l'est de l'Arctique canadien, à partir des connaissances limitées actuellement disponibles. Le rétablissement est défini comme l'augmentation de la population jusqu'à 70 % de l'abondance présumée d'avant l'exploitation. La simulation, effectuée au moyen d'un modèle logistique généralisé stochastique, a permis d'examiner des hypothèses différentes à propos des valeurs des paramètres : la situation actuelle et les niveaux futurs possibles de capture. On a supposé qu'un seul stock constituait la population de baleines boréales dans l'est de l'Arctique canadien qui comprend l'inlet Prince-Régent, la baie Baffin, le détroit de Davis, la baie d'Hudson et le bassin Foxe. L'incertitude associée aux connaissances actuelles de la dynamique de la population et de la situation de la population de baleine boréales de l'est de l'Arctique canadien donne lieu à un large éventail de délais de rétablissement possibles. Les résultats montrent que l'amélioration de l'estimation de la taille de la population resserrerait considérablement l'éventail des délais de rétablissement. Parmi tous les niveaux d'exploitation évalués, un retrait de 50 bêtes entraînerait le plus long délai de rétablissement. Le fait de retirer 15 animaux par année peut causer un délai considérable dans le contexte de certains paramètres, mais si les prises sont inférieures à 10 animaux, il n'y aurait à peu près pas de délai de rétablissement. Ce résultat est valable dans la mesure où l'on suppose que la population est correctement décrite par un modèle logistique utilisant des valeurs de paramètres se situant dans l'échelle utilisée pour la présente analyse, que les conditions actuelles de l'environnement ne dépasseront pas les limites imposées par le modèle (y compris l'occurrence d'événements catastrophiques) et qu'il n'y a pas d'autre source importante de mortalité. Enfin, le comportement de la composante de l'erreur de traitement dans le modèle de population a indiqué que des valeurs de $\sigma_{process}$ de 0,015 et plus entraînaient des valeurs de croissance annuelle de la population qui peuvent être irréalistes pour la population de baleines boréales de l'est de l'Arctique canadien. Par ailleurs, toutes les valeurs utilisées de $\sigma_{process}$ permettent une croissance négative quand la population approche de la capacité de charge, mais c'est uniquement à 0,2 ou plus que la population présente une croissance négative à des niveaux de population inférieurs. Bien que cette situation puisse susciter une mise en garde à l'égard de cette composante du modèle, celui-ci est jugé acceptable pour représenter la variabilité naturelle. Les fluctuations de la croissance annuelle dues à l'erreur de traitement devraient être inférieures aux fluctuations observées au sein du stock de l'est de baleines grises et un choix de $\sigma_{process}$ de 0,01 et de ρ de 0,8 a été fait pour l'analyse.

INTRODUCTION

The present report includes results of analyses that are an extension and a review of the previous efforts to evaluate time to recovery of bowhead whales in the eastern Canadian Arctic (Alvarez-Flores 2006). The analyses reported here include additional catch options and a revised estimate of abundance. The description of the process error term is also presented with additional figures and explanations that aim to clarify previous questions regarding its influence on annual growth. A good portion of the content in this report is taken from the previous one, allowing the report to be a stand alone document. Although times to recovery presented here are different from those in the previous report, the main conclusions remain the same and only a few additions are made.

METHODS

Time to Recovery

A simulation model was built and coded using the C++ computer language. The overall structure of the model is represented in Fig. 1 and appendix 1 presents a description and a guide to the use of the software. The program requires an input file to feed the all assumptions for parameter values, the alternative catch levels and all necessary variables to control the simulations. Values used in the present analysis are shown in Table 1.

The Conservation Strategy considers a time frame of 100 years to monitor recovery because of the estimated lifespan of the bowhead whale and its slow population growth rate. For this reason, the simulation model projected the population 100 years using different combinations of parameters ψ, K, R_{max} (see the description of the population model below for parameter definitions) as well as all alternative catch levels. Each population trajectory spanning 100 years for each set of parameters and catch was repeated 5000 times. For each trajectory, the number of years that it took the population to be equal or greater than $0.7K$ was stored. Next, the 5000 values of time to recovery obtained for each set of parameters and catch were used to create a frequency distribution histogram with a bin size of one year and then standardized to obtain probability and cumulative probability distributions. From the cumulative probability distribution the year to recovery (YTR) corresponding to the 95th percentile was arbitrarily chosen as the acceptance level to decide that the population had recovered to the selected target level.

Decline

When a deterministic logistic model is used to project a population subject to an unsustainable constant catch level, it is enough to check if the abundance at the beginning of the projection N_0 is smaller than N_{0+1} because the declining trend will continue at least for part of the projection. In a stochastic logistic model however, this is not useful because chance will determine the outcome for any single realization. In this way, a large number of simulations are run to determine

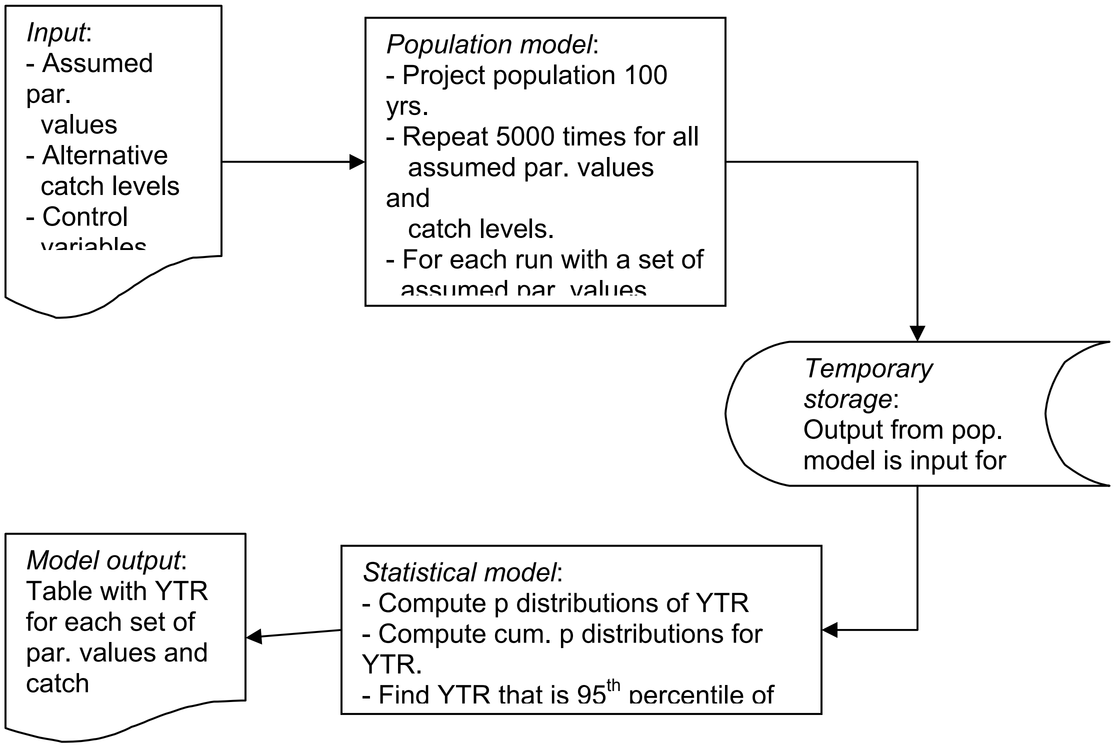


Fig. 1. Flow chart describing the general structure of the simulation model to compute the time to recovery of bowhead whales in the eastern Canadian Arctic.

if the population is recovering or declining with some projections within a trial presenting an increasing trend and others a declining one. The decision to determine that under a certain combination of parameters and catch a population has a high probability of declining was built in two steps. First, a single population trajectory had a declining trend if the projection reached 100 years without recovery and the abundance at time N_{100} was smaller than N_0. Secondly, during a trial, the number of trajectories resulting in a decline was counted. If 95% or more of the projections resulted in a decline, then the result of that trial was a decline.

Population model
A single population of bowhead whales in the eastern Canadian Arctic was projected using a generalized logistic model with lognormal process error (Hilborn and Mangel 1997):

$$N_{t+1} = \left[N_t + N_t \ R_{\max} \left[1 - \left(\frac{N_t}{K} \right)^{\psi} \right] \right] e^{u_t} - C_t$$

Where the process residual u_t is serially correlated and computed as:

$$\boldsymbol{u_t = u_{t-1} \ \rho + \sqrt{1 - \rho^2} \ \ x \ \sigma_{process}}$$

such that $\boldsymbol{VAR(u_t) = \sigma^2_{process}}$ and $\boldsymbol{cor(u_t, u_{t-1}) = \rho\sigma^2_{process}}$
(Punt pers. comm.; see Appendix 2 for proof).

Also:
N_t = Abundance at time t or t + 1; time in years.
R_{max} = The discrete-time maximum annual population growth.
K = The pre-exploitation population size.
ψ = A parameter that determines the population level where productivity is maximum, also known as the “shape parameter”, usually called ‘*z*’ but here given a different name to distinguish it from the statistic ‘*z*’ used in the previous report during the sampling process to compute PBR.
C_t = The number of whales killed in year t.
ρ = The strength of the autocorrelation in the process error.
$\sigma_{process}$ = The standard deviation of the process error representing the level of natural variability.
x_t = A random number drawn from a standard normal distribution.

Table 1 shows the alternative values assumed for the parameters of the logistic model together with catch options and all other control variables.

Selecting values of the population model parameters
Although alternatives for the parameter values in the logistic model are somehow arbitrary, an effort was made to use guidelines based on current knowledge about marine mammals, other stocks of bowhead whales or about the eastern Canadian Arctic stock itself.

Feasible values for the proportion of MNPL/*K* in marine mammals have been suggested to fluctuate within a range of 0.5 to 0.8 (Taylor and De Master 1993), corresponding to ψ values of 1 and 11.22. For the present analysis, the selected ratios of MNPL/*K* were 0.5, 0.675, and 0.85, corresponding to ψ values of 1, 4.2 and 18.18 respectively.

Table 1. Parameter values, alternative catch levels and variables to control the simulations to calculate time to recovery of bowhead whales in the eastern Canadian Arctic assuming a single stock. Parameters are used in a generalized logistic model with ψ = shaping parameter, K = pre-exploitation population level or carrying capacity, R_{max} = maximum annual population growth, N_0 = initial population size, ρ = correlation level in process error and $\sigma_{process}$ = variability in process error.

Parameter values					
ψ	K	R_{max}	ρ	$\sigma_{process}$	N_0
1	9000	0.01	0.8	0.01	5100
4.2	12300	0.03			
18.18	15000	0.05			
Catch					
Whales killed (or struck and lost) yearly					
0					
2					
4					
8					
15					
50					
Control variables					
Target fraction of K for recovery	0.7				
Acceptance level for YTR	0.95				
Initial year of projection	2005				
Years to project	100				
Number of simulations	5000				

Selecting values for the maximum annual per capita population increase was based on current knowledge about the Western Arctic stock of bowhead whales. The most recent stock assessment for the Western stock conducted by the US NOAA Fisheries suggests an R_{max} of 0.04 (Anglis and Lodge 2004). For the present analysis, DFO requested that values of 0.01, 0.03 and 0.05 were used.

