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Evaluation of the sustainability of a flexible system of total allowable annual catches of narwhals (*Monodon monoceros*)

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Foreword

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

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ABSTRACT

In response to Resource Management's requests for science advice on a proposed system of flexible catch limits of narwhals, various model scenarios were run to determine the sustainability of allowable harvest limit carry-overs or credits between years over a five-year period. The modelling was similar to the robustness trial method used for Potential Biological Removal (PBR) calculations. Population numbers are projected over a period of 100 years with harvest rates based on PBR updated from estimates of the population every ten years. Results of model runs indicate that modelling scenarios with harvest debits or credits from year to year were not different from the base model with no credit or debit between years. All runs projected above Maximum Net Productivity Level (MNPL); the population size at which the combined size and growth rate of the population produces the largest number of animals per year, i.e., largest productivity. These results indicate that a flexible harvest limit system can be sustainable, as long as the five year total remains less than or equal to five times the PBR, as was the case in our model runs. To add realism to these long-term population projections, the model scenarios were also run with process error $\sigma_{process} = 0.05$. Results of the various scenarios were close to or better than the base model case, with no credits or debits from year to year. Model runs with a recovery factor fixed at 1 had a reduced number of end populations above MNPL but the debit or credit scenarios gave similar results to the base model without credit or debit between years. These results assume that actual hunting losses (i.e., struck and lost) are not different from those used to calculate Total Allowable Landed Catches in previous science advice and that there are no implementation errors in this flexible catch limit system.

Évaluation de la durabilité d’un système de limites flexibles de captures de narvals (*Monodon monoceros*)

RÉSUMÉ

Suite à la demande de la Gestion des Ressources de leur fournir un avis scientifique sur un système proposé de limites flexibles de captures de narvals, une série de scénarios de modélisation ont été effectués pour déterminer si des reports ou des emprunts de limites de captures entre années durant des périodes de cinq ans seraient durables. La modélisation suit l’approche de tests de robustesse du niveau de Retrait Biologique Potentiel (RBP) de Wade. Elle projette le nombre de populations sur cent ans avec des mises à jour du niveau de RBP faites à partir d’un échantillonnage de la population à intervalles réguliers. Les résultats des passages de modèles suggèrent que les scénarios avec débits ou crédits de captures d’une année à l’autre ne sont pas différents du modèle de base sans crédits ou débits entre années. Toutes les projections ont dépassé le Niveau Maximum de Productivité Nette (NMPN). Ces résultats suggèrent qu’un système de niveau de chasse flexible peut être durable, en autant que le niveau total de mortalité sur cinq ans est égal ou inférieur à cinq fois le RBP, ce qui était le cas dans nos scénarios de modélisation. Pour ajouter du réalisme à ces projections à long terme, nous avons ajouté de nouveaux passages de modèle des mêmes scénarios avec un facteur d’erreur de processus σprocess = 0.05. Les résultats sont semblables à ceux des modèles sans ce facteur, avec la plupart des projections finissant au-dessus du NMPN, comme dans le cas du modèle de base. Les projections faites avec un facteur de rétablissement fixé à 1 avaient moins de populations finales au-dessus du NMPN mais les résultats des projections avec débits ou crédits ne différaient pas sensiblement des modèles de base sans débit ou crédit. Ces résultats supposent que les pertes de chasse réelles ne sont pas trop différentes de celles utilisées pour calculer le niveau de débarquements autorisé et qu’il n’y a pas d’erreur de mise en œuvre de ce système flexible de limites de captures.

INTRODUCTION

There are presently five recognized narwhal summering stocks in the Canadian Arctic: Somerset Island, Admiralty Inlet, Eclipse Sound, East Baffin Island, Northern Hudson Bay (DFO 2010, Richard 2010). Hunts on these narwhal stocks are managed by setting an annual Total Allowable Landed Catch (TALC) for each stock for a five-year period. The TALC is based on a Potential Biological Removal (PBR) calculated for each stock, minus estimated hunting losses (i.e., struck and lost) (Asselin et al. 2012, DFO 2012a, 2012b, Richard 2008). The present analysis is in response to requests by Resource Management (RM) for peer reviewed science to address the following questions:

Question 1: Is it sustainable if Arctic Bay and Pond Inlet exchange their unused spring and fall Marine Mammal Tags for use by either community during their migratory (spring/fall) narwhal hunts? The same question was also posed for Clyde River and Qikiqtarjuaq.

