An exploratory assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using a stochastic population dynamics model

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ABSTRACT

The stochastic population dynamics model used by Aboriginal Whaling Management Procedure developers is revised to correct weaknesses related to uncertainty parameterisation and replacement yield estimation. Two variants of this model, along with the standard deterministic version, are used to assess the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The variants differ with respect to the magnitude and complexity of the stochastic variation they introduce into natural mortality and birth/calf survival processes. An allowable catch statistic, $E\ (Q_0)$, is defined for appropriate use with stochastic model assessments. Using the same assessment methods, likelihood and priors as IWC (1999a), 5th percentiles of $E\ (Q_0)$ were found to be 117, 106 and 91 for the deterministic, simpler stochastic and extreme stochastic models, respectively. Bayes factor results show that there is no evidence suggesting that either stochastic model should be favoured over any simpler alternative, and the deterministic model yielded the best fit overall. The $E\ (Q_0)$ estimates confirm and strengthen past IWC Scientific Committee inference that under current bowhead subsistence hunting levels the stock should continue to increase towards stabilisation above its maximum sustainable yield level.

KEYWORDS: ARCTIC; BOWHEAD WHALE; MODELLING; POPULATION ASSESSMENT; STATISTICS; WHALING-ABORIGINAL

INTRODUCTION

In-depth assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales, *Balaena mysticetus*, are carried out by the IWC Scientific Committee (SC) periodically. The last two major assessments took place in 1994 (e.g. Raftery *et al.*, 1995; Givens *et al.*, 1995; Butterworth and Punt, 1995) and 1998 (e.g. Breiwick, 1998; Schweder and Ianelli, 1998; Wade, 1998; Poole, 1999; Punt and Butterworth, 1999). Both Bayesian and frequentist techniques have been used to estimate important quantities of interest such as the 5th percentiles of replacement yield (RY) and allowable catch Q_0 (Wade and Givens, 1997), which are used in setting the catch limits for aboriginal subsistence whaling. Regardless of the statistical methodology employed, all the assessments have been based on versions of the population dynamics model (PDM) encoded in the BALEEN II computer program (de la Mare, 1989; Punt, 1999b). This is an age-structured, density-dependent deterministic model designed to project the population from some starting year, typically the first year of the commercial fishery, through to the present time and beyond. The population is assumed to be at pre-exploitation equilibrium in the initial year of the projection.

The Scientific Committee is currently in the process of developing an Aboriginal Whaling Management Procedure (AWMP) that will eventually be used to set whaling catch limits. As part of this process, a stochastic version of the PDM has been developed (see IWC, 2000) based on earlier work by Givens (1999) and Punt (1999a). This model allows for random variation in the natural mortality and birthing/calf survival processes. In this paper, problems with some parameters and output statistics used by the stochastic model are identified and corrections are suggested. The results of an assessment using the revised stochastic model are then presented. Two cases are considered: (i) demographic stochasticity only; and (ii) demographic plus environmental stochasticity with autocorrelation. Demographic stochasticity is the variability associated with the birth and death processes in the population. When the parameters that control the demographic stochasticity are themselves subject to serially correlated variation over time, the model is said to incorporate environmental stochasticity with autocorrelation. This extra variation might model trends or variations in the basic stochastic dynamics due to environmental or other unexplained factors.

For each of these two cases a Bayesian analysis using the 'backwards' approach is performed. In contrast to the standard projection of the population from a point in the past through to the present time, this approach selects a value of current abundance and then solves for the initial population size that, together with fixed values of biological parameters, gives rise to the chosen current abundance. The 'backwards' approach is described in further detail by Butterworth and Punt (1995).