A significant difference from the previous analysis is that only a single assumption about the present abundance was made. Current abundance of bowhead whales is estimated to be 7,309 (CV = 44.8), and DFO decided that the 20th percentile of the distribution of abundance should be used as input to the model, therefore N_0 was set to 5,100.

The pre-exploitation abundance for the eastern Canadian Arctic stock has been estimated to be of 12,300 whales (Woodby and Botkin 1993; COSEWIC 2005).

To choose alternative values, it was decided to take approximately the 60% CI from a normal distribution (the approximation would be about the same using a lognormal distribution) assuming a CV of 0.3 and a mean of 12,300. This resulted in a low value of 9,000 and a high value of 15,000.

Selecting values of ρ and $\sigma_{process}$

In the equation to compute the serially correlated process residual, parameter ρ determines the degree to which a residual is correlated to the previous one, in other words, to what extent a residual will likely be followed by another residual of similar magnitude and sign. On the other hand, parameter $\sigma_{process}$ determines the magnitude of the natural variability or the size of the residuals.

When this lognormal process error is applied to the logistic model, it is important to note first that the error is applied to the whole population and not explicitly to the parameter of growth R_{max}. This means that if environmental conditions are appropriate, subsequent states of the population (e.g. N_t, N_{t+1}) may follow each other to conform some trend for a period of time. However, because $\ln(N_{t+1} / N_t)$ is the annual growth r_t, it follows that the population growth is autocorrelated in the same way as the abundance. Recall also that R_{max} = maximum expected value of $(N_{t+1} / N_t) - 1$ which is an approximation of $\ln(N_{t+1} / N_t)$. Observe now in Fig. 2 the plots of $\ln(N_{t+1} / N_t)$ vs. time (with K = 12,300, R_{max} = 0.04 and ψ = 4.2). For reference, the graphs overlap the resulting deterministic and the stochastic trajectories of r_t. These stochastic curves were generated with a single set of random numbers and are useful only to exemplify the effect of using different combinations of ρ and $\sigma_{process}$. In these curves, the left part of the plot corresponds to the growth at low population levels compared to K (N_0 = 3,154) and therefore it approaches R_{max}. Notice that a small $\sigma_{process}$ = 0.0005 introduced a level of variability in r_t that made the stochastic growth almost indistinct from the deterministic. On the contrary a larger value of $\sigma_{process}$ = 0.05 created extremely large fluctuations in the value of r_t, in some cases making it reach values of 0.1 or more which may be very unrealistic for the bowhead whale. An intermediate value of $\sigma_{process}$ = 0.005 produced interesting fluctuations in r_t with maximum values that didn't go over 0.05 which is a fairly plausible value for bowhead whales and was the maximum value assumed for R_{max} in the analyses of recovery.

A better description of the behavior of the population model under different levels of process error an autocorrelation was developed running a series of simulation trials. In these simulations, a population was projected with the parameters of dynamics K = 12,300, R_{max} = 0.04 and ψ = 4.2. The initial population size was set to 500 to observe the response from severely depleted levels and was

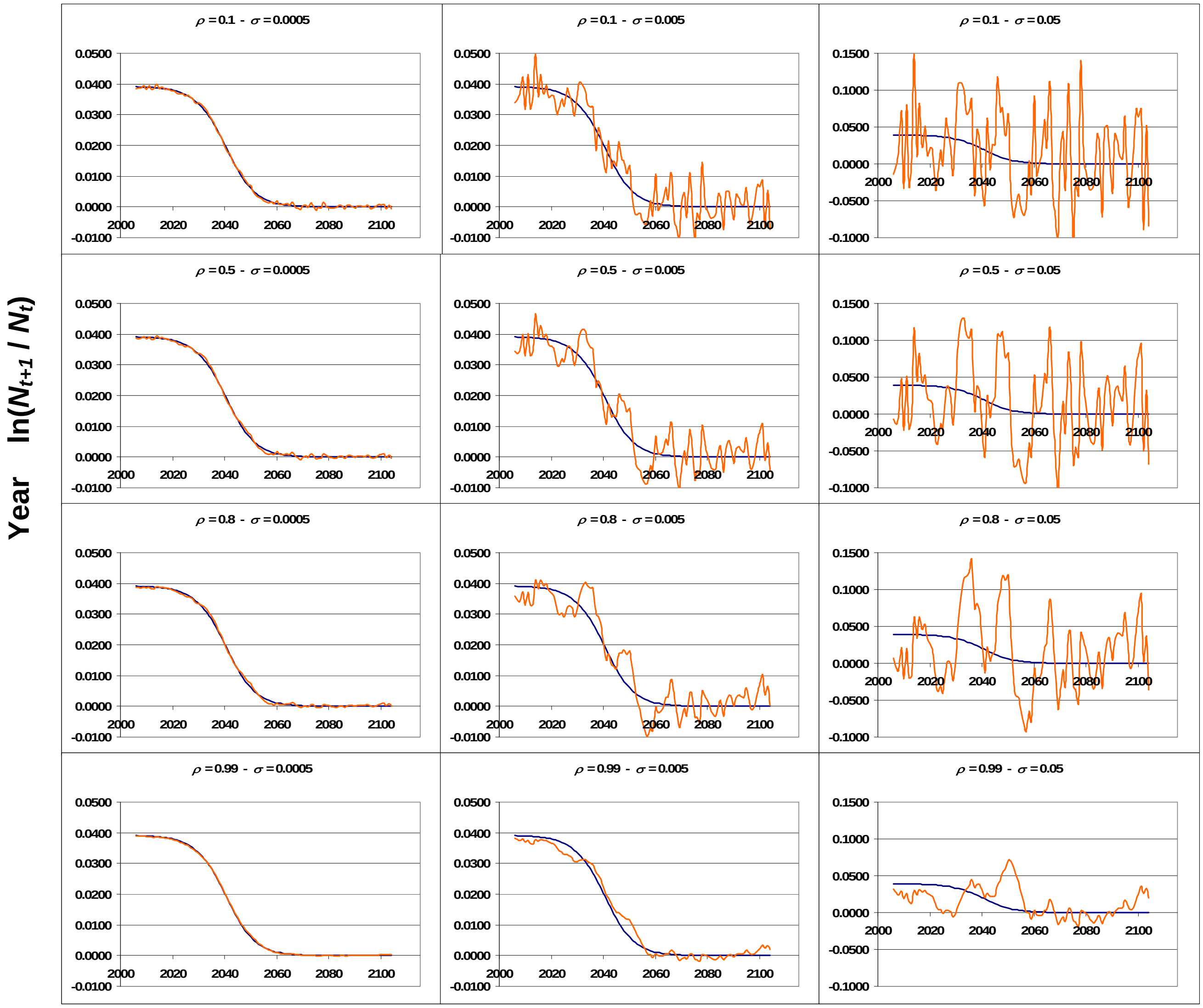


Fig. 2. Effect of stochasticity on annual population growth as determined by alternative parameter values. Dark line is the deterministic trend, light colored line is stochastic.

projected for 100 years. Each projection with a single combination of $\sigma_{process}$ and ρ was repeated 5000 times. Bounds of -0.1 to 0.1 were set to the annual growth and if exceeded the projection was discarded. These bounds allow a considerable margin of fluctuation in the annual growth but don't allow implausible (although not impossible) growth levels. Each projection was divided in three sections. The first section went from the initial population size of 500 to the inflection point of the population curve at MNPL where density dependent effects start causing a decline in productivity. The second section went from the MNPL to half the distance between MNPL and K for moderate density dependent effects. The last level went up to K to observe maximum density dependent effects. For each section of the projection, the maximum and the minimum growth values were saved, therefore, for every combination of process error parameters, the distribution and summary statistics were obtained for the maximum and minimum at each section of the population trajectory.

To facilitate interpretation of the results of the simulations, the information is presented in different ways. First, the distributions of three parameter combinations were selected to present a graphical picture of the possibilities of maximum and minimum values of growth during the three different stages of the projection. The selected cases were high variance and moderate correlation ($\sigma_{process}$ =0.05 and ρ=0.8); moderate variance and moderate correlation ($\sigma_{process}$ =0.02 and ρ =0.8); finally, low variance and high correlation ($\sigma_{process}$ =0.01 and ρ=0.95). Each set of graphs in figures 3 to 5 include their corresponding summary statistics to aid in the interpretation of both the graphs and the summary statistics table.

In the first case ($\sigma_{process}$ =0.05 and ρ=0.8), both maximum and minimum values fell heavily towards the bounds, meaning that in many cases the population exceeded the established limits to annual growth (both increasing and decreasing) and therefore considered unlikely for bowhead whales on a regular basis. Additionally, a wide range of values were observed with this selection of parameters with a lager spread of the distributions in the case of the minimums. In the second case ($\sigma_{process}$ =0.02 and ρ =0.8), reducing the process error moved the distributions away from the bounds, although the maximums at low population levels were still considerably close to the upper bound.

Finally, setting $\sigma_{process}$ to 0.01 and ρ to 0.95 not only narrowed the spread of the distributions limiting the range of possible annual growth, but centered the distributions on values that are considered more realistic for bowhead whales. For the same three cases above, the distribution of the deviation from the deterministic projection is presented in Fig. 6. Values in the *x* axis of the charts are deviations at all times during the projections. They can be a deviation when the population is at low levels and therefore the deterministic annual growth was close to R_{max}, but could also be a deviation from the growth when the population was approaching *K* and therefore the annual growth was low. Observe that when process error was large (0.05), the stochastic growth could depart considerably from the deterministic values causing unrealistic population fluctuations. Moderate levels of process error (0.02) restricted the departures to more realistic scenarios, but if the departure was positive at low population levels, the maximum growth values could be above 9% (0.04 + 0.05). Under this level of process error, an extreme negative departure can be considered reasonable if caused by rare catastrophic events. When process error was set to (0.01), level of fluctuation in the annual growth appeared more constrained to fluctuations that can be more easily explained by the biology of the species and environmental conditions. However, negative departures from the deterministic growth may still be considered insufficient because strong catastrophic events may not be properly represented.