This question was in fact addressed by previous science advice (Richard 2011). In short, each community pair likely hunts from a different stock mixture in spring and fall and therefore is taking from its stock mixture's combined TALC. Consequently, harvest credits are transferable between community pairs without invalidating previous advice on the sustainability of the affected stocks. As such, we did not address this question any further.

The remaining RM questions, on the other hand, required new analyses:

Question 2: Harvest credit (or carry-over) in a five year period:

a. Is 100% carry-over for one year sustainable?
b. What % carry-over for one year is sustainable?
c. What % cumulative carry-over is sustainable over consecutive years (up to five years)?

Question 3: Harvest debit (or borrow-back) in a five year period:

a. Is 100% borrowing from the following year sustainable once in a five year period?
b. What % borrowing from the following year is sustainable?
c. Can the total five consecutive years' total allowable catch be allocated to each year, in a five year period, any way the hunters chose as long as the sum of the five-years of catch does not exceed that total?

Question 4: How sustainable would a hunting mortality of five times the total allowable catch if applied to any one year of a five year period?

METHODS

SIMULATION MODEL

The model used for robustness simulations of flexible quota questions was first described by Wade (1998). His model used the discrete form of the generalized logistic equation less an annual mortality factor called Potential Biological Removal (PBR). We added an offset factor to the PBR to simulate credits or debits between years.

The model used here is therefore:

$$N_{t+1} = N_t + N_t \bullet R_{max} \, [\, 1 - (N_t / K)^{\theta}] - O_t \bullet PBR$$

where:

N_t = population size at year t; N_0 is fixed at 5,000, 10,000 (below MNPL[1] or 12,500) or at 15,000 (above MNPL or 12,500) depending on the modelling scenario

R_{max} = maximum net recruitment rate which is FIXED at a cetacean default value = 0.04

K = the pre-exploitation size or carrying capacity of the population = 25,000 for these simulated populations (FIXED)

θ = the density dependent shape parameter = 1 in this case for Maximum Net Productivity at 50% K (i.e., 0.5 K) (logistic growth) (FIXED)

O_t = offset factor in year t= 1, x times the PBR that year (to simulate credits or debits between years). O_t varies according to the scenarios outlined below

PBR_t = Potential Biological Removal in year t, calculated every tenth year (starting at t= 0) and applied for the ten years between surveys

$PBR_t = N_{min,t} \bullet 0.5 \bullet R_{max} \bullet F_r$ where:

$N_{min,t}$ is the 20% percentile of the log-normal distribution of the estimated population size an estimate $E(N_t)$ with a FIXED CV of 30%

$N_{min,t} = E(N_t) / [\exp(z \bullet \mathrm{sqrt}[\ln(1+CV^2)])]$, which simply = $E(N_t) / 1.280407$ with z = 0.842 (standard normal variate for 20th percentile) and a CV = 0.3

The estimated $E(N_t)$ used to update $N_{min,t}$ and PBR is sampled from a lognormal distribution of mean N_t and CV of 30%, as follows:

$E(N_t) = \mathrm{Exp}(\mathrm{Log}(N_t / (1 + (CV^{0.5}))) + z \bullet ((\mathrm{Log}(1 + CV^2))^{0.5}))$

where z is a random normal deviate = (-2*Log(Uniform(0,1))*Cos(2*π*Uniform(0,1))

R_{max} = is the maximum rate of increase for the population

F_r = recovery factor = 0.5 or 1, depending if the scenario puts the starting population (N_0) below MNPL (0.5 K or 12,500) then F_r = 0.5, or above MNPL then F_r = 1

The science advice questions relate to the sustainability of the TALC (TALC = PBR – hunting losses[2]). For simplicity, modelling was done on total hunting mortality, assuming that hunting losses are a constant fraction of hunting mortality, as was done for the original advice on TALC (DFO 2008, Richard 2008). Consequently, total hunting mortality each year is equal to a multiple or a fraction of PBR, depending on the scenarios.

