

Constructing a coherent joint prior while respecting biological realism: application to marine mammal stock assessments

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Brandon, J. R., Breiwick, J. M., Punt, A. E., and Wade, P. R. 2007. Constructing a coherent joint prior while respecting biological realism: application to marine mammal stock assessments. – *ICES Journal of Marine Science*, 64: 1085–1100.

Bayesian estimation methods, employing the Sampling–Importance–Resampling algorithm, are currently used to perform stock assessments for several stocks of marine mammals, including the Bering–Chukchi–Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) and walrus (*Odobenus rosmarus rosmarus*) off Greenland. However, owing to the functional relationships among parameters in deterministic age-structured population dynamics models, placing explicit priors on each life history parameter in addition to the population growth rate parameter results in an incoherent joint prior distribution (i.e. two different priors on the estimated parameters). One solution to constructing a coherent joint prior is to solve for juvenile survival analytically, using values generated from the prior distributions for the remaining parameters. However, certain combinations of model parameter values result in values for juvenile survival that are larger than adult survival, which is biologically implausible. Therefore, to respect biological realism, certain parameter values must be rejected for some or all the remaining parameters. This study investigates several alternative resampling schemes for obtaining a realistic joint prior distribution, given the constraint on survival rates. The sensitivity of assessment results is investigated for data-rich (bowhead) and data-poor (walrus) scenarios. The results based on limited data are especially sensitive to the choice of alternative resampling scheme.

Keywords: age-structured population dynamics model, Bayesian statistics, biological realism, bowhead whale, coherent joint prior, marine mammal, modelling, sensitivity analyses, stock assessment, walrus.

Received 3 October 2006; accepted 5 June 2007; advance access publication 16 July 2007.

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Introduction

Bayesian methods utilizing age-structured population dynamics models (PDMs) have formed the basis for recent stock assessments of several marine mammal populations, including those for Atlantic walrus (*Odobenus rosmarus rosmarus*) in Greenland (Witting and Born, 2005), the Bering–Chukchi–Beaufort Seas (B–C–B) stock of bowhead whales (*Balaena mysticetus*) (Brandon and Wade, 2006), British grey seals (*Halichoerus grypus*) (Thomas *et al.*, 2005), the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) (Punt *et al.*, 2004), New Zealand sea lions (*Phocarcos hookeri*) (Breen and Kim, 2006), northeastern offshore spotted and eastern spinner dolphins (*Stenella attenuata* and *Stenella longirostris orientalis*) (Hoyle and Maunder, 2004), and Steller sea lions (*Eumetopias jubatus*) (Fay and Punt, 2006; Winship and Trites, 2006). These assessments use Bayesian estimation methods to calculate posterior probability distributions for model parameters and management-related quantities, and to form the basis for risk analyses to evaluate the implications of potential management actions (Hilborn and Walters, 1992; Ellison, 1996). A brief review is provided for the developments required for commonly used Bayesian methods when applied to age-structured PDMs for stock assessments: the necessity of constructing a coherent joint prior distribution; one solution to this challenge that has been employed in several

recent stock assessments; and, finally, the importance of investigating the sensitivity of those results to alternative schemes for constructing a coherent joint prior while respecting biological realism.

Adopting similar approaches to Butterworth *et al.* (1987) and Nakamura *et al.* (1989), Raftery *et al.* (1995) and Givens *et al.* (1995) developed and influenced the application of Bayesian methods to age-structured PDMs for marine mammal stock assessment. The method developed, “Bayesian synthesis”, was a departure from the “standard” Bayesian approach in that it allowed explicit prior distributions on model inputs and outputs. During the development of these methods, it was shown that Bayesian synthesis (as originally proposed) is inappropriate on theoretical grounds (Wolpert, 1995; Schweder and Hjort, 1996). Raftery and Givens (1997) clarified the concerns by distinguishing two hurdles: (i) Borel’s paradox (i.e. conditioning on an ill-defined distribution, resulting in this case from explicit priors on both model inputs and outputs, and ultimately leading to posterior distributions that are not invariant to model parameterization); and (ii) prior incoherence (i.e. the implicit presence of two different prior distributions on the same parameter). Bravington (1996) provides illustrative examples of these issues using a simple model of exponential population growth. Borel’s paradox does not apply to a standard Bayesian analysis.

However, the issue of prior incoherence is a potential concern for all Bayesian stock assessments. As Givens and Roback (1999) stress, simultaneous and competing prior distributions for the same parameters are common occurrences in Bayesian modelling.

A coherent joint prior must be constructed before inference may be drawn from Bayesian analyses. Punt and Hilborn (1997) advise that care needs to be taken to avoid implicitly specifying contradictory priors for the same model parameter in Bayesian stock assessments. Those authors demonstrate how explicit prior distributions on both unexploited biomass and current depletion (the ratio of current biomass to unexploited biomass) lead to incoherent joint priors. Such subtleties become more insidious as PDMs (and the functional relationships among parameters therein) increase in complexity. Several approaches have been developed to address this issue in the context of age-structured PDMs. However, we postpone consideration of alternative methods at this stage, and instead return to this during the concluding discussion. The sensitivity analyses presented here focus on just one approach for constructing a coherent joint prior while respecting biological realism: the most commonly employed during recent assessments of large whales, as outlined below (e.g. Punt and Butterworth, 1999, 2002; Wade, 2002; Punt *et al.*, 2004; Brandon and Wade, 2006; Punt, 2006).

Owing to the functional relationships among life history parameters and the parameter related to population growth rate in a deterministic age-structured PDM (Lotka, 1907; Euler, 1970), placing priors on life history parameters in addition to a prior on the population growth rate would result in effectively placing two (most likely incoherent) priors on the same parameter. Therefore, an option for constructing a coherent joint prior is to place marginal priors on all but one of these parameters, then to solve for the value of the remaining parameter analytically. Given that many of the key model outputs (e.g. the current rate of increase) are almost directly proportional to the population growth rate, having an explicit prior on the latter parameter allows clear consideration of the impact of the priors on these model outputs. For example, placing a uniform prior on the population growth rate, to the extent possible, essentially imposes a non-informative prior on some of the model outputs of interest to management.

There exists very little information on which to base a prior on juvenile survival S_{juv} for most marine mammal populations. Therefore, it has been argued that placing an explicit prior on this life history parameter is unfounded for most species, and that a more appealing approach would be simply to impose some biological bounds instead of a full probability distribution (Butterworth, 1995). Additionally, a common assumption in age-structured PDMs for marine mammals is that juvenile survival is less than adult survival S_a (e.g. IWC, 1995; Chivers, 1999; Witting and Born, 2005). This assumption is based on observed mammalian mortality patterns, which are typically U-shaped with age (Caughley, 1966; Barlow and Boveng, 1991). Therefore, one solution to constructing a coherent joint prior is not to place an explicit prior on S_{juv} (Punt and Butterworth, 1996), but instead to solve for this parameter analytically given the values for the other life history parameters and the population growth rate (Breiwick *et al.*, 1984; Punt, 1999). This is equivalent to determining the coherent joint prior implied by the remaining explicit marginals. Additionally, the solution for S_{juv} is subject to the constraint, $S_{juv} < S_a$. This approach is appealing because it is relatively simple, minimizes the influence of marginal priors for life history

parameters on key model outputs of interest to management, and results in a coherent joint prior distribution that also respects biological realism. However, certain combinations of otherwise reasonable parameter values result in solutions for S_{juv} which seem biologically implausible, if not completely impossible. Specifically, solutions for S_{juv} may result that are larger than those for adult survival (including values > 1.0 ; Figure 1).

Sensitivity tests to alternative prior specifications should be conducted during the assessment processes to ensure that inference is robust. Effectively, the constraint $S_{juv} < S_a$ is an element of the joint prior on the life history parameters. There are several ways to construct a coherent joint prior in cases where the constraint becomes active. For example, in addition to completely ignoring the parameter space that violates the constraint, one could also resample values for different subsets of the life history parameters (effectively re-weighting the marginals) until a feasible solution for S_{juv} is attained. Both approaches have been applied in marine mammal stock assessments. However, the question of sensitivity to such alternative resampling schemes has not been explored in any detail to date.

The Sampling–Importance–Resampling (SIR) algorithm (“Resampling” parameters values to find a feasible solution for S_{juv} should not be confused with the “resampling” step in the SIR algorithm) for approximating Bayesian posterior distributions is employed here to generate realized joint prior distributions (also referred to as post-model-pre-data distributions). These distributions represent the actual (implicit) marginal prior distribution for each parameter after the explicit marginal prior distributions have been reconciled (via the model and resampling schemes)

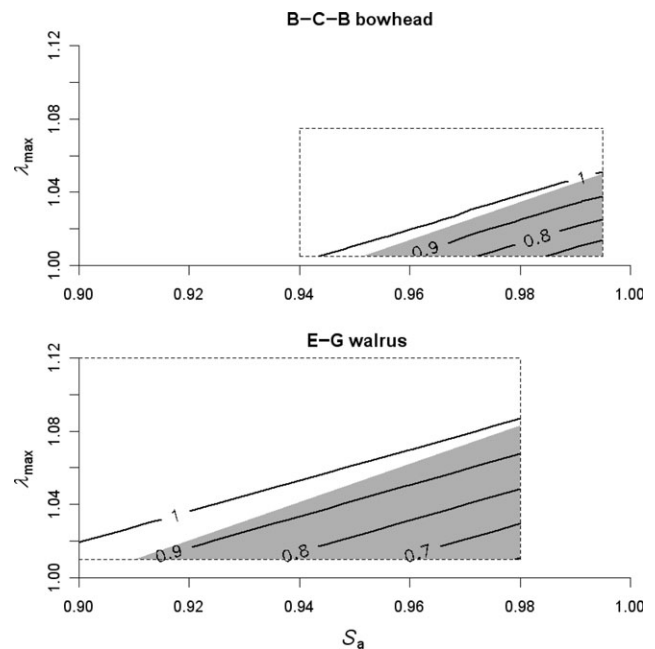


Figure 1. Contour plots showing solutions for S_{juv} [from Equation (4)] given a range of values for S_a and λ_{max} . These diagrams are created by setting the remaining life history parameters constant, equal to the expectation of their explicit prior marginal distribution (e.g. $a_m = 20$ for B–C–B bowheads). The shaded triangular region is the feasible parameter space, subject to the constraint on survival rates. The area between the contour of 1.0 and the shaded region shows the biologically implausible region where $S_{juv} > S_a$.

into a coherent joint probability distribution. It would be expected that the realized prior distribution will differ under alternative resampling schemes, but little is known about whether and how, if at all, the posteriors for the quantities of management interest are affected. The results of these interactions are potentially relevant to the calculation of management-related quantities, and hence to the provision of management advice.