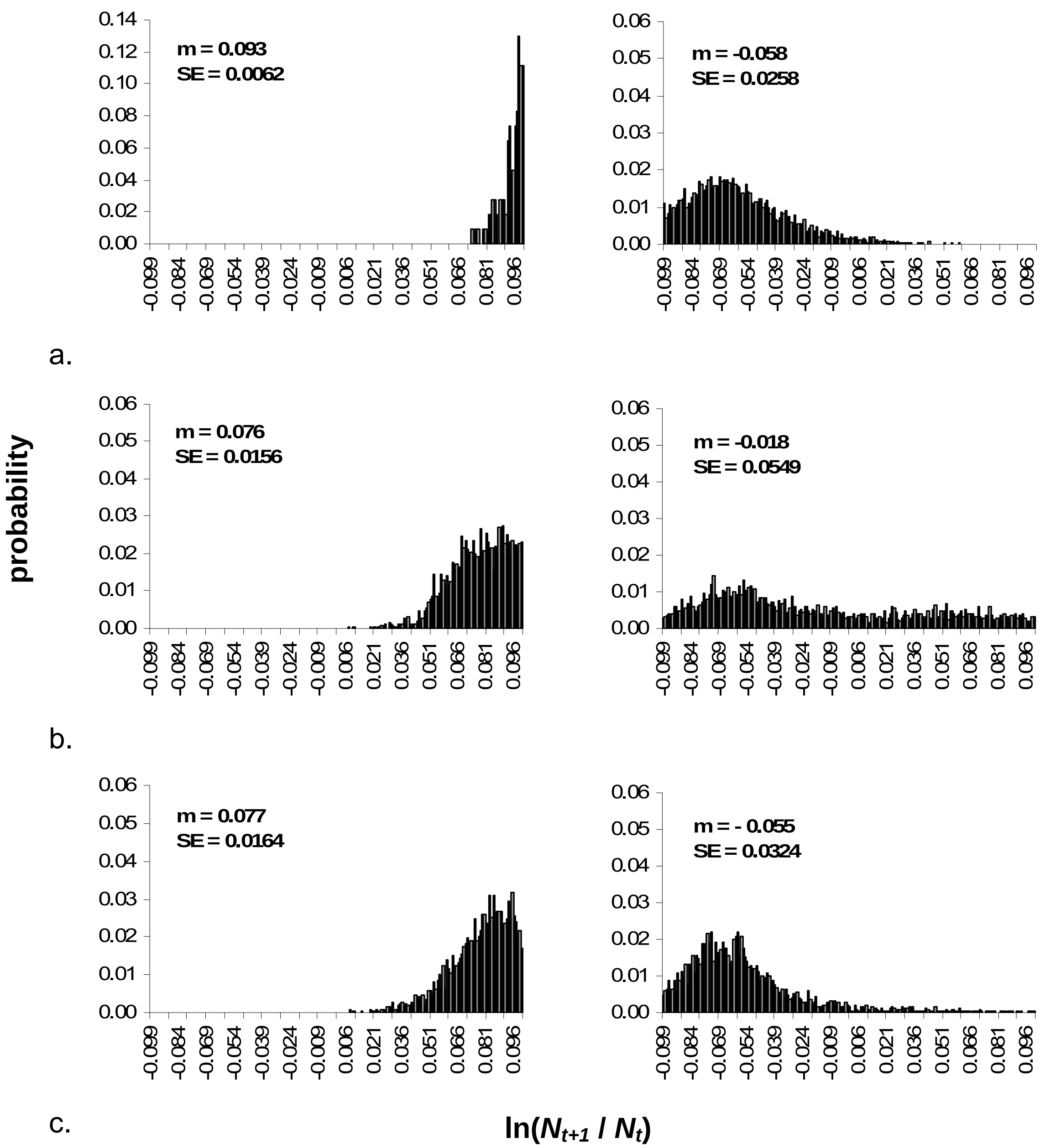


Fig. 3. Distribution of the maximum (left panels) and minimum (right panels) annual growth obtained during simulations of stochastic projections of bowhead whales. The projections in this figure were made using parameters $\sigma_{process}$ =0.05 and ρ=0.8 and are presented for the cases where the population was below MNPL (a), between MNPL and 0.5(*K*-MNPL) (b) and above 0.5(*K*-MNPL) (c).

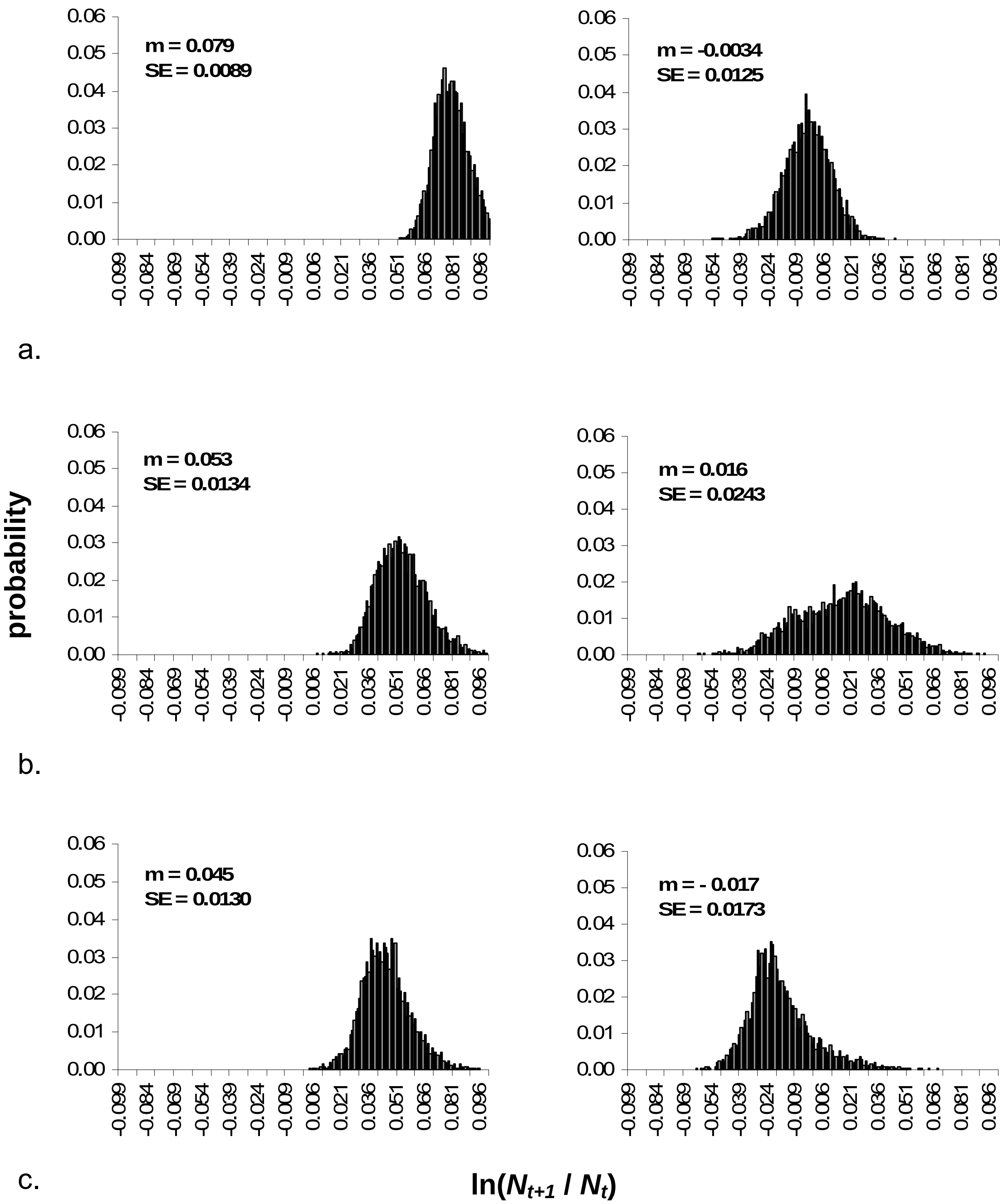


Fig. 4. Distribution of the maximum (left panels) and minimum (right panels) annual growth obtained during simulations of stochastic projections of bowhead whales. The projections in this figure were made using parameters $\sigma_{process}$ =0.02 and ρ =0.8 and are presented for the cases where the population was below MNPL (a), between MNPL and 0.5(*K*-MNPL) (b) and above 0.5(*K*-MNPL) (c).

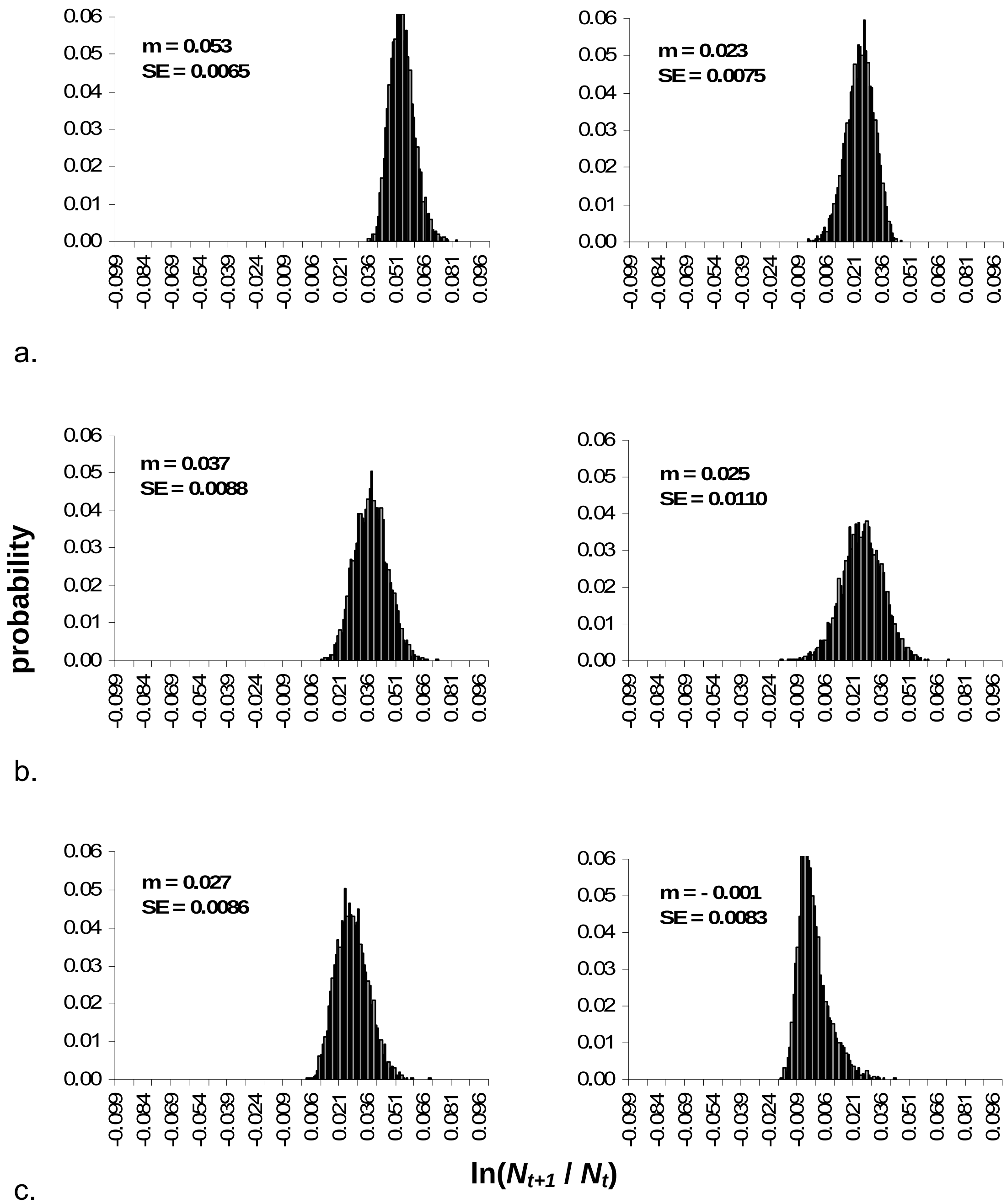
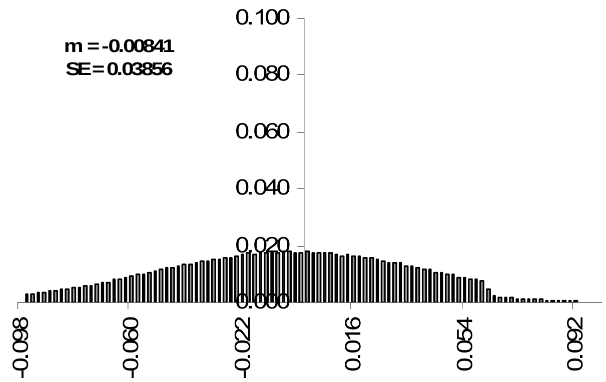
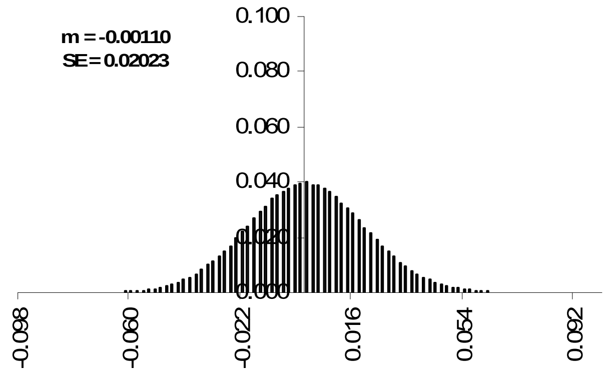