Modelling scenarios were developed to address each question as follows:

Question 2: Harvest credit (or carry-over):

a. Scenario 1
b. Scenario 2
c. Scenario 3

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[1] MNPL (Maximum Net Productivity Level) is the population size at which the combined size and growth rate of the population produces the largest number of animals per year, i.e., largest productivity

[2] Potential Biological Removal (PBR) is a method initially developed in the United States for the regulation of human-induced mortality on marine mammals. For narwhal and beluga in Nunavut the principal human induced mortality is assumed to be from hunting and hunting losses.

Question 3: Harvest debit (or borrow-back):

a. Scenario 4
b. Scenario 5
c. Scenario 6

Question 4: Scenario 7

In all seven scenarios, 10,000 projections were run and a projection was carried for 100 years with PBR updates every ten years. As in Wade (1998), a scenario was considered sustainable if 95% or more of the deterministic projections' N_{100} were greater than MNPL, or 0.5 K =12,500. Conversely, the proportion of deterministic projections whose $N_{100} \leq 12{,}500$ gives the risk of overexploitation for a particular scenario. The Wade (1998) PBR robustness trial approach, on which the above scenario runs are based, is essentially deterministic (except for the PBR updating).

1) O_t = 0, 2, 1, 1, 1
   1a) N_0 = 5,000, F_r = 0.5 (i.e., N < MNPL (0.5 K) at start)
   1b) N_0 = 10,000, F_r = 0.5 (i.e., N < MNPL (0.5 K) at start)
   1c) N_0 = 15,000, F_r = 1 (i.e., N > MNPL (0.5 K) at start)
   The O_t are fixed and repeated every five years for each run

Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K

2) O_t = 1-x, 1+x, 1, 1, 1 where x = Rand(0…1)
   2a) N_0 = 5,000, F_r = 0.5
   2b) N_0 = 10,000, F_r = 0.5
   2c) N_0 = 15,000, F_r = 1
   Set x_n is fixed and repeated every five years for each run;
   Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K
3) O_t = x_1, x_2, x_3, x_4, x_5 (harvest credit accumulation for 5 years)

   where:
   x_1 = Rand(0..1)
   x_2 = Rand(0..1) • [1+(1-x_1)]
   x_3 = Rand(0..1) • [1+(1-x_2)]
   x_4 = Rand(0..1) • [1+(1-x_3)]
   x_5 = Rand(0..1) • [1+(1-x_4)]
   3a) N_0 = 5,000, F_r = 0.5
   3b) N_0 = 10,000, F_r = 0.5
   3b) N_0 = 15,000, F_r = 1
   Set x_n is fixed and repeated every five years for each run;
   Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K
4) O_t = 2, 0, 1, 1, 1
   4a) N_0 = 5,000, F_r = 0.5
   4b) N_0 = 10,000, F_r = 0.5
   4b) N_0 = 15,000, F_r = 1
   The O_t are fixed and repeated every five years for each run
   Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K
5) O_t = 1+x, 1-x, 1, 1, 1 where x = Rand(0…1)
   5a) N_0 = 5,000, F_r = 0.5
   5b) N_0 = 10,000, F_r = 0.5
   5b) N_0 = 15,000, F_r = 1
   Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K

6) $O_t = x_1, x_2, x_3, x_{4,}, x_5$ where:
    x_1 = Rand(0…5)
    x_2 = Rand(0..1)*(5- x_1)
    x_3 = Rand(0..1)*(5- x_1- x_2)
    x_4 = Rand(0..1)*(1-x_1- x_2- x_3)
    x_5 = Rand(0..1)*(1-x_1- x_2- x_3- x_4)
    6a) N_0 = 10,000, F_r = 0.5
    6b) N_0 = 10,000, F_r = 0.5
    6b) N_0 = 15,000, F_r = 1
    Set x_n is fixed and repeated every five years for each run
    Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K
7) A five year set x = (O_1, O_2, O_3, $O_{4,}$, O_5) is selected at random for each run, where sets are:
    x_1 = (5,0,0,0,0)
    x_2 = (0,5,0,0,0)
    x_3 = (0,0,5,0,0)
    x_4 = (0,0,0,5,0)
    x_5 = (0,0,0,0,5)
    7a) N_0 = 5,000, F_r = 0.5
    7b) N_0 = 10,000, F_r = 0.5
    7b) N_0 = 15,000, F_r = 1
    Set x_n is fixed and repeated every five years for each run
    Do 10,000 runs to t=100 and calculate how many N_{100} > 0.5 K

For comparison with the debit or credit scenarios, a separate set of projections, or base models, were also run using PBR without any offset factor but with the same range of start populations and recovery factors. To determine if credit or debit scenarios had noticeable effects on population projections, the results were compared to these base model scenario results.

