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Stock-Dynamic Model for the Northern Hudson Bay Narwhal Population Based on 1982-2008 Aerial Surveys

Modèle de dynamique de stock pour la population de narvals du nord de la baie d'Hudson selon les relevés aériens de 1982 à 2008

Michael C.S. Kingsley[1], Pierre Richard[2] and Steven H. Ferguson[2]

[1]Rua Principal, Cortiça, P.O. Box 3, 3300–357 São Martinho da Cortiça Portugal

[2]Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba Canada R3T 2N6

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ABSTRACT

The Northern Hudson Bay narwhal population was previously assessed from aerial photographic surveys of summer aggregations in 1984, 2000, and 2008. The August 2008 survey was intended to provide information necessary for a full assessment of the population, but owing to camera malfunction, sea ice conditions, and poor weather a partial estimate using the 21–22 August survey provided an estimate of only 610 surface-visible narwhals (95% CI: 376–989), suggesting a loss of half of the population since the previous survey in 2000. A stock-dynamic model using Bayesian methods and run on the WinBUGS platform was developed to assess the population size indices updated with the catch history to inform management of this population. First, models were run using all three surveys and updated catch history. Second, the models were run without the 2008 survey. Third, the model was run using all three survey results and adding killer whale predation to understand its possible influence on the time series of population size estimates. The hunting levels of recent years, mean reported landings of 89 narwhals a year since 1998, appear from these results to be sustainable using model results from the model run without the 2008 survey information. The low result of the 2008 survey is not to be explained by the higher catches since 1998. The few survey estimates and the lack of good information on loss rates in hunting limited the ability of model results to estimate the present status of the population. The recent 2008 survey appeared incompatible with earlier survey estimates and reported catches. Model results could match the 2008 survey estimate by introducing predation since the preceding survey in 2000. However, the predation required to fit the survey results was high and would indicate that the population is unlikely to sustain even low catches. The results from this modelling exercise are uncertain and do not provide reliable estimates of future sustainable catches; we conclude that a further survey is required.

RÉSUMÉ

La population de narvals du nord de la baie d'Hudson a été évaluée avec des relevés aériens photographiques des agrégations estivales en 1984, 2000 et 2008. Le relevé d'août 2008 avait pour but de fournir des renseignements nécessaires à l'évaluation complète de la population, mais compte tenu du mauvais fonctionnement d'un appareil photo, de l'état des glaces de mer et des mauvaises conditions météorologiques, une estimation partielle, en utilisant le relevé des 21 et 22 août, a fourni une estimation de 610 narvals visibles à la surface (IC de 95 % : 376-989), ce qui suggérait une perte de la moitié de la population depuis le relevé précédent, effectué en 2000. On a conçu un modèle de la dynamique de la population en utilisant les méthodes bayésiennes et on l'a exécuté sur la plateforme WinBUGS pour évaluer les indices de l'effectif de la population mis à jour avec l'historique des prises pour informer la gestion sur l’état de cette population. D'abord, les modèles étaient exécutés en utilisant les trois relevés ainsi que l'historique mis à jour des prises. Ensuite, les modèles étaient exécutés sans le relevé de 2008. Enfin, le modèle était exécuté en utilisant les résultats des trois relevés et en ajoutant la prédation de l'épaulard pour comprendre son incidence possible sur les séries chronologiques de l'estimation de l'effectif de la population. Les niveaux de chasse des dernières années, qui représentent des débarquements déclarés moyens de 89 narvals par année depuis 1998, semblent être durables selon les résultats de l'exécution du modèle sans le relevé de 2008. Le faible résultat du relevé de 2008 ne peut être justifié par la hausse des prises depuis 1998. Le peu de relevés et le manque de renseignements pertinents sur les taux de pertes attribuables à la chasse ont limité la capacité des résultats de modèles à estimer l'état actuel de la population. Le récent relevé de 2008 semblait incompatible avec les estimations précédentes et les prises déclarées. Les résultats de modèles pourraient être compatibles avec l'estimation du relevé de 2008 en introduisant de la prédation à partir de l’année 2000. Toutefois, la prédation requise pour ajuster le modèle aux résultats du relevé de 2008 était élevée et indiquerait qu'il est peu probable que la population puisse soutenir même un faible taux de prises. Les résultats de cet exercice de modélisation sont incertains et ne fournissent pas pour l’avenir d'estimations fiables de niveaux de captures durables; nous avons donc conclu qu'un autre relevé est nécessaire.

INTRODUCTION

A stock-dynamic model of the population of narwhals in northern Hudson Bay was built and run. Among the objectives were: to review the sustainability of hunting at the levels of recent years, which appear to have been on average significantly bigger than before about 1999; to evaluate the most recent survey, flown in 2008, which returned a low estimate of population size, but was plagued with problems of weather, sea-ice and equipment, and to consider whether the low estimate from that survey might be explained by a serious decrease in population size due either to the recent increases in reported takes or by increased predation; and to estimate a sustainable take from the population (Richard 2010).

It has been reported that these days there are more and more killer whales summering in the eastern Canadian Arctic and they prey on narwhals. What effect this possibly increased predation level might be having on the dynamics and status of this quite small population of narwhals is not well known. However, it is thought possible that the low result of the 2008 survey could have been due, or partly due, to a real reduction of the population by sustained, and increased, predation (Richard 2010).

MATERIALS AND METHODS

A model was built to be fitted to the available data by Bayesian methods and coded for the WinBUGS platform (Lunn et al. 2000).

Data on catches were taken from the Table that is Appendix 4 of an unpublished report on harvests of narwhals prepared by D.B. Stewart (Arctic Biological Consultants, unpubl. data), updated with recent data from Fisheries and Oceans Canada (DFO) harvest reports (see Appendix 1 in this document). Catches in 1977–2009 were included. Going further back in time the number of missing reports increases, and as there are no surveys before 1982, using earlier data would provide no useful information on stock dynamics. The mean level of reported catches increased from 21 in 1977–98 to 89 in 1998–2009. In both periods the coefficient of variation (CV) of the reported catch was 40–50% but in neither was there any increasing or decreasing trend.

Survey data and information on survey coverage were taken from Richard (1991) and Bourassa (2003), updated with information on the 2008 survey from Richard (2010). The surveys constitute only two closely grouped sets of data points. The surveys flown in 1982–84 have such similar results and span so short an interval that their relative results give little information on stock dynamics, although they do contain information on the precisions of different types of survey and the relative visibility of narwhals to them. Similarly, the three results from 2000 yield information on survey precision and relative visibility. Information on stock dynamics comes only from the difference between the 1982–84 surveys and those flown in 2000, combined with statistics on landed catch. Given the sparseness of the data and its small range, it did not look as though the data was likely to contain useful information on any effect of population size on stock dynamics. Therefore, the dynamics of the population was modelled as a constant growth rate and we did not consider including in the model any effect of large numbers in reducing or limiting growth rate.

The prior distributions selected were in general cast as uninformative. One exception was that for process error. Narwhals have a gross annual birth-rate somewhere near 10% and are long-lived, so it was appropriate to model the process error as small, in default of making the stock dynamics deterministic.