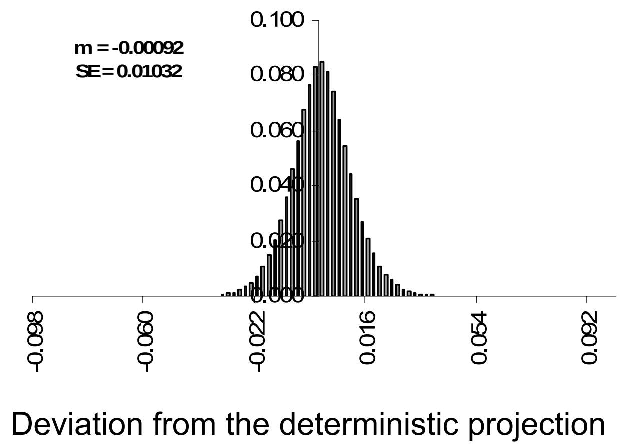
Fig. 5. Distribution of the maximum (left panels) and minimum (right panels) annual growth obtained during simulations of stochastic projections of bowhead whales. The projections in this figure were made using parameters $\sigma_{process}$ =0.01 and ρ=0.95 and are presented for the cases where the population was below MNPL (a), between MNPL and 0.5(K-MNPL) (b) and above 0.5(K-MNPL) (c).



a.



b.



c.

Fig. 6. Distribution of the deviations from the deterministic projected annual growth of bowhead whales in stochastic simulations using parameters $\sigma_{process}$ =0.05 and ρ=0.8 (a), $\sigma_{process}$ =0.02 and ρ =0.8 (b) and $\sigma_{process}$ =0.01 and ρ=0.95 (c).

An alternative way to present the results of these simulations was to plot the mean maximum and minimum values (Fig. 7). In each section of this figure, the upper panel shows the maximum values and lower shows the minimums. The values in the charts are ordered and included in boxes representing the level of process error. Within a box, three distinct sequences of dots are observable, the upper one corresponding to the maximum or minimums for the segment of the projection when the population is below MNPL, the sequence in the middle representing the projection section when the population is between MNPL and half the distance between MNPL and *K*, and the lower sequence for the remaining of the population projection as it approaches *K*. Each dot in the sequence is the mean for the respective $\sigma_{process}$ and each value of ρ (from left to right 0.5, 0.8, 0.9 and 0.95). The plots show that as expected, when process error was low (0.005), at low population levels the observed mean maximum growth was close to R_{max}, particularly if the level of autocorrelation was high. On the other hand, maximum growth values had a tendency to be higher the more the population was allowed to fluctuate with higher values of process error. Also as expected, the maximum annual growth declined as the population approached *K*. Practically all minimum mean growth values allowed declines (they were negative) if the population was approaching *K*. However, when the population was below half the distance between MNPL and *K*, only if the level was at least 0.02 the growth could be negative. This may be a caveat of the model that may require further development to allow more cases with negative annual growth when the population is not too close to *K*. Notice that when $\sigma_{process}$ was set to 0.015 and 0.02 the mean minimum growth at low population levels was smaller than at medium population levels. This is due to a wider spread of the distribution at medium population levels for which there's no apparent explanation.

After the first report proposed the use of a component of process error in the model, the discussion that followed suggested comparing the results of the predicted annual growth in the bowhead whale in the eastern Canadian Arctic with the observed growth in the gray whale of the eastern Pacific Ocean. Data for the gray whale were taken from Rugh *et al*. (2005). As pointed out elsewhere, the data shows that from 1970 to 1997 the population grew at a rate of approximately 0.025, whereas from 1997 to 2001 the population declined at an average rate of approximately -0.123. Several things need to be considered about this data before it is used to compare growth in the bowhead whale simulations. For example, the time series of estimates of abundance show fluctuations at different times which certainly may reflect the natural variability in the population, at least in part. However annual growth of 0.436 between 1971 and 1972; 0.253 between 1977 and 1978 and 0.268 between 1992 and 1993 were observed. The maximum growth (R_{max}) adopted by the US NOAA Fisheries for gray whales has a value of 0.047 which is the 10^{th} percentile of the error distribution around the best estimate of 0.072. If gray whales have an R_{max} of 0.07, then the high annual growth values observed are probably biologically

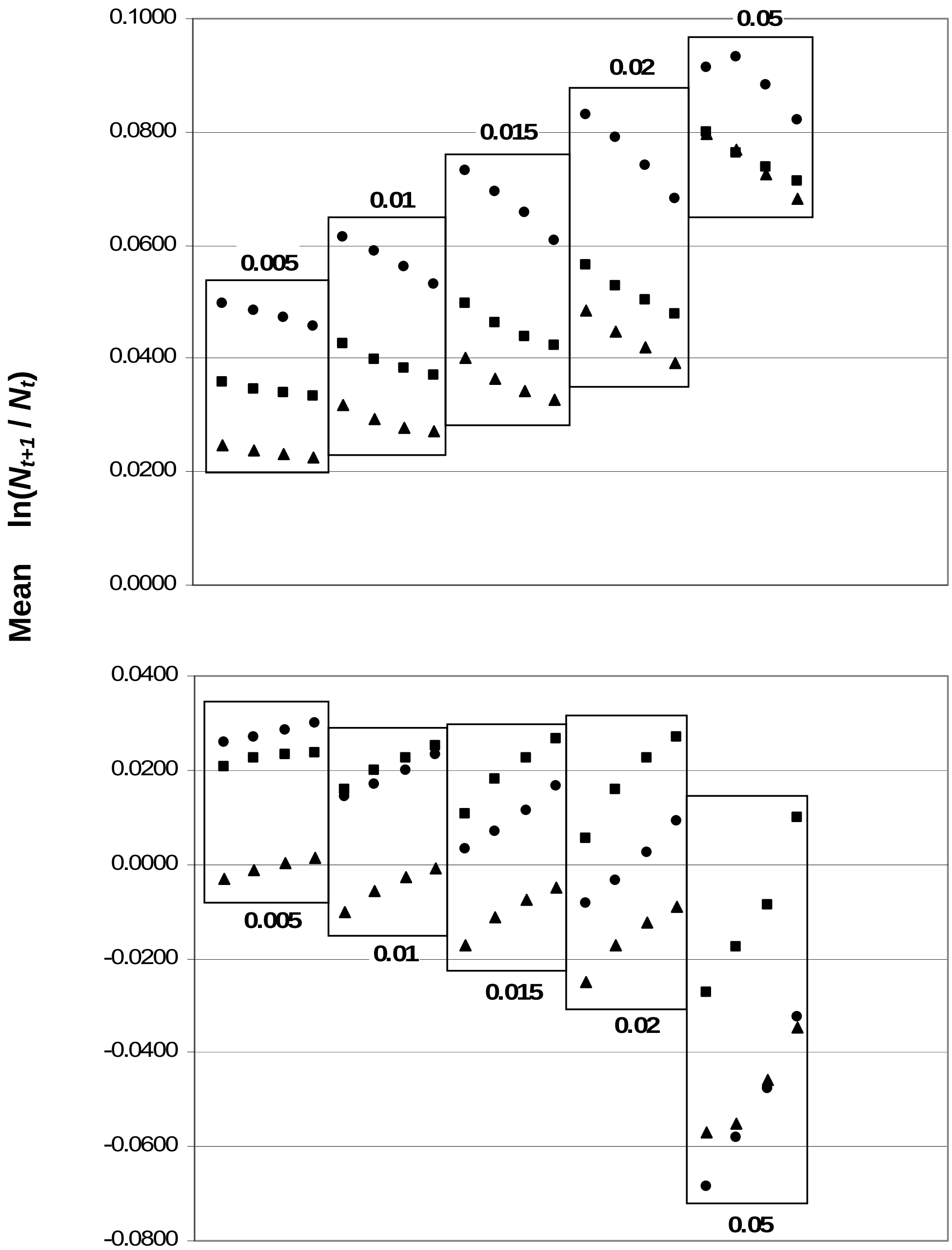


Fig. 7. Mean maximum (upper panel) and minimum (lower panel) annual growth of a simulated population of bowhead whales projected with a stochastic logistic model. Each box aggregates values obtained with specific levels of $\sigma_{process}$. Dots are the mean maximum and minimums when the population was below MNPL, squares when the population was between MNPL and half the distance between MNPL and *K* and triangles for values as the population approached *K*. Within a box, each mark from left to right represent the value for autocorrelation (ρ) levels of 0.5, 0.8, 0.9 and 0.95.

implausible and may be a result of observation error more than process error. Also, if the decline between 1997 and 2001 is certainly the longest sustained population decline recorded, another decline spanning three years was also recorded between 1969 and 1971 with annual growth values that averaged -0.128. The lowest growth was -0.253 observed between 1977 and 1978, but was immediately followed by an increase of almost the same magnitude. The decline in 1977-78 could then be subject of debate as to whether the population might have actually declined more than 25% in a single year only to recover that loss the following year. Shelden *et al*. (2004) associated this decline with the appearance of an environmentally anomalous year and report unusual numbers of calf carcasses along the migratory route. No adult carcasses were reported, therefore, the observed environmental fluctuation may have slowed down the recovery process but caused a minor (if any) decline in the total population. Additionally, Shelden *et al*. (2004) also report a change in whale distribution and the timing of migration, which may influence the abundance estimation process and therefore a better explanation to the observed decline. As for the decline observed in the last years, Rugh *et al*. (2005) suggest that it may be an indication that the population is currently approaching carrying capacity which was combined with unusually poor environmental conditions. Although the time series of abundance estimates for the gray whale are the most complete and one of the best available for large whales, it is still questionable if direct observation of the sequence of estimates leads to reliable estimates of the annual growth because their variability may be confounded with unaccounted uncertainty in the abundance estimates. Wade (2002) fitted alternative models to the catch and abundance data and found that the model that best fitted the data had to include a parameter that incorporated additional variance to the estimates of abundance. An attempt to separate the effects of process and observation error was made by Punt and Butterworth (2002), concluding that for the most part, parameter estimates were insensitive to alternative choices of increasing values of process error and those that showed some response were considered only “a little less optimistic”. Because of this, it was concluded that the effect of process error was insufficient to explain the discrepancy between the catch and the abundance data, and that it appeared that the inclusion of the additional variance proposed by Wade (2002) was justified. Although additional improvements have been made to the estimated abundance and its variance (Hobbs *et al*., 2004 and Rough *et al*., 2005), no consideration was made as to what extent the improvement matched the required additional variance that made a model, which included a parameter representing the addition, a better fit to the data.