There is a growing recognition in ecology that such deterministic models are unrealistic because they do not reflect natural variation in population processes (Dennis et al. 2006). To simulate natural variability, a separate set of the debit and credit scenarios were run with an additional random parameter for process error W_t, as follows:

$$N_{t+1} = W_t * [N_t + N_t * R_{max} * (1 – ((N_t /K)\text{^}1)) - (O_t\text{*}PBR)]$$

where $W_t = Exp(z_* s_{pro} – s_{pro}^2/2)$, s_{pro} is the process error, and z is a normal deviate (Hilborn and Mangel 1997 Equation 7.39 and 7.40).

Unfortunately, there is little guidance in the population dynamic literature on what amount of process error is realistic for narwhal populations, let alone for any marine mammal population. For their Bayesian model of beluga dynamics, Doniol-Valcroze et al. (2013) used an informative prior distribution of process error, which resulted in quartiles of 0.055 and 0.087. In their model runs, this prior distribution was not updated by posterior distributions of process error, so it remains unknown if their choice of process error distribution was correct. Ahrestani et al. (2013) estimated process error from population data of two species of elk (*Cervus elaphus* and *Cervus canadensis*) and several caribou or reindeer (*Rangifer tarandus*) subspecies across the northern hemisphere. With a few exceptions, estimated process errors in most of these ungulate populations were less than 0.05.

In our model runs, we chose to use an arbitrary process error of 0.05, consistent with our belief that population dynamics of the long-lived narwhals, and probably many long-lived slow-reproducing mammals, are not highly variable. To determine if the different credit and debit scenarios with process error had an effect on population projections, we compared their results to those of base model projections with process error.

Finally, we evaluated the effect of using a fixed recovery factor in our model projections, It is often impossible to ascertain whether a population is above MNPL with the assessment data available, therefore we undertook another set of runs with start populations N_0= 5,000 and 10,000 and a fixed recovery factor F_r=1, with and without process error. To determine the impact of incorrectly assuming a start population is above MNPL, and consequently incorrectly assigning it a recovery factor F_r =1, the scenario results were compared to their corresponding base models and to the runs with F_r = 0.5.

RESULTS

In the first set of runs with deterministic projections (without process error), each scenario (and sub-scenario) resulted in all, or practically all, projections reaching population numbers (N_{100}) above MNPL of 12,500 narwhals after 100 years (Table 1). All exceeded the Wade (1998) criterion (95%) for robustness for deterministic trials. When compared to the base model, the scenario runs resulted in little or no differences in the proportions above MNPL.

As expected, the runs with process error gave more variable results (Table 2), but a large proportion of the projections reached above 12,500 narwhals after 100 years (Table 2), and almost all exceeded the Wade criterion (95%) for robustness. Comparing the base model with the seven scenario runs with process error resulted only in small negative deviations, (range -0.2% to -1.9%) (Figure 1). In fact, several scenarios had positive deviations from base models, i.e., a larger proportion of N_{100} > 12,500.

The additional set of deterministic runs with a recovery factor F_r = 1 for population sizes 5,000 and 10,000 gave similar results to the first set of deterministic runs with F_r = 0.5. All or all but a few of N_{100} > 12,500 (range 98.7%-100%). The run with N_{100} = 15,000 and F_r = 1 is shown for comparison (Table 3).

On the other hand, the runs with process error and F_r = 1 for N_{100} = 5,000 and 10,000 resulted in significantly fewer N_{100} > 12,500 (76.8%-98.3%) (Table 4), compared to runs with F_r=0.5 (range 96.3%-98.9%) (Table 2). This is evident in all scenarios, including the base scenarios where there are no credits or debits between years. Nevertheless, the results of scenario runs with debits or credits were again not much different or better than corresponding base scenario runs. There were small negative deviations (range -0.5% to -2.9%) from base scenarios and several scenarios had larger proportions of N_{100} > above 12,500 (Figure 2).