Here, therefore, we explore the sensitivity of Bayesian assessments for marine mammal populations to several alternative resampling schemes used to construct a coherent joint prior, while simultaneously respecting biological realism. Results are provided for two populations that differ in terms of the amount of available data to illustrate the consequences in terms of quantities of management interest. The B–C–B bowhead population is data-rich in that considerable information is available on abundance and trends in abundance (e.g. Zeh and Punt, 2005); in contrast, the walrus population off East Greenland (EG) is data-poor, with only one (fairly imprecise) estimate of abundance on which to base assessments, and hence management advice (Born *et al.*, 1997; Witting and Born, 2005).

Methods

To ease subsequent comparison, similar methods are used for the analyses of both the bowhead and the walrus data. Hence, unless noted otherwise, the methods described here apply to both populations. Similarly, all parameters related to abundance or catch statistics are reported in terms of the 1+ component of the population (all age groups except calves), except for the trajectories of walrus population size, which are plotted on the same scale as the prior for recent abundance (total population size including calves).

Available data

B–C–B bowhead whales

The PDMs utilize three sources of data: (i) abundance estimates from ice-based surveys at Point Barrow, Alaska, between 1978 and 2001 (Table 1); (ii) average proportion of calves and mature animals in the population from 1985 to 1994 (Table 2); and (iii) annual catches in numbers from 1848 to 2002 (Punt, 2006).

EG walrus

A single abundance estimate of 1000 exists for the EG walrus population in 1995. This estimate is based on opportunistic and systematic observations (Born *et al.*, 1997; Witting and Born,

2005), and is assumed to relate to the total population (i.e. including young of the year). Following Witting and Born (2005), the coefficient of variation for this estimate is arbitrarily set to 0.35, to encompass the plausible range for abundance in 1995. This estimate forms the basis for the prior on abundance in 1995 (see below).

Born *et al.* (1997) report, or in some years estimate, catches of walrus off EG for the period 1889–1999. These catches are treated as known (estimated without error) in the model. No attempt has been made in this analysis to take into account the potential number of animals struck and lost, or the numbers landed and not reported in a given year [i.e. the data correspond to the “low” catch history analysed by Witting and Born (2005)]. The reader is referred to Born *et al.* (1997) and Witting and Born (2005) for the catch table and a detailed list of sources regarding these catches.

Before 1956, there was no information on the sex ratio of the catch. In 1956, walrus off EG were protected north of ca. 72°N, effectively ending the foreign hunt on this population. After 1956, the sex ratio in the Greenland catch is highly skewed towards males (~90%; Born *et al.*, 1997). Therefore, we follow the methods of Witting and Born (2005), and assume an even sex ratio before 1956, and a 9:1 male:female sex ratio thereafter.

Inflated catches

The implications of higher levels of catch on model outputs are examined by multiplying the catch history by five, for both B–C–B bowheads and EG walrus.

Population dynamics model

The underlying PDM is an age- and sex-structured Leslie matrix (Leslie, 1945, 1948) projected as

$$N_{t+1} = (A_t N_t) - C_t, \tag{1}$$

where N_t is the matrix of population size by sex and age class at the start of year t (defined when births and natural mortality occur), A_t the Leslie matrix for year t , and C_t the matrix of sex- and age-specific catches during year t .

The parameters that define the entries of the Leslie matrix are: (i) S_{juv} , the survival rate of immature animals (assumed identical for calves and juveniles); (ii) a_T , the last age with survival rate S_{juv} ; (iii) S_a , the survival rate of mature animals; (iv) a_m , the age at sexual maturity (the last age class with zero fecundity, i.e.

Table 1. Data inputs for B–C–B bowhead whales: estimates, CVs (actually the standard errors of the log-abundance estimates, to which these are approximately equal), and a correlation matrix for the indices of abundance (Zeh and Punt, 2005).

Year	Estimate	CV	Correlation matrix											
1978	4 765	0.305	1.000											
1980	3 885	0.343	0.118	1.000										
1981	4 467	0.273	0.056	0.050	1.000									
1982	7 395	0.281	0.094	0.084	0.035	1.000								
1983	6 573	0.345	0.117	0.104	0.049	0.084	1.000							
1985	5 762	0.253	0.070	0.062	0.020	0.078	0.062	1.000						
1986	8 917	0.215	0.072	0.064	0.017	0.092	0.064	0.113	1.000					
1987	5 298	0.327	0.124	0.110	0.052	0.088	0.110	0.065	0.067	1.000				
1988	6 928	0.120	0.028	0.025	0.013	0.017	0.024	0.009	0.007	0.026	1.000			
2001	10 545	0.128	0.008	0.007	0.005	0.001	0.007	−0.004	−0.008	0.008	0.003	1.000		

Table 2. Average proportion of observed calves (p_c^{obs}) and mature (p_m^{obs}) animals, with associated standard errors, for the years 1985–1994.

p_c^{obs}	σ_{p_c}	p_m^{obs}	σ_{p_m}
0.0580	0.0062	0.4366	0.0106

Proportions are given based on ignoring the potentially anomalous dataset for 1985 (IWC, 1999; Koski *et al.*, 2006).

birth occurs at $a_m + 1$ year, the age at first parturition); (v) f_{max} the maximum fecundity rate; and (vi) a_{max} , the age after which survival becomes zero. Fecundity is assumed to be identical for all mature animals, and is calculated as the number of female calves per mature female. The sex ratio at birth is assumed to be 50:50 male:female. Recruitment to the fishery is assumed to be knife-edged and to occur at age 1, and the catch is therefore distributed uniformly over all recruited age classes.

Density-dependence and initial conditions

Density-dependence is assumed to influence fecundity according to a Pella–Tomlinson functional relationship based on the depletion of the 1+ component of the population (Pella and Tomlinson, 1969; Allen, 1976):

$$f_t = f_0 + (f_{\text{max}} - f_0) \left[1 - \left(\frac{N_t^{1+}}{K^{1+}} \right)^z \right], \quad (2)$$

where f_t is the fecundity during year t , N_t^{1+} the (1 +) population size at the start of year t , K^{1+} the pre-exploitation (1 +) population size, z the Pella–Tomlinson shape parameter, and f_0 the fecundity at carrying capacity. Given values of the life history parameters, the value for f_0 is determined from the characteristic equation of the Leslie matrix given equilibrium conditions (Breiwick *et al.*, 1984; Punt, 1999):

$$f_0 = \frac{1 - S_a}{S_{\text{juv}}^{(a_T)} S_a^{(a_m - a_T)} [1 - S_a^{(a_{\text{max}} - a_m - 1)}]}. \quad (3)$$

The population projections are initialized from a stable age distribution at the start of the year before the first catch is removed, given values for the parameters sampled from the joint prior distribution.

Modelling approaches

B–C–B bowhead whales

The population trajectory is modelled in two ways: (i) a density-dependent model initialized in 1848 (abbreviated as 1848 Bkwd) and (ii) a density-dependent model initialized in 1978 (1978 Fwd). The six life history parameters of the Leslie model are included in each model. However, the approach used to estimate the equilibrium population size, or carrying capacity, K , differs between the two models. The 1848 Bkwd model includes a parameter with associated prior for the population size in 1993, N_{1993} , and the backwards method (Butterworth and Punt, 1995; Punt and Butterworth, 1999) is used to back-calculate to the population size in 1848 (assumed to be equal to K). Instead of placing a prior on N_{1993} , the 1978 Fwd model involves placing a prior on the population size in 1978, N_{1978} , and projecting forwards from that initial year (Wade, 2002). This model includes an additional (explicit) prior on K . However, unlike the

1848 Bkwd model, it does not make the assumption that the catch history is known without error or that K has remained unchanged over the past 150 years. Both models include a parameter for the depletion at which maximum sustainable yield (MSY) is achieved (referred to as the MSY level, or MSYL), and one for the maximum population growth rate in the limit of no density-dependence, λ_{max} (the dominant real eigenvalue of the Leslie matrix). These two modelling approaches have been used in recent assessments of B–C–B bowhead whale (e.g. Brandon and Wade, 2006); it is therefore of interest to include them both in this analysis for the sake of comparison.

EG walrus

The analyses for this population are based on a density-dependent model initialized in 1899 (corresponding to the model 1848 Bkwd for B–C–B bowheads). In addition to the six life history parameters and MSYL, this model also includes a parameter for the population size in 1995, N_{1995} . Note that the assumption that harvest selectivity is uniform above age 1 differs from the assumption that selectivity increases with age from age 0 to age 10 made by Witting and Born (2005). However, this difference is inconsequential for the analyses here.

Model parameters and prior distributions

Calves are defined as young of the year (i.e. age 0), and f_{max} is specified in the standard Leslie matrix formulation as female calves per female per year (e.g. a fecundity rate of 0.125 implies a female calving interval of 8 years, and therefore a total calving interval of 4 years, assuming an equal sex ratio of calves).