Stochastic population dynamics models have a history in the fisheries assessment literature. The estimation of parameters in these applications has typically been based on maximum-likelihood or least-squares methods. Emlen (1995) used a density-dependent, age-structured stochastic PDM, with autocorrelated environmental variability, to model a species of salmon and to examine the consequences of various management options. Freeman and Kirkwood (1995) developed a time-series approach to abundance estimation (from catch and effort data) that incorporated stochastic population dynamics. Outside of fisheries, Sæther *et al.* (2000) used a simple stochastic PDM to project a population of sparrows through time. They showed that ignoring the uncertainty in population dynamics can lead to major underestimation of the extinction risk. Engen and Sæther (1998) provided a good general review and discussion of stochastic population models.

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The AWMP stochastic model was designed primarily for use in AWMP trials rather than as a new tool for more traditional assessments. However, until the AWMP is in place, the aboriginal whaling catch limits will continue to be based on traditional assessments and it is therefore of interest to investigate the degree to which demographic and/or environmental stochasticity might affect the results of the assessment. However, it is premature to deem stochastic PDM assessment results as reliable as deterministic PDM results. Our analysis has identified several areas where the stochastic PDM appears to require improvement; these are detailed in the next section.

SPECIFICATION OF THE STOCHASTIC ASSESSMENT MODEL AND METHODS

The stochastic model of the AWMP Standing Working Group

A technical description of the current stochastic model used in the AWMP development process is given in IWC (2000), and so the details are not repeated here. What distinguishes a stochastic model from its deterministic counterpart is that the sizes of the recruited and unrecruited populations in any given year are random variables with means equal to the sizes specified in the deterministic model. The stochastic model achieves this through several probabilistic assumptions, which are summarised informally below.

(1) The numbers of whales of each age class that die of natural causes during a year are realisations of binomial random variables with means equal to the corresponding numbers of deaths for that year in the deterministic model.
(2) The total number of births in a given year is the realisation of a binomial random variable with mean equal to the total number of births for that year in the deterministic model.
(3) The number of female births in a given year is the realisation of a binomial random variable with mean equal to half the total number of births in that year. In the deterministic model the number of female births is simply half of the total.
(4) The model allows for environmental variability in the birthing/calf survival process by selecting the probability of birth/calf survival in a given year to be the realisation of a random process rather than as a fixed value. This random process can incorporate autocorrelation (over time) if desired.

Such stochastic dynamics require a change in the interpretation of some model parameters. For example, the maximum sustainable yield rate (MSYR) of production, which is an input to both models, must be interpreted as a generic productivity parameter for the stochastic model, rather than as the actual productivity rate at the stock's maximum net production level as is the interpretation for the deterministic model.

The deterministic model (denoted 'D') and the two stochastic model variants described earlier are considered here. These two variants are currently under consideration as part of the AWMP development process. The simpler case is to assume demographic stochasticity only: binomial births and deaths. Denote this model as 'SD'. A more far-reaching generalisation is to assume that the parameters controlling demographic stochasticity are themselves subject to serially correlated stochastic variation over time. Denote this model as 'SE'. There are other variants that could also be considered. For example, the probabilities of death could be treated as serially correlated random variables. For the purposes of this paper, the focus is restricted to the SD and SE variants.

Corrections to the stochastic models

Variance estimation

The excess variation in the SE model is controlled by two parameters: σ_ε^2 and ρ. σ_ε^2 determines the variability of the process generating the probability of birth/calf survival, and ρ controls the serial correlation in that process. The value of b_t, the probability of birth/calf survival in year t, is generated according to the random process:

$$b_t = \frac{e^{q_t}}{1+e^{q_t}}$$

where

$$q_t = \mu_t + \rho(q_{t-1} - \mu_{t-1}) + \varepsilon_t, \quad \varepsilon_t \sim N(0,\sigma_\varepsilon^2).$$

σ_ε^2 and ρ need to be specified, while μ_t is chosen such that $E(b_t)$ equals the corresponding birth/calf survival rate in the deterministic model.

