Why do Bayesian and maximum likelihood assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales differ?

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ABSTRACT

An approach to baleen whale stock assessment based on maximum likelihood estimation is outlined. This approach is able to consider uncertainty in all of the parameters of the BALEEN II population dynamics model used for the assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales. It replaces the prior distributions used in the Bayesian analyses to incorporate indirect information by bounds (only) on model quantities. The results from this approach are notably different from Bayesian analyses based on the same data/assumptions. These differences result from two factors: the specific shapes chosen for the priors for biological parameters needed for the Bayesian approach, and the updating of these priors, together with the covariance introduced between them, by the exclusion process which ensures consistency of parameter sets generated from these priors with the population model, before the data are taken into account in the assessment. The second of these factors is shown to be much more important in accounting for the difference between the results. However, it is unclear whether this exclusion process is defensibly accorded the probabilistic interpretation that the Bayesian approach assumes of it. Until this question is satisfactorily settled, the bounded maximum likelihood method introduced in this paper may provide a more defensible basis for assessment of the B-C-B bowhead population, even though it may be unable to take account of some information which could be incorporated in a Bayesian approach.

KEYWORDS: BOWHEAD WHALE; POPULATION ASSESSMENT; MODELLING; TRENDS; BIOLOGICAL PARAMETERS; WHALING-ABORIGINAL; ARCTIC

INTRODUCTION

Assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales involves estimation of the values for the parameters of the BALEEN II population dynamics model. These parameters are:

K^{1+}	the total (1+) pre-exploitation size of the resource;
$MSYL_{1+}$	the ratio of the total (1+) population size at which MSY is achieved to K^{1+};
$MSYR_{1+}$	the ratio of MSY to the total (1+) population size at which it occurs;
a_m	the age-at-maturity;
$S_{adult} = \exp(-M_{adult})$	the survival rate of adults in the absence of exploitation;
$S_{juv} = \exp(-M_{juv})$	the survival rate of juveniles in the absence of exploitation; and
a_T	the greatest age to which juvenile natural mortality applies.

Recent advice from the Scientific Committee of the International Whaling Commission (IWC) on this stock has been based on applications of a Bayesian approach to stock assessment using the BALEEN II model (e.g. Givens *et al.*, 1995; Givens and Thompson, 1996).

A particular concern about Bayesian methods is the specification of a (multivariate) prior to represent ‘indirect’ (*sensu* Bravington, 1996; Punt and Butterworth, 1999) information concerning biological parameters. This would not be a problem had an appropriate joint prior been derived from experiments on other stocks of bowhead whales (or on the B-C-B stock itself). However, problems of interpretation can arise when the multivariate joint prior is obtained by multiplying univariate priors for each of the parameters, each univariate prior being based on analogy with other populations of (non-bowhead) baleen whales. Furthermore, failure to take adequate account of covariance (non-independence) between the parameters can give rise to difficulties. Concern regarding the specification of an appropriate prior is the main reason why investigation into likelihood-based methods (e.g. Butterworth and Punt, 1992; 1995; Punt and Butterworth, 1996; 1997) continues for the B-C-B bowhead stock.

Results from maximum likelihood assessments of the B-C-B Seas bowhead stock have differed notably from those of Bayesian assessments, in general suggesting that the productivity of the population is higher. To date, however, such methods have either been based on pre-specifying values for the ‘biological’ parameters of the BALEEN II model (i.e. $MSYL_{1+}$, a_m, a_T, S_{adult}, and S_{juv})[1] and examining the sensitivity of the results to different choices for these pre-specified values, or trying to ‘integrate’ these parameters out using the approach of Restrepo *et al.* (1991; 1992). Pre-specifying values for model parameters can be criticised because uncertainty about these parameters is then not fully reflected in the results of the analyses. Furthermore, since sensitivity tests usually involve changing the value of only a single parameter (Punt and Hilborn, 1997), such results do not guarantee that some (reasonably plausible) combination of parameter values will not give rise to behaviour that is not evident in the results produced. Finally, it is often difficult to summarise the management implications of those tests that exhibit considerable sensitivity without some form of weighted integration across those tests (Punt and Hilborn, 1997). While the approach of Restrepo *et al.* (1991; 1992) is not subject to these concerns, it can be shown (Poole *et al.*, 1999) that this method is biased when the assessment data

[1] Hence these approaches are termed ‘conditioned’ maximum likelihood methods, as their results are conditional on the values pre-specified.

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are informative about the ‘biological parameters’, which appears to be the case for the B-C-B bowhead stock (Punt and Butterworth, 1997; 1999).

Schweder and Hjort (1997) introduced the ‘likelihood synthesis’ approach. This involves estimating values for all of the parameters of the BALEEN II population model (Punt, 1999) by maximising the likelihood function while incorporating the information that is represented in the prior distribution for a Bayesian assessment as ‘data’ in the likelihood function. Schweder and Ianelli (1998) were able to apply this approach to the B-C-B bowhead stock but were unable to assess the uncertainty using likelihood profiling due to difficulties with the curvilinear surface of the likelihood function.

This paper first outlines an alternative, yet similar, approach to that of Schweder and Hjort (1997): to estimate all the parameters of the BALEEN II model, but, instead of including the prior distributions selected by IWC (1999) as ‘data’, to merely apply the weaker constraint that these priors provide bounds on the parameters concerned. Applications of this ‘bounded’ maximum likelihood assessment method to the B-C-B Seas bowhead stock are then compared with those of a Bayesian assessment method that is identical in all respects, except in the nature of the estimator. It will be shown that the two methods lead to notably different results. The reasons for this difference are then discussed.

METHODS

Re-formulation of the BALEEN II model

It is necessary for the (constrained) likelihood function to be continuous and differentiable with respect to the seven model parameters to be able to apply efficient numerical methods to find the maximum of the likelihood function. Unfortunately this is not the case for the B-C-B assessment conducted by IWC (1999) for the following three reasons:

(a) the age-at-maturity, a_m, was assumed to be an integer and maturation was assumed to be a knife-edged function of age;

(b) the greatest age to which juvenile natural mortality applies, a_T, was assumed to be an integer and the transition from juvenile to adult survival was assumed to be a knife-edged function of age;

(c) it is necessary to solve the equation that relates $MSYL_{1+}$ and $MSYR_{1+}$ to the resilience and degree of compensation parameters numerically (Punt, 1999).