Reported landed catches were available. While it is known that losses occur, and that in some hunts they are large, there is little accurate information on rates. This is a perennial problem in modelling the dynamics of hunted Arctic stocks of small cetaceans. Average ratios of lost:landed of 28% are reported by Richard (2008). These rates have been reported by the hunters themselves in association with community-based narwhal management systems. They are low compared with those of observed[1] floe-edge hunts but similar to those of observed open-water hunts (Weaver and Walker 1988, Roberge and Dunn 1990). Given that in Northern Hudson Bay most narwhals are taken in open-water hunts, a highly informative prior was assigned to loss rates.

Different versions of the eventual final model were run. The basic model included only the surveys flown in the early 1980s and in 2000. A second version included the 2008 survey to find out whether its low result could be due to the increased hunting in 1998–2008. A third version accommodated the low 2008 survey by modelling a step increase in (predation) mortality from 2000.

One set of statistics of use in judging management options and the sustainability of possible future catch levels comprises the risks of decline below given thresholds. For this assessment, risks of any decline, and of decline to less than 90% of the 2009 number, within 10 years, were calculated for a range of catch levels. Probabilities of future states, as estimated by this kind of model, depend on the process error, which is sampled independently for each consecutive year. Therefore a fourth version of the model was run in which there was no process error and the stock dynamics were deterministic; other uncertainties, and their prior distributions, were left unchanged. Code for both stochastic and deterministic stock dynamics is included in Appendix 2.

Survey coverage was planned in concert with the Repulse Bay Hunters and Trappers Organisation. But the realised coverage had also been affected by the weather and by the extent of small-floe pack ice, in which narwhals are much more difficult to detect (P. Richard., DFO, pers. comm.). Consequently survey coverage varied and results were not exactly comparable with one another. To deal with this problem, a standard stratification for surveys was defined for this model, and a coverage table that listed the strata covered by each past survey was included in the data made available to the model. On the basis of the survey results, the model made its best estimate of how the numbers were, on average, distributed between these strata; a somewhat informative prior was placed on this distribution. (As formulated, and with the data now available, the model is not able to take account of narwhals in areas that were never surveyed; cf Westdal 2008). A standardised photographic survey estimate was calculated for each survey by correcting its coverage to be Repulse Bay, Frozen Strait, Gore Bay and Lyon Inlet, and, if it was a visual survey, adjusting again for the model's estimate of visibility difference between the two types of survey; a standardised corresponding total population estimate was also calculated.

The model scaled survey results to true population size by using a set of visibility parameters. The base visibility was that pertaining to photographic surveys. Values were obtained from a single tagging study on this population (Westdal 2008). This base visibility parameter represented the overall average visibility of narwhals to photographic survey, and an uninformative gamma prior was given to its uncertainty. Each of the tagged whales was treated as an independent observation of the average visibility. Visual surveys were fitted by applying a visibility-ratio parameter, which was given an uninformative prior; the data, however, contains

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[1] By independent observers systematically recording shots fired and their effects.

information on the relative visibility of narwhals to the two types of survey and the distribution was strongly updated by the model fitting. Between-survey variation in average visibility is subsumed in the survey-variation parameter, along with other between-survey differences such as variations in the distribution of narwhals between strata and the survey sampling error.

The model was coded for fitting by Bayesian methods. The Bayesian equation was integrated by Markov-chain Monte-Carlo methods using WinBUGS 1.4.3. Automatic generation of initial values worked well enough for the basic run in which the 2008 survey was not fitted. But for the other three cases considered, initial values had to be saved from the basic run and provided to the model; if not, the model failed to converge to satisfactory solutions and as a result ran hesitantly or not at all. The model was burnt in for 50,000 iterations and run for 25,000,000 of which every 500th was saved.

MATHEMATICAL DESCRIPTION OF THE MODEL

The following equations specify the model. The parameters for the prior distributions used for the most recent runs of the model are tabulated at the end of the description (Table 1).

Table 1. Prior distributions for parameters of a stock-dynamic model for northern Hudson Bay narwhals.

Symbol	Name	Distribution	Parameters[1]	Limits
P_1	Starting true number	Uniform in log space		100, 10,000
k	Killer whale predation	Uniform		0, 1,000
$\varepsilon 1$	Process error	Log-normal	$0, 1/\sigma 1^2$	
$1/\sigma 1^2$	Process precision	Gamma	2, 0.0048[2]	
r	Population annual growth	Uniform		–0.1, 0.1
L	Hunting loss rate	Log-normal	–1.55, 1.45	
p	Population distribution between strata	Dirichlet	(3, 2.4, 0.3, 0.3)	
$\varepsilon 2$	Survey error	Log-normal	$0, 1/\sigma 2^2$	
$1/\sigma 2^2$	Survey precision	Gamma	0.01, 0.01	
v_2	Visibility to photographic survey	Uniform in log space		0.1, 1
$\varepsilon 3$	Experimental error in estimating visibility	Normal	$0, 1/\sigma 3^2$	
$1/\sigma 3^2$	Precision of visibility estimation	Gamma	0.01, 0.01	$10^{-8}, \infty$
Δ	Visibility difference factor, visual: photo	Uniform in log space		0.316, 3.16

[1] Parameters tabulated are as follows: for log-normal distributions the mean and precision of the corresponding Normal distribution in log space, for Normal distributions mean and precision—i.e., the reciprocal of the variance—and for gamma distributions shape and rate.

[2] Process precision was kept fairly high, considering narwhals to have high survival and low birth-rate.

The central variable in the model was an unknown quantity, the true population in the total survey area, implicitly at survey time. The true population for the next year, P_{y+1}, was predicted from the present year's population, P_y, by subtracting 25% of this year's true catch, adding a natural increase, subtracting 75% of next year's true catch, and multiplying by a (nominally) stochastic and independent lognormal error in the stock-dynamic process. I.e., it was assumed that on average 75% of a year's catch is taken before survey time and 25% after it, but that all births and natural deaths take place shortly before surveys are flown. The realised value of the error term $\varepsilon 1$ was, however, fitted by the model to the data series, and the series of process error values fitted is one diagnostic of the fit of the model to the data. A step in killer whale predation (to be effective from 2000) was added to the model in order to find out whether the low count made in the 2008 survey could be due to a recent increase in predation.

$$P_{y+1} = \left(P_y - 0.25T_y - 0.75T_{y+1} - k \cdot f_{y+1}\right) \cdot \left(1 + r\right) \cdot \varepsilon 1_y$$

where k is killer whale predation and f_y is a binary variable showing whether narwhals were preyed upon in year y[2]. The true catch T_y is related to the reported catch R_y by a stochastic loss factor:

$$T_y = R_y \cdot \left(1 + L_y\right)$$

Population numbers are anchored to survey results. As mentioned above, survey data present problems in that no fixed stratification for the surveys was established, and survey coverage varied from survey to survey. For the present analysis, the following strata were defined: 1) Repulse Bay and Frozen Strait, as far south as the south-eastern end of White Island; 2) Gore Bay and Lyon Inlet; 3) northern Foxe Channel (i.e., any effort applied south of the southern end of White I.) and 4) north-eastern Roes Welcome Sound. Maps in Richard (1991) and Bourassa (2003) were interpreted to develop a matrix of survey coverage (Table 2).