A third parameter, $\sigma_q^2 = \sigma_\varepsilon^2/(1-\rho^2)$, summarises the total marginal extra-binomial variation in the birth/calf survival process (i.e. the variation beyond typical binomial randomness). Suitable values for σ_ε^2 and ρ, and hence also σ_q^2, are suggested by the following analysis.

Givens *et al.* (1995) assessed the variability in bowhead calf counts from 1985, 1986, 1989, 1990, 1991 and 1992 resulting from the aerial photogrammetry work of Angliss *et al.* (1995). This variability has three main components along with possible sub-components:

(1) binomial counting, or sampling, variability;
(2) counting process error, including variation due to survey timing relative to migratory patterns, missed survey days, ice conditions, etc.; and
(3) variation in the true proportions of calves, due to:
    (a) trend in proportion of calves due to population dynamics; and
    (b) stochastic variation in calf production, including:
        (i) binomial birthing/calf survival process; and
        (ii) extra-binomial variation in birthing/calf-survival process (possibly serially correlated), parameterised by σ_ε^2 and ρ in the SE model.

Givens *et al.* (1995) estimated that the 1985-1992 mean proportion of calves in the stock was 0.052, with an estimated CV of 0.41. This CV estimate reflects variance components 1-3 and all their sub-items above[1]. Each AWMP stochastic model sets σ_ε^2 at a value which yields 0.41 as the coefficient of variation (CV) for only component 3(b)(ii). Clearly this is excessive since 3(b)(ii) is only one of many contributors to the overall CV, and other sources - especially (2) - likely dominate. Thus, the SE model as prescribed for AWMP simulations seems to allow too much calf productivity variation. This is important for both AWMP development and for assessment since it would bias downwards the 5th percentiles for management quantities of interest.

Corrections to σ_ε^2 and ρ are therefore required. Some of the above variance components can be estimated from data and simulations. The calculations of Givens *et al.* (1995) indicate that component (1) accounts for 6% of the total.

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[1] The Givens *et al.* (1995) analysis assumed that component 3(a) was negligible. That assumption is approximately removed here by considering such variation to be another contributor to the random variables denoted S_i in their work, which were used to drive the process error accounted for in their analysis.

Clearly the remaining variance components are not likely additive, but in the absence of a better model, the remaining variation is decomposed additively to provide at least a rough gauge of their relative sizes.

Using the base-case AWMP evaluation, deterministic simulations provide typical 'true' calf proportions in the years matching the Angliss *et al.* (1995) data. Typical simulated trajectories showed calf percentages changing by about 0.24% over this time span. The average within-simulation variance of calf proportions over these years suggests that roughly 6% of the total variation is attributable to component 3(a). The same simulations provide the binomial sample sizes and probabilities that would be used to simulate stochastic birth/calf survival. Typical values were 1,175 eligible mature females and 0.23 mean calving probability. This provides an estimate that roughly 1% of the total variation is likely due to component 3(b)(i).

This leaves components (2) and 3(b)(ii). Although the former source is believed to be dominant, there are no data available to quantify either. Therefore, the residual 87% of the total observed variation is divided equally between these two sources. In summary, then, the observed data CV is 0.41, of which 0.18 is attributed to 3(b)(ii) and 0.23 to other sources.

Thus, to match the AWMP Standing Working Group strategy, σ_ε^2 and ρ were derived to yield a stochastic birth/calf survival process whose probability parameter had a mean of 0.25, serial correlation of 0.75, and variance corresponding to a CV of 0.18 (see IWC, 2000). The estimates were $\sigma_q^2 = 0.0585$ and $\rho = 0.752$, yielding $\sigma_\varepsilon^2 = 0.0254$.