The first two problems have been overcome, following Schweder and Ianelli (1998), by making the probability of maturation and the transition from juvenile to adult survival smooth (logistic) functions of age:

$$\beta_a = (1 + e^{-\ln 19(a - a_m)/0.5})^{-1} \tag{1a}$$

$$S_a = S_{juv} + (S_{adult} - S_{juv})(1 + e^{-\ln 19(a - a_T)/0.5})^{-1} \tag{1b}$$

where:

β_a is the probability of being ‘mature’ (strictly, having reached the age-at-first-parturition) as a function of age; and

S_a is the annual survival rate of animals of age a in the absence of exploitation.

The choice of a value of 0.5 for the steepness-related parameter of the logistic equation above ensures that the transition from immaturity to maturity, and from juvenile to adult survival, occurs over a very small range of ages, thus approximating the conventional knife-edge assumption.

The problem related to $MSYL_{1+}$ and $MSYR_{1+}$ has been overcome by parameterising the model in terms of the maximum possible pregnancy rate, $f_{\max}$ ($= 1/c_{\min}$, where $c_{\min}$ is the minimum calving interval) and the degree of compensation, z. It is still necessary to calculate $MSYL_{1+}$ and $MSYR_{1+}$ as functions of $f_{\max}$, z and the other biological parameters (see appendix 3 of Punt, 1999), but the result of this calculation is needed only to check that $MSYL_{1+}$ lies within its pre-specified range.

The data included in the likelihood function are the information on absolute abundance from counts at Point Barrow, Alaska and the fraction of calves and mature animals in counts from 1985-92. The former are incorporated using equation (9) of Punt and Butterworth (1999), while the latter are assumed to be independent t-distributed random variables with 5 degrees of freedom (for the rationale for this choice, see IWC, 1995).

Selection of priors/bounds

Table 1 lists the base-case priors and bounds for the parameters of the model. The bounds on the parameters S_{adult}, S_{juv}/S_{adult}, a_m, a_T, and $f_{\max}$ for the bounded maximum likelihood approach correspond directly to the limits of the priors selected by IWC (1999), except that the upper limit for the uniform prior on $MSYL_{1+}$ has been extended from 0.8 to 0.95. This extension is based partly on numerical convenience and partly because the data suggest that values for $MSYL_{1+}$ larger than the upper bound for the prior selected by IWC (1999) should not be excluded.

The bounds on the first five quantities are implemented by constraining the range of these parameters directly, whereas the last (which is not a parameter of the model estimated

Table 1

The base-case prior distributions assumed when conducting the Bayesian assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales, and the bounds inferred from these priors that are imposed on the biological parameters for the bounded maximum likelihood assessments.

Parameter	Prior distribution	Base-case bounds
S_{adult}	N(0.99; 0.02^2) $S_{adult} \le 0.995$	$0 < S_{adult} \le 0.995$
S_{juv}	$S_{juv} \le S_{adult}$	$0 < S_{juv} / S_{adult} \le 1$
Minimum calving interval, $c_{\min}$	$c_{\min} \sim$ U[2.5; 4]	$2.5 \le c_{\min} \le 4$
Transition age, a_T	1,2, … , 9 equally likely	$1 \le a_T \le 9$
Age-at-maturity, a_m	N(20;3^2) $13.5 \le a_m \le 26.5$	$13.5 \le a_m \le 26.5$
K^{1+}	N/a	$0 < K^{1+}$
Total (1+) population size in 1993, P_{1993}	$\ell n P_{1993} \sim N(\ell n 7{,}800, 0.167^2)$	N/a
$MSYL_{1+}$	U[0.4; 0.95]	$0.4 \le \text{MSYL}_{1+} \le 0.95$
$MSYR_{1+}$	U[0.01; 0.07]	$0 < \text{MSYR}_{1+}$

directly in the fitting process) is implemented by adding the following term to the negative of the logarithm of the likelihood function:

$$\left[\frac{(2MSYL-(MSYL_{\max}+MSYL_{\min}))}{MSYL_{\max}-MSYL_{\min}}\right]^{20} \qquad (2)$$

where:

$MSYL_{\min}$ is the lower bound for $MSYL_{1+}$; and
$MSYL_{\max}$ is the upper bound for $MSYL_{1+}$.

Equation 2 provides values very close to zero for all values of $MSYL$ within the range [$MSYL_{\min}$; $MSYL_{\max}$], but very large values for $MSYL$ outside this range. No bounds are placed on $MSYR_{1+}$ and K^{1+} because there is little ($MSYR_{1+}$) or no (K^{1+}) basis for specifying these (independent of historical catches, but their information content is taken into account through the population model utilised), except (trivially) that they are required to be positive.

The bootstrap procedure

The uncertainty associated with the estimates for the model outputs for the maximum likelihood procedure is evaluated using a (conditioned) parametric bootstrap procedure. This procedure involves generating 250 pseudo-datasets and applying the estimator to each. Each pseudo-dataset contains information on relative abundance, the bias factor that relates the relative abundance indices to absolute abundance, and the proportion data (Punt and Butterworth, 1999). The relative abundance indices are drawn from a multivariate normal distribution with mean given by the point estimates obtained by fitting the model to the actual data for the B-C-B bowhead stock, and variance co-variance matrix equal to that assumed when fitting the model (see appendix A of Punt and Butterworth, 1999). The pseudo-bias factor is drawn from a log-normal distribution with median given by the point estimate and a CV of 0.026 (Punt and Butterworth, 1999), while the pseudo-proportion data are drawn from independent t-distributions with means given by the point estimates and variances equal to those assumed when fitting the model. The bootstrap estimates of confidence intervals will be negatively biased because of the bounds placed on the model parameters. In the current study, some of the bootstrap replicates led to values for a_m, $f_{\max}$ and S_{adult} on their boundaries.

RESULTS AND DISCUSSION

Comparison of assessment results

Table 2 lists results for 13 management-related quantities for the analyses based on Bayesian and bounded maximum likelihood assessments that use the modified models and priors (bounds). The base-case Bayesian analysis is based on

Table 2

Estimates of the 13 management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. Results are shown for four Bayesian assessments and one bounded maximum likelihood assessment. For the Bayesian analysis, which uses the 'backwards' procedure, posterior medians, means and 90% credibility intervals are shown, whereas, for the maximum likelihood analysis, the point estimate and bootstrap 90% confidence intervals are listed. The 'Max($MSYL$)=0.8' sensitivity test replaces the upper limit of 0.95 on the prior for $MSYL$ by 0.8; 'Original' refers to the procedures and priors used for the 1998 assessment conducted by the IWC Scientific Committee, and 'Uniform priors' involves replacing the priors for S_{adult} and a_m in Table 1 by uniform priors.