B–C–B bowhead whales

Data-based prior distributions are assigned to adult survival rate and age-at-maturity (Table 3), and the maximum age in the Leslie matrix is set to 200 years following the results of recent research on age determination (George *et al.*, 1999).

EG walrus

The prior distributions for the life history parameters for walrus are based on various field and modelling studies (Table 4). The age at which survival changes from immature to adult is fixed, and set to age 3. The maximum age after which survival becomes zero is set to 60 years.

Although we attempt to follow the methods of Witting and Born (2005) in most regards, this study treats the juvenile survival rate differently. We choose to follow methods recently employed in stock assessments used by the International Whaling Commission (IWC, e.g. Punt and Butterworth, 1999; Wade, 2002), i.e. we place a uniform prior from 1.01 to 1.12 on λ_{max} and do not place a prior on juvenile survival. The details of this treatment are given in the following section (and apply to the bowhead analyses as well).

Alternative resampling schemes

The constraint that juvenile survival must be less than adult survival is implemented here. However, as Punt and Butterworth (1999) note, placing an explicit prior on S_{juv} (in addition to priors on the remaining life history parameters, and a prior on the population growth rate) would result in an incoherent prior because of the functional relationships among life history parameters. Instead, the value of S_{juv} is calculated analytically by rearranging the characteristic equation of the Leslie matrix given

Table 3. Prior distributions for B–C–B bowhead whales. Sources are given below.

Parameter	Model type	
	1848 Bkwd	1978 Fwd
S_a (Adult survival)	$N(0.990, 0.02^2)$, truncated at 0.940 and 0.995 ^a	–
f_{max} (Maximum fecundity)	$U[0.125, 0.200]$ ^b	–
a_T (Age-at-transition to adult survival)	$DU[1, 9]$ ^c	–
a_m (Age-at-maturity)	$N(20.0, 3.0^2)$, truncated at 13.0 and 26.0 ^d	–
λ_{max} (Intrinsic population growth rate)	$U[1.005, 1.075]$ ^e	–
N_{1978} (Population size in 1978)	N/A	$U[3000, 9000]$ ^f
N_{1993} (Population size in 1993)	$N(7800, 1200^2)$ ^g	N/A
K (Carrying capacity)	N/A	$U[8000, 30000]$ ^h
MSYL (MSYL in terms of the 1+ population component)	$U[0.40, 0.80]$ ^h	–

Dashes (–) represent prior distributions that are equal to those from the model in the column to the left. N/A indicates a prior that is not required for the model concerned. Fecundity is defined as female calves per mature female. The abbreviations for these distributions are: U, Uniform; DU, Discrete uniform; and N, Normal.

^aBased on the posterior distribution for adult survival rate obtained by Zeh *et al.* (2002).

^bThe prior for the maximum number of calves (of both sexes) per mature female selected by the Scientific Committee of the IWC was $U(0.25, 0.4)$ (IWC, 1995). This is the corresponding prior given fecundity has been defined here as female calves per mature female per year.

^cSelected by the Scientific Committee of the IWC (IWC, 1995), although there is little information on the value of this parameter (Givens *et al.*, 1995).

^dBased on a best estimate of 20 years and a lower confidence interval for the age at first parturition (age at sexual maturity + 1 year) of 14 years (IWC, 1995).

^ePreliminary analyses indicated that there was no posterior probability outside this range, which was confirmed in the final analyses. This range was therefore selected to improve the efficiency of the numerical integration while not affecting the results.

^fSelected to encompass a plausible range of values for 1+ population size in 1978.

^gSelected by the Scientific Committee of the IWC (IWC, 1995) based on the posterior distribution resulting from an independent estimate of abundance.

^hBased on the prior selected by the Scientific Committee of the IWC (IWC, 1995).

the values for the remaining five life history parameters and λ_{max} (Breiwick *et al.*, 1984):

$$S_{juv} = \left[\frac{\lambda_{max}^{(a_m+1)} - S_a \lambda_{max}^{(a_m)}}{S_a^{(a_m-a_T)} f_{max} [1 - (S_a/\lambda_{max})^{(a_{max}-a_m-1)}]} \right]^{1/a_T} \quad (4)$$

The resulting value for S_{juv} is constrained to be less than that of S_a through one of the alternative resampling schemes.

These schemes involve resampling the following parameters from their prior distributions while keeping the values of all other parameters if $S_{juv} > S_a$:

- (1) f_{max} , S_a , and a_m ;
- (2) f_{max} and S_a ; and
- (3) no parameters (abbreviation None), meaning that the current set of life history values is simply ignored and a completely new set of values is drawn from the marginals (see Parameter estimation).

Table 4. Prior distributions for EG walrus.

Parameter	Prior
S_a (adult survival)	$U[0.900, 0.980]$ ^a
f_{max} (maximum fecundity)	$U[0.167, 0.250]$ ^b
a_m (age-at-maturity)	$DU[5, 9]$ ^b
λ_{max} (intrinsic population growth rate)	$U[1.01, 1.12]$ ^c
N_{1995} (population size in 1995)	$LN[\ln(1\ 000), 0.35^2]$ ^d
MSYL (MSYL in terms of 1+ abundance)	$U[0.50, 0.80]$ ^e

The abbreviations for these distributions are: U, Uniform; DU, Discrete uniform; and LN, Log-normal.

^aPrior assumed by Witting and Born (2005), with ranges set wide enough to encompass plausible values as no direct evidence is available for this parameter.

^bThe range of fecundity values used by Witting and Born (2005) has been divided by 2 because these values are taken here to relate to the number of female calves per mature female per year.

^cPreliminary analyses indicated that there was no posterior probability outside this range, which was confirmed in the final analyses. This range was therefore selected to improve the efficiency of the numerical integration while not affecting the results.

^dAfter Born *et al.* (1997); the abundance estimate used for 1995 by Witting and Born (2005), where the CV is taken to be approximately equal to the standard error of the logarithm.

^ePrior assumed by Witting and Born (2005).

For resampling schemes 1 and 2, values for the parameters are resampled until $S_{juv} < S_a$, or 1000 resamples occur. If this maximum is reached, a new value for λ_{max} is drawn from its prior distribution, and the process is repeated until an acceptable sample from the joint prior is obtained.

The rejection rate is calculated for each scheme. This rate is the average proportion of resample attempts needed before a feasible solution for juvenile survival is achieved (e.g. a rejection rate of 50% corresponds to a feasible solution every other attempt).

Output quantities

Posterior distributions are calculated for several output quantities that are derived from the parameters in Tables 3 and 4. The MSY rate (MSYR) is calculated as $(\lambda_{MSY} - 1)$ based on the fecundity value, f_{MSY} , associated with MSYL. The quantity Q_1 , designed to meet the intent of IWC aboriginal whaling management objectives (Wade and Givens, 1997), is also calculated. This quantity has the property that the proportion of net production allocated to recovery increases the more depleted a population is assessed to be [this definition applies to a population above some minimum level, P_{min} (assumed here to be 0.1K), below which catches are

set to zero]. Specifically,

$$Q_1 = \min(\text{MSYR} \times N_t, 0.9\text{MSY}), \quad (5)$$

where N_t is the population size in 2000 for walrus or 2002 for bowheads.

The realized prior is reported for the parameters. This distribution arises after conditioning the specified priors on the model and the resampling scheme by eliminating combinations of parameters for which (i) the juvenile survival rate implied by Equation (4) exceeds the adult survival rate drawn from the joint prior distribution and (ii) population trajectories go extinct before the final year of the projection period. Likewise, post-model-pre-data distributions for output quantities are calculated as the distributions for these quantities in the sampled joint prior space.

Parameter estimation

The SIR algorithm (Rubin, 1988; Smith and Gelfand, 1992) is used to generate samples of parameter vectors (and output quantities of interest) from the joint posterior distribution. This algorithm involves randomly sampling a large number of parameter vectors from the prior distribution. A population trajectory is then calculated for each vector of parameter values, and this trajectory is used to determine the likelihood of the data for each random draw (the likelihood is 1 for the walrus case because there are no abundance data for this population except for that on which the prior for the abundance in 1995 is based). In all, 10 000 draws (which form a numerical representation of the posterior distribution) are selected by sampling (with replacement) from the initial samples from the prior, with probability proportional to the likelihood (i.e. the importance function is set equal to the joint prior, so the importance weight is the likelihood). Following Raftery *et al.* (1995) and Punt and Butterworth (1999), the SIR algorithm is considered to have converged if the number of unique parameter vectors in the sample from the posterior is fairly high (>5000) and if the most frequently resampled parameter vector does not occur in the posterior sample more than ten times.

B–C–B bowhead whales

The total negative log-likelihood of a model trajectory, given a vector of parameters and the data, consists of contributions from four data sources: (i) an estimate of abundance for 1993; (ii) estimates of abundance for the remaining years; (iii) the proportion of calves in the population; and (iv) the proportion of mature animals in the population. The abundance estimates are assumed to be indices of the 1+ component of the population. The scientific surveys at Point Barrow are assumed to have occurred after the aboriginal catch [in reality, there are two seasonal (spring and autumn) hunts each year, with the survey immediately following the spring hunt. However, as catches are a relatively small proportion of the total population size, the simplification made will hardly affect the quantitative results], and the likelihood function is calculated therefore (i.e. catches are removed before calculating the likelihood of the data for a given year). Model-predicted proportions are calculated over the period 1985–1994, because the actual stage proportions are based on data for these years.