Replacement yield and Q_0 estimation

For a given year *t*, the deterministic model calculates RY as the number of recruits minus the number of deaths, divided by the weighted mean survival. In the stochastic case, however, such a calculation is dominated by the random fluctuations in the birth and death processes that occur during the given year. Therefore, the *expectation* of RY should be calculated in order to average over the randomness in these processes. No single simulated value of RY_t is guaranteed to adequately reflect the expected dynamics in year *t*. The expected RY cannot be obtained as the expected number of recruits minus the expected number of deaths, divided by the expected weighted mean survival[2]. Instead, the expected value of RY_t, denoted $E(\mathrm{RY}_t)$, using the Monte Carlo average of 150 realised values of RY_t is estimated.

A key quantity of interest for the Bering-Chukchi-Beaufort stock of bowhead whales is the allowable catch, Q_0, defined in the deterministic case (Wade and Givens, 1997) as:

$$Q_{0,t} = \begin{cases} 0 & \text{if } N_t^{1+} < 2{,}000 \\ \min\ (\mathrm{RY}_t - 1,\ 0.9\ \mathrm{MSY}) & \text{if } 2{,}000 \le N_t^{1+} < \mathrm{MSYL}^{1+} \\ 0.9\ \mathrm{MSY} & \text{if } N_t^{1+} > \mathrm{MSYL}^{1+} \end{cases}$$

where RY_t is the replacement yield as defined above, N_t^{1+} is the number of whales aged 1 or more in year *t*, MSY is maximum sustainable yield and MSYL^{1+} is the MSY level relative to the 1+ stock and expressed as a number of whales rather than as a proportion of carrying capacity. In the stochastic case, the expected value of $Q_{0,t}$, denoted $E(Q_{0,t})$, can be estimated by averaging the 150 values of $Q_{0,t}$ obtained from the 150 values of RY_t generated earlier. These estimates, $E(\mathrm{RY}_t)$ and $E(Q_{0,t})$, were used for all the analyses involving stochastic models in this paper[3].

Assessment method

The intention was to replicate the method used in IWC (1999b). Thus, the 'backwards' Bayesian analysis and the prior distributions for model parameters that were used in that assessment were also used, listed here in Table 1[4].

The data were treated in the same way as they were used in IWC (1999b). The age data for the proportions of calves and mature animals were taken from IWC (1995). The likelihoods for these data are shown in Table 2, where t_5 signifies a *t*-distribution with five degrees of freedom. The series of N_4/P_4 survey abundance estimates and their pairwise correlations were taken from Punt and Butterworth (1999), and are shown here in Tables 3 and 4. The logarithms of the survey estimates were assumed to jointly follow a multivariate normal distribution with means given by the logarithms of the point estimates and correlation matrix as in Table 4.

It is also necessary to incorporate the Bayes Empirical Bayes (BEB) likelihood for 1993 abundance (Raftery and Zeh, 1998) into the likelihood; this is the estimate agreed by the Scientific Committee to be the best single estimate of abundance in 1993. The N_4/P_4 estimate for 1993 is essentially independent (on the log scale) of the estimates in all the previous years. (This is evident from an inspection of the final row of the correlation matrix in Table 4). Under independence, 1993 can be treated separately from the years 1978-1988, and the BEB likelihood for 1993 can be explicitly included in place of the log-normal distribution assumed for the N_4/P_4 estimate. In this case, the N_4/P_4

Table 1

Prior distributions for bowhead PDM parameters.

Parameter	Prior
MSYL^{1+}	U[0.4; 0.8]
MSYR^{1+}	U[0.01; 0.07]
Survival transition age (a)	Discrete U[1; 9]
Age at sexual maturity (ASM)	Grouped N(20; 3^2) truncated at 13.5 and 26.5
Adult survival (*s*)	N(0.99; 0.02^2) truncated at 0.995
Maximum theoretical pregnancy rate (f_{max})	$1/f_{max} \sim$ U[2.5; 4]
1+ abundance in 1993 (P_{93})	N(7,800; $1{,}300^2$)

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[2] This is because the expected value of a non-linear function of random quantities is generally unequal to the value of that function evaluated at the expected value of each component quantity.

