Assessment of BCB bowheads: including estimates of calf production and environmental stochasticity

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ABSTRACT

A stochastic population dynamics model for the BCB bowhead whales which keeps track of the reproductive stage of females is developed. This model is fitted to a variety of data sources, including estimates of total (1+) abundance, the fraction of calves based on aerial surveys, and a potential index of deviations in birth rates (sea-ice on the eastern Beaufort Sea feeding grounds) using penalized maximum likelihood. The results from the extended assessment are compared with analyses which mimic those on which previous assessments have been based. All model configurations fit the abundance data well. However, only the stochastic models are able to mimic the inter-annual changes in the proportion of calves adequately. Although currently preliminary, this model framework could be extended and used as the basis to evaluate some of the potential impacts of climate change of the dynamics of the BCB bowhead whales, and hence the performance of the Bowhead *SLA*.

KEYWORDS: BIRTH RATE; BOWHEAD WHALE; ICE; MODELLING; NORTHERN HEMISPHERE; WHALING – ABORIGINAL

INTRODUCTION

The Bering-Chukchi-Beaufort Seas (BCB) stock of bowhead whales was severely depleted by commercial hunting during the late 1800's, but the current trend in abundance estimates indicates that the population has been growing at a steady rate (George *et al.*, 2004) and recent assessments based on historic catch records suggest that abundance may be approaching pre-exploitation levels (e.g., Brandon and Wade, 2006). Aboriginal subsistence hunting currently occurs during the spring and fall migrations (between wintering and feeding grounds in the Bering and eastern Beaufort Seas, respectively), with the majority of catches taken off the coast of Barrow, Alaska. The most recent ice-based survey estimate of stock size in 2001 is about 10,000 animals (Zeh and Punt, 2005) and recent catches are on the order of 40-70 individuals per year, under quotas based on the *Bowhead Strike Limit Algorithm* (*SLA*) of the IWC (IWC, 2003).

Bowheads are the only baleen whales which spend their entire life in the Arctic seas, where the effects of global warming are expected to be pronounced (IPCC, 2007). Therefore, they are ranked as one of the arctic marine mammals most susceptible to the impacts of climate change (Laidre *et al*., 2008). Moore and Laidre (2006) provide an analysis of trends in sea-ice for BCB bowhead habitat and a conceptual model for how future changes in sea-ice might impact the population. Further, George *et al.* (2005) have found some evidence that the body condition of animals killed in the hunt may be related to sea-ice conditions in the eastern Beaufort Sea, an important feeding ground in the fall (Ljungblad *et al.*, 1986). Those findings are consistent with the conceptual model of Moore and Laidre (2006); less sea-ice appears to have a beneficial effect on body condition, presumably through increases in prey availability and/or abundance. Although the potential mechanisms are not well understood in either case, a similar pattern has

hypothesized for eastern North Pacific (ENP) gray whales, where calf production appears to be related to sea-ice conditions on the feeding grounds during the previous year (Perryman *et al*., 2002).

Under the Aboriginal Whaling Management Procedure (AWMP) of the IWC, the Bowhead *SLA* is scheduled for regular *Implementation Reviews* to re-examine the current state of knowledge about this stock and hence assess the adequacy of the *Bowhead SLA* (and the simulation trials used to evaluate the ability of candidate *SLA*s to achieve the management objectives for the BCB bowhead whales) in light of any new information (IWC, 2003). As research continues on the effects of environmental variability on bowhead population dynamics and new information becomes available on sea-ice loss in the Arctic, it is likely that future *Implementation Reviews* will need to consider whether such information means that the set of plausible hypothesis on which the trials used to develop the *Bowhead SLA* remain appropriate or whether these need to be revised.