Table 2. Survey coverage as used in a model of the stock dynamics of northern Hudson Bay narwhals (derived by interpreting maps in Richard (1991) and Bourassa (2003)).

Year	Method	Repulse Bay and Frozen Strait	Gore Bay and Lyon Inlet	north-western Foxe Channel	north-eastern Roes Welcome Sound
1982	Visual	Yes	Yes	Yes	No
1982	Photo	Yes	Yes	Yes	Yes
1983	Photo	Yes	No	Yes	Yes
1984	Photo	Yes	Yes	No	No
2000	Photo	Yes	Yes	Yes	No
2000	Visual	Yes	Yes	Yes	No
2000	Visual	Yes	Yes	Yes	No
2008	Photo	Yes	Yes	Yes	No

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Then the expected true population N_S in the area covered by a survey would be given by:

$$N_S = \sum_A p_A \cdot C_{A,S} \cdot P_{Y_S}$$

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[2] The killer-whale predation term could be, and was, made ineffective by setting *k* equal to zero without otherwise changing the model code.

where $C_{A,S}$ is a binary variable indicating whether stratum A, which holds a proportion p_A of the population, was covered by survey S, which was flown in year Y_S. And the survey result V_S was then estimated by:

$$V_S = \left(N_S \cdot v_{K_S}\right) \cdot \varepsilon 2_S$$

where v_K is the visibility[3] of narwhals to surveys of type K, either photographic or visual, and the $\varepsilon 2_S$ are lognormal($0,\sigma 2^2$). Values for average visibility from Westdal (2008) were used, with an uninformative prior distribution on the uncertainty.

$$O_i = v_2 + \varepsilon 3_i$$

where O_i was the proportion of time that the i^{th} narwhal in Westdal's study was estimated to be visible to vertical aerial photography. Values for O ranged from 0.26 to 0.40.

The visibility to visual survey was expressed by putting a difference factor on the photographic-survey visibility:

$$v_1 = v_2 \cdot \Delta$$

The difference factor, Δ, was given a prior distribution uniform in log space between about 0.3 and 3.

To facilitate the graphical presentation of results, standard survey results U that would be expected from photographic surveys over Repulse Bay, Frozen Strait, Gore Bay and Lyon Inlet, were calculated from modelled population numbers P, including numbers in future years, by:

$$U = P(p_1 + p_2)v_2$$

(p_A being defined above) and standardised photographic survey results corresponding to each survey available to be used as data by:

$$D_S = V_S \cdot \frac{\left(p_1 + p_2\right)}{\sum C_{AS}\, p_A} \cdot \frac{v_2}{v_S}$$

corresponding to the expected result from a photographic survey over Repulse Bay, Frozen Strait, Gore Bay and Lyon Inlet.

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[3] 'Visibility' here is the ratio of animals counted on a survey to animals in the surveyed area i.e., a single correction factor to be applied to counts.

RESULTS

MODEL RUN BEHAVIOUR

The model could be compiled, initialised and run with few problems, provided that the 2008 survey was omitted or its result accommodated by increased predation after 2000. If not, the model needed to be supplied with good starting values, otherwise it failed to run, ran very slowly, or failed to converge.

The model fitted more parameters than there were observations, so many correlations between parameter estimates were significant and some were high. However, in spite of the many parameters to be fitted to so little data, most of the prior distributions were markedly updated by the Bayesian fit. There were two principal exceptions. One was the loss correction to reported catches. The data contains no information on loss rates of struck animals, so the posterior distribution of this parameter was essentially the unchanged prior. However, it had only one significant correlation, of +6.5% with the population growth rate.

The other was the process error. This was given an informative prior, narwhal having low birth- and death-rates[4]. When the 2008 survey was omitted, the population trajectory was fitted essentially to two survey points, so there was no pressure for the process error to be updated. However, when the 2008 survey was included, the process error distribution was updated to higher values, the model needing to make large adjustments to numbers in order to reduce them from the high values of the 2000 survey to the low 2008 value.

In general, there was not much data, and what there was had large uncertainties. Therefore it is not surprising that parameter estimates are generally associated with large standard errors. The model considered that it was only estimating about 8 effective parameters.

MODEL RESULTS, OMITTING THE 2008 SURVEY AND WITH NO PREDATION ALLOWANCE

The model ran easily and converged well with low autocorrelations in the MCMC chains. The fitted trajectory showed a steady increase until 1998; the population growth rate was fitted to the (fairly constant) catches in this period and to the change in survey index between the surveys of the early 1980s and those carried out in 2000. The resulting estimate of annual growth in numbers was 2.4%, which, although somewhat low, is not substantially out of agreement with accepted views on population dynamics of monodontid whales (Table 3). After 1998, the fourfold increase in catches in the most recent 10 years lessened the rate of increase in the median estimate of numbers (Figure 1). Between the survey points, i.e., early 1980s and 2000, the uncertainty in numbers did not increase much, but uncertainty increased markedly as the most recent survey data point was left further behind and by 2009 the estimate of population size—as indexed by a hypothetical photo survey—has a relative interquartile range (IQR)[5] of more than 60% (Figure 1).

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[4] Runs with uninformative priors for the process error tended to hang, having too much freedom and not enough direction.

[5] Relative IQR = IQR divided by the median.

Table 3. Parameter estimates from model run without the 2008 survey and with no added predation.

	Mean	S.D.	Median	Relative IQR (%)
Population growth rate (%)	2.4	2.3	2.4	117
Starting number, true pop. ('00)	46.0	14.0	44.0	38
Stock-dynamic process error, CV (%)	6.1	2.9	5.3	53
Lost, per landed (%)	29.4	28.9	21.0	117
Photo visibility std. err. (pctge points)	7.8	2.3	7.4	36
Visibility difference (visual:photo) (%)	89.3	37.5	82.3	44
Visual survey visibility (%)	28.0	12.1	25.7	46
Photo survey visibility (%)	31.4	2.7	31.4	11
Visual survey error CV (%)	56.7	49.9	43.3	81
Photo survey error CV (%)	32.7	26.3	25.6	86
Population proportions: (%)				
Repulse Bay and Frozen Strait	65.2	16.8	67.3	35
Gore Bay and Lyon Inlet	23.4	13.2	21.2	84
north-western Foxe Channel	5.2	7.7	1.7	426
north-eastern Roes Welcome Sound	6.1	8.6	2.1	408