Assuming that the population is at or near K (with annual growth close to zero or even negative), and assuming also that the estimated abundance in the last 5 years are unbiased or at least contain biases of similar nature and magnitude and that their variances are better estimated than in the past, then a decline of -0.123 may be realistic although there’s no undisputable evidence that the decline was actually of this magnitude. On the other hand, a decline of similar or greater magnitude while the population was well below K, is more difficult to explain and allowing annual abundance declines as large as 0.1 is only justified when the population is close to *K*.

The most recent stock assessment on bowhead whales of the western Arctic stock published by NOAA Fisheries also show large fluctuations in the time series of estimated abundance (Anglis and Outlaw 2005), but it is possible that estimating abundance of these whales is more problematic than for gray whales and that this problem complicates even more the interpretation of the observed annual change. If bowhead whales have an R_{max} value around 0.04 as assumed by the US NOAA Fisheries, then it may be expected that fluctuations due to process error are smaller than in the gray whale population. In this way, looking at the level of variability shown in figure 7 a choice of $\sigma_{process}$ = 0.01 and □ = 0.8 allowed for maximum growth that had a mean value of nearly 0.06 with a range of 0.044 to 0.084 and 95% of the simulations falling below 0.069. This choice of parameters for process error also allows minimum growth values that have a mean of -0.009 with the lowest observed value of -0.028. As mentioned before, the limit in the lower annual growth can be a caveat if negative values may be expected to be even smaller near *K* and occur more often at population levels away from *K* and not properly represented by the model.

Finally, the complete results of the simulations are presented in the form of summary statistics in Table 2.

RESULTS AND DISCUSSION

Table 3 shows the estimated times to recovery (YTR) for all combinations of parameter values and alternative catch quotas. In this table, YTR values represent the time needed to find 95% of the simulations yielding a population at or above the recovery target of 0.7 of *K*. The model was programmed to project the population only for 100 years, therefore, if a population takes longer than that to recover it is reported as 100+.

A quick look at table 3 shows that YTR values ranged from 5 to 100+. This result is expected given the equally wide range in the combination of parameter values and initial abundance. For example, given that the initial abundance was assumed to be 5,100 and no catch was applied, a combination of ψ = 18.18, *K* = 9,000 and R_{max} = 0.05 yielded a recovery time of 5 years. This is expected given that in this case the target population level was 6,300 and the population is growing faster from the initial 5,100. In contrast, if the parameters were set

Table 2. Summary statistics of simulations to test the influence of different parameter values to compute process error on the annual population growth of bowhead whales. ρ is the residual correlation coefficient and $\sigma_{process}$ its standard error; mean and standard errors of the 5000 maximum values of r_t obtained for each combination of parameters are presented.

		Max below MNPL		Max MNPL - 0.5(K-MNPL)		Max 0.5(K-MNPL) - K		Min below MNPL		Min MNPL - 0.5(K-MNPL)		Min 0.5(K-MNPL) - K	
$\sigma_{process}$	ρ	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
0.005	0.5	0.0498	0.0024	0.0358	0.0037	0.0248	0.0039	0.0259	0.0026	0.0207	0.0045	-0.0032	0.0034
	0.8	0.0486	0.0028	0.0346	0.0043	0.0236	0.0043	0.0272	0.0030	0.0225	0.0052	-0.0011	0.0039
	0.9	0.0473	0.0032	0.0340	0.0046	0.0230	0.0047	0.0286	0.0034	0.0233	0.0054	0.0003	0.0042
	0.95	0.0456	0.0035	0.0333	0.0048	0.0226	0.0049	0.0300	0.0037	0.0238	0.0054	0.0015	0.0044
0.01	0.5	0.0614	0.0048	0.0425	0.0068	0.0319	0.0066	0.0145	0.0050	0.0159	0.0092	-0.0103	0.0068
	0.8	0.0589	0.0055	0.0399	0.0076	0.0294	0.0075	0.0171	0.0060	0.0200	0.0108	-0.0058	0.0084
	0.9	0.0563	0.0059	0.0382	0.0082	0.0277	0.0081	0.0201	0.0069	0.0227	0.0111	-0.0029	0.0088
	0.95	0.0532	0.0065	0.0371	0.0088	0.0270	0.0086	0.0233	0.0075	0.0250	0.0110	-0.0010	0.0083
0.015	0.5	0.0730	0.0069	0.0496	0.0099	0.0402	0.0092	0.0031	0.0075	0.0107	0.0151	-0.0173	0.0112
	0.8	0.0695	0.0080	0.0463	0.0108	0.0364	0.0103	0.0071	0.0091	0.0181	0.0174	-0.0114	0.0129
	0.9	0.0657	0.0087	0.0439	0.0116	0.0342	0.0109	0.0114	0.0105	0.0226	0.0175	-0.0075	0.0126
	0.95	0.0607	0.0092	0.0424	0.0120	0.0328	0.0114	0.0165	0.0114	0.0267	0.0168	-0.0051	0.0109
0.02	0.5	0.0831	0.0077	0.0566	0.0120	0.0486	0.0117	-0.0082	0.0099	0.0053	0.0209	-0.0250	0.0160
	0.8	0.0791	0.0089	0.0529	0.0134	0.0447	0.0130	-0.0034	0.0125	0.0157	0.0243	-0.0173	0.0173
	0.9	0.0740	0.0105	0.0502	0.0141	0.0418	0.0139	0.0024	0.0148	0.0225	0.0250	-0.0125	0.0163
	0.95	0.0681	0.0114	0.0478	0.0148	0.0391	0.0142	0.0093	0.0156	0.0270	0.0232	-0.0090	0.0138
0.05	0.5	0.0915	0.0000	0.0799	0.0137	0.0797	0.0160	-0.0684	0.0189	-0.0274	0.0501	-0.0570	0.0353
	0.8	0.0931	0.0062	0.0762	0.0156	0.0769	0.0164	-0.0579	0.0258	-0.0178	0.0549	-0.0552	0.0324
	0.9	0.0883	0.0111	0.0738	0.0167	0.0726	0.0170	-0.0477	0.0320	-0.0087	0.0565	-0.0459	0.0297
	0.95	0.0821	0.0149	0.0712	0.0178	0.0683	0.0179	-0.0325	0.0364	0.0100	0.0542	-0.0348	0.0244

Table 3. Estimated time to recovery (YTR) of bowhead whales in the eastern Canadian Arctic for different combinations of population parameter values and catch assuming that N_0 = 5,100. For comparison, the stochastic output of the model (column S) is presented together with the deterministic time to recovery (column D).

Parameter values			YTR											
			Annual Catch											
			0		2		4		8		15		50	
ψ	K	R_{max}	S	D	S	D	S	D	S	D	S	D	S	D
1	9000	0.01	100+	58	100+	64	100+	72	100+	95	100+	100+	Decline	Decline
1	9000	0.03	44	20	45	20	49	21	53	23	63	26	100+	100+
1	9000	0.05	22	12	23	12	23	12	24	13	28	14	53	23
1	12300	0.01	100+	100+	100+	100+	100+	100+	100+	100+	100+	100+	Decline	Decline
1	12300	0.03	68	40	70	41	71	42	76	44	87	48	100+	93
1	12300	0.05	37	24	37	25	38	25	39	26	42	27	61	37
1	15000	0.01	100+	100+	100+	100+	100+	100+	100+	100+	100+	100+	Decline	Decline
1	15000	0.03	80	51	82	52	83	53	90	55	97	59	100+	95
1	15000	0.05	43	31	44	31	45	31	46	32	48	33	65	42
4.2	9000	0.01	60	25	65	26	71	28	79	30	100+	37	100+	Decline
4.2	9000	0.03	13	9	13	9	14	9	14	9	16	10	25	13
4.2	9000	0.05	6	5	6	6	6	6	7	6	7	6	9	7
4.2	12300	0.01	100+	58	100+	60	100+	63	100+	67	100+	78	100+	Decline
4.2	12300	0.03	28	20	28	20	28	20	29	21	31	22	41	27
4.2	12300	0.05	15	12	15	12	15	12	15	13	15	13	18	15
4.2	15000	0.01	100+	79	100+	81	100+	84	100+	89	100+	100+	Decline	100+
4.2	15000	0.03	35	27	36	27	36	27	37	28	39	29	50	35
4.2	15000	0.05	19	16	20	16	20	17	20	17	20	17	24	19
18.18	9000	0.01	53	22	55	23	57	23	63	25	80	29	100+	100+
18.18	9000	0.03	10	8	11	8	11	8	11	8	12	8	18	11
18.18	9000	0.05	5	5	5	5	5	5	5	5	5	5	7	6
18.18	12300	0.01	95	53	100+	55	100+	57	100+	60	100+	69	100+	100+
18.18	12300	0.03	24	18	25	18	25	19	25	19	27	20	35	24
18.18	12300	0.05	13	11	13	11	13	11	13	12	14	12	16	13
18.18	15000	0.01	100+	73	100+	75	100+	77	100+	82	100+	93	100+	100+
18.18	15000	0.03	32	25	33	25	33	25	34	26	35	27	45	32
18.18	15000	0.05	18	15	18	15	18	15	18	16	19	16	21	18

to $\psi = 1$, $K = 15,000$ and $R_{max} = 0.01$, the population was very far from the target level and growing slowly, taking 100+ years to recover even without removals.

Table 3 also shows that when $\psi = 1$, there's a tendency for YTR to differ more from all other YTR values, than the difference between times to recovery when $\psi = 4.2$ and $\psi = 18.18$. For example, if the catch was 4 and parameter values were $\psi = 1$, $K = 9,000$ and $R_{max} = 0.03$, the time to recovery was 48 years, whereas YTR was 14 if $\psi = 4.2$ and 11 if $\psi = 18.18$ with everything else kept equal. This difference is a direct consequence of one of the effects of the shape parameter on the population behavior as described with a generalized logistic model. For one single growth value, the population increases faster with larger values of ψ, but the difference in the increase is smaller between larger ψ values.

Regarding the influence of the different assumptions about parameter values, the conditions in this report differ from the previous analysis in that only a single assumption was made here about the initial population size. If the combination of K and N_0 influenced the results more strongly in the past, throughout table 3 it is seen that it is the whole set of parameters of the logistic model that can be considered important. Lower values of K implied that the current population was closer to the target and took less time to recover. In the same way, the larger ψ and R_{max} were, the less it took the population to reach the recovery target. This result doesn't contradict the conclusion in the past report, it only highlights the relevance of having a reliable estimate of the present whale abundance and ideally to have a complete reliable record to estimate model parameters instead of assuming their values in a simulation analysis.