	Estimation procedure				
	Bayesian				Maximum likelihood
Quantity	Base-case	Max($MSYL$) = 0.8	Original	Uniform priors	Base-case
K^{1+}	12,065 (12,331)	12,335 (12,628)	12,405 (12,674)	12,069 (12,375)	10,146
	[9,674 15,838]	[9,868 16,062]	[9,964 16,088]	[9,533 15,983]	[8,596, 13,516]
Q_0 (1998)	215 (215)	192 (190)	191 (189)	215 (216)	267
	[108 309]	[105 260]	[106 257]	[104 316]	[164, 370]
RY (1998)	200 (203)	185 (183)	185 (183)	197 (201)	178
	[91 306]	[107 239]	[109 236]	[92 306]	[66, 276]
P^{1+}_{1998} / K^{1+}	73.6 (73.6)	70.8 (70.3)	70.1 (70.1)	73.3 (73.4)	90.1
	[48.2 96.3]	[47.4 90.2]	[47.8 89.8]	[47.2 96.8]	[65.9, 99.3]
P^{f}_{1998} / K^{f}	42.4 (42.8)	42.1 (42.7)	41.6 (42.2)	43.4 (43.7)	56.5
	[34.0 52.2]	[33.6 52.8]	[33.6 51.7]	[33.6 53.5]	[41.3, 75.2]
$P^{1+}_{1998} / MSYL_{1+}$	94.7 (93.5)	100.4 (99.3)	99.7 (98.9)	94.9 (93.7)	123.0
	[59.8 117.7]	[67.9 122.2]	[68.7 121.7]	[58.8 118.7]	[90.2, 128.1]
$MSYR_{1+}$ (%)	2.58 (2.61)	2.45 (2.46)	2.40 (2.43)	2.59 (2.63)	3.99
	[1.21 3.94]	[1.18 3.73]	[1.17 3.68]	[1.19 4.09]	[1.91, 5.47]
$Slope$ (%)	2.38 (2.40)	2.30 (2.29)	2.25 (2.27)	2.40 (2.42)	3.72
	[1.03 3.68]	[1.03 3.48]	[1.02 3.43]	[0.98 3.80]	[1.79, 4.65]
$MSYL_{1+}$	0.798 (0.792)	0.718 (0.708)	0.719 (0.709)	0.795 (0.788)	0.732
	[0.594 0.937]	[0.573 0.792]	[0.572 0.791]	[0.586 0.936]	[0.663, 0.909]
a_m	19.0 (19.3)	20.0 (19.9)	19.0 (19.4)	18.0 (19.1)	14.5
	[15.0 24.0]	[15.0 24.0]	[15.0 24.0]	[15.0 26.0]	[13.5, 20.8]
S_{juv}	0.914 (0.901)	0.923 (0.914)	0.916 (0.905)	0.918 (0.905)	0.969
	[0.739 0.973]	[0.782 0.976]	[0.750 0.975]	[0.740 0.974]	[0.869, 0.990]
S_{adult}	0.986 (0.985)	0.985 (0.984)	0.986 (0.985)	0.985 (0.983)	0.985
	[0.968 0.994]	[0.967 0.994]	[0.969 0.994]	[0.963 0.994]	[0.974, 0.995]
$f_{\max}$	0.300 (0.307)	0.308 (0.314)	0.309 (0.314)	0.302 (0.309)	0.322
	[0.252 0.383]	[0.253 0.387]	[0.253 0.388]	[0.253 0.383]	[0.25, 0.40]

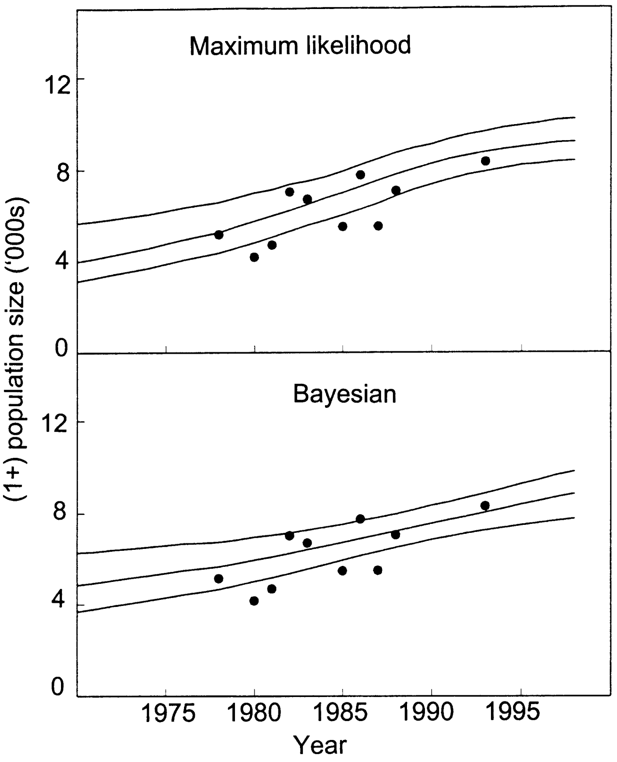

Fig. 1. Median and 90% confidence intervals for the time-trajectory of 1+ population size from the base-case bounded maximum likelihood analysis, and median and 90% credibility intervals for the posterior for this time-trajectory based on the corresponding 'backwards' Bayesian analysis. The black dots indicate the available relative abundance data, adjusted by the bias factor of 0.936 derived from the relative and absolute estimates for 1993 (Punt and Butterworth, 1999).

an application of the 'backwards' approach to a Bayesian assessment of the B-C-B bowhead stock[2]. The 13 quantities include six of the seven model parameters, $MSYL_{1+}$, and the following six additional quantities.