The estimate of abundance for 1993 is assumed to be independent of the remaining estimates (Punt and Butterworth, 1999),

and to have normally rather than log-normally distributed sampling error. The contribution of the abundance estimates to the negative of the log-likelihood function is (ignoring constants independent of model parameters):

$$L_1 = 0.5 \frac{(\hat{N}_{1993} - 8293)^2}{626^2}$$

$$L_2 = 0.5 \sum_{t_1} \sum_{t_2} (\ln \hat{N}_{t_1} - \ln N_{t_1}^{\text{obs}})^T \mathbf{V}_{t_1, t_2}^{-1} (\ln \hat{N}_{t_2} - \ln N_{t_2}^{\text{obs}}), \quad (6)$$

where N_t^{obs} is the survey estimate of abundance for year t , \hat{N}_t the model estimate of 1+ abundance for year t , and \mathbf{V} is the variance-covariance matrix for the logarithms of the estimates of abundance (excluding 1993).

The estimates of abundance (Table 1) are based on combining the data from visual counts at Point Barrow, Alaska, and estimates of the proportion of animals that passed within visual range based on acoustic data. Equation (6) accounts for the correlation among the non-1993 estimates of abundance that arises because the proportion within visual range is treated as a random effect when constructing the estimates of abundance (Zeh and Punt, 2005).

The contribution of the proportion data to the likelihood function follows Punt (2006). As a bootstrapping approach was adopted to calculate the length-frequency distributions from which the proportion data were calculated (Koski *et al.*, 2006), it is reasonable to assume that the estimates are normally distributed:

$$L_3 = 0.5 \frac{(p_c - p_c^{\text{obs}})^2}{(\sigma_{p_c})^2}$$

$$L_4 = 0.5 \frac{(p_m - p_m^{\text{obs}})^2}{(\sigma_{p_m})^2}, \quad (7)$$

where p_c^{obs} is the observed average fraction of the population that consists of calves between 1985 and 1994, σ_{p_c} the standard deviation of p_c^{obs} , p_c the model estimate of the average fraction of the population that consists of calves between 1985 and 1994, p_m^{obs} the observed average fraction of the population that consists of mature animals between 1985 and 1994, σ_{p_m} the standard deviation of p_m^{obs} , and p_m the model estimate of the average fraction of the population that consists of mature animals between 1985 and 1994.

Risk analysis

Forward projections are initialized from the posterior distribution corresponding to the status of the stock at the start of 2000 (walrus) or 2002 (bowheads). Following Witting and Born (2005), the catch during the first 5 years of the projection period is set equal to that for the last year of the assessment (e.g. 80 walrus, with a sex ratio 9:1 male:female), and the population is then projected forward under different levels of constant catch C , for another 5 years (applying the assumed sex ratio and the selectivity pattern of the current hunt). The management objective, ob , used to summarize the results of the decision analysis follows the aboriginal whaling guidelines of the IWC (2000), as interpreted by Witting and Born (2005):

$$ob = \begin{cases} N_{\text{yr}+5} > N_{\text{yr}} & \text{if } N_{\text{yr}} < N_{\text{MSYL}} \\ C \leq 0.9\text{MSY} & \text{if } N_{\text{yr}} \geq N_{\text{MSYL}} \end{cases} \quad (8)$$

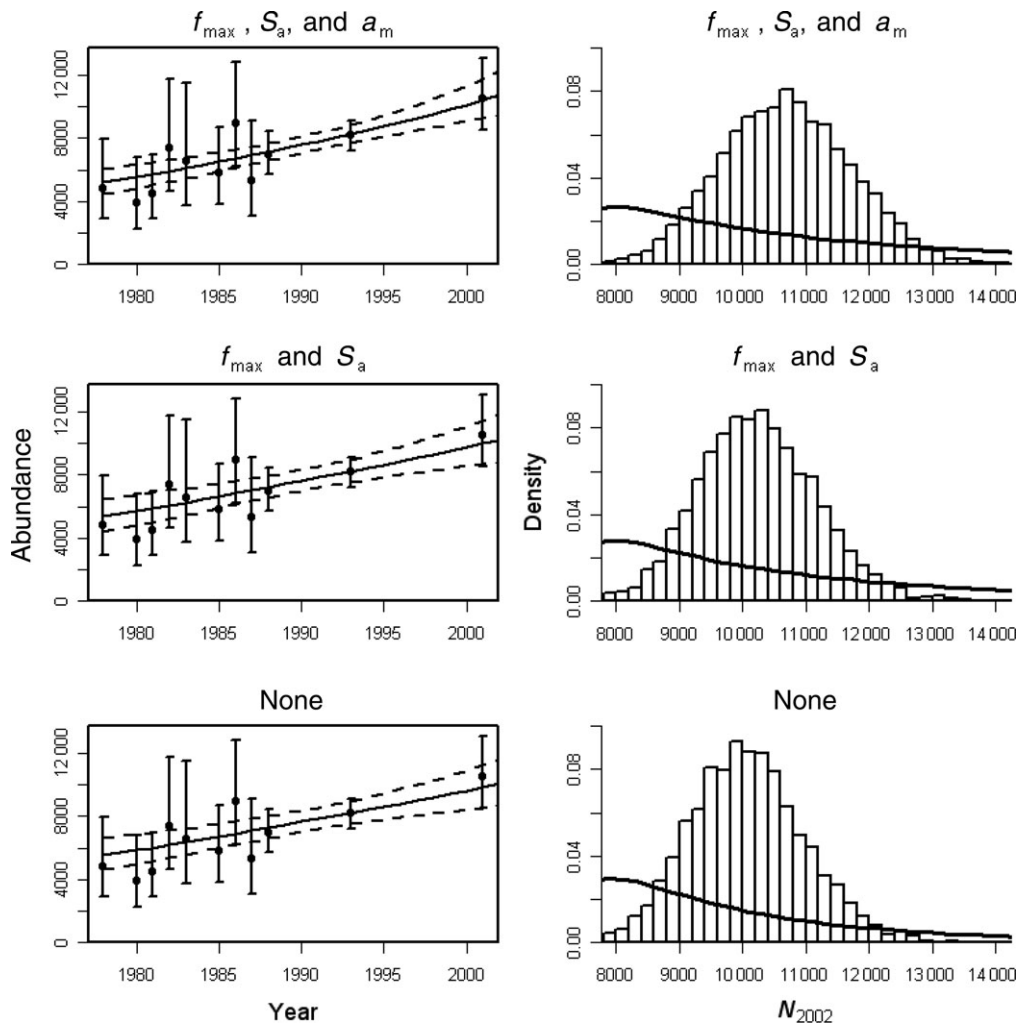


Figure 2. Model fits and estimates of recent abundance according to the 1978 Fwd model for B–C–B bowheads. The left panels show the posterior distributions (medians and 90% credibility intervals) for the time-trajectory of population size obtained for three resampling schemes. Error bars represent 90% CIs from survey estimates, and are assumed to be log-normally distributed for all abundance estimates except 1993 (second to last), which is assumed to be normally distributed. The right panels show the posterior distribution of population size in 2002. The solid lines are the realized prior distributions, and the bars the posterior probabilities.

Here N_{yr} is the population size in 2005 for EG walrus, and in 2007 for B–C–B bowheads. The probability of meeting the objective, given a future catch level and one of the alternative resampling schemes, is calculated as the proportion of trajectories at the start of N_{yr+5} that meet the objective. These probabilities are conditioned on reported catch history.

Results
B–C–B bowhead whales

In general, all three resampling schemes lead to reasonable fits to the data (see, for example, the results for the 1978 Fwd model in Figure 2). However, there are certain notable differences in the outputs of the models among resampling schemes, especially those from the 1978 Fwd model. Specifically, resampling f_{max} , S_a , and a_m leads consistently to higher values of stock productivity, as quantified by λ_{max} , and hence to better fits to the estimate of abundance for 2001 and as a consequence to the largest estimate

of 2002 population size for the 1978 Fwd model (Figure 2 and Table 5).

As expected from previous research (e.g. Punt and Butterworth, 1999), the 1848 Bkwd model is relatively insensitive to modifications to the prior. This is likely the result of conditioning the model on the historical catch record from 1848, which is assumed known without error. There are basically no differences between median estimates of current population size among resampling schemes for this model (although the CV of current population size for the first resampling scheme is ~20% smaller than that for resampling None). The posterior median for K is also slightly lower when f_{max} , S_a , and a_m are resampled, resulting in greater probability that the stock is less depleted according to this resampling scheme (Table 5; Figure 3).

It is useful to examine the original (explicit) priors, the realized priors, and the posteriors for the model parameters to understand better the reasons for the differences among the three resampling schemes for some of the model outputs. Qualitatively, the results

Table 5. Posterior medians [5th, 95th percentiles] for five management-related quantities for the B–C–B bowhead population for all models and alternative resampling schemes.

Model and resampling scheme	N_{2002}	K	N_{2002}/K	λ_{\max}	Q_1
1848 Bkwd					
Reported catches					
$f_{\max}, S_a,$ and a_m	9 496 [8 750, 10 180]	10 960 [9 190, 13 950]	0.888 [0.647, 0.985]	1.041 [1.024, 1.059]	228 [149, 296]
f_{\max} and S_a	9 571 [8 030, 10 360]	11 670 [9 252, 15 630]	0.826 [0.459, 0.977]	1.036 [1.014, 1.053]	208 [92, 276]
None	9 579 [7 974, 10 400]	11 960 [9 562, 16 150]	0.809 [0.434, 0.973]	1.034 [1.012, 1.050]	203 [83, 271]
Inflated catches					
$f_{\max}, S_a,$ and a_m	10 140 [7 957, 11 840]	56 870 [44 750, 66 170]	0.180 [0.119, 0.245]	1.058 [1.034, 1.067]	330 [215, 506]
f_{\max} and S_a	9 611 [7 457, 11 410]	58 430 [46 240, 70 070]	0.166 [0.105, 0.226]	1.050 [1.028, 1.067]	290 [177, 441]
None	9 364 [7 320, 11 180]	57 550 [46 550, 70 760]	0.162 [0.101, 0.222]	1.045 [1.026, 1.060]	282 [167, 436]
1978 Fwd					
$f_{\max}, S_a,$ and a_m	10 670 [9 042, 12 410]	20 510 [11 010, 29 120]	0.530 [0.356, 0.925]	1.045 [1.025, 1.063]	295 [160, 439]
f_{\max} and S_a	10 210 [7 989, 12 160]	20 890 [9 403, 29 510]	0.498 [0.302, 0.915]	1.037 [1.015, 1.058]	246 [84, 420]
None	10 050 [7 949, 11 930]	20 880 [9 253, 29 500]	0.487 [0.296, 0.912]	1.034 [1.013, 1.051]	232 [73, 402]

Rejection rates: None (63%); f_{\max} and S_a (99%); $f_{\max}, S_a,$ and a_m (99%). Note, these rates are identical between models and catch histories.

for age-at-maturity are relatively insensitive to the resampling scheme (Figure 4, left panels), both the realized prior and posterior distributions being unimodal. Closer inspection of the results reveals, however, that resampling $f_{\max}, S_a,$ and a_m leads to lower posterior medians than the other schemes. The situation for f_{\max}

is similar, with this scheme again leading to the most optimistic posterior (Figure 4, right panels). Likewise, the realized priors and posterior distributions assign less probability to the highest values of adult and juvenile survival when none of the parameters are resampled (scheme None) (Figure 5).