In the same way as in the past report, from the practical point of view, a critical result of the exercise is the fact that for any particular combination of parameters, as long as the catch is lower than 10 animals, the delay in time to recovery is minimal compared to YTR values with no catch. For example, in Table 3 if $\psi = 1$, $K = 9,000$ and $R_{max} = 0.03$, time to recovery is 46 years if no catch is allowed. With the same combination of parameters, YTR values with catch levels of 2, 4 and 8 animals were 46, 48 and 52 respectively, increasing to 63 and more than 100 years when the catch was set to 15 and 50 whales. If the parameter combination was $\psi = 4.2$, $K = 12,300$ and $R_{max} = 0.03$, time to recovery was 27, 27, 28, 29 and 30 for no catch, and catches 2, 4 8 and 15 respectively and only when the catch was 50, time to recovery went up to 41 years. As concluded in the past report, because the recovery goal in the Conservation Strategy is not specific about the time to reach the target, regardless of what parameters govern the real world population of whales, if they are within the limits of the model, catches smaller than 10 whales, allow adopting an acceptable level of confidence that such management action is compatible with the goals outlined in the Conservation Strategy for the bowhead whale.

A catch of 50 whales was also the only level that resulted in population decline. This situation occurred in all cases when R_{max} was assumed to be 0.01. This is an interesting result because if the management goal is not explicit about the timeframe to observe recovery, even if the population takes more than 100 years to recover, as long as there is recovery the management goal is met. Under these assumptions, the only circumstance that can lead to a decline with an annual removal of 50 animals is that this particular whale population does have indeed low annual growth. The declining populations occur in the stochastic model under conditions coinciding with the resulting declines in the deterministic model. However, a decline in the deterministic model resulted in a population taking more than 100 years to recover and another one that in the deterministic model took more 100 years to recover but in the stochastic model resulted in a decline. Both of these cases occurred as well when R_{max} was set to 0.01. These differences don't imply inconsistencies between the two models and are only a consequence of the natural variability represented by the process error.

The conclusion that low catch levels won't cause marked delays in time to recovery holds under the assumptions that aside from the catch there are no other significant sources of mortality that go unrecorded; that this bowhead whale population is appropriately described by the model with parameters within the range used in the present analysis. This implies the assumption that environmental conditions won't change beyond the limits imposed on the model parameters.

The comparison of the times to recovery obtained with the model including process error with results using a deterministic model show that YTR values in the first case tend to be considerably larger as time to recovery increases. The reason for this divergence is found in the way times to recovery are recorded in the stochastic model. Recall that in the stochastic model YTR is the time where 95% of the projected populations (5000) during a simulation trial were above the recovery target. In this way, a population that takes longer to recover undergoes a longer process of fluctuation producing a broader distribution of times to recovery. Observing one such distribution illustrates this point. Figure 8 presents the distribution of YTR with $\psi = 1$, $K = 9{,}000$ and $R_{max} = 0.03$ and no catch. Time to recovery from the stochastic model was 46 years (light colored bar) whereas the deterministic time to recovery is 20, which as expected is at the mode of the distribution (patterned bar). In contrast, figure 9 presents the distribution of times to recovery with $\psi = 4.2$, $K = 9{,}000$ and $R_{max} = 0.05$ where the time to recovery from the stochastic model was 6 years and 5 from the deterministic model. Notice the narrow distribution that makes both results to be very close. The observed differences in the predicted times to recovery between the two population models certainly reflect the relevance of considering the effect of natural variability when projecting animal populations of long life span. However, the magnitude if the divergence from the deterministic model is determined by a choice that is more political than biological, the larger the acceptance level is the more conservative the policy is.

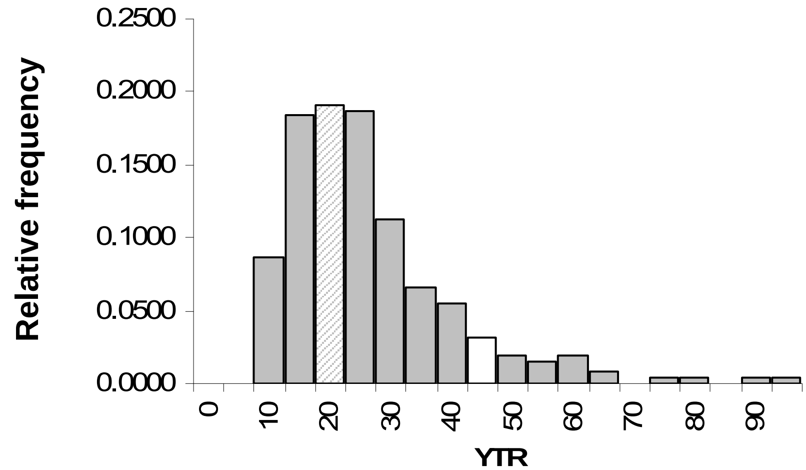


Fig. 8. Relative frequency distribution of time to recovery of bowhead whales in the eastern Canadian Arctic if no catch was allowed and parameters of dynamics were set to $\psi = 1$, $K = 9,000$ and $R_{max} = 0.03$. Light colored bar is the time to recovery where 95% of the simulations fell above the recovery target. Patterned bar is the mode of the distribution corresponding to the deterministic prediction.

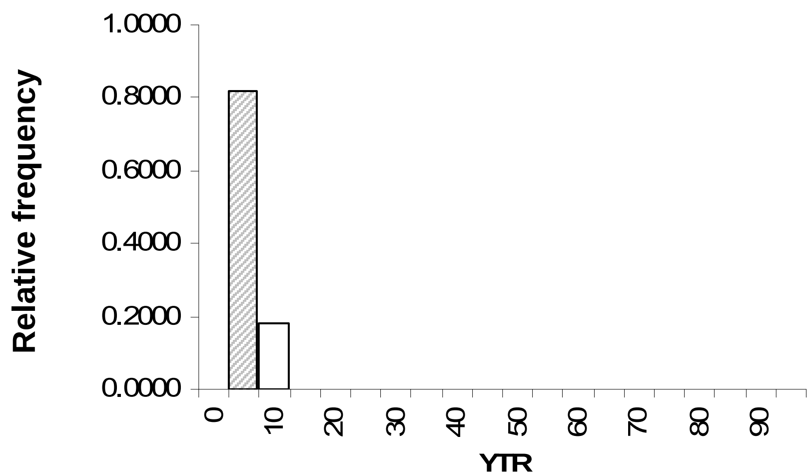


Fig. 9. Relative frequency distribution of time to recovery of bowhead whales in the eastern Canadian Arctic if no catch was allowed and parameters of dynamics were set to $\psi = 4.2$, $K = 9,000$ and $R_{max} = 0.05$. Light colored bar is the time to recovery where 95% of the simulations fell above the recovery target. Patterned bar is the mode of the distribution corresponding to the deterministic prediction.

Selecting an acceptance level lower than 95% will make the predicted time to recovery closer to the deterministic prediction. On the other hand, if management goals are set to be achieved in the short term, it is possible to ignore the effects of process error, but if the goal is expected to be reached in the long term, then natural variability introduces a source of uncertainty that is difficult to ignore.

Finally, it is important to keep in mind that the results presented in this report are valid only under the assumed parameter values of process error. Larger values of $\sigma_{process}$ can certainly modify these results. Observing the population response under a different assumption about the magnitude of process error however would work in the same way as with the selection of alternative population parameter values to explore feasible future scenarios.

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Appendix 1

Instructions to use the program to run simulations that compute time to recovery under different assumptions of population parameters and catch levels

The program was coded in C++ using an object oriented approach. The code includes a typical header file (BHWREC.H); a main file (MAIN_BHWREC.CPP); a file with the functions required to simulate the population dynamics and catch as well as a random number generator (POPSIM.CPP); a file to create the probability distributions (PDF.CPP) and a file for data management (DATA_MANAG.CPP). An external input data file is required to read the alternative parameter values as well as the control variables (BHW.dat). All the functions, the global variables and variables used in files other than the main are declared in the header file. Variables of local scope are declared in the functions where they are used. The program is commented as much as necessary to facilitate understanding of its different components.

Two sets of files are provided. A “clean” set includes only the principal code files as well as the executable file and the input and output folders. The second set includes the same files as the clean set plus all other files produced by the compilation process, provided only in case the Microsoft Visual C++ 6.0 ® compiler is used to modify the code. In this case, the MAIN_BHWREC.DSW workspace opens with all the code files. Of course, the clean set is enough to use the Microsoft compiler, but a new workspace needs to be created. If changes to the code are required later on, it isn’t necessary to use the Microsoft Visual C++ 6.0 ® compiler but it is highly recommended. It is possible that earlier versions of the Microsoft compiler may present incompatibilities and it is unknown if newer versions such as 7.0 (Visual C++ .NET 2002), 7.1 (Visual C++ .NET 2003) or 8.0 (Visual C++ 2005) will compile the code.

The overall structure of the program is outlined in Fig. 1. The main file controls the central flow of the program by starting the simulations for each catch level. The program first runs the *popsim* function to project the population as many years as determined in the input file and repeats the projection as many times as declared in the same input file. The output of the *popsim* function is stored in the file RawYrToRecovLook.out and then read by the *pdf* function called in the main file immediately after *popsim*. The content in the file RawYrToRecovLook.out could be used to generate the probability distributions and to obtain the times to recovery externally if desired but maybe cumbersome given the amount of data produced. Finally, after simulations have been run for all catch levels in the main, the final data with times to recovery are written by the *write_data* function into the YTR.out file and the program terminates. Tables 3a and b are basically the same YTR.out output file simplified to facilitate their reading.

The random number generator uses two additional files with the functions *gasdev* which draws numbers from a standard normal distribution and *ran1* which draws random numbers from a uniform distribution. Both functions for random numbers are from Numerical Recipes in C++ (Press, W. H., S. A. Teukolsky, W. T. Vetterling and B. P. Flannery . 2002. Numerical Recipes in C++. The art of scientific computing. Cambridge.).

The *pdf* function produces an output file with the probability distributions of time to recovery (PDF.out) and another one with the cumulative probability distributions (CPROB.out). In these two files, there are as many columns as years the population was projected. Each row includes the distributions for each combination of parameters. The arrangement is hierarchical with catch on the top, followed by ψ, K and R_{max}. The order of the rows resembles the parameter combinations in Tables 3a and b. Note that the Tables have 27 rows corresponding to each parameter combination. In the probability distribution files, the same sequence is represented for each catch level (5 total) in the same order as in Table 3 for a total of 135 rows. Although the user doesn't need these two files to extract the times to recovery, they are provided in case a plot of one or more of such distributions is required to visualize or explore their behavior or any other use as desired.

Before running the program it is necessary to verify that the location of the input and output files are consistent with the path of all stream declarations in the code (for both input and output). The simplest way to do this is to create new folders with the same paths as in the code. Default paths (folders that need to be created) are C:\Bowheads\Recovery\Input and C:\Bowheads\Recovery\Output. Note that if these paths need to be changed in the code, the paths must have double backslashes. For example, the path for data input would be C:\\Bowheads\\Recovery\\Input\\BHW.dat. If the output of a program run is to be kept, it is necessary to move it to a different location taking care of including information in the new folder about the specific parameter settings used in that run. If the output is not moved to a different folder location and the program is run again with different settings, the previous output will be lost. An alternative way to assure that file locations and program path declarations are the same is to modify the program with the desired new paths and recompile the program. This method has the advantage of providing the possibility of making multiple copies of the program in different locations for each run eliminating the need of moving the output to a new folder.