$P^{1+}{}_{1998} / K^{1+}$	the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 1998 to K^{1+};
p^{f}_{1988} / K^{f}	the ratio (expressed as percentage) of the size of the mature female component of the population at the start of 1998 to the corresponding pre-exploitation size;
$P^{1+}_{1998} / MSYL_{1+}$	the ratio (expressed as percentage) of the size of the 1+ component of the population at the start of 1998 to *MSYL;*
RY (1998)	the replacement yield for 1998;
Q_0 (1998)	the value of the quantity Q_0 (Wade and Givens, 1997) for 1998:

$$Q_0(1998) = \begin{cases} 0.9MSY_{1+} & \text{if } P^{1+}_{1998} / K^{1+} > MYSL_{1+} \\ \min(RY(1998) - 1, 0.9MSY_{1+}) & \text{otherwise} \end{cases}$$

where $MSY_{1+} = MSYR_{1+}\ MSYL_{1+}\ K^{1+}$.

Slope	the annual rate of increase of the 1+ population from 1978-1993, expressed as a percentage.

The results from the base-case bounded maximum likelihood and Bayesian analyses are directly comparable and exhibit some notable qualitative differences. In particular, the base-case maximum likelihood analysis leads to much larger values for *Slope* (see also Figs 1 and 2). The point estimate for the maximum likelihood analysis is much nearer to the slope estimate that follows from placing a log-linear regression line through the relative abundance data, taking account of their variance-covariance structure (3.50%, 90% CI = 1.41, 5.58). The corresponding 90% confidence intervals for the maximum likelihood analysis are narrower than those based solely on the relative abundance data because other information (including that on the magnitude of the bias factor which relates absolute and relative abundance information) further constrains the value for *Slope*.

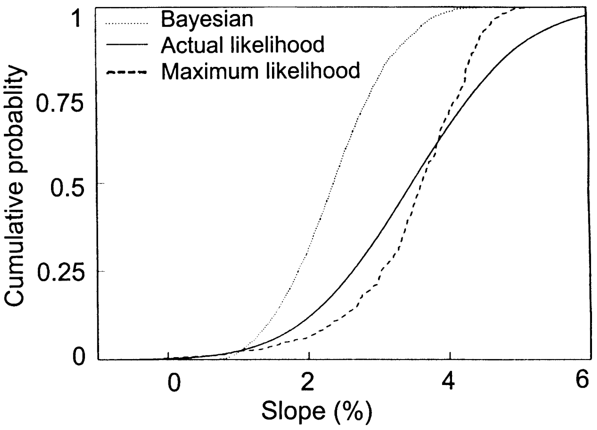

Fig. 2. Cumulative probability/credibility ogives for the 1978-93 annual rate of increase of the 1+ population (*Slope*) as determined from the relative abundance data alone by the likelihood profile method ('Actual likelihood'), and after application of the population model using either the base-case bounded maximum likelihood ('Maximum likelihood'), or corresponding 'backwards' Bayesian ('Bayesian') approaches.

Another notable difference between results for the base-case Bayesian and bounded maximum likelihood analyses is that the latter leads to the conclusion that bowheads are more productive and less depleted than does the Bayesian (Fig. 3; Table 2). Furthermore, the maximum likelihood results suggest the population to have been at a considerably lower level in 1910 (roughly when it reached its minimum size) than do those for the Bayesian analysis, and hence seem more consistent with the commercial extinction of the resource at that time. Unlike the case for the Bayesian analysis (Fig. 3), the maximum likelihood analysis suggests that there is a relatively high probability that the 1+ population is now above *MSYL* and, indeed, is quite close to *K* in terms of the 1+ (although not the mature female) component of the population. This leads the maximum likelihood analysis to suggest a lower replacement yield for 1998 than the Bayesian analysis, despite indicating a much higher value for Q_0 (1998). Both the maximum likelihood and the Bayesian analyses suggest that $MSYL_{1+}$ is near the upper end of the range considered. The maximum likelihood method leads to a lower point estimate for the age-at-maturity, a higher point estimate for S_{juv}, and a lower point estimate for a_T (which increases the net survival rate) than the corresponding Bayesian method medians, to allow a better fit to the observed rate of increase.

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[2] The 'backwards' approach effectively projects population trajectories backwards from a population estimate generated from a prior for the population size in 1993.

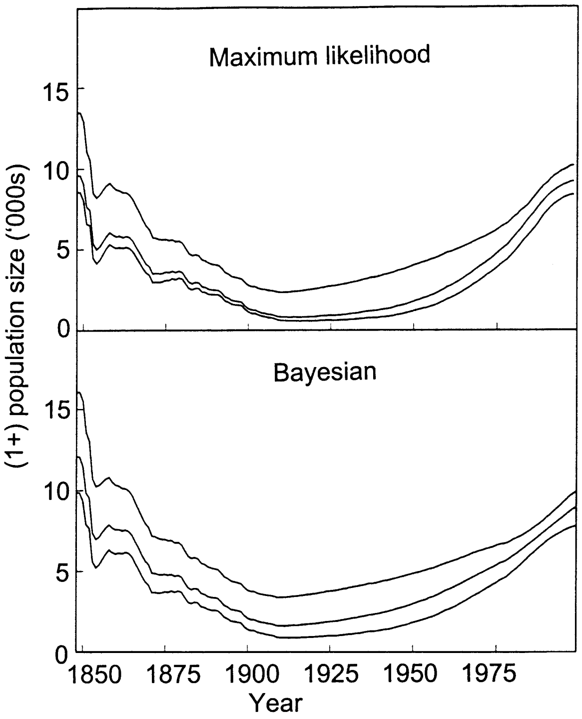

Fig. 3. Median and 90% confidence intervals for the time-trajectory from the commencement of harvesting until the present of 1+ population size from the base-case bounded maximum likelihood analysis and median and 90% credibility intervals for the posterior for this time-trajectory based on the corresponding 'backwards' Bayesian analysis.

Table 2 also contrasts the results for the base-case Bayesian analysis with those for three sensitivity tests. Forcing the upper bound for the prior for $MSYL_{1+}$ to occur at 0.8 rather than 0.95 (denoted 'Max($MSYL$) = 0.8' in Table 2), leads, in general, to less optimistic results (lower values for $MSYR_{1+}$, current depletion, and Q_0(1998)), although the population is assessed to be less depleted relative to $MSYL_{1+}$ (in contrast, the estimated present population status expressed relative to K hardly changes). Replacing the functional forms for the age-dependence in the survival rate and the probability of maturity (Equation 1) by knife-edged functions (as was the case for the 1998 assessment of the B-C-B bowhead stock, denoted 'Original' in Table 2) has negligible impact on the overall results - compare this column with 'Max($MSYL$) = 0.8', as that bound applied also to the 1998 assessment. Somewhat surprisingly, replacing the priors for S_{adult} and a_m by uniform distributions does not impact the results markedly; furthermore, it does not result in a Bayesian assessment that is any closer to the maximum likelihood analysis (which ignores the shape of the priors).