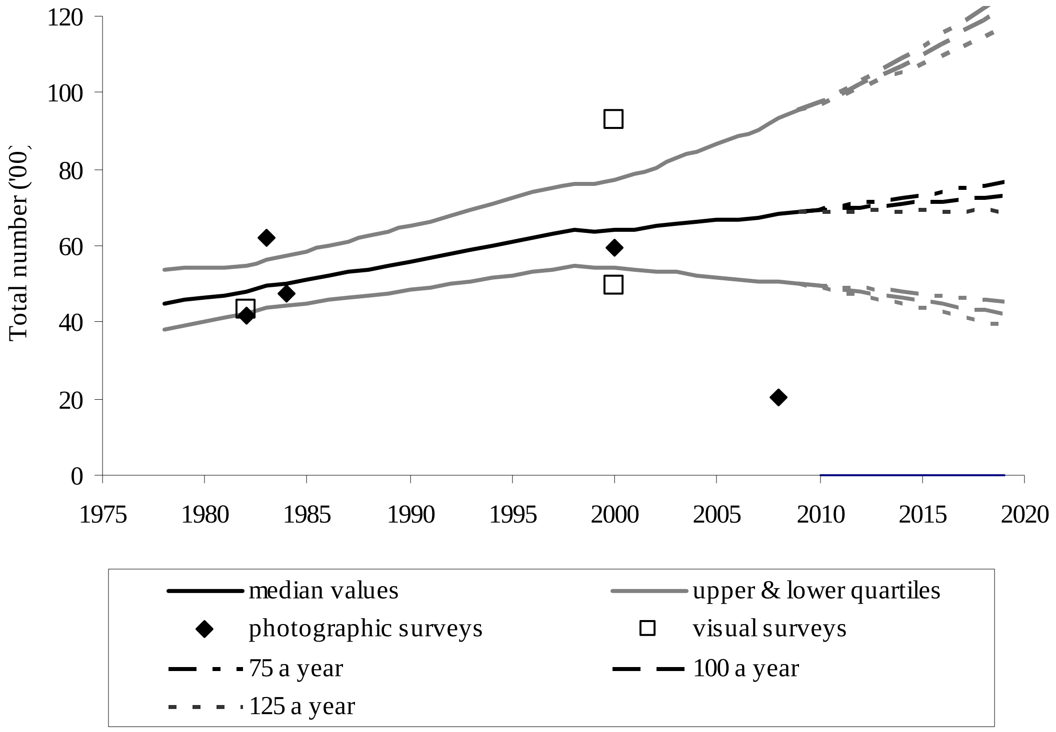

Figure 1. Modelled trajectory of estimated total number of narwhals in surveyed area, with 10-year projections for reported annual landings of 75, 100 and 125 narwhals. 2008 survey not fitted. Survey results standardised to median estimates of equivalent total number.

In this model, the estimate of photo survey visibility was fixed by experimental results from tagging studies of dive behaviour, which limited the model's freedom. There were therefore few large correlations (Table 4). Large correlations were estimated between the starting population size and the growth rate—negative, since a larger starting population would imply a trajectory sitting high on the early survey results and then low on the later ones; and between the visibilities of the two types of surveys, since they did on the whole agree fairly well in their estimates of population trend. Other correlations were low; even the loss rate had only one significant correlation, with the growth rate—positive, since higher losses had to be compensated by greater production from the population.

Table 4. Correlations (%)[1] between parameter estimates; model run with no 2008 survey and no extra predation after 2000.

	Survey error		Survey visibility		Visibility difference	Visibility error	Loss rate	Start number
	photo	visual	photo	visual				
Growth rate	8.0	-5.6		-12.7	-13.4		6.5	-55.0
Start number		4.4	-27.5	-15.8	-10.6			
Visibility error			-5.7					
Visibility difference		17.6		97.6				
Visibility, visual		17.2	20.2					

[1] Correlations over 5% are tabulated.

Predicted population trajectories were calculated for a range of reported landings. However, uncertainty about the present size and status of the population greatly outweighed likely differences between proposed catch limits (Figure 1). The available data provides only a poor basis for estimating sustainable catches for this population.

MODEL RESULTS, INCLUDING THE 2008 SURVEY BUT WITH NO PREDATION ALLOWANCE

The 2008 survey result is incompatible with the other seven. The higher catches in 1998–2009 are insufficient to explain its low estimate (Figure 1). To attempt to fit it, therefore, the model had to take violent action, adjusting the values of most parameters (Table 5) and also forcing adjustments to the stock dynamics to achieve some kind of fit. It was necessary to find means of making it look possible that the survey result decreased by a factor of nearly 3 between 2000 and 2008 even though survey results increased between the early 1980s and 2000.

Among the adjusted parameters were the following.

- Population growth rate, median -0.2%, down from 2.4%. This made it easier for the survey result to decrease between 2000 and 2008, and fitted better to the entire series of 8 surveys in 1992–2008.
- Start population 5,090, up from 4,410. This helped the population to sustain the catches between the early 1980s and 2000 without decreasing.
- Stock-dynamic process CV 5.7%, up from 5.3%. The process error CV had an informative prior which made it difficult for the model to fit large values. However, the model would have liked to have a larger CV for the process error so that it could, with reasonably high likelihood, fit large positive process errors between the early 1980s and 2000 to maintain numbers, and large negative ones between 2000 and 2008. This increase was as much as the informative prior distribution would allow.

Table 5. Parameter estimates from the model run with the 2008 survey but with no added predation.

	Mean	S.D.	Median	Change (%)	Relative IQR (%)
Population growth rate (%)	0.0	2.4	-0.2	-107	-1,663
Starting number, true pop. ('00)	52.4	18.1	51.0	16	49
Stock-dynamic process error, CV (%)	6.8	3.7	5.7	7	61
Lost, per landed (%)	32.2	34.3	22.2	6	121
Photo visibility std. err. (pctge points)	7.8	2.3	7.4	0	35
Visibility difference (visual:photo) (%)	112.0	48.7	102.4	24	54
Visual survey visibility (%)	35.3	15.6	32.1	25	55
Photo survey visibility (%)	31.5	2.7	31.5	0	11
Visual survey error CV (%)	68.6	59.5	52.9	22	82
Photo survey error CV (%)	48.3	31.0	40.5	58	74
Population proportions: (%)					
Repulse Bay and Frozen Strait	60.8	17.2	62.1	-8	40
Gore Bay and Lyon Inlet	28.4	14.3	26.7	26	75
north-western Foxe Channel	5.3	8.1	1.6	-4	438
north-eastern Roes Welcome Sound	5.5	8.4	1.7	-20	416

- Loss rate increased as much as the prior would allow. This increased the effect of the larger reported catches after 1998 in driving numbers down.
- Visibility in visual surveys increased to 102% of that of photographic surveys from 82%. The highest proportion of visual-survey data points—2 out of 3—was in 2000. By raising the visibility ratio the model reduced the overall estimate of true numbers in 2000, as the visual-survey results became due to high visibility, not to large numbers. So the difference in estimated true numbers between the early 1980s and 2000 was also reduced, and this fitted better to a population with a very low rate of growth. This change also reduced the difference in estimated true numbers between 2000 and 2008, thus reducing, slightly, the drastic actions needed to bring the numbers down to fit the 2008 survey.
- Error CVs greater for both visual and photographic surveys (medians 53% and 40% instead of 43% and 26%). The surveys in the early 1980s agreed fairly well with one another and those in 2000 weren't too badly out of agreement, and the model had to find a compromise between this agreement and the large *dis*agreement between the survey trajectory and that derived from the stock-dynamic model. It found the best compromise at different values from those fitted when the 2008 survey was not around to cause problems.