DISCUSSION

These results indicate that a system of flexible total allowable landed catch is robust, as long as the total hunting mortality within each five year period does not exceed five times the PBR. The PBR update that takes place every 10 years in our model runs ensures that hunting pressure diminishes if the population is not assessed as increasing above MNPL (12,500) in a ten year period. In the deterministic runs (Table 1 and 3), more than 95% of the runs ended with N_{100} > MNPL, no matter what the starting population N_0 or recovery factor F_r set at the beginning of the projections. In the runs with process error (Tables 2 and 4), the proportions of N_{100} > MNPL were lower than the deterministic runs, as expected, but all scenarios performed almost as well or, in some cases, better than the base scenario (Figure 1).

It may seem counter-intuitive that several credit or debit scenarios actually do better than base models, but it makes sense if one considers that the base scenario assumes that 100% of the

PBR is used every year. In contrast, scenarios that give better results have a random proportion of the PBR < 100%, utilized in any specific year.

One aspect of these analyses that was not entirely realistic, is that the recovery factor was kept constant, even when the projections with an initial population size N_0 of 15,000 dip below MNPL (12,500), or when projections with an initial population size N_0 of 10,000 or 5,000 climb above 12,500. In a real-life implementation, with enough information on historical levels of the population, the recovery factor might be adjusted if the sampled population was thought to be above or below MNPL in a ten-year assessment. In the case where a population was deemed to be declining below MNPL, we can expect that a population with lesser recovery factor (from F_r=1 to F_r=0.5) at the ten-year PBR update would recover even faster than in our projections. One can also expect that as increasing populations exceed 12,500 their growth trend would slow down if the recovery factor was adjusted from 0.5 to 1 after a ten-year assessment. But the lesson from our N_0=15,000, F_r=1 deterministic runs is that such a recovery factor adjustment is not likely to cause a population decline below MNPL.

The deterministic run with a fixed recovery factor F_r = 1 (Table 3) show that the PBR method is robust to the choice of recovery factor, with 98.7% or more runs above MNPL after 100 years. The runs with process error are a little more sensitive to the choice of recovery factor but the scenario runs with a recovery factor F_r = 1 vary at worst by no more than -1% from scenario runs with F_r =0.5 (Table 4, Figure 2). Consequently, there is little indication that a flexible catch limit system will significantly increase the risk to sustainability, with a recovery factor of F_r = 1.

In response to questions from Fishery Management, the model runs have explored the risk of a range of moderate to extreme credit or debit options in five-year periods. In reality, one of the most likely events is that the total annual hunting mortality (landed catch and hunting loss) is frequently lower than the PBR. This is likely because in recent years several narwhal hunting communities in Nunavut have not reached their Total Allowable Landed Catch limit. In response to question 2, our scenarios 1 to 3 modelled a range of credit (carry-over) possibilities: all of which gave results close to or above the base model, where no credits were applies.

In response to Question 3 and 4, our scenarios 4 to 7 modelled a range of debit (borrow-back) possibilities, where excess hunting mortality could be debited from the following year. Such a situation could occur when there is an influx of large numbers of narwhals in a hunting area and it is later determined that total hunting mortality (landed catch and hunting loss) has exceeded the stock's PBR in a given year. Scenario 7 is an extreme case of that situation while scenarios 5 and 6 model random events of excess catch followed by debits in subsequent years. All gave results ± 3% of the base model where no debits were applied.

These results are encouraging, as they show little additional risk to the population from the implementation of flexible TALCs. Nevertheless, one should keep in mind that the above conclusions are based on models with some important assumptions. The first is that TALCs are a constant fraction of total hunting mortality, i.e., that hunting losses are constant and very similar to what was used to provide TALC advice for narwhal stocks (0.28 from Richard 2008). Hunting losses may in fact vary from area to area, from season to season and with different hunting methods. Unfortunately, we have insufficient data at present to determine those variations and apply them in modelling. Nevertheless, the PBR method has been shown to be robust to under-estimates of actual hunt mortality (Wade 1998).

Second, we assume that sources of human-induced narwhal mortality other than total hunting mortality (landed catch and hunting loss) are negligible. We have no reason to believe otherwise at present.