Therefore, we provide a stochastic population dynamics modeling framework which is able to incorporate recent estimates of calf production from aerial surveys (Koski *et al*., 2008) and an index of sea-ice on the eastern Beaufort Sea feeding grounds (Moore and Laidre, 2006). The modeling framework differs from previous stochastic models applied to this stock (e.g., Poole and Givens, 2001; IWC, 2003) in that the model developed here explicitly keeps track of the numbers of females in each reproductive stage in a given year. Calf production is then a product of the stochastic birth rate and the number of surviving receptive females (as opposed to assuming that all reproductive females are able to give birth in a given year). Additionally, the framework allows the observations of sea-ice to be related to the deviations in the process error in birth rates.

While development is preliminary at this stage, we anticipate that this framework can potentially form the foundation for an operating model with which to test the performance of the *Bowhead SLA*, given global climate model forecasts of sea-ice on the feeding grounds or other potentially important indices of environmental variability, and hypotheses regarding their influences on population dynamics.

METHODS

Population dynamics model

The analyses were based on a sex- and age-structured population dynamics model with an annual time-step. The model included stochastic birth rates and explicitly considered the transition between receptive, resting and calving stages for mature females (Fig. 1). The total number of animals in the population was consequently divided into the number of males by age and year $N_{a,t}^{male}$, the number of immature females by age and year $N_{a,t}^{i}$, the number of reproductively receptive females by year N_t^r, the number of reproductively resting females by year N_t^R ,and the number of cows with calves by year N_t^c (the age-structure of receptive, resting and calving females was not tracked explicitly because all such animals were aged equal to the plus-group age or older).

Density dependence
Density dependence was assumed to act through the birth rate[1] according to the Pella-Tomlinson model:

$$b_t = \max\left\{0,\ b_{\text{eq}} + (b_{\max} - b_{\text{eq}})\left[1 - \left(\frac{N_{1+,t}}{K_{1+}}\right)^z\right]\right\} \tag{1}$$

where:

$b_{\max}$ is the maximum birth rate (in the limit of zero population size);

K_{1+} is the carrying capacity of the 1+ component of the population (all animals aged 1 yr and older);

b_{eq} is the equilibrium birth rate at carrying capacity;

z is the degree of density-dependent compensation (assumed to equal 2.39, which implies maximum sustainable yield at population density approximately 60% of K_{1+}), and;

$N_{1+,t}$ is the size of the 1+ component of the population (both sexes combined) in year *t*.

Stochastic birth rates
Birth rates varied annually about the deterministic value given by Eqn. 1. Since this rate must lie between zero and one, its realization in any one year was calculated using a logistic transformation:

$$b_t^* = \left[1 + \exp(-(\Phi^{-1}(b_t)\sqrt{2.76 + \sigma_\varepsilon^2} + \varepsilon_t))\right]^{-1} \tag{2}$$

where:

Φ^{-1} is the inverse standard normal cumulative distribution function;

ε_t is the process error deviation for year *t*, such that $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$, and;

σ_ε is a measure of the extent of variability in the process error.

This formulation of stochastic birth rates ensured that the expected birth rate in a given year was equal to the deterministic value from Eqn. 1 (Brandon and Punt, 2009). This transformation leads to a realized standard deviation $`\sigma_\varepsilon$ (taken across years) of the process error deviations that is less than $\sigma_\varepsilon$ (Punt, 2008). Therefore, the realized standard deviation $`\sigma_\varepsilon$ was also calculated for comparison.

[1] This is really the rate at which receptive females successfully conceive and then survive with calf to be counted during the aerial surveys. Therefore, this is rate will be less than the true birth rate due to early calf mortality, and even more so less than pregnancy rates due to the combined effects of prenatal mortality. Also note that, a constant birth rate of 1.0 corresponds with roughly one-third of mature females having a calf in any given year, due the structure of the population dynamics model.