Why do the bounded maximum likelihood and Bayesian assessments differ?

First, it is important to understand why the values of biological parameters do influence the results of assessments of the B-C-B bowhead stock, unlike the situation for many other baleen whale populations. The reason is that these parameters place bounds on the maximum rate of population growth. If G is the annual proportional growth per year in the 1+ population, then for a steady age-structure (i.e. ignoring transients), it can be shown (Butterworth and Best, 1990) that:

$$(1+G)^{a_m} = (1+G)^{a_m-1} S_{adult} + 0.5 f (S_{juv})^{a_T} (S_{adult})^{a_m-a_T} \quad (3)$$

where f is the annual pregnancy rate of mature females, and 50% of births are assumed to be female.

If $f_{\max}$ is the maximum value of f, and $S_{juv} \le S_{adult}$, it follows that the maximum possible steady growth rate for the population ($G_{\max}$) is given by the appropriate solution of:

$$(1+G_{\max})^{a_m} = (1+G_{\max})^{a_m-1} S_{adult} + 0.5 f_{\max} (S_{adult})^{a_m} \quad (4)$$

Furthermore, since $S_{adult} \le 1$, the upper bound for $G_{\max}$ is obtained from:

$$(1+G_{\max})^{a_m} = (1+G_{\max})^{a_m-1} + 0.5 f_{\max} \quad (5)$$

Thus if, purely for illustrative purposes, it is assumed that a_m and $f_{\max}$ for the B-C-B bowheads were known to be exactly equal to the mid-points of the ranges given for their priors in Table 1 (20 and 0.325 respectively), Equation (5) would lead to the conclusion that $G_{\max} \le 5.68\%$. If it was considered that S_{adult} could not exceed 0.99 per annum, then Equation (5) would indicate $G_{\max} \le 4.63\%$.

Now the estimate of the growth rate for the B-C-B stock of bowhead whales from 1978-93 (*Slope*), as estimated from the available relative abundance information when taking the associated variance-covariance structure into account, is 3.50% with a 95% CI = 1.41, 5.86. The role then, of adding the further information on biological parameters to a composite age-structured population model such as BALEEN II, is effectively to truncate the upper tail of this distribution at $G_{\max}$. If probability statements can be made about the various possible values for these biological parameters (i.e. if justifiable prior distributions can be provided for each for a Bayesian assessment), these statements translate through Equation (3) to a probability distribution for an upper bound on the *Slope* distribution. The BALEEN II model then effectively applies this bound distribution to the trend estimate (and its distribution) derived from the relative abundance information.

This suggests that the forms chosen for the prior distributions, which are needed for the Bayesian but not the bounded maximum likelihood approach, could be a key reason for the difference in results between the two. However, when the two informative priors for biological parameters (those for S_{adult} and a_m, see Table 1) are changed to uniform distributions, Table 2 shows that results are hardly affected, so that this cannot be the primary explanation for the difference.

Table 3 lists results for the Bayesian and maximum likelihood analyses when the coefficients of variation (*CV*s) associated with the abundance data are first halved and then doubled. These tests have been conducted not because it is believed that the *CV*s for these abundance estimates are biased, but rather to examine the behaviour of the estimator as the information content of the data is varied. The results for the maximum likelihood analysis behave as customary, i.e. decreasing the *CV*s has little impact on the point estimates, but the 90% confidence intervals contract. While the contraction of credibility intervals is also a feature of the Bayesian analysis as the *CV*s are decreased, in addition the posterior medians and means change systematically. If the *CV*s are halved, the results for the maximum likelihood and Bayesian analyses become more similar. This is hardly surprising; the two types of analyses converge as the *CV*s are reduced to zero, and the data dominate any other information provided to the assessment process.

The difference in the results of the two approaches must therefore lie in the different ways in which they are taking information on the biological parameters into account. As

Table 3

Distributions of four management-related quantities inferred from the base-case Bayesian and bounded maximum likelihood approaches. For the Bayesian analyses, which use the ‘backwards’ procedure, posterior medians, means and 90% credibility intervals are shown, while, for the maximum likelihood analysis, the point estimate and bootstrap 90% confidence intervals are listed.

Specification	----	Q_0 (1998)	$MSYR_{1+}$ (%)	*Slope* (%)
Bayesian				
Base-case	73.6 (73.6)	215 (215)	2.58 (2.61)	2.38 (2.40)
	[48.2 96.3]	[108 309]	[1.21 3.94]	[1.03 3.68]
Post-model-pre-data	60.8 (63.0)	161 (172)	1.92 (2.09)	1.68 (1.82)
	[37.5 92.7]	[84 286]	[1.04 3.67]	[0.74 3.37]
Double CVs	67.2 (68.0)	189 (192)	2.25 (2.30)	2.04 (2.09)
	[44.3 93.6]	[94 295]	[1.09 3.69]	[0.88 3.45]
Halve CVs	85.0 (84.3)	260 (258)	3.23 (3.24)	3.02 (3.02)
	[65.5 98.2]	[176 322]	[2.15 4.11]	[1.96 3.85]
Maximum likelihood				
Base-case	90.1	267	3.99	3.72
	[65.9, 99.3]	[164, 370]	[1.91, 5.47]	[1.79, 4.65]
Double CVs	90.1	267	3.99	3.73
	[31.9, 99.3]	[28, 370]	[0.27, 5.47]	[0.08, 4.73]
Halve CVs	90.1	267	3.99	3.73
	[82.3, 99.3]	[221, 365]	[3.03, 5.28]	[2.68, 4.50]

discussed above, it does not appear to be the choices for the prior distributions *per se* which are causing the difference, so that it must be the manner in which the BALEEN II population model is introducing constraints in modifying these priors to the ‘post-model-pre-data’ joint distribution[3] (summarised in Fig. 4 and Table 3). Note, for example, that the mean of the post-model-pre-data distribution for $MSYR_{1+}$

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[3] The distribution which arises after parameter combinations not consistent with the population dynamics model are excluded.