All these parameter adjustments were not enough to come close to fitting the 2008 survey. Making even larger adjustments to parameters values would have made the parameter set very improbable as defined by the assigned prior distributions. In this model, the stock dynamics are not deterministic, but an adjustment, the 'process error' is made to the population numbers each year. To fit the 2008 survey, these 'process errors' were also forced to participate in adjusting the population size. When the 2008 survey was not fitted, the process errors formed a close-to-random series, except for excursions where the model sought to fit the survey results of 1983 and 1984 (Figure 2). When the 2008 survey was fitted, a string of positive process errors—gratis additions to the population—were needed to maintain the population against the catches before 2000 (the population growth rate having been fitted at a negative value), i.e., to provide the narwhals taken by the hunters. After 2000, the model fitted a series of large negative process errors—gratuitously subtracting animals from the population—as numbers were forced down to fit the 2008 survey (Figures 2 and 3). The large size of the process errors contributed to standard diagnostics of model fit, but the low likelihood of such a clearly non-random sequence of supposedly independently and identically distributed variates did not. The mean deviance of this model was 39.0 compared with 29.3 when the 2008 survey was not fitted.

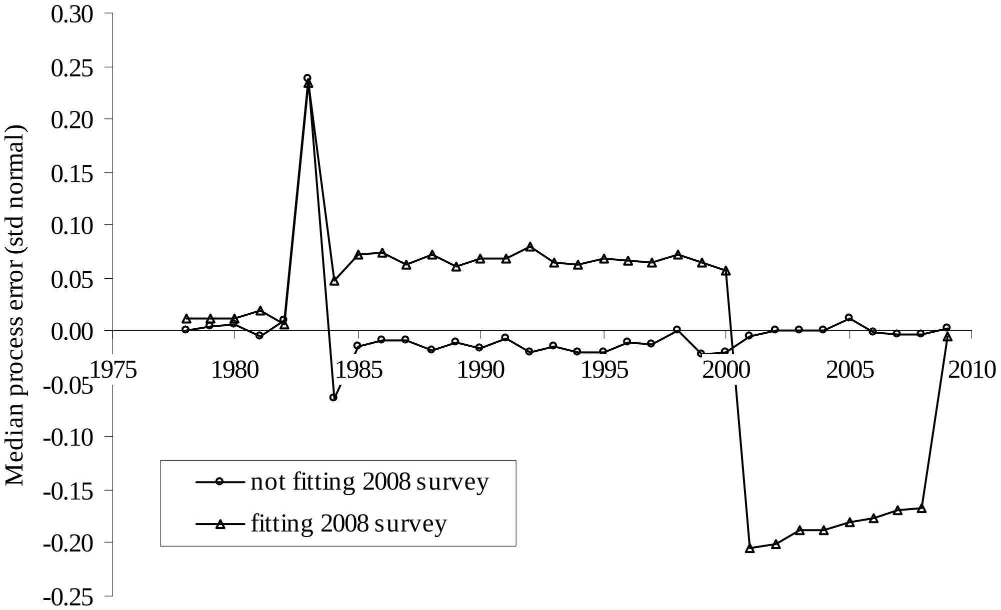

Figure 2. Stock-dynamic process errors when fitting, or not fitting, the 2008 narwhal survey result.

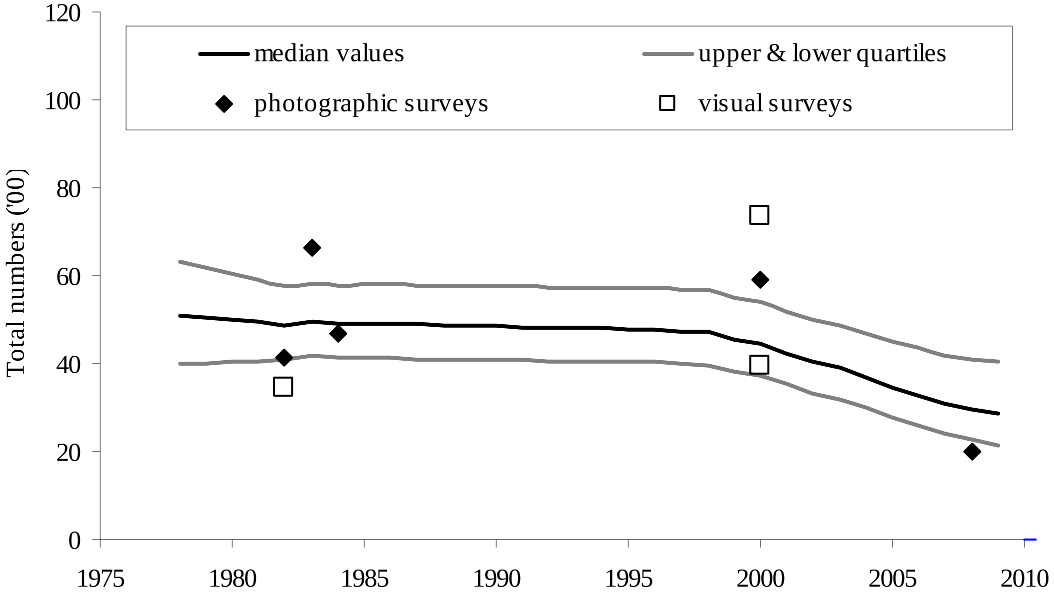

Figure 3. Trajectory of estimated total numbers fitted by a stock-dynamic model to all available narwhal survey results. Survey results standardised to median estimates of equivalent total number.

RESULTS WITH EXTRA KILLER WHALE PREDATION AFTER 2000

Adding a predation parameter from 2000 and on allowed the population to be easily brought down to fit the 2008 survey. The flexibility added by this parameter allowed the 2008 survey to be fitted with parameter values close to those obtained when the 2008 survey was omitted (Table 6, Figure 4). The biggest change in the stock-dynamic modelling parameters was a reduction of 6.9% in the error CV of photographic surveys. Other values were changed by less than 5%. The process errors were close to a random series (allowing for the excursions to fit the 1983–84 surveys) but median process errors after 1999 were again generally negative owing to the influence of the 2008 survey value; the model fit ignores the low likelihood of a series of consecutive values with the same sign, being only concerned with the distribution of the values.

Table 6. Stock-dynamic parameters from fitting a stock trajectory to all surveys, fitting additional predation from 2000 onwards.

	Mean	S.D.	Median	Change (%)	Relative IQR (%)
Population growth rate (%)	2.5	2.0	2.5	3.1	105
Starting number, true pop. ('00)	46.1	13.5	44.1	0.2	37
Stock-dynamic process error, CV (%)	6.0	2.7	5.3	-0.4	52
Lost, per landed (%)	29.0	27.9	20.8	-1.0	117
Photo visibility std. err. (pctge points)	7.8	2.3	7.4	-0.1	36
Visibility difference (visual:photo) (%)	90.9	35.8	84.2	2.3	42
Annual kill by killer whales	5.0	2.3	4.9		70
Visual survey visibility (%)	28.4	11.5	26.2	1.9	44
Photo survey visibility (%)	31.2	2.7	31.3	-0.4	11
Visual survey error CV (%)	55.9	50.7	42.8	-1.2	80
Photo survey error CV (%)	29.8	21.7	23.9	-6.9	81
Population proportions: (%)					
Repulse Bay and Frozen Strait	65.7	16.6	67.7	0.5	34
Gore Bay and Lyon Inlet	22.6	12.8	20.5	-3.6	84
north-western Foxe Channel	5.3	7.8	1.7	2.8	419
north-eastern Roes Welcome Sound	6.4	8.7	2.4	12.7	386

With an uninformative prior—uniform in the range 0–1,000—the median predation was 489 narwhals a year, the upper quartile point 665. An earlier analysis of killer whale feeding (Kingsley, unpubl. data) modelled different bases for prey selection by killer whales. The greatest mortality of narwhals was found when this species composed 32% of the diet, and was 8% (median estimate) from a population assumed to number 5,100, i.e., 408 narwhals a year. Other compositions of diet or attacks yielded lower estimates of the number of narwhals killed by killer whales.