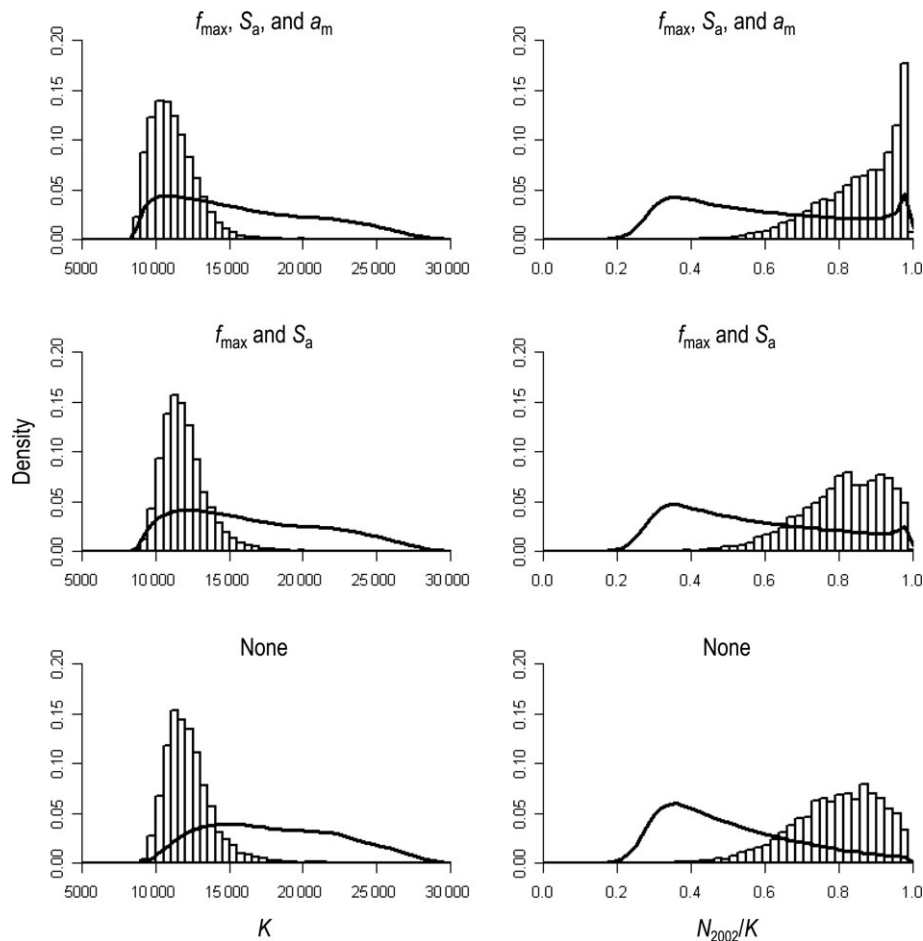


Figure 3. Realized prior distributions (solid lines) and posterior distributions (bars) for K and depletion in 2002, according to the 1848 Bkwd model for the B–C–B bowhead population for three resampling schemes.

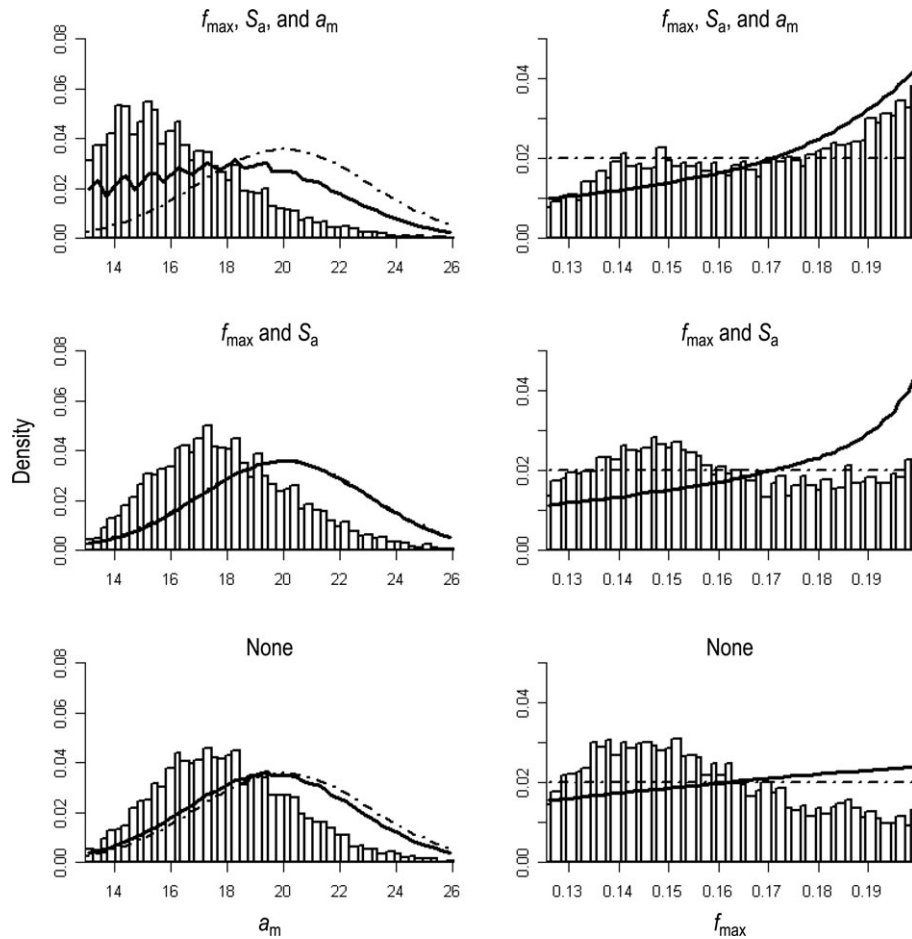


Figure 4. Explicit priors (dash-dot lines), realized priors (solid lines), and posterior distributions (bars) for a_m and f_{max} according to the 1978 Fwd model for the B–C–B bowhead population for three resampling schemes.

The realized prior for the maximum rate of increase differs substantially from the explicit prior when no parameters are resampled. Resampling None assigns almost no realized prior probability to high (≥ 1.05) values for λ_{max} , but this is not the case when f_{max} and S_a , and (particularly) when f_{max} , S_a , and a_m are resampled (Figure 6). The rejection rates between resampling schemes exhibit a similar pattern: None (63%), f_{max} and S_a (99%), and f_{max} , S_a , and a_m (99%). These rates are positively correlated with the value drawn for λ_{max} .

Sensitivity analyses

Figure 7 compares the posterior distributions for the time-trajectory of 1+ population size given the reported catch history (top panel) with that from the analyses in which the catch history is increased fivefold (bottom panel). The estimates of K are obviously very different between catch histories. However, these estimates are effectively insensitive to the choice of resampling scheme for each catch history (Table 5). The estimates of the catch quantity Q_1 are only moderately more sensitive to the choice of resampling scheme than those given the reported catch history (Table 5).

There is essentially no difference among resampling schemes in the probability of meeting the management objective (i.e. all predict $\sim 100\%$ success) for future catches as high as 100 whales (Figure 8, left panel). Regardless of the resampling scheme, the

resulting prediction is consistent across a wide range of plausible future catch levels. At greater catch levels, resampling None leads to more conservative results.

EG walrus

The results for EG walrus illustrate how alternative resampling schemes may potentially impact posterior distributions when the dataset is uninformative (Table 6). Given the reported catches, the population trajectories for EG walrus show little sensitivity to alternative resampling schemes (Figure 9, top panel). The median and 90% credibility intervals for N_{2000} are nearly identical for all three schemes. This is perhaps not unexpected because the population is estimated to be at a large fraction of K (Table 6). As expected from the bowhead analyses, the results of resampling only a subset of the life history parameters are more similar, and differ from those for resampling None. Resampling f_{max} and S_a , and (particularly) f_{max} , S_a , and a_m , are again more optimistic in terms of management-related quantities such as Q_1 . However, unlike the case for the B–C–B bowheads, the impact of the choice of resampling scheme on management-related quantities can be quite large (e.g. $\sim 50\%$ differences among schemes in the posterior median for Q_1 ; Table 6).