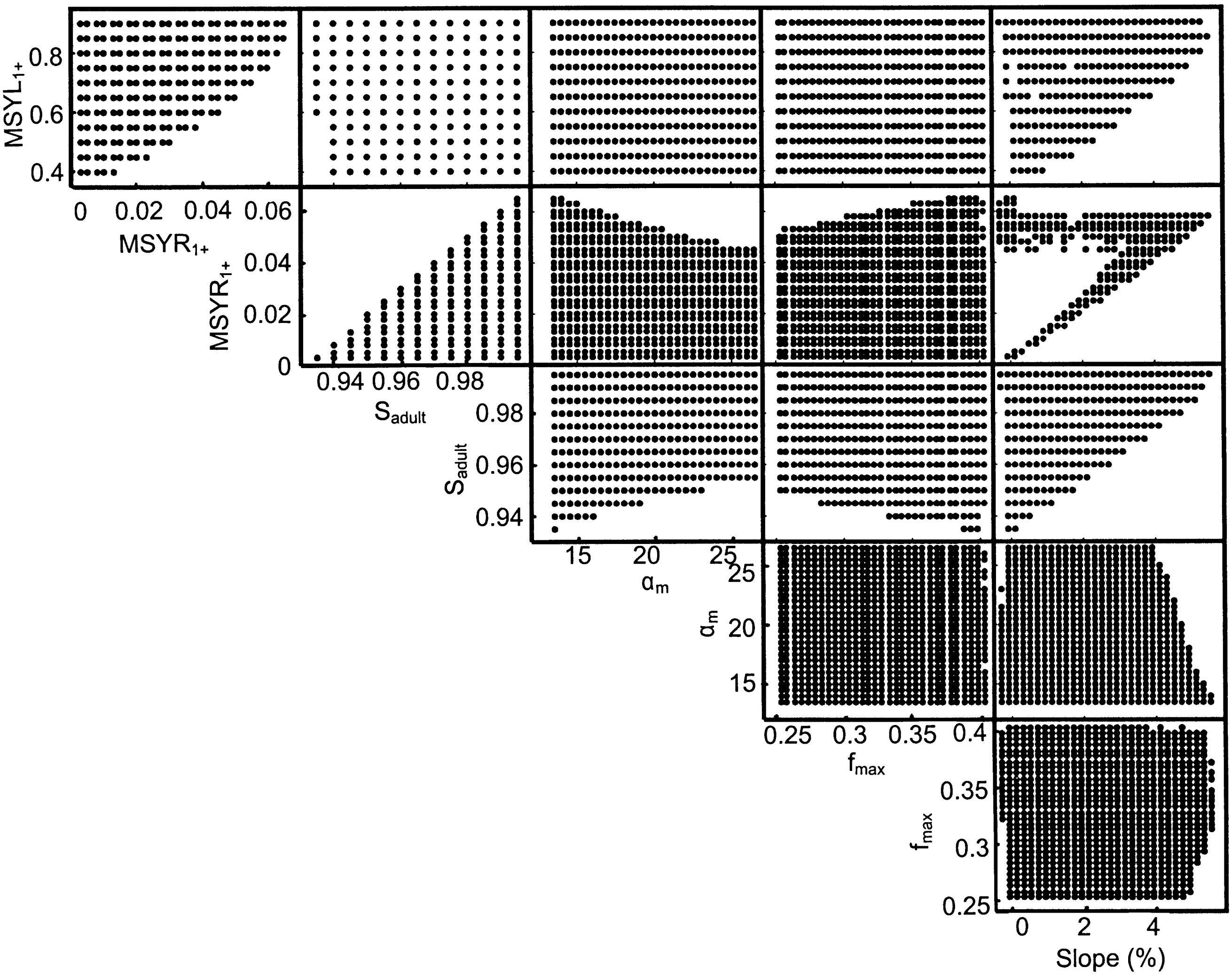

Fig. 4. Cross correlations among five biological parameters of the BALEEN II population model and *Slope* for the post-model-pre-data distribution for the ‘backwards’ Bayesian analysis. The plots show the boundaries of the feasible space that follow from the constraints introduced by the population model, but do not reflect differences in probability density within those regions.

is only 2.09%, compared to the mean of the associated prior of 3.5%. The post-model-pre-data distribution is placing much greater probability on less optimistic (in terms of resource productivity) values for biological parameters than is implied by the initial priors specified (see Table 1). This is because, for example, the low values for $MSYR_{1+}$ are consistent with all the values for the other parameters, but this is not the case for the high values of $MSYR_{1+}$ considered (see Fig. 4). Hence the posterior medians and means for the Bayesian assessments in Table 3 change systematically as the *CV*s for the abundance data are reduced - the increasingly informative data (with their associated *Slope* estimate of 3.50%) then proceed to further outweigh the contrary trend implied by the post-model-pre-data distribution with its median of 1.68% (see Table 3).

It is illuminating to examine Fig. 4, which plots cross correlations among six quantities (five of the biological parameters of the BALEEN II population model and *Slope*), more closely. Points are plotted in Fig. 4 when the parameter combination concerned, generated from the independent priors in Table 1 (for a Bayesian analysis), is consistent with this population model. Thus, the figure indicates the boundaries of post-model-pre-data parameter feasibility space (although it does not attempt to illustrate differences in probability density within those regions). Both the maximum likelihood and Bayesian analyses exclude any parameter combinations outside these bounds. However, only the Bayesian analyses assign different *a priori* weights to these parameter combinations through the post-model-pre-data distributions. There are some strong inter-relationships evident in Fig. 4. The most obvious of these is the one between $MSYR_{1+}$ and $MSYL_{1+}$; values of $MSYR_{1+} < 0.01$ are consistent with all values of $MSYL_{1+}$ between 0.4 and 0.95. In contrast, values of $MSYR_{1+} > 0.05$ automatically imply that $MSYL_{1+} > 0.65$. The value of S_{adult} also places strong constraints on the allowable value for $MSYR_{1+}$. Similar, though less marked, inter-relationships exist between $MSYR_{1+}$ and a_m, and between S_{adult} and a_m. The values of S_{adult}, $MSYR_{1+}$ and $MSYL_{1+}$ can place marked constraints on the possible value of *Slope*, in some instances forcing it below the best estimate from the data (alone) of 3.50%. The somewhat peculiar '7' shape of the $MSYR_{1+}$ *vs Slope* inter-relationship merits explanation. For any particular value for *Slope*, there are in effect two alternative 'explanations'. The first is that the resource is recovering and in the vicinity of its *MSYL*, so that $MSYR_{1+}$ and *Slope* values are near identical. The other is that the population has a high *MSYR*, has already recovered to well above its *MSYL*, and accordingly can manifest a low *Slope* because it is now approaching *K*. The feasibility regions shown in Fig. 4 differ markedly from those implied by the selected independent prior distributions of Table 1, so that the covariance introduced by the exclusion process which leads to the post-model-pre-data distribution, is playing a key role.