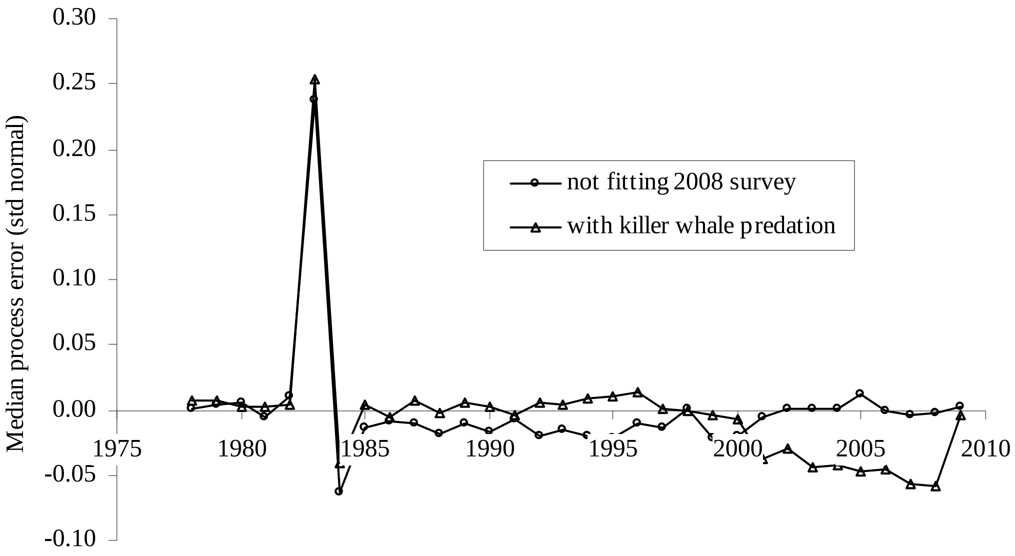

Figure 4. Median stock-dynamic process errors from a run including the 2008 survey with an additional predation term from 2000 onwards.

Lower predation levels could be combined with an intermediate level of distrust of the 2008 survey result, but modelling the spectrum of possibilities would produce little additional information.

If the 2008 survey result were to be deemed explained by killer whale predation during 2000–09 and not by survey error, it would be necessary to infer that the population was now at such a low level that it could not sustain landed catches of 60/yr (Figure 5). If killer whales kept on preying on narwhals at the rate needed to bring the numbers down to fit the 2008 survey, the population would be well on its way to becoming extinct.

RESULTS WITH DETERMINISTIC STOCK DYNAMICS

When process error was set to zero and the stock dynamics made deterministic, median trajectories were not much changed, but IQRs of both historic and future trajectories became narrower. Estimates of the probabilities of future decrease also changed. The risks of decrease, and of decrease to less than 90% of present size, were estimated to be lower if stock dynamics were assumed to be deterministic (provided catches were on average sustainable) (Table 7).

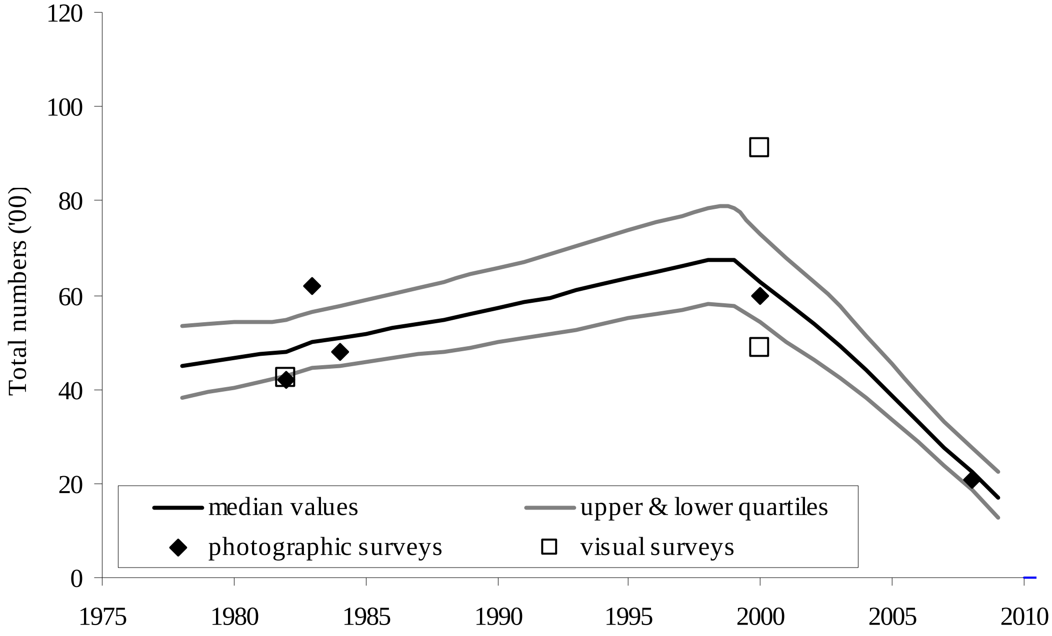

Figure 5. Population trajectories fitted to all surveys, with predation by killer whales added from 2000 onwards. Survey results standardised to median estimates of equivalent total number.

Table 7. Estimated risks of decrease, and of decrease to less than 90% of 2009 numbers, under different levels of landed catch and assuming stochastic and deterministic stock dynamics.

	Probability (%) of population size in 2019 less than:			
	estimated 2009 population size		90% of estimated 2009 population size	
Landed catch	Model with no process error (deterministic)	Model with process error (stochastic)	Model with no process error (deterministic)	Model with process error (stochastic)
10	9.8	22.6	3.8	13.5
20	12.5	24.9	5.4	15.5
40	18.5	29.9	9.1	19.8
60	26.6	35.4	13.8	24.8
80	34.4	40.7	19.8	29.8
100	42.0	45.2	26.4	34.5
120	49.3	49.8	33.0	39.3
140	55.6	54.3	40.0	44.2

DISCUSSION

The history of reported landings comprises two periods, in both of which landings were fairly constant, but at different levels. There is therefore only one change in catch rate. Without a usable survey since 2000, estimating the effect of this change on the population trend depends, completely, on the assumptions about visibility and loss rate. Trying to calculate what other change in catch rate might have a specified effect on population trend—for example, no change in size—is therefore both difficult and conditioned on these same assumptions. Partly as a result of the shortage of data, uncertainty as to the present state of the population and its future trend is much larger than the differences in trend that might be associated with different future catch rates. In other words, estimating future sustainable catch is difficult and the result uncertain.