The posterior distributions for some of the management-related quantities are nearly identical among the three resampling schemes. For example, the posterior distribution for K is centred

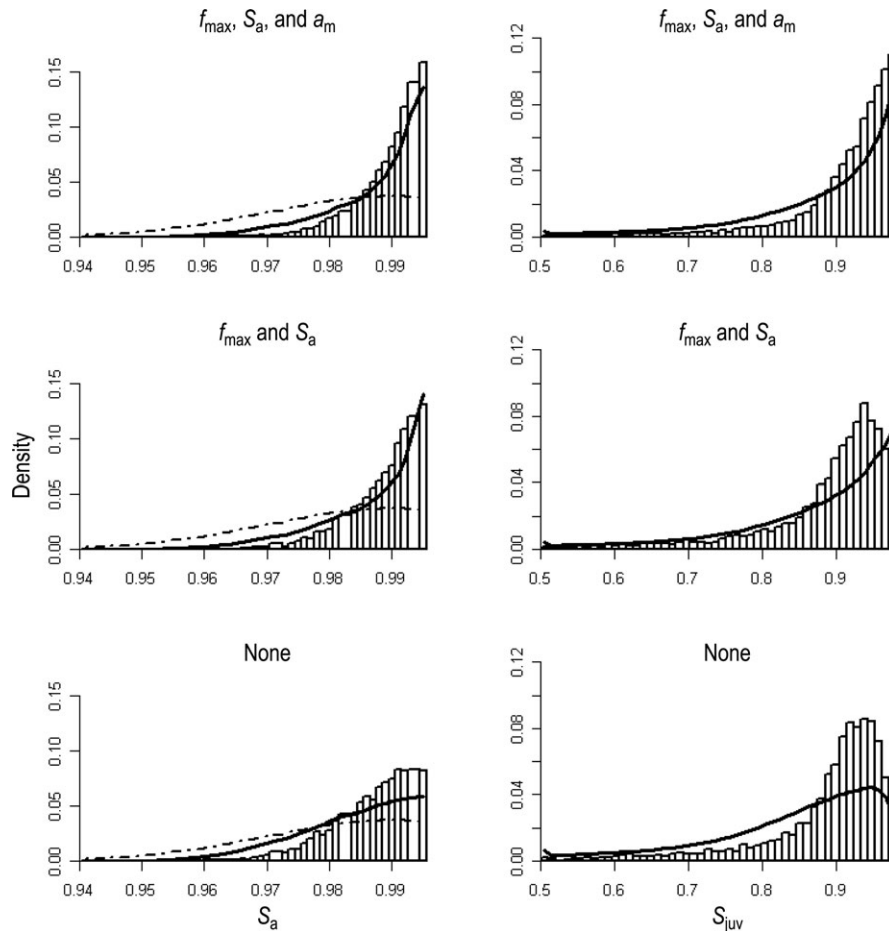


Figure 5. Explicit priors (dash-dot lines—left panels only), realized priors (solid lines), and posterior distributions (bars) for S_a and S_{juv} according to the 1978 Fwd model for the B–C–B bowhead population for three resampling schemes. Note that the ranges of the x-axes differ between parameters.

around 1000 (slightly higher for None) and skewed to the right, that for MSYL is very similar to its prior, and the posterior for the catch-related quantity Q_1 is skewed to the right and its median differs among resampling schemes (Table 6).

The rejection rates are similar to those for bowheads: None (60%), f_{max} and S_a (97%), and f_{max} , S_a , and a_m (97%). Again, these rates are positively correlated with the value drawn for λ_{max} . The sensitivity of the posterior distribution for λ_{max} to the choice of resampling scheme is consistent with that observed for B–C–B bowheads, although the size of the effect is much larger for E–G walrus (Table 6).

Sensitivity analyses

Figure 9 (bottom panel) shows the posterior distributions for the time trajectory of 0+ population size from the analyses in which the historical catches are increased fivefold. In contrast to the situation for the low catches on which Figure 9 (top panel) was based, the estimates of historical population size are sensitive (i.e. >20% difference in median terms) to the choice of resampling scheme. This sensitivity arises because the catches are now large enough to have reduced the population to well below its carrying capacity; in this situation, the stock's current status does depend on how productive the resource is assessed to be which, in turn, depends on λ_{max} , and hence the choice of resampling scheme.

The diverging population trajectories in recent years among resampling schemes for the analyses based on the higher catches (Figure 9, bottom panel) are notable. This pattern is much more pronounced than that for B–C–B bowheads (Figure 7, bottom panel) and has implications for management advice. Therefore, it is not surprising that the results of the risk analysis (e.g. calculating the probability of achieving a management objective given different levels of catch) are also sensitive to the choice of resampling scheme, even when the analyses are based on the reported (rather than increased) catches. Again, resampling None leads to more conservative results (Figure 8, right panel).

Discussion

The sensitivity analyses suggest that the choice of resampling scheme for implementing the constraint $S_{juv} < S_a$ can impact the results of stock assessments and hence the scientific management advice arising from such assessments. In particular, resampling f_{max} , S_a , and a_m to achieve a near-uniform realized prior distribution for λ_{max} consistently leads to more optimistic results given the ranges of the prior distributions considered here (which are representative of many marine mammal populations). The effect can be marked in cases for which the data are uninformative. This is an example of a well-known property

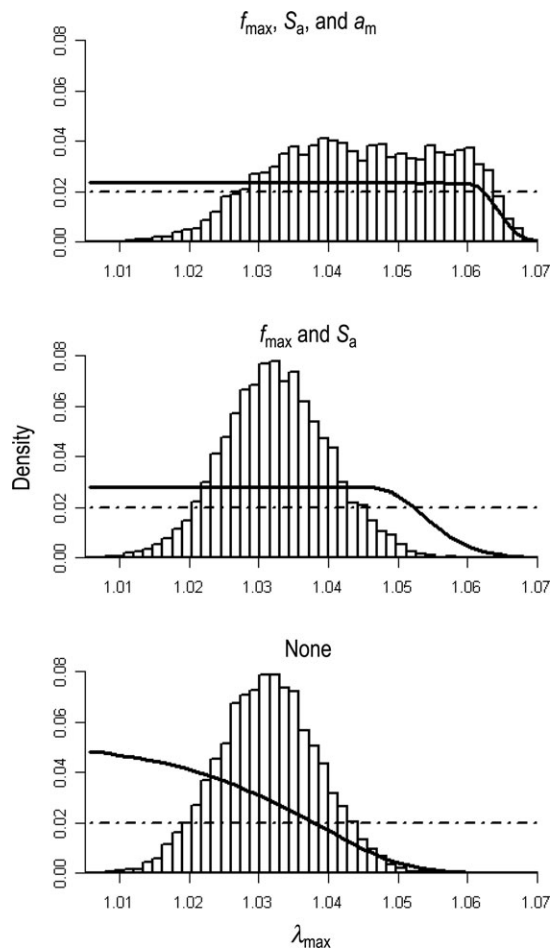


Figure 6. Explicit priors (dash-dot lines), realized priors (solid lines), and posterior distributions (bars) for the intrinsic rate of growth λ_{max} according to the 1978 Fwd model for the B–C–B bowhead population for three resampling schemes.

of Bayesian analyses: when the information content in the likelihood is low, the prior will dominate the resulting posterior.

It is of note that the realized prior distribution for λ_{max} when resampling life history parameters assigns greater prior probability to large values. It is also well known that there are fewer combinations of parameter values for which $S_{juv} < S_a$ when the intrinsic rate of growth is high (Figure 1; Punt and Butterworth, 2000), explaining the discrepancy in rejection rates between resampling schemes (Tables 5 and 6) and the correlation between rejection rates and λ_{max} . The scheme (None) that does not retain the original value drawn from the prior for λ_{max} to find a feasible solution for S_{juv} is assigning greater prior probability to low values for the intrinsic rate of growth. This is because the other two resampling schemes continue to resample the life history parameters when the intrinsic rate of growth is high—in order to sample that part of parameter space that satisfies the constraint on S_{juv} —but are not having to do this when the intrinsic rate of growth is low.

In essence, resampling schemes are a way of re-weighting marginal priors. The issue is whether one considers the fact that there is less feasible parameter space for larger values of λ_{max} , means that larger values are less likely. Resampling None accepts with equal weight all points of parameter space which respect biological realism. The other extreme is to resample values for all life

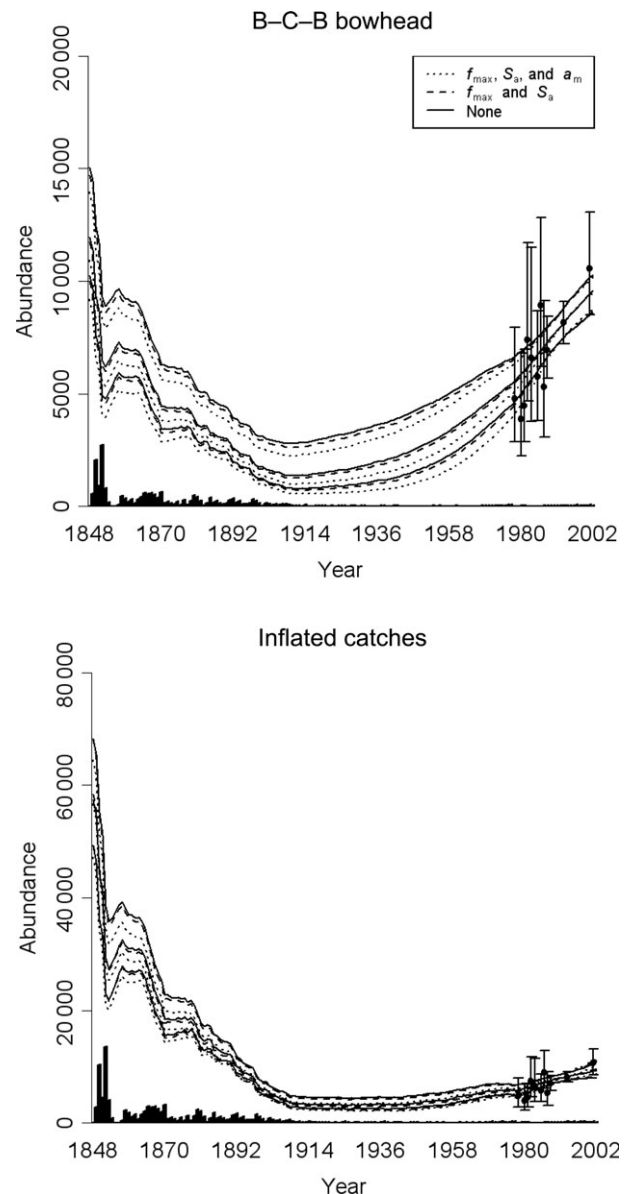


Figure 7. Time trajectories of 1+ abundance (medians and 90% credibility intervals) for the B–C–B bowhead population when the reported catch history is used (top panel), and when the inflated catch history is used (bottom panel). Note the ranges are different for each y-axis. Catches are plotted along the x-axes. Abundance estimates are shown with error bars representing 90% CI.

history parameters, which to the maximum extent possible maintains the prior on λ_{max} . This approach basically ignores the drop in feasible parameter space for larger values of λ_{max} , and appears (for the cases investigated here) to lead to the least conservative outcome.