Female dynamics

The number of immature females by age depended on the number of births, an assumed 50:50 sex ratio at birth, maturation, and mortality from natural causes and hunting:

$$N^{i}_{a,t+1} = \begin{cases} 0.5N^{c}_{t+1} & \text{if } a = 0 \\ N^{i}_{a-1,t} S_{a-1,t} \left(1 - E^{fem}_{t} V_{a-1}\right) & \text{if } 1 \le a \le 19 \end{cases} \tag{3}$$

where:

E^{fem}_{t} is the exploitation rate during year *t* on females:

$$E^{fem}_{t} = C^{fem}_{t} / \left(N^{r}_{t} + N^{R}_{t} + N^{c}_{t} + \sum_{a} V_{a} N^{i}_{a,t} \right) \tag{4}$$

V_a is the selectivity on animals of age *a*, assumed to be constant with regard to sex and time, and uniform on ages 1+, following the approach of previous assessments (e.g., Brandon and Wade, 2006):

$$V_{a} = \begin{cases} 0 & \text{if } a < 1 \\ 1 & \text{if } a \ge 1 \end{cases} \tag{5}$$

C^{fem}_{t} is the total catch of females during year *t*.

This formulation assumed that selectivity was the same for all animals of a given age, and was independent of sex, time, and reproductive condition. Maturity was assumed to be knife-edged at age 19 (i.e. all females reached the age at first estrous at age 19). The plus-group age (denoted as age *x*) was set equal to the assumed age at maturity, so there was no need to implement a plus group for the immature stage. The gestation period was assumed to be one year, so the age at first possible parturition was age 20, which was equivalent to the median of the prior distribution for this life history parameter adopted in previous assessments (IWC, 1995; Brandon and Wade, 2006).

The number of resting, receptive and calving females are given by:

$$N^{R}_{t+1} = S_{4+,t} N^{c}_{t} \left(1 - E^{fem}_{t} V_{1+}\right) \tag{6}$$

$$N^{r}_{t+1} = S_{4+,t} \left[\left(1 - b^{*}_{t}\right) \left(N^{i}_{19,t} + N^{r}_{t} \right) + N^{c}_{t} + N^{R}_{t} \right] \left(1 - E^{fem}_{t} V_{1+}\right) \tag{7}$$

$$N^{c}_{t+1} = S_{4+,t} b^{*}_{t} \left(N^{i}_{19,t} + N^{r}_{t} \right) \left(1 - E^{fem}_{t} V_{1+}\right) \tag{8}$$

Male dynamics
Males were modeled using an age-structured model that ignored maturity because the number of males was assumed not to be a limiting factor for female reproductive success:

$$N_{a,t+1}^{\text{male}} = \begin{cases} 0.5N_{t+1}^{c} & \text{if } a = 0 \\ N_{a-1,t}^{\text{male}} S_{a-1,t}\left(1 - E_t^{\text{male}} V_{a-1}\right) & \text{if } 1 \le a < x \\ S_{4+,t}\left(1 - E_t^{\text{male}} V_{1+}\right)\left(N_{19,t}^{\text{male}} + N_{x,t}^{\text{male}}\right) & \text{if } a = x \end{cases} \quad (9)$$

where:
E_t^{male} is the exploitation rate during year *t* on males:

$$E_t^{male} = C_t^{male} / \sum_a V_a N_{a,t}^{male} \quad (10)$$

C_t^{male} is the total catch of males during year *t*.

Initial conditions
Population trajectories were initiated in 1848, under the assumption of a stable-age-distribution and no hunting mortality. A numbers-per-female-calf (i.e., numbers-per-recruit) approach was taken to solve for the numbers-at-age in 1848 given values for the life-history parameters of the model, and the assumption that the population was at pre-exploitation equilibrium in 1848. The number of females per calf is given by:

$$NPR_a = \begin{cases} 0.5 & \text{if } a = 0 \\ NPR_{a-1} S_{a-1} & \text{if } 1 \le a < x \\ NPR_x S_{4+} \big/ \left(1 - S_{4+}\right) & \text{if } a = x \end{cases} \quad (11)$$