The hunting levels of recent years—mean reported landings of 89 narwhals a year since 1998—appear from these results to be sustainable. The median, and mean, estimates of numbers continue to increase. However, the modal[6] estimates—i.e., the most likely values—decrease after 1998 as the uncertainty increases and the mode and median diverge. These results are contingent on the input values for photographic survey visibility, which governs the true numbers estimated to be in the population, and for the loss rate, which governs the effect of a given reported catch. A low value for visibility increases estimates of true numbers and makes catches easier to sustain. A low loss rate reduces the effect on numbers of the increase in reported landings after 1998. In these model runs, both of these parameters have been given informative priors at low values.

The low result of the 2008 survey is not to be explained by the higher catches since 1998. The model could be persuaded to fit a trajectory to the complete set of surveys, but not only needed to adjust many of the basic parameters as much as their prior distributions would allow, but also imposed large process errors in trying to force the population trajectory to conform to the survey series. Another way of interpreting this is to say that the model requires an unknown external influence to force the numbers down to near the 2008 estimate. The low likelihood of the process-error series was not captured by the deviance value, which was, however, higher at 39.0 than the mean of 29.3 when the 2008 survey was not fitted.

Adding a fixed killer-whale predation on narwhals from 2000—with a very uninformative prior distribution—made it easy for the model to fit the population trajectory to the 2008 survey, but the predation was high, with a median estimate of about 490 narwhals a year. The unfortunate corollary was that if predation were in fact both constant in numbers and high enough to explain the 2008 survey result the population would still be rapidly decreasing and by now imperilled. Various compromise models might be tried but would require informative prior distributions, with sound quantitative bases, on the relative badness of the 2008 survey, or on the number of narwhals that killer whales take a year, or both. And even if such priors were available, the conclusion would probably remain inescapable that the 2008 survey was not fully comparable with the other photographic surveys.

When stock dynamics was modelled as stochastic, the prior distribution of process error was not updated at all, the posterior completely overlapping the prior. This is not surprising, as the available data contains no information on process error. However, it appears that process error and the way it is included in stock-dynamic models are important in estimating probabilities of future states of the population. If such probabilities are to form a basis for the formulation of

---

[6] The mode has been estimated both as median minus twice the difference between mean and median and as median divided by the square of the ratio of mean to median.

advice, it will be necessary to develop a reliable and scientifically sound way of estimating and describing process error—i.e., the stochastic component of population dynamics—that can be included in stock-dynamic models.

CONCLUSIONS

A simple stock-dynamic model for the narwhals of Northern Hudson Bay could easily be designed using Bayesian methods and run on the WinBUGS platform. It provided some information on the relative visibility and error levels of photographic and visual surveys. The sparsity of survey data and the lack of good information on loss rates in hunting, and therefore on true levels of catches, hindered getting accurate results on the present status of the population, and predictions of population trend for different levels of landings differed by much less than their associated uncertainty. The most recent survey in 2008, appeared incompatible with earlier surveys and reported catches. It could be made compatible by introducing an elevated level of predation since the preceding survey in 2000. However, the predation required fully to fit the survey was rather high. Furthermore, if the survey result were thus to be made to seem accurate the population would now be so small that it would be unlikely to sustain even low catches, especially if predation were assumed to be continuing.

ACKNOWLEDGEMENTS

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APPENDICES

Appendix 1. Landed harvests from the northern Hudson Bay narwhal population by community (0 = no harvest, blank cell = no report) (from Appendix 4 in Stewart unpubl. report (2008) and DFO unpubl. data).The model used the catch series presented in the "Total" column.

Year	Cape Dorset	Chesterfield Inlet	Coral Harbour	Kimmirut	Rankin Inlet	Repulse Bay	Whale Cove	Total
2009	0	4	0	0	8	97	0	**109**
2008	0	2	1	0	2	25	0	**30**
2007	0	3	3	1	9	72	0	**88**
2006	0	4	3	0	10	72	5	**94**
2005	0	4	6	0	7	72	1	**90**
2004	0	3	3	0	7	106	0	**119**
2003	0	2	1	0	3	38	2	**46**
2002	0	4	4	1	2	57	2	**70**
2001	1	2	0	0	3	100	2	**108**
2000	0	3	0	0	7	49	0	**59**
1999	0	5	0	0	2	156	2	**165**
1998	0	3	4	0	2	18	0	**27**
1997	0	0	9	0	0	35	1	**45**
1996	0	0	10	0	7	10	0	**27**
1995	0	0	10	0	6	4	0	**20**
1994	1	0	0	0	0	5	0	**6**
1993	0	0	1	0	0	13	0	**14**
1992	0	0	0	0	0	20	0	**20**
1991	16	0	0	0	0	3	0	**19**
1990	0	0	0	0	0	17	0	**17**
1989	0	0	0	0	0	16	0	**16**
1988	1	0	0	0	0	25	0	**26**
1987	0		12	7	0	16	0	**35**
1986	0		0	0	0	7	0	**7**
1985	0		0	0	1	15	0	**16**
1984			0	0	2	25	0	**27**
1983	0		0		2	11	0	**13**
1982	0		0	0	0	21	1	**22**
1981	0		6	0	5	29	0	**34**
1980	1		0	0	0	25	0	**26**
1979	1		0	0	0	30	0	**31**
1978	2		0	0	0	4	0	**6**
1977	0		0	0	0	8	0	**8**