These schemes (except resampling only f_{max} and S_a) have been employed at one time or another during recent assessments of marine mammals: Punt and Butterworth (1999) based their analyses on resampling None, and Wade (2002) resampled f_{max} , S_a , and a_m . The choice among resampling schemes depends on several factors. The realized prior distributions for the intrinsic rate of growth are nearly uniform when f_{max} , S_a , and a_m , or f_{max}

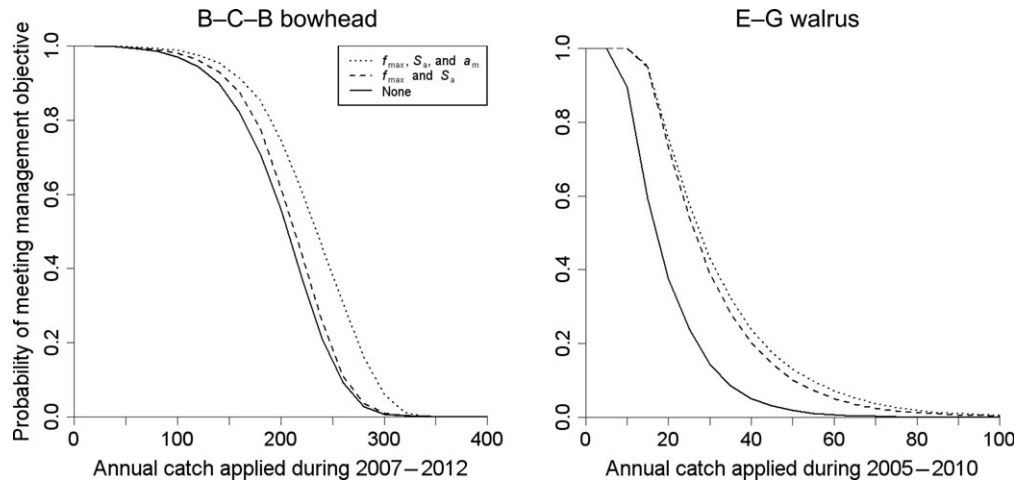


Figure 8. The probability of meeting the management objective selected by Witting and Born (2005) for each alternative resampling scheme as a function of constant future catch for B–C–B bowhead (left panel) and EG walrus (right panel). Probabilities are shown for each analysis using the reported catch history.

and S_a , are resampled (Figure 6). Such distributions are therefore more consistent with the intended prior for λ_{max} . Choosing a resampling scheme that maintains a near-uniform prior on λ_{max} is defensible if it is believed that the resampled life history parameters are essentially nuisance parameters, recognizing that the status of a population depends critically on the value of the parameter that determines productivity, which is λ_{max} in these models. Such an alternative might be appealing, if, for example, there is limited prior information on life history parameters, and instead there exist a precise series of abundance estimates over a relatively long period. In fact, this approach appears to provide a better fit to recent abundance estimates for the B–C–B bowhead stock (Figure 2).

This study was originally motivated by a desire to ensure that, based on the results of recent stock assessments (e.g. Brandon and Wade, 2006), current aboriginal quotas for the B–C–B bowhead whale are well-founded and sustainable. We emphasize here that this is certainly the case. However, the B–C–B bowhead whale is one of the most well-studied populations of marine mammal in the world, so its stock assessments are exceptionally data-rich, the exception rather than the rule. As we have shown, there are other populations of marine mammals for which these issues are an important consideration.

It is not our intention that the results presented here for E–G walrus are directly comparable with those of Witting and Born (2005). The selectivity ogive assumed here for E–G walrus is probably oversimplified (certainly different), and likewise, we explore a catch series that is five times the reported (or estimated) values, purely to illustrate the potential sensitivity of these results. Although the increase in catches is obviously exaggerated, there is undoubtedly considerable uncertainty in the catch history (e.g. Witting and Born, 2005, explore a struck and lost rate of up to 25%). It is of note that the estimates of the quantity Q_1 for bowheads are only moderately sensitive to the inflated catch history (Table 5). This result is consistent with previous analyses which show that, given uncertainty or bias in the catch record before 1915, abundance estimates from survey data are the dominant influence on the posterior distributions for quantities related to management (Givens and Thompson, 1996; Givens, 1999).

We have attempted to apply the methods explored here to both case studies consistently. However, it is not practical to use the “forwards from recent” modelling approach for E–G walrus. There are insufficient data from which to specify independently a prior on recent abundance for this stock and hence to fit a population trajectory. If this technique had been used to estimate management quantities for E–G walrus, the results would have been even more

Table 6. Posterior medians [5th, 95th percentiles] for five management-related quantities for EG walrus based on reported and inflated catches.

Model and resampling scheme	N_{2000}	K	N_{2000}/K	λ_{max}	Q_1
Reported catches					
f_{max} , S_a , and a_m	1 011 [613, 1 814]	1 067 [661, 1 786]	0.98 [0.56, 1.00]	1.059 [1.015, 1.103]	21 [8, 61]
f_{max} and S_a	1 022 [619, 1 787]	1 082 [681, 1 779]	0.98 [0.55, 1.00]	1.053 [1.015, 1.096]	19 [8, 55]
None	1 036 [624, 1 805]	1 176 [751, 1 838]	0.91 [0.48, 1.00]	1.033 [1.012, 1.073]	14 [6, 38]
Inflated catches					
f_{max} , S_a , and a_m	1 335 [715, 2 361]	3 680 [2 503, 5 906]	0.31 [0.12, 0.72]	1.059 [1.015, 1.103]	50 [10, 122]
f_{max} and S_a	1 312 [701, 2 281]	3 852 [2 627, 5 955]	0.29 [0.12, 0.66]	1.053 [1.015, 1.096]	44 [10, 115]
None	1 208 [654, 2 137]	4 575 [3 072, 6 263]	0.22 [0.10, 0.50]	1.033 [1.012, 1.073]	27 [8, 84]

Rejection rates: None (60%); f_{max} and S_a (97%); f_{max} , S_a , and a_m (97%). These rates are identical between catch histories.

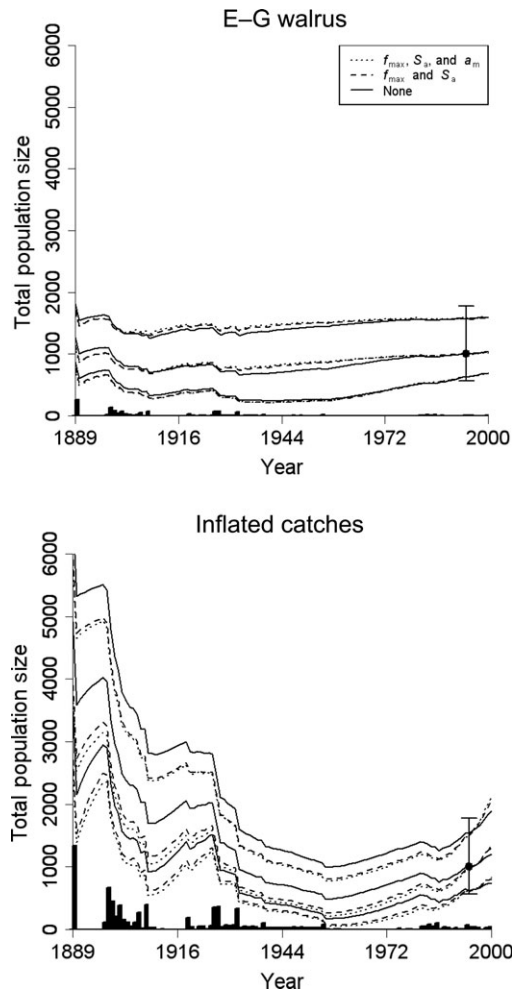


Figure 9. Time trajectories of 0+ population size (medians and 90% credibility intervals) for the EG walrus population when the reported catch history is used (top panel), and when the inflated catch history is used (bottom panel). Catches are plotted along the x-axes. The mean of the prior for 1995 abundance (0+) is shown with error bars delimiting the 90th percentiles for the sampling distribution.

sensitive to the specification of priors than was the case for the backwards method. Another difference between the case studies is the prior chosen for λ_{max} . However, both are uniform, with an upper bound chosen to coincide with the realized upper bound dictated by the constraint on S_{juv} (Figure 1). Although different, the upper bounds do not constrain the results, but they do make numerical integration more efficient. The method investigated here is perhaps the most common approach to constructing a coherent prior for marine mammals in recent years, largely based on assessments performed for the IWC. The consistent methodology allows for comparison between a data-rich and a data-poor scenario, highlighting the sensitivity of data-poor scenarios to an easily overlooked aspect of constructing a coherent joint prior while respecting biological realism.