Fig. 4 for the Bayesian approach is to be contrasted with Fig. 5, which shows likelihood profiles for $MSYL_{1+}$, a_m,

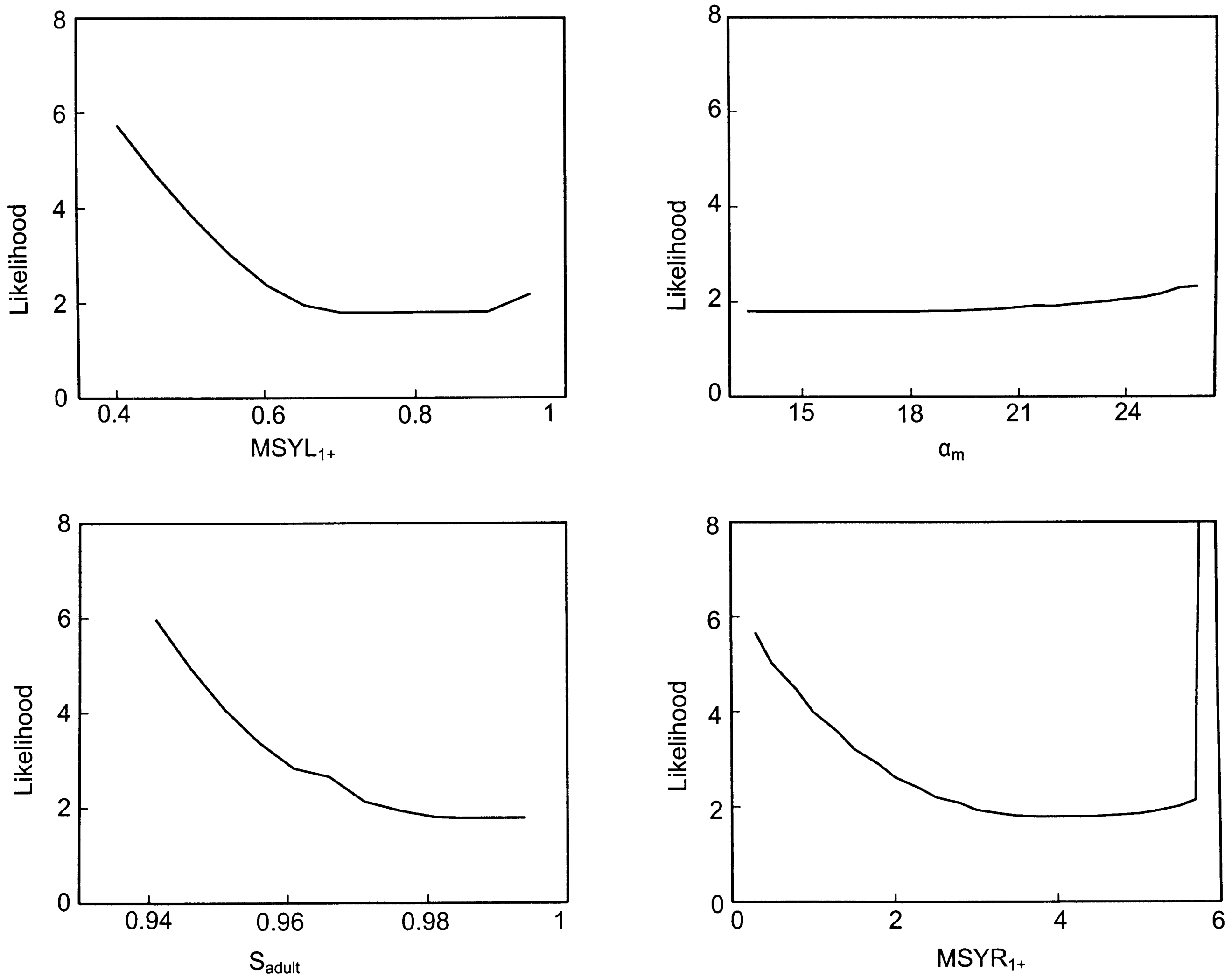

Fig. 5. Likelihood profiles for $MSYL_{1+}$, a_m, S_{adult}, and $MSYR_{1+}$.

Table 4

Estimates of six management-related quantities for the Bering-Chukchi-Beaufort Seas stock of bowhead whales based on the Schaefer population dynamics model. Results are shown in this table for a Bayesian and a bounded maximum likelihood assessment. For the Bayesian analysis, which uses the 'backwards' procedure, posterior medians, means and 90% credibility intervals are shown, while, for the maximum likelihood analysis, the point estimate and bootstrap 90% confidence intervals are listed.

	Estimation procedure	
Quantity	Bayesian	Maximum likelihood
K^{1+}	10,906 (11,432)	10,292
	[9,005 16,433]	[8,877 15,488]
$MSYR_{1+}$ (%)	4.4 (4.3)	5.0
	[1.5 6.8]	[1.8 7.0]
Slope (%)	2.88 (2.83)	3.24
	[1.34 4.20]	[0.93 3.77]
Q_0 (1998)	216 (209)	233
	[112 275]	[124 280]
RY (1998)	148 (144)	138
	[89 181]	[55 170]
P^{1+}_{1998} / K^{1+}	89 (85)	83
	[56 94]	[54 95]

S_{adult} and $MSYR_{1+}$ arising from the bounded maximum likelihood approach[4]. It is clear from Fig. 5 that the data are not particularly informative about the values for these parameters over a wide range. For example, the data have essentially no ability to distinguish among alternative values for a_m. This is in stark contrast to the results from the Bayesian analysis which suggest that high values for a_m are more likely than low values (Table 2). The informative posterior for a_m from the Bayesian approach is therefore not a consequence of the data included in the likelihood function, but rather of the form of the post-model-pre-data distribution (Fig. 4).