Before running the program it is also necessary to carefully create the input file. The following table is an example of the format of one such file.

```
1.0
4.2
18.18
-9999

9000
12300
15000
-9999

0.03
0.04
0.05
-9999

7104
-9999

1
1
-9999

0
0
-9999

2
13
-9999

0.8 0.005 0.7 0.41 2005 100 0.5 10 0.95 5000 1

0.0
1.0
8.0
```

The data are arranged in 9 distinct blocks that correspond to the following information:

1. Alternative values for ψ.
2. Alternative values for K.
3. Alternative values for R_{max}.
4. Alternative values for N_0.
5. The maximum catch for the two areas contributing to the "irregular" catch schedule. More on this in the description of block 7.
6. The minimum catch for the two areas contributing to the "irregular" catch schedule.
7. The periodicity with which the maximum catches occur. Blocks 5 to 7 in this example are interpreted so that in one area one whale is removed in the first line every two years and zero otherwise. In the same way, for the other area, one whale is removed every 13 years and zero otherwise. However, the catch options can be set in different ways. For example, if the numbers in block 5 were 4 and 10, the numbers in block 6 were one and two and the numbers in block 7 were 5 and 15, it would mean that in one area 4 whales are removed every 5 years and one otherwise whereas in the other area 10 whales would be removed every 15 years and two otherwise.

Note also that up to block 7 the last number in the series is -9999. This number is a tag that tells the program it is the end of each block and must be present, otherwise numbers in the following block will be interpreted as part of the last block and will cause the program to fail the execution. Note also that between blocks there is an empty row. This blank row is not necessary but recommended to facilitate the order and control in the file.

The next block is the series of the so called "control variables". The sequence is for the autocorrelation parameter ρ, the magnitude of the natural variability □, the management goal as a proportion of K, the CV of the surveys, the initial year, the number of years to project the population, the recovery factor F_r for PBR, the periodicity of future surveys, the critical probability value to accept that recovery occurred, the number of simulations and the bin size for the probability distributions. No end of block tag is included.

The final block corresponds to the fixed catch quotas. In this block, the last value must be the fixed PBR harvest level. No end of block tag is included. It is very important that at the end of this block there must be NO return, space or any other character after the last number, otherwise the program will crash.

Blocks 1 trough 4 and 9 can have any number of alternative values of parameters and catch, the program is not restricted to work with the same number of options as in the example provided. The only requirements are that for blocks 1 through 4 the end of block tag is included and that in block 9 nothing else is added after the last number.

The program can be run in windows simply by double clicking on the icon for the executable file. However, it can also be run by typing the name of the executable in the command line of a DOS console after entering the correct path or by clicking the start and run windows buttons and going to the folder where the executable is stored.

Once the program starts, it opens a DOS console and shows on the screen the parameter values, the control variables and the catch so that the user is able to take a quick look and verify that parameter and variable assignments are correct. If something looks wrong, the program can be stopped by pressing ctrl c or ctrl brake.

All output files are found in the Outputs folder and are text files that can be opened with any word editor or spreadsheet program. Columns in the YTR.out and RawYrToRecovLook.out files are separated by tabs. Columns in the PDF.out and CPROB.out files are separated by single blank spaces.

Appendix 2

Proof of the equation for serially correlated residuals of process error[1]

The aim is to generate a time-series of residuals so that $VAR(\varepsilon_t) = \sigma^2$ and $cor(\varepsilon_t, \varepsilon_{t-1}) = \rho\sigma^2$. The proposed solution is
$\varepsilon_t = \rho\varepsilon_{t-1} + \sqrt{1-\rho^2}\,\eta_t$ where $\eta_t \sim N(0;\sigma^2)$

Now:

$$VAR(\varepsilon_t) = E([\rho\varepsilon_{t-1} + \sqrt{1-\rho^2}\,\eta_t][\rho\varepsilon_{t-1} + \sqrt{1-\rho^2}\,\eta_t])$$

$$= E(\rho^2\varepsilon_{t-1}^2 + 2\rho\varepsilon_{t-1}\sqrt{1-\rho^2}\,\eta_t + (1-\rho^2)\eta^2)$$

$$= E(\rho^2\varepsilon_{t-1}^2) + E(2\rho\varepsilon_{t-1}\sqrt{1-\rho^2}\,\eta_t) + E((1-\rho^2)\eta^2)$$

$$= \rho^2 VAR(\varepsilon_{t-1}) + (1-\rho^2)\sigma^2$$

Now, for a stationary process, $VAR(\varepsilon_t) = VAR(\varepsilon_{t-1}) = VAR(\varepsilon)$. This is achieved by setting $\varepsilon_0 \sim N(0;\sigma^2)$

So

$$VAR(\varepsilon)(1-\rho^2) = (1-\rho^2)\sigma^2$$

or

$$VAR(\varepsilon) = \sigma^2$$

Similarly,

$$cor(\varepsilon_t, \varepsilon_{t-1}) = E([\rho\varepsilon_{t-1} + \sqrt{1-\rho^2}\,\eta_t]\varepsilon_{t-1})$$

$$= E(\rho\varepsilon_{t-1}\varepsilon_{t-1} + \varepsilon_{t-1}\sqrt{1-\rho^2}\,\eta_t)$$

$$= E(\rho\varepsilon_{t-1}^2) + E(\varepsilon_{t-1}\sqrt{1-\rho^2}\,\eta_t)$$

$$= \rho E(\varepsilon_{t-1}^2) + 0$$

$$= \rho\sigma^2$$

[1] This proof was kindly provided as personal communication by Andre Punt (School of Fisheries, University of Washington).

Appendix 3
Criticisms and comments, and responses by the author.

Page numbers refer to relevant text in the present document.

Criticism or comment (p. 1), regarding how decline was detected. Quoted original text with suggested text and comments shown in bold.

> When **the** deterministic **portion of this** model is used to project a population subject to an unsustainable constant catch level, it is **sufficient** to check if the abundance at any given time N_t is smaller than N_{t+1} **and that net productivity declines as well (Comment: a sustainable harvest will cause a decline from K)** because the declining trend will continue for the rest of the projection. In **the** stochastic model below, this is not useful **because chance will determine the outcome for any one realization thus** a large number of simulations are run to determine **the likelihood that** the population is recovering or declining **estimated by the fraction of projections** within a trial presenting an increasing trend and others a declining one.

Author's response: Actually, this comment is not entirely accurate. A sustainable catch (or yield, SY_t) is defined as the catch that makes $N_{t+1} = N_t$. Using a deterministic logistic model therefore, such condition is met when $R_{max} * N_t * (1-(N_t/K)^z) = C_t=SY_t$. With this in mind, no sustainable catch would cause a decline no matter where the population is. Possibly he is thinking of a catch that is between the *maximum* sustainable yield and the sustainable yield for a population between K and MSYL. Under those conditions, the population will decline to a certain level where it will stabilize and therefore the statements in the paragraph hold with a couple of precisions. Instead of "check if the abundance at any given time N_t is smaller than N_{t+1}" it should say "check if the abundance at the beginning of the projection N_0 is smaller than N_{0+1}" and instead of "because the declining trend will continue for the rest of the projection" say "because the declining trend will continue at least for part of the projection".

Criticism or comment (p. 3), regarding the reference to the process error equations. Quoted original text with comments shown in bold.

$$u_t = u_{t-1}\ \rho + x_t \left(\sqrt{1-\rho^2}\right)\ \sigma_{process}$$

> **(Unclear how this relates to actual processes in marine mammal populations)**

such that $VAR(u_t) = \sigma^2_{process}$ *and* $cor(u_t, u_{t-1}) = \rho\sigma^2_{process}$

(Punt pers. comm.; see Appendix 2 for proof) **(Comment: a well known result from time series analysis. Discard the pers com and reference a text such as Schumway that is readily available)**

Author's response: This was requested originally by Pierre and will stay as it is. Since I don't have access to the referred book I prefer not to include the recommended reference.

Criticism or comment (p. 3), regarding the objection on the choice of process error distribution.

I object to this choice of error term e^u . It is biased positive and skewed to allow larger increases than declines both of which have significant consequences when the lower 5th percentile of a distribution is used as a criterion for a safe harvest. It does have some convenient mathematical properties but these are of limited value when compared to the effort required to describe it and the caveats required to interpret the results. There are a variety of simple options that are easy to describe and give results that can be interpreted directly.

Examples:
1) replace e^u with a binomial draw (p(1)=0.95, p(0.80)=0.05) this gives a deterministic growth with a 1 in 20 chance of a 20% decline resulting in an expected maximum annual per capita increase of R_{max}=0.01. This model will not exceed R_{max} in any runs and models a process of concern to managers.

2) discard e^u $R_{\max}\left[1-\left(\frac{N_t}{K}\right)^{\psi}\right]$ and replace in the projection with

$$\left[R_{\max}\left[1-\left(\frac{N_t}{K}\right)^{\psi}\right]+U(-0.01,+0.01)\right]$$ where U(-a,+a) is a

random draw from a uniform distribution between -a and +a. This can be drawn every year or for 5 or 10 or 20 year blocks to recreate periods of good and bad environmental conditions. This gives an expected maximum annual per capita increase of R_{max} and allows a constant range of variation through out. This model will not exceed R_{max} +a in any runs. Could use a=0.01, 0.02, etc to provide a range of variabilities.

3) Replace U(-a,+a) with a Beta distribution scaled to fit the preferred range of variation with parameters selected for the chosen mean and variance. This can be set so that the maximum annual increase is not greater than 6% and yet significant declines can occur.

4) combine 1) and 2) or 1) and 3), their effects are independent.

Author's response: (also applies to other sections of the review where the same objection is presented.) The main objection to the analysis refers to the assumption about the distribution of the process error. In principle, I share his concerns and already have included in the discussion the downside of the approach. However, from the first time he presented his opinion about this issue, he hasn't provided yet with evidence to support his claim that natural variability in the bowhead whale is not properly represented by log-normal error. As I said in the first reply to the objection, there's virtually no useful information to determine the magnitude of fluctuation in whale populations. The gray whale data which would be the most promising to get some insights about natural fluctuations turns out to be difficult to use to such purpose (will get back to this further down).

He suggests looking at papers such as Breiwick *et al.* (no year or any further reference on this or any other paper), but I was unable to find such paper. There are other papers where Breiwick coauthors analyses on the gray whale abundance series. Some have already been referred to in the report, but they mostly focus on improvements to reduce biases in the estimates of abundance and their variance. He says that the papers he recommends "include attempts to tease apart the effects of measurement and process error". My literature review includes the following papers: Buckland and Breiwick (2002); Butterworth *et al.* (2002); Gerber *et al.* (1999); Gerber *et al.* (2000); Hobbs *et al.* (2004); Norris (2002); Punt *et al.* (2004); Punt and Butterworth (2002); Rough *et al.* (2005); Shelden *et al.* (2004); Wade (2002); Witting (2003).