Appendix 2. WinBUGS code for the model. This model is the most developed, i.e., that which uses data from all surveys flown and includes a term for killer whale predation. The model calls on other files for data on survey coverage and results, expecting that any surveys not to be fitted will be at the end of the file, on catches, and on the incidence of killer whale predation.

```
#data
list(area.pct=c(50,40,5,5), area.obs=6,
Nsurv=8, Nuse=8, Nyears=33,  #Nuse = 7 to omit 2008 survey (last in the file)
N.fut.years=10,Nlevel=3,
set.catch=c(0.75, 1.0 , 1.25),
N.vis.obs = 9,
vis.obs=c(0.349, 0.286, 0.314, 0.4, 0.27, 0.382, 0.305, 0.261, 0.279),  # Westdal data
fut.surv.cover = c(1,1,0,0) )


# areas are 1. R.B & F.S. (always surveyed together); 2. Gore B. and Lyon In.;
3. N.W. Foxe Chann.; 4. N.E. Roes Welcome Sound.


model  {

lgt.true.pop.1 ~ dunif(0,2)
lgt.true.pop.1.prior ~ dunif(0,2)
true.pop[1] <- pow(10, lgt.true.pop.1)
true.pop.1.prior <- pow(10, lgt.true.pop.1.prior)



true.catch[1] <- report.catch[1] * (1 + struck.and.lost)

for (i in 1:N.vis.obs)
{     vis.obs[i] ~ dnorm(vis[2],prec.vis)I(1.0E-1,)
}


for (yr in 2:Nyears)
{     true.pop.pred[yr] <- (true.pop[yr-1] - 0.25 * true.catch[yr-1]) * (1 +
r) - 0.75 * true.catch[yr]- k.w.step * k.w.cover[yr]
      true.pop.med[yr] <- log(max(1.E-3,true.pop.pred[yr]))

# the following line is used in modelling stochastic stock dynamics
      true.pop[yr] ~ dlnorm(true.pop.med[yr],prec.proc)
# the following line is used in modelling deterministic stock dynamics
#     true.pop[yr] <- exp(true.pop.med[yr])

      std.vis.pop[yr] <- true.pop[yr] * vis[2] * inprod(area.prop[],
fut.surv.cover[])  # result of standard photo survey
      true.pop.offset[yr] <- (log(true.pop[yr]) - true.pop.med[yr] ) *
sqrt(prec.proc)
      true.catch[yr] <- report.catch[yr] * (1 + struck.and.lost)
      for (area in 1:4)
      {     area.true.pop[yr,area] <- true.pop[yr] * area.prop[area]
      }

}

for (surv in 1:Nuse)  # visual surveys have code 1, photo. have code 2
            # fit only the surveys to be fitted
{     surv.vis.pop[surv] ~ dlnorm(surv.vis.pop.med[surv],
prec.type.surv[type[surv]])
      }

for (surv in 1:Nsurv)  # calculate stats for all surveys, incl. those not
fitted
```

```
{
      surv.vis.pop.pred[surv] <- inprod(area.true.pop[surv.year[surv],],
surv.cover[surv,]) * vis[type[surv]]
      surv.vis.pop.med[surv] <- log(surv.vis.pop.pred[surv])
      prec.surv[surv] <- prec.type.surv[type[surv]]
      std.surv[surv] <- surv.vis.pop[surv]/inprod(area.prop[],
surv.cover[surv,]) * inprod(area.prop[],fut.surv.cover[]) # corrected for
coverage
      std.foto.surv[surv] <- std.surv[surv]*vis[2]/vis[type[surv]] # corr. for
cover and type visibility
      std.totpop.surv[surv] <- surv.vis.pop[surv] / inprod(area.prop[],
surv.cover[surv,])  / vis[type[surv]]  # convert to equivalent estimated
numbers
}


# this block predicts future evolution
base.vis.pop <- true.pop[Nyears] *  inprod(area.prop[],fut.surv.cover[]) *
vis[2]
for (level in 1:Nlevel)
{     true.fut.catch[level] <- set.catch[level] * (1 + struck.and.lost)
      for (yr in 1:1)
      {     true.fut.pop.pred[level,yr] <- (true.pop[Nyears] - 0.25 *
true.catch[Nyears]) * (1 + r) - 0.75 * true.fut.catch[level]- k.w.step
            true.fut.pop.med[level,yr] <- log(max(1.E-
3,true.fut.pop.pred[level,yr]))

# the following line is used in modelling stochastic stock dynamics
            true.fut.pop[level,yr] ~
dlnorm(true.fut.pop.med[level,yr],prec.proc)
# the following line is used in modelling deterministic stock dynamics
#           true.fut.pop[level,yr] <- exp(true.fut.pop.med[level,yr])

            fut.vis.pop[level,yr] <- true.fut.pop[level,yr] *
inprod(area.prop[],fut.surv.cover[]) * vis[2]
      }
      for (yr in 2:N.fut.years)
      {     true.fut.pop.pred[level,yr] <- (true.fut.pop[level,yr-1] - 0.25 *
true.fut.catch[level]) * (1 + r) - 0.75 * true.fut.catch[level]- k.w.step
            true.fut.pop.med[level,yr] <- log(max(1.E-
3,true.fut.pop.pred[level,yr]))

# the following line is used in modelling stochastic stock dynamics
            true.fut.pop[level,yr] ~ dlnorm(true.fut.pop.med[level,yr],
prec.proc)
# the following line is used in modelling deterministic stock dynamics
#           true.fut.pop[level,yr] <- exp(true.fut.pop.med[level,yr])

            fut.vis.pop[level,yr] <- true.fut.pop[level,yr] *
inprod(area.prop[],fut.surv.cover[]) * vis[2]
      }
      rate.of.change[level] <-   ( log(fut.vis.pop[level, N.fut.years]) -
log(base.vis.pop)) / N.fut.years
      extinct[level] <- step(-0.6 - rate.of.change[level])
}


#proportions in areas

for (area in 1:4)
{     area.prop.base[area] <- area.pct[area]/sum(area.pct[]) * area.obs
      area.prop.gamma[area] ~ dgamma(area.prop.base[area],1)
      area.prop[area] <- area.prop.gamma[area]/sum(area.prop.gamma[])  #
}
```

```
#priors

r ~ dunif(-0.1,0.100)

r.prior ~ dunif(-0.1,0.100)

shape <- 2
rate <- .0016 * (shape + 1) # mode for process CV at 4%
prec.proc.prior ~ dgamma(shape , rate)
prec.proc ~ dgamma(shape , rate)

prec.vis ~ dgamma(0.01, 0.01)I(1.0E-8,)

lgt.vis.2 ~ dunif(-1,0)
vis[2] <- pow(10,lgt.vis.2)
vis[1] <- vis[2] * vis.diff

lgt.vis.diff ~ dunif(-.5,.5)
vis.diff <- pow(10, lgt.vis.diff)

for (i in 1:2)
{     prec.type.surv[i] ~ dgamma(.01,.01)I(1.E-8,)
}

k.w.step ~ dunif(0,10)  # k.w.step <- 0 for no predation

struck.and.lost ~ dlnorm(-1.55,1.45)  # PRR recommendation 11/06/10
struck.and.lost.prior ~ dlnorm(-1.55,1.45)


prec.surv.prior ~ dgamma(.01,.01)I(1.0E-8,)


#bookkeeping

w[1]<-r
w[2]<-true.pop[1]

w[3]<-1/sqrt(prec.proc)

w[4]<-struck.and.lost
w[5] <- 1/sqrt(prec.vis)
w[6] <- vis.diff
w[7] <- k.w.step
w[8] <- base.vis.pop
w[11]<-vis[1]
w[12]<-vis[2]  #vis[2] is photographic
w[21]<-1/sqrt(prec.surv[1])
w[22]<-1/sqrt(prec.surv[2])

w1[1]<-r.prior
w1[2] <- true.pop.1.prior
w1[3]<-1/sqrt(prec.proc.prior)
w1[4]<-struck.and.lost.prior


for (i in 1:4)
{     y[i] <- area.prop[i]
}

for (i in 1:Nsurv)
{     y1[100+i] <- std.surv[i] # standardised for coverage only
      y1[200+i] <- std.foto.surv[i]  # standardised for coverage and
visibility
      y1[300+i] <- std.totpop.surv[i]  # standardised to total numbers, all
areas
```

```
}

for (i in 2:Nyears)
{     x[100+i] <- true.pop[i]
      x[200+i] <- std.vis.pop[i] # expected result from photo survey in areas
1 & 2
      x[300+i] <- true.pop.offset[i]
}

for (level in 1:Nlevel)
{     z2[level,1] <- rate.of.change[level]
      z2[level,2] <- extinct[level]
      for (yr in 1:N.fut.years)
      {     z[level,100+yr] <- true.fut.pop.pred[level,yr]
            z[level,200+yr] <- fut.vis.pop[level,yr] # expected result from
photo survey in areas 1 & 2
      }
}


#end of model
}}}
```