[3] At present, the AWMP program does not calculate $E(Q_{0,t})$. A routine was created specifically for the analyses in this paper.

[4] An alternate formulation allowed the adult survival *s* to approach 1 while enforcing a maximum age of $w = 100$. The two formulations gave very similar results, so this case was not considered further in the stochastic assessment.

Table 2

Likelihoods for bowhead age data.

Data	Distribution
Proportion of calves (1985-1992)	$0.0164t_5+0.052$
Proportion of matures (1985-1992)	$0.0286t_5+0.411$

Table 3

Estimates and standard errors of logarithms of abundance indices for the Bering-Chukchi-Beaufort Seas bowhead stock. These values were obtained from Punt and Butterworth (1999).

Year	Estimate	SE of logarithm ≈ CV
1978	4,820	0.273
1980	3,900	0.314
1981	4,389	0.253
1982	6,572	0.311
1983	6,268	0.321
1985	5,132	0.269
1986	7,251	0.186
1987	5,151	0.298
1988	6,609	0.113
1993	7,778	0.071

estimates for 1978-1988 are still assumed to follow a joint distribution with correlation matrix from Table 4 (now excluding the final row), and they are multiplied by a 'bias' factor b. The bias factor re-scales the 1978-1988 N_4/P_4 estimates to reflect the difference between the 1993 BEB and N_4/P_4 point estimates.

The contribution of the abundance data to the negative log-likelihood function was (excluding constants) therefore:

$$-\log L = \frac{1}{2(\sigma_{93}^{BEB})^2}(N_{93}^{BEB} - \hat{N}_{93})^2 + \frac{1}{2}(\log(b\underline{N}^{surv}) - \log \hat{\underline{N}})^T(\Sigma^{surv})^{-1}(\log(b\underline{N}^{surv}) - \log \hat{\underline{N}})$$

where

N_{93}^{BEB} is the BEB point estimate of 1+ abundance in 1993, set equal to 8,293, the mean of the BEB likelihood;

$\hat{N}_{93}$ is the 1+ abundance for 1993 generated by the BALEEN II population dynamics model;

σ_{93}^{BEB} is the standard error of N_{93}^{BEB}, set equal to 626, the standard deviation of the BEB likelihood;

b is taken to be 8,200/7,778, the ratio of the 1993 BEB posterior and N_4/P_4 point estimates;

$\underline{N}^{\mathrm{surv}}$ is the vector of N_4/P_4 estimates for the years 1978-1988;

$\hat{\underline{N}}$ is the vector of 1+ abundances for 1978-1988 generated by the BALEEN II population dynamics model;

Σ^{surv} is the covariance matrix for the logarithms of the N_4/P_4 estimates for the years 1978-1988.

This expression is equivalent to Equation (9) of Punt and Butterworth (1999) except that:

(1) the value of the bias factor b was fixed (= 8,200/7,778) and its normal likelihood thus ignored - this source of variability is very small compared to the uncertainty associated with other parameters and data;

(2) the likelihood for 1993 abundance was assumed to be independent of the other estimates and was explicitly included in place of the likelihood for the 1993 N_4/P_4 estimate.

RESULTS

The results are presented in Table 5. Here, K^{1+} and K^f are the 1+ and mature female carrying capacities respectively, MSYR^{1+} is the net productivity rate at MSYL^{1+}, P_t^f is the number of mature female whales in year t, the ROI is the geometric mean population growth rate in years 1978-1993. Quantities shown are the medians and bounds of the 90% Bayesian posterior probability intervals. As expected, the results for the deterministic model (D) are almost identical to those of the 'backwards' assessment in IWC (1999a).