Out of the reviewed papers, Gerber's don't address in any way the problem of confounding errors in the time series nor any attempt to separate them. Wade (2002) notes that "the mechanism that causes process error is unknown and is not explicitly modeled here". However, he introduced an additional error term to include unaccounted *observation* error and concluded that "an additional variance term should be included in the population dynamics models fitted to the gray whale abundance data. In other words, it is clear that not all of the variance associated with the abundance estimate has been included in previous estimates".

Of all examined papers, only Punt and Butterworth (2002) used a model that explicitly included specifications of process error and explore the behavior of different parameters to alternative error levels. In spite of this attempt, it is still difficult to know to what extent abundance may deviate from an expected deterministic trajectory and their work only looked at the general behavior of parameters such as MSYR, the average trend (their “slope” parameter) and others. Results of the analysis in that paper lead to two conclusions relevant to our discussion. First, for the most part, parameter estimates were insensitive to alternative choices of increasing values of process error and those that showed some response were considered only “a little less optimistic” but there is no indication that fluctuations in the abundance could be of the magnitude claimed. Their second conclusion relevant to our concerns was that their results indicate that “process error effects alone are not sufficient to resolve the discrepancy between the historical catches and the trend in the abundance estimates”. Furthermore, the authors add that the results “confirm that the inclusion of the term in equation (7) for additional variance [to the abundance estimates] is justified. Wade and DeMaster (1996) showed using Bayesian factors that models that included the possibility of additional variance provided more satisfactory fits to the abundance data”. In other words, even in the case where an extraordinarily good data set is available, it has been impossible to determine the magnitude of the acting process error, and the variability in the abundance estimates is most likely confounded with still unaccounted observation error.

I understand that Hobbs *et al.* (2004) and Rough *et al.* (2005) included in their analyses improvements in the estimates of abundance and their variances, but they don’t specify to what extent such improvements match the additional variance that has been deemed necessary in models to better explained the abundance and catch data.

The choice of log-normal process error is a common practice for population trends in general (Hilborn and Mangel, 1997) and other components of marine mammal population dynamics (Punt and Butterworth, 2002). I understand that use of any particular form of error distribution on different elements of a population model can lead to different population behavior and agree that log-normal error distribution can be skewed, however, such considerations don’t fully justify rejecting the choice. Observe that in the report’s figure 6 the plots of deviations of the annual growth from the deterministic projection are almost symmetrical. I believe that the concerns however, are not so much about the symmetry of the deviations but as to the possibility that annual changes could be highly negative. Throughout the reviewed literature, the only discussion about observed decline in the estimated abundance refers to the cases where the population is approaching K. For example, Rough *et al.* (2005) discuss the possibility that the decline in the last abundance estimates can be explained by a population approaching carrying capacity. However, there’s no discussion as to what extent the actual population response may still be confounded by yet unaccounted observation errors. Moreover, Shelden *et al.* (2004) are the only authors that provide some insights about how such density dependent mechanisms may be acting on the gray whale by reporting increasing numbers of calves being born outside the traditional breeding grounds in Baja California, Mexico. The authors highlight the relevance that such population behavior change may have on calf survivorship as a mechanism of density regulation. There’s very little information as to what other processes may have affected the population while well below K. Shelden *et al.* (2004) include a discussion on the potential effects of environmental conditions on different elements of the population. They point out to the shift that occurred in 1977 that led to the appearance of calf carcasses along the migratory route. This event coincides with a decline of about 25% in the estimated abundance in 1978 but is followed by an increase of almost the same magnitude the following year, an increment that seems to be biologically implausible. Additionally, Shelden *et al.* (2004) indicate that the general behavior of the whales also changed with increased dispersion and changes in the timing of migration, factors that may affect the estimated abundance. Therefore, the hypothesis of increased observation error due to factors such as changes in the population behavior appears to be more useful to interpret the trends in those years than a real decline and increase in three consecutive years.

In conclusion, although the suggestion of a different error distribution may have some potential, switching to any of his recommendations now doesn't appear to have solid justification to describe natural population variability in the bowhead whale (e.g. the claim that "declines in excess of 10% are entirely plausible") and can be equally problematic to interpret simulation results. If he has information that goes beyond the referred papers, it would be more useful to present it properly to aid in the discussion.

As for the current contents of the report regarding this issue, I admit overlooking the Punt and Butterworth (2002) and Wade (2002) discussions about the need to include additional variance terms while fitting population models to the abundance data, which supports the argument that observation and process errors can be confounded making difficult to interpret the level of actual fluctuation attributed only to natural effects. I'll include them in the report together with Shelden *et al.* (2004) to support the proposition that large fluctuations when the gray whale population was well below K are not easily identifiable.

Criticism or comment (p. 3), regarding the use of the word "rate" to refer to R_{max}.

> R_{max} = *The discrete*-**time** ~~intrinsic rate of~~ **deterministic maximum annual per capita** increase, ~~similar to (r-1), the maximum growth rate of a population the continuous parameter.~~ **Note: In the standard vocabulary of mathematical modeling, this is not a rate. The term rate is used for growth parameters in a continuous time model not a discrete time model the terminology should be corrected throughout the paper.**

Author's response: I don't object to the recommendation, but do suggest that a paper be written to change the widespread practice of using the word "rate" to define R_{max}. The precision in the definition of R_{max} however doesn't invalidate the statement that it is equivalent to its continuous counterpart.

Criticism or comment (p. 3), regarding adding N(0,1) to the term x_t .

> x_t = A random number drawn from a standard normal distribution, **N(0,1).**

Author's response: Addition of **N(0,1)** makes the phrase redundant. By definition a standard normal distribution is **N(0,1)**.

Criticism or comment (p. 5), regarding correlation in N_t and r_t. Quoted original text with suggested text and comments shown in bold.

> When this lognormal process error is applied to the logistic model, it is important to note first that the error is applied to the whole population and not explicitly to the parameter of growth R_{max}. This means that if environmental conditions are appropriate, subsequent states of the population (e.g. N_t, N_{t+1}) may follow each other to conform some trend for a period of time. However, because ln(N_{t+1} / N_t) is the annual growth rate r_t, it follows that the population growth is autocorrelated in the same way as the abundance **(Comment: not true, r_t can be uncorrelated and Nt will still be correlated)**. Recall also that R_{max} = maximum **expected** value of (N_{t+1} / N_t) – (**1 +bias in lognormal process error**) which is an approximation of ln(Nt+1 / Nt). Observe now in Fig 2 the plots of ln(N_{t+1} / N_t) vs. time (with K = 12,300, R_{max} = 0.04 and □ = 4.2).

Author's response: I don't see how can r_t be uncorrelated if N_t is correlated when r_t = ln(N_{t+1}/N_t).

Criticism or comment (p. 5), regarding the discussion to select parameters of process error. Quoted original text with comments shown in bold.

> A better description of the behavior of the population model under different levels of process error an autocorrelation was developed running a series of simulation trials. In these simulations, a population was projected with the parameters of dynamics K = 12,300, R_{max} = 0.04 and □ = 4.2. The initial population size was set to 500 to observe the response from severely depleted levels and was projected for 100 years. Each projection with a single combination of $\sigma_{process}$ and ρ was repeated 5000 times. Bounds of -0.1 to 0.1 were set to the annual growth rate and if exceeded the projection was discarded. Note: This is a condition on the error term of the model and should be included with the model description above. Also sustained growth in excess of 6% is impossible based on our current knowledge of bowhead biology but declines in excess of 10% are entirely plausible. ~~These bounds allow a considerable margin of fluctuation in the growth rate but don't allow implausible (although not~~

> ~~impossible) growth levels~~ (**Comment: the discussion of possible and plausible values should be in the parameter section. All of this discussion and demonstration of simulation results is useful to provide examples to none modelers, but should not be used to tune the model. Given the model description above it is quite simple to calculate directly the likelihood of implausible and impossible values, which should be the basis for tuning the model).**

Author's response: I think that the comment is a matter of preferences and therefore I choose to leave it as it is.

Criticism or comment (p. 6), regarding where density dependent effects start to act. Quoted text with suggested text and comments shown in bold.

> Each projection was divided in three sections. The first section went from the initial population size of 500 to the inflection point of the **deterministic** population curve at MNPL where density dependent effects start to act **(Not true! density dependence acts throughout the range of N, NMPL is the point where the decline in population annual increase resulting from increasing density dependence of adding one individual matches the increase in the annual increase resulting from the addition of that individual)**.

Author's response: I agree that density dependence acts throughout the whole population trajectory, I meant to say that MNPL is the point where density dependent effects start to cause a decline in productivity… will modify the text accordingly.

Criticism or comment (p. 12), regarding the paragraph beginning with "After the first report proposed the use of a component of process error in the model…".

> The paragraph is bad science and should be re written or removed. Much of the variation that is discussed is measurement error not process error. There are several good papers reviewing this time series Breiwick *et al.*, Wade *et al.*, Gerber *et al*. come to mind (and I'm sure that there are others). These include attempts to tease apart the effects of measurement and process error. Carlos should review these before launching into his own analysis. Rather than discussing each data point separately I would like to see him fit his model to the data so that we get some fitted values from real data for σ and ρ.

Author's response: I certainly missed the inclusion of a couple of papers that support the idea put forward, "much of the variation that is discussed is measurement error and not process error". That is exactly the point, it is very difficult to separate the two errors to determine what the magnitude of natural variability is and therefore tune the model accordingly (see discussion above). In practice, the papers that support the proposition that there's more observation error than reported and the difficulties to separate the effect of the two errors only add to what is observable in the data series and I don't see anything wrong with observing what's conspicuous. The suggestion to fit the model to the data may be tempting, however, such thing isn't possible given the constraints in the Canadian Arctic bowhead whale data. If the necessary data were available, a full parameter estimation would have been done instead of a simulation. Finally, as discussed above, I understand and even share to some extent the concerns about the choice of process error distribution, but the preference for other distributions is not supported by data or any other verifiable piece of information. I think it would be more productive to provide either the data or the proper references to pertinent papers to support a claim or proposition.

Criticism or comment (p. 18), regarding the effect of the shape parameter on growth. Quoted original text with comment shown in bold.

> For one single growth rate, the population increases faster with larger values of ψ but the difference in the increase rate is smaller between larger ψ values **(Not True! For any given R_{max} the per capita annual increase in the deterministic model is close to R_{max} for small values of R_{max}. For larger values of ψ, the per capita annual increase remains close to R_{max} through a larger range of N before dropping to zero at N=K).**

Author's response: When he says "Not True! For any given R_{max} the per capita annual increase in the deterministic model is close to R_{max} for small values of R_{max}" I'm not sure what he wants to say here. My guess is that he made a mistake and typed R_{max} at the end of his sentence when he meant N_t… but then, although correct, his comment is irrelevant to the statement under scrutiny. He adds, "For larger values of ψ the per capita annual increase remains close to R_{max} through a larger range of N before dropping to zero at N=K)". This is actually not only correct but a confirmation of the statement he claims as untrue.

Criticism or comment, regarding assumptions on σ and ρ.

Author's response: I'm adding a paragraph at the end of the results-discussion section to warn that results are only valid under the choice of assumed parameter values and that increasing process error may certainly lead to different results.

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