Third, we assume that flexible hunting limits are adhered to by all and that landed catches are reported exactly, that there are no implementation errors. Presently, we know of no reason to believe that narwhal landed catches are not reported accurately, but there have been no independent studies to verify this assumption. Perhaps this concern is moot as the latest records of narwhal catches (DFO) indicate that landed catches are, in many cases, lower than TALCs.

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TABLES

Table 1. Percentage of population projections runs (n=10,000) greater than MNPL (12,500) after 100 years, with no process error

Start parameters	**N_0 = 5,000, F_r = 0.5**	**N_0 = 10,000, F_r = 0.5**	**N_0 = 15,000, F_r = 1**
Scenario	**% N_{100} > 12,500**	**% N_{100} > 12,500**	**% N_{100} > 12,500**
Base: PBR harvest all years	100%	100%	100%
1) 0 harvest in year 1, 2 x PBR in year 2, PBR other years for 5-year period	100%	100%	100%
2) Random unused harvest in year 1 carried to year 2, otherwise PBR in 5-year period	100%	100%	100%
3) Random unused harvest carried over year to year over 5-year period	100%	100%	100%
4) 2 x PBR in year 1, 0 harvest in year 2, PBR other years for 5-year period	100%	100%	100%
5) Random excess harvest in year 1 debited from year 2, otherwise PBR	100%	100%	100%
6) Random annual harvest (0 to 5 x PBR) debited or credited over 5-year period, so total for 5-year period ≤ 5xPBR	100%	100%	99.9%
7) 5xPBR in one random year every 5-year period, 0 harvest in other years	100%	100%	99.7%

Table 2. Percentage of population projections runs (n=10,000) greater than MNPL (12,500) after 100 years, with process error (0.05).

Start parameters	**N_0 = 5,000, F_r = 0.5**	**N_0 = 10,000, F_r = 0.5**	**N_0 = 15,000, F_r = 1**
Scenario	**% N_{100} > 12,500**	**% N_{100} > 12,500**	**% N_{100} > 12,500**
Base: PBR harvest all years	96.3%	98.8%	91.9%
1) 0 harvest in year 1, 2 x PBR in year 2, PBR other years for 5-year period	96.0%	98.6%	91.4%
2) Random unused harvest in year 1 carried to year 2, otherwise PBR in 5-year period	96.8%	99.0%	93.0%
3) Random unused harvest carried over year to year over 5-year period	99.0%	99.6%	98.3%
4) 2 x PBR in year 1, 0 harvest in year 2, PBR other years for 5-year period	96.3%	98.6%	92.5%
5) Random excess harvest in year 1 debited from year 2, otherwise PBR	96.8%	98.9%	93.1%
6) Random annual harvest (0 to 5 x PBR) debited or credited over 5-year period, so total for 5 years ≤ 5xPBR	97.0%	98.9%	91.0%
7) 5 x PBR in one random year every 5-year period, 0 harvest in other years	96.3%	98.4%	90.0%

Table 3. Percentage of population projections runs (n=10,000) greater than MNPL (12,500) after 100 years, with Fr= 1 fixed and no process error

Start parameters	**N_0 = 5,000, F_r = 1**	**N_0 = 10,000, F_r = 1**	**N_0 = 15,000, F_r = 1**
Scenario	**% N_{100} > 12,500**	**% N_{100} > 12,500**	**% N_{100} > 12,500**
Base: PBR harvest all years	100%	100%	100%
1) 0 harvest in year 1, 2 x PBR in year 2, PBR other years for 5-year period	100%	100%	100%
2) Random unused harvest in year 1 carried to year 2, otherwise PBR in 5-year period	100%	100%	100%
3) Random unused harvest carried over year to year over 5-year period	100%	100%	100%
4) 2 x PBR in year 1, 0 harvest in year 2, PBR other years for 5-year periods	100%	100%	100%
5) Random excess harvest in year 1 debited from year 2, otherwise PBR	100%	100%	100%
6) Random annual harvest (0 to 5 x PBR) debited or credited over 5-year period, so total for 5-year period ≤ 5 x PBR	99.4%	99.9%	99.9%
7) 5xPBR in one random year every 5-year period, 0 harvest in other years	98.7%	99.5%	99.7%

Table 4. Percentage of population projections runs (n=10,000) greater than MNPL (12,500) after 100 years, with Fr=1 fixed and process error (0.05).