In mathematical terms, the difference between the Bayesian and maximum likelihood approaches is formally that of integration *vs* maximisation. Nevertheless, the likelihood profile method used for confidence interval estimation for the latter approach does, like integration, also take account of the shape of the likelihood function. Thus, the key difference between the two approaches still comes down to the post-model-pre-data joint distribution, which adds a differential weighting to different parts of parameter space - a feature that is absent from any likelihood-based approach. There are two components to this weighting; first the forms selected for the prior distributions, and then the population-model-based exclusion process that introduces covariance between them. The results above show that it is this latter factor that is the dominant cause of the difference between the results of the Bayesian and bounded maximum likelihood assessments of the B-C-B bowhead stock, when both are based upon the BALEEN II population model.

The key role played by this introduction of covariance is evident from considering the application of a simpler population model. Here the assessment is conducted based upon the dynamic logistic (or Schaefer) model in place of BALEEN II. This model has only two parameters: the intrinsic growth rate, r (= 2*MSYR*), and a recent population size, P_{1993}. The prior for P_{1993} is chosen to be that given in Table 1, while that for r is taken to be U[0.02, 0.14]. The results for the ('backwards') Bayesian and bounded maximum likelihood approaches in this case are compared in Table 4. These results are not strictly comparable to those in Table 2, *inter alia* because the assessments based upon the simpler Schaefer model are unable to take the 'proportion' data into account. Nevertheless it is clear that the results of the two approaches for the Schaefer model differ far less than for the corresponding BALEEN II model based assessments. For example, the point estimates (posterior medians for the Bayesian assessment) for Q_0(1998) are 216 and 233 in Table 4 compared to 215 and 267 in Table 2. Similar results are evident for the quantities K^{1+}, $MSYR_{1+}$, *Slope*, *RY* (1998) and P^{1+}_{1998}/K^{1+}. Note that the key difference between these two cases is that the one based on the Schaefer model does not involve any updating of the priors when the population model is applied (to provide the post-model-pre-data distribution), because all parameter combinations implied by these priors remain consistent with this model.

The relative merits of the two approaches

In principle, a Bayesian approach is preferable to the bounded maximum likelihood one, in that it can take additional information (the shapes of the priors) about biological parameters into account, which the likelihood-based one ignores by considering only the prior boundaries. The practical question, however, is whether there really is additional information available in the form of the probability statements about parameter values which the Bayesian approach is implicitly assuming in its use of priors, and whether the exclusions effected by application of the population dynamics model are updating and introducing covariances between these priors in a reliable way.

Stepping back from the B-C-B bowhead assessment for the moment, imagine a situation in which all biological parameter values were known exactly for every baleen whale population except the one under assessment, and there were no reasons to consider that last population atypical. Then the empirical joint distribution provided by those known parameter values would provide a totally defensible joint prior for a Bayesian assessment of the population in question. Note, in particular, that this joint prior would manifest non-zero covariances, for example, because populations with higher ages at maturity would tend to have higher survival rates. Furthermore, application of the population model would produce *no* exclusions, because the sets of known biological parameter values for each population would all be consistent with the model, i.e. there would be no updating in moving from the joint prior to the post-model-pre-data joint distribution for a 'backwards' Bayesian assessment.

How closely does the application of Bayesian methods to the B-C-B bowhead population approach this ideal? First, B-C-B bowheads are clearly *not* typical of other baleen whale populations, given, for example, that their age at maturity (albeit not accurately known) is still clearly larger than that for most if not all other such populations. Thus, choices of prior distributions based upon analogy with other baleen whales (e.g. that for S_{adult} in Table 1) become questionable, and it is debatable whether the probability statements implicit in such priors are defensible.

What of priors in Table 1 developed from information on the B-C-B bowhead population itself? Although their use circumvents the problem raised above of the atypicality of

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[4] The 90% confidence intervals that can be inferred from Fig. 5 differ from those derived from bootstrap procedure. This may be a result of occasional failure to find the true minimum of the likelihood function for some of the bootstrap replicates when this function is very flat.

bowheads, it raises another in that such priors are *independent* of each other. Covariances are introduced by the exclusion process that accompanies the application of the population model, but what guarantee is there that the (very influential) covariance structure to which this process leads is reliably representative of the covariance that might *a priori* be anticipated? Thus, for example, Fig. 4 shows that the prior for S_{adult}, through the exclusion process, introduces covariance between S_{adult} and *MSYR*, and in consequence downweights higher *MSYR* values compared to lower ones in the Bayesian integration, 'contrary' to the intent of the uniform prior originally specified for *MSYR* that all such values were *a priori* equally likely. In this sense then, specification of the forms for the prior distributions may be important, because a uniform distribution, chosen with the intent of its being uninformative, can become informative about key quantities of management interest through the exclusion process. Can the results of this process defensibly be accorded a probabilistic interpretation, or do they provide no more than bounds to feasible parameter space (which is as far as the bounded maximum likelihood approach admits their interpretation)?

There is a further concern with the exclusion process as applied in the B-C-B bowhead case. Were there a firm basis for all biological parameter prior distribution choices bar one, with bounds available only for this last, those bounds provide the basis for the exclusions, and hence a unique post-model-pre-data distribution. However, there is no supporting evidence for the choice of a *uniform* distribution for the prior for $c_{\min}$ in Table 1. One could equally well have defended a uniform distribution choice for S_{juv} over $[0, S_{adult}]$, and then used the bounds of 2.5 and 4 for $c_{\min}$ to provide the basis for exclusions when checking consistency with the population model. The problem then is that this process would have resulted in a *different* post-model-pre-data distribution to the one that uses S_{juv} as the basis for exclusions - which is to be preferred?

In summary, it would appear that substantial questions remain to be resolved on how priors for biological parameters for Bayesian B-C-B bowhead assessments based on the age-structured BALEEN II population model should best be formulated, in particular as regards incorporating an appropriate covariance structure (given the considerable influence that this can have on results). This poses the question of whether, until such issues have been satisfactorily settled, the bounded maximum likelihood approach would constitute a more defensible basis for Scientific Committee assessments of this resource, even though it may be unable to take account of some information which could be incorporated in a Bayesian approach.

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