When demographic stochasticity (SD) is introduced, the results reflect a slightly less productive stock than is indicated by the deterministic (D) model. The additional environmental variation (SE) produces no further effect on the estimates of depletion, ROI, MSYR^{1+} or K^{1+}, but it does cause a slight increase in the uncertainty of $E(\mathrm{RY}_{1998})$ and $E(Q_{0,1998})$. The relative abundance estimates provide a point estimate for ROI of approximately 3.20% (Raftery and Zeh, 1998). The model-based point estimates (medians) of ROI are all considerably lower than this figure, and it is noticeable that the point estimates from the stochastic models are even lower than that of the deterministic model.

DISCUSSION

Several issues are noted concerning the results produced by these stochastic models.

First, care needs to be taken in the use of the 5th percentile of $E(Q_0)$ as a 'rule' for setting a catch limit. Changes in the lower bound are expected as a natural byproduct of adding more uncertainty to the model. Thus, such changes probably do not warrant any important revision to past beliefs about

Table 4

Correlation matrix of the logarithms of the bowhead abundance indices. These values were obtained from Punt and Butterworth (1999).

Year	Correlation matrix									
1978	1.000									
1980	0.166	1.000								
1981	0.054	0.047	1.000							
1982	0.168	0.146	0.047	1.000						
1983	0.163	0.141	0.046	0.143	1.000					
1985	0.126	0.109	0.025	0.110	0.107	1.000				
1986	0.080	0.070	0.012	0.070	0.068	0.108	1.000			
1987	0.175	0.152	0.049	0.154	0.149	0.115	0.074	1.000		
1988	0.038	0.033	0.012	0.033	0.032	0.018	0.009	0.035	1.000	
1993	0.002	0.001	0.001	0.001	0.001	-0.002	-0.002	0.001	0.001	1.000

Table 5

Medians and 90% Bayesian posterior probability interval bounds for management-related quantities.

Quantity	Model specification Deterministic (D)	 Stochastic (SD)	 Stochastic (SE)
$\mathcal{E}$ (RY$_{1998}$)	118	110	106
	187	182	178
	236	233	240
$\mathcal{E}$ ($Q_{0,1998}$)	117	106	91
	192	178	166
	251	245	247
P^{1+}_{1998} / K^{1+} (%)	49.6	47.9	47.2
	69.4	66.6	66.1
	88.3	85.1	86.2
P^{f}_{1998} / K^{f} (%)	33.9	33.3	33.4
	40.9	40.2	40.0
	50.6	50.2	49.5
$P^{1+}_{1998} / MSYL^{1+}$ (%)	71.5	70.5	69.1
	98.3	94.4	93.6
	119.1	117.1	116.1
ROI (1978-1993) (%)	1.20	1.12	1.09
	2.30	2.12	2.11
	3.39	3.18	3.16
MSYR^{1+}	0.013	0.012	0.012
	0.024	0.022	0.022
	0.035	0.034	0.034
K^{1+}	10,335	10,552	10,644
	12,307	12,733	12,814
	16,026	16,346	16,569

bowhead productivity; for example, note that the results for MSYR^{1+} are rather insensitive to model choice. Furthermore, the transition from traditional assessment and estimation of the 5th percentile of allowable catch to AWMP implementation will probably encompass more than the type of modelling shown here. For example, an AWMP is unlikely to be so conservative as to focus exclusively on the 5th percentile of an estimated allowable catch. Thus, the stochastic PDM results provided here are not a harbinger of eventual AWMP results.

Although the AWMP serial correlation target of 0.75 was used here, no bowhead whale data are known to indicate that positive serial correlation exists at all. The value of 0.75 was adopted in the AWMP development process only because it represented moderately strong correlation that should be substantially different from zero. Furthermore, $\rho = 0.75$ means that about 50% of the variation in q_t (and hence about that amount of variation for b_t) is attributable to last year's outcome, and the rest is attributable to independent randomness. Several authors have hypothesised that this stock of bowheads might exhibit a four-year cycle in calf productivity (Koski *et al.*, 1993; George *et al.*, 1995). If a strong, brief cycle existed, ρ might even be negative if any synchronisation in breeding cycles was introduced, say, by a sudden depletion due to natural factors or historical whaling, like these authors speculate. Thus, even the corrected version of the SE model is still speculative with respect to ρ.