Start parameters	**N_0 = 5,000, F_r = 1**	**N_0 = 10,000, F_r = 1**	**N_0 = 15,000, F_r = 1**
Scenario	**% N_{100} > 12,500**	**% N_{100} > 12,500**	**% N_{100} > 12,500**
Base: PBR harvest all years	79.7%	89.6%	91.9%
1) 0 harvest in year 1, 2 x PBR in year 2, PBR other years for 5-year period	79.9%	89.1%	91.4%
2) Random unused harvest in year 1 carried to year 2, otherwise PBR in 5-year period	80.1%	91.0%	93.0%
3) Random unused harvest carried over year to year over 5-year period	93.2%	97.5%	98.3%
4) 2 x PBR in year 1, 0 harvest in year 2, PBR other years for 5-year periods	78.1%	92.7%	95.1%
5) Random excess harvest in year 1 debited from year 2, otherwise PBR	79.4%	90.1%	93.1%
6) Random annual harvest (0 to 5 x PBR) debited or credited over 5-year period, so total for 5-year ≤ 5 x PBR	80.2%	88.4%	91.0%
7) 5xPBR in one random year every 5-year period, 0 harvest in other years	76.8%	87.6%	90.0%

FIGURES

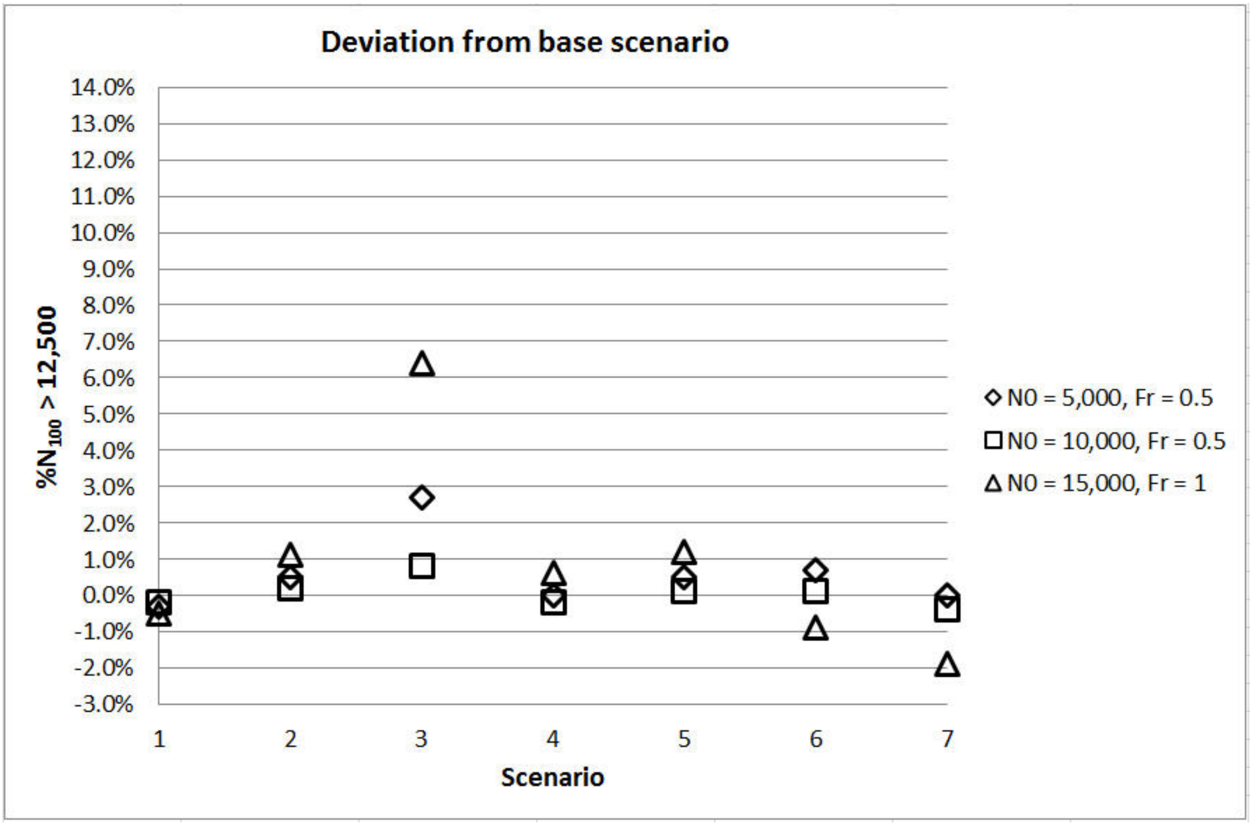

Figure 1. Percent probability deviation (N_{100} > 12,500) from base scenario in the seven credit or debit scenarios with process error and with F_r =0.5 for N_{100} = 5,000 and 10,000 (from Table 2 results).

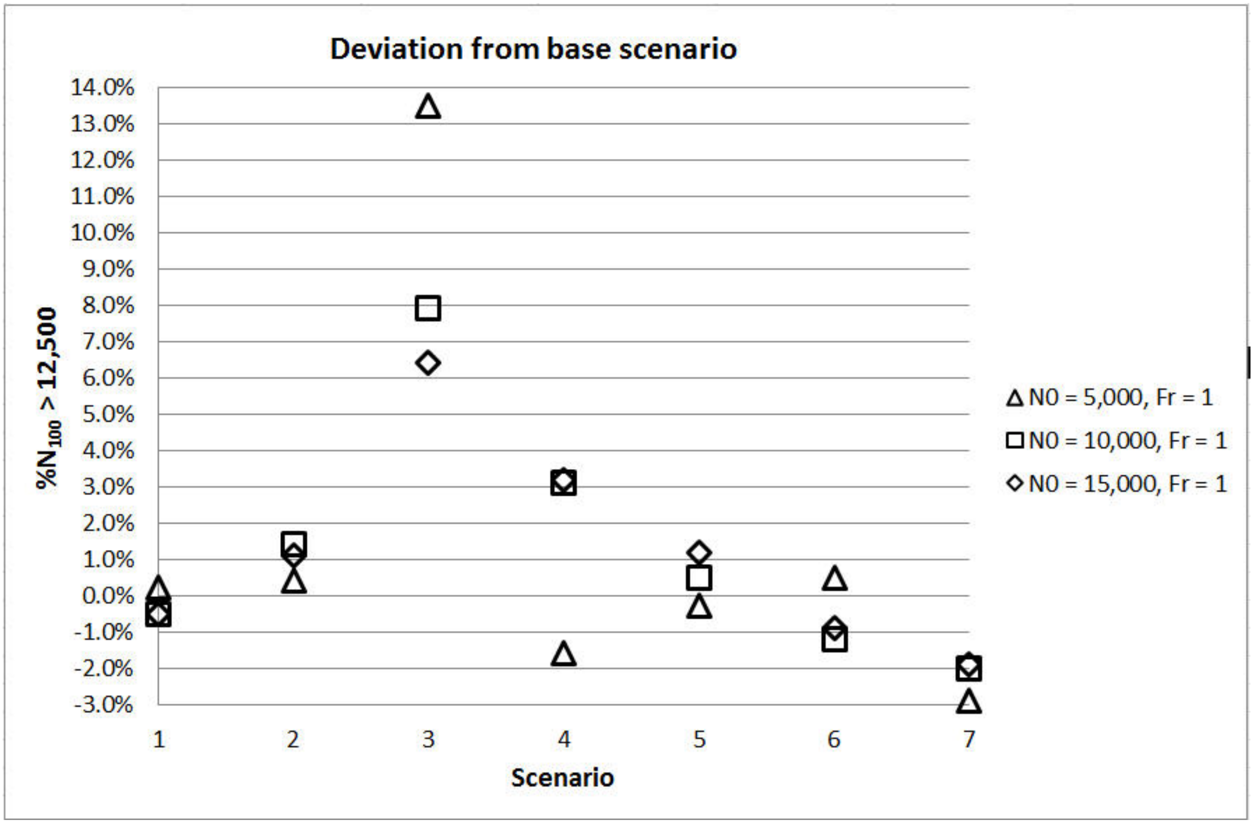

Figure 2. Percent probability deviation (N_{100} > 12,500) from base scenario in the seven credit or debit scenarios with process error and Fr = 1 for all runs (from Table 4 results).