The birth rate at unexploited equilibrium b_{eq} is the inverse of the number of receptive females per-calf which can give birth. Since the maturity ogive was assumed to be knife-edged and the age at first parturition was assumed equal to the age at which individuals entered the plus group, the number of mature females-per-calf was NPR_x. Given this, and that the number of calves is 1, b_{eq} is the reciprocal of the number of mature females $NPR_x - 1$, i.e.

$$b_{eq} = \left(NPR_x - 1\right)^{-1} \quad (12)$$

The age- and sex-structure at the start of the 1848 was then calculated by scaling the numbers-per-calf by K_{1+}. The numbers–at-age of each sex in 1848 was then the total numbers-at-age divided by two. The numbers of calving females at equilibrium equaled

the product of the equilibrium birth rate and the numbers of mature females at equilibrium. The numbers of resting females was assumed to equal the number of calving females, and the numbers receptive was then calculated as the remainder of the numbers mature which were not calving or resting. These assumptions resulted in numbers at stage that approximated the equilibrium stage structure.

Data and likelihood function

Three sources of data were considered when fitting the model: (1) estimates of population size during 1978-2001 from the spring surveys at Point Barrow, AK (Zeh and Punt, 2005)(Table 1); (2) estimates of calf production (percentage calves in the population) during 1985-2004 from aerial surveys (Koski *et al*., 2009)(Table 2); and (3) estimated fraction of open water in the eastern Beaufort Sea in September during 1979-2002 (data not available for 1987) (Moore and Laidre, 2006) (Fig. 2, left panel).

Annual catches were available from 1848-2007 (Fig. 2, right panel). The catch records used by Brandon and Wade (2006) were also used here, except for those for 1985-2007. The updated catches from these more recent years were obtained from the IWC website[2]. Selectivity-at-age resulting in the observed catches was treated as known (knife-edge and uniform on 1+). Hence no attempt was made to fit the catch data. Instead, catches were simply subtracted from the population each year according to the assumed selectivity ogive.

The negative of the logarithm of the likelihood function was the sum of the contributions for each data source. Trajectories resulting in extinction were assigned zero likelihood. Previous studies using similar, but not identical ways of including process error in the population dynamics have assigned values for σ_ε using an approach which relies on the convergence of the root-mean-squared-error between the logarithms of expected vs. observed recruitment (Methot, 2000; Brandon *et al.*, 2007). However, this approach is not suitable given the transformation applied here (Equation 2). Instead, a default value for σ_ε of 0.50 was used for the base case scenarios, following the analyses of Brandon and Punt (2009), which suggested that this value was consistent with observed inter-annual variability in ENP gray whale data. Analyses were also conducted in which σ_ε = 0.30 and 0.60 to assess the sensitivity of the results to the value assumed for σ_ε (Table 3).

Abundance estimates

The abundance estimates were assumed to be indices of the 1+ component of the population. The estimate from 1993 was assumed to be independent of the other years, and the residuals of the model fits to this year were assumed to be normally distributed. Hence the negative log-likelihood component for this abundance estimate is[3]:

$$L_1 = 0.5\frac{\left(N_{1+,1993} - 8167\right)^2}{580^2} \tag{13}$$

[2] http://www.iwcoffice.co.uk/conservation/table_aboriginal.htm

[3] The likelihood components were calculated ignoring constants independent of the parameters of the model.

The residuals of the model fit to the remaining abundance estimates were assumed to be correlated among years and log-normally distributed (Zeh and Punt, 2005). These assumptions led to the following component of the negative log-likelihood function:

$$L_2 = 0.5\sum_{t_1}\sum_{t_2}\left(\ln N_{1+,t_1}^{\text{obs}} - \ln N_{1+,t_1}\right)^T \Sigma_{t_1,t2}^{-1}\left(\ln N_{1+,t2}^{\text{obs}} - \ln N_