A fundamental tenet of statistical estimation is that one should favour the most parsimonious model for which there is no convincing evidence of its inadequacy. In the present context, the simplest model is D and the most complex one is SE. Consider the following three null hypotheses: H_0: D is not inferior to SD; H_0: D is not inferior to SE; and H_0: SD is not inferior to SE. The models can be compared using Bayes factors (Jeffreys, 1961; Kass and Raftery, 1995). The Bayes factor for a model M_0 against an alternative model M_1 is defined as the posterior odds for M_0 against M_1 when the prior odds are equal to one. This is:

$$B_{0,1} = p(D|M_0) \,/\, p(D|M_1)$$

where $p(D|M_k)$ is the integrated likelihood of model M_k defined by

$$p(D|M_k) = \int L(\theta_k|D,M_k)\,p(\theta_k|M_k)\,d\theta_k. \qquad (1)$$

D denotes the data, and θ_k is the vector of parameters for model M_k ($k = 0,1$). Equation (1) says that the integrated likelihood is the integral over the parameter space of the ordinary likelihood, $L(\theta_k|D,M_k)$, multiplied by the prior density, $p(\theta_k|M_k)$. The integral in equation (1) can be approximated by generating a sample from the prior and calculating the average of the likelihoods for those sampled values. If $\theta_{1,k},\ldots,\theta_{l,k}$ is a sample from $p(\theta_k|M_k)$, then:

$$p(D|M_k) \approx \frac{\sum_{i=1}^{\ell} L(\theta_{i,k}|D,M_k)}{\ell}.$$

Note that the prior distributions for the model parameters are the same for each of the three models considered here (Table 1).

Applying this procedure, the following values were obtained for the respective null hypotheses: $B_{D,SD} = 1.27$; $B_{D,SE} = 1.42$; and $B_{SD,SE} = 1.12$. Kass and Raftery (1995) suggested that values between 1 and 3 provide slight evidence in favour of the null hypothesis. Additionally, since none of the values are less than 1, there is no evidence against any of the three null hypotheses. It is concluded that there is no evidence suggesting that SE should be favoured over the simpler alternative models; indeed the other models provide a superior fit to the observed data and D yields the best fit overall.

Therefore, for assessment purposes, the results from the deterministic model seem most defensible. Consideration of the stochastic variants is more relevant in the AWMP development context, which is characterised by its wide-ranging exploratory trials and its robustness concerns. Nevertheless, it is reassuring that even models that extend to the plausible limits of uncertainty or beyond yield assessment results confirming that current bowhead subsistence hunting levels will not deplete the stock and will allow continued increase towards stabilisation above MSYL.

There are a number of ways in which the approach adopted here could be extended. For example, the values of the parameters that control environmental variability (σ_ε^2 and ρ) were fixed on an analysis of available data. One possible extension would be to treat these parameters as unknown and to estimate them along with the parameters of the PDM. In a Bayesian context, data-based priors could be constructed whose mean values correspond to the point estimates used here. Another possibility would be to experiment with alternative forms of stochasticity in the population dynamics, particularly with a view to improving the fit of the models to the available data.

ACKNOWLEDGEMENTS

This work was partially supported by the North Slope Borough (Alaska), the State of Alaska (through the Alaska Department of Community and Regional Affairs) and the National Oceanic and Atmospheric Administration (through the National Marine Mammal Laboratory to the Alaska Eskimo Whaling Commission). The computer coding of the stochastic model was carried out by Cherry Allison of the IWC Secretariat, with notable assistance from André Punt. Their coding has been an enormous and complicated task and we are thankful to them for their work, for providing the software to us, and for helpful comments on implementation.

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