The degree of sensitivity between data-rich and data-poor scenarios is well illustrated by the results of the risk analyses, which are based on the reported catch history. A future catch of 100 bowheads (a catch larger than the current catch) would lead one to predict a consistent ~100% chance of meeting the management objective, regardless of the resampling scheme used

(Figure 8, left panel). In contrast, there are large differences in the probability of meeting the management objective for EG walrus, depending on which resampling scheme is used to construct a coherent joint prior while applying the constraint on juvenile survival (Figure 8, right panel). For example, given an annual catch of 15 animals, resampling None indicates that the management objective will be met with only a 60% probability, whereas resampling f_{max} and S_a (and a_m) would lead one to predict a greater than 90% probability. If the technique examined here, solving for a free parameter, is to be used to construct a coherent joint prior given a biological constraint, we recommend exploring different resampling schemes during the initial phase of the stock assessment to determine the sensitivity of the results to this choice. Given the results of these analyses, it seems that two coherent joint priors that respect biological realism could be constructed and the assessment run twice, resampling f_{max} , S_a , and a_m , or resampling None. This amounts to a sensitivity analysis to alternative joint priors. These two schemes are likely to bracket intermediately conservative weightings of the marginals. If the results are not consistent between these two schemes, then some consideration should be given to the sensitivity of the assessment results to the priors. We emphasize this recommendation for data-poor stock assessments.

Alternative approaches are available to construct a coherent joint prior distribution. For example, a variant of the technique explored here was used by Witting and Born (2005). They imposed a joint prior distribution on (S_{juv}, S_a) , with S_{juv} conditional on S_a such that values of S_{juv} greater than S_a were set equal to S_a . Then, given values of the life history parameters from the prior, they solved for the productivity parameter MSYR [the population growth rate (population growth rate in this discussion corresponds to a percentage, e.g. a growth rate of $0.04 = 4\%$ growth, whereas λ_{max} is conventionally described as the population multiplier, e.g. 1.04) at MSY]. Such an approach is appealing if there is good prior information on life history, but not population growth rate. Indeed, walrus populations are an example of this: there exist reliable measurements of life history parameters (e.g. fecundity and age-at-maturity), but accurate surveys of abundance have proven elusive. Solving for MSYR will more closely maintain the explicit priors on life history parameters, for which there is a greater degree of confidence.

Solving for the intrinsic population growth rate analytically (instead of a life history parameter) does not circumvent biologically impossible solutions (e.g. $\lambda_{max} < 1.0$). Goodman (1984) clearly demonstrated this fact using Monte Carlo simulation with life history parameters for the spotted dolphin (*Stenella attenuata*). Witting and Born (2005) rejected a parameter set (i.e. resampled None of the parameters) when they arrived at a solution for the maximum population growth rate that was negative. It is just as conceivable to resample only a subset of life history parameters until a feasible solution for population growth rate is obtained. This approach would result in certain realized priors on life history parameters being more consistent with their intended distributions.

Obviously, the population growth rate is an extremely influential parameter with regards to model outputs important to management. However, if this parameter is solved for analytically to construct a coherent joint prior, it must be recognized that the resulting implicit prior will be sensitive to the limits placed on the priors for the life history parameters. For instance, given uniform priors on all life history parameters, the resulting implicit

prior distribution for population growth rate will be bell-shaped, with a mean and variance that shifts according to the upper and lower limits of the uniform priors for life history parameters (cf. Figure 1 of Goodman, 1984). Hence, while very little is often known about certain life history parameters, the range for which such ignorance is bounded may be more informative than desired. For example, the resulting implicit prior distribution for the intrinsic population growth rate will differ substantially (all else being equal) between priors for $S_{\text{juv}} \sim U[0.70, 0.90]$ or $\sim U[0.10, 0.90]$. This sensitivity is likely to be unsatisfactory.

If a life history parameter is solved for, then the prior distribution on population growth rate, or at least its upper bounds, could be based on a meta-analysis for related species for which there exist trend data from populations recovering from depletion (e.g. Best, 1993). Unfortunately, reliable trend information does not exist for most walrus populations. However, it is worth noting that the constraint on juvenile survival rate, in concert with the ranges of other life history parameters, is what effectively imposes the upper bound on the realized prior for λ_{max} (Figure 1). Therefore, any uniform prior on λ_{max} will lead to the same results, as long as the upper bound on the explicit prior provides support up to those values for λ_{max} beyond which there is zero realized prior probability. Following the prior distributions for life history parameters used by Witting and Born (2005), we chose a suitable upper limit for EG walrus, $\lambda_{\text{max}} = 1.12$. It is clear from the values for the upper 95th percentiles of the posteriors for this parameter (Table 6) that the upper bound on this prior does not constrain the results for the stock.

Setting one parameter to be calculated, given values from the priors of the remaining parameters, ignores potential information. In certain cases, this might be justifiable (e.g. given a lack of knowledge of juvenile survival). However, there are other methods for constructing a coherent joint prior while retaining explicit prior distributions on all inputs (and outputs). Poole and Raftery (2000) extend Bayesian synthesis to include logarithmic pooling of priors (French, 1985; Genest and Zidek, 1986). This technique, termed Bayesian melding, provides a coherent joint prior on model inputs and outputs and is not subject to Borel's paradox. To our knowledge, this method has only been applied to an age-aggregated surplus production model for the B–C–B stock of bowhead whale (Givens and Roback, 1999; Poole and Raftery, 2000). It remains to be seen how a biological constraint like $S_{\text{juv}} < S_a$ could be implemented using Bayesian melding with an age-structured PDM. Moreover, it is not obvious how any approach can escape the necessity of resampling (or not) parameter values given that parts of the prior space violate biological realism.

Ideally, whatever method is used to construct a coherent joint prior, an explicit correlation structure between the parameters is involved, given observed and hypothesized relationships among model parameters (e.g. between fecundity and adult survival). However, completely specifying a joint prior distribution with explicit correlations among the parameters is a complex endeavour for age-structured PDMs. It is interesting that implementing the constraint on juvenile survival imposes a correlation structure among the parameters (Figure 10; Punt and Butterworth, 1999), and this is probably an improvement over a naive assumption of independence.

In addition to incorporating correlations between life history parameters, it is desirable that the method used to construct the prior should change the explicit marginal priors as little as

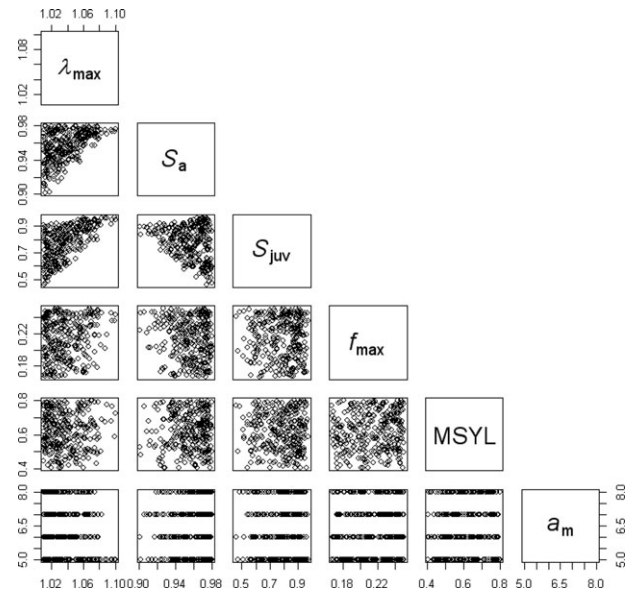


Figure 10. Bivariate scatterplots of parameter values from the coherent joint prior achieved by the resampling scheme None for EG walrus.

possible. However, it is apparent that resampling (or not) updates the explicit marginal priors, resulting in different realized marginal priors. Further, different resampling schemes change the marginals of the parameters differently. For example, compare the explicit and realized marginals for B–C–B bowhead S_a and λ_{max} (Figures 5 and 6). Radke *et al.* (2002), in an example from another field of natural resource modelling, achieve a coherent joint prior distribution using Bayesian melding (via SIR), while explicitly incorporating rank correlations among input parameters (Iman and Conover, 1982; Guan, 2000). The method is analogous to a “normal copula” (e.g. Wang, 1999), which induces a target correlation structure between parameters while retaining the explicit marginal priors. We tested this approach, but it does not appear to be a valid substitution for the constraint on S_{juv} (at least for the cases investigated in our analyses). However, application of a copula before resampling could reduce the rejection rate, so this methodology deserves consideration in future research.

It seems certain that the number of assessments using similar Bayesian methods will increase in future. Our objective is not to advocate a single best approach for constructing a coherent joint prior while respecting biological realism. However, as we have shown, Bayesian inference based on assessment scenarios for which data are limited is likely to be sensitive to the issues explored here. Likewise, these issues are also relevant to other long-lived marine taxa, for which similar biological assumptions, PDMs, and assessment methodologies are appealing, but time-series of abundance and anthropogenic mortality are likely to be limited and imprecise (e.g. some seabirds, sharks, and sea turtles).

Acknowledgements

Support for JRB was provided during the course of this research by MMS, NOAA/NMFS, and an NMFS–Sea Grant Fellowship in population dynamics. Matthew Alford, Jaime Kelso, and Jeremy Sterling are thanked for providing support at certain points, as well as participating in the exploration of some areas which would still be around the corner otherwise. An anonymous

reviewer suggested copulas and Janna Wemmer inspired JRB to make a connection on that subject. Thanks also to Sonja Kromman at the NMML library for valuable help attaining reference material, to Eric Ward for patience in the computing laboratory, and the Punt Laboratory at the University of Washington for necessary computing and intellectual support. Judy Zeh stimulated thought on this subject. Comments from Geoff Givens during an IWC Scientific Committee meeting enhanced an earlier draft of the work. We especially thank Doug Butterworth, Lars Witting, and an anonymous referee for reviews that substantially improved the paper. However, the views presented here should not be taken to be other than those of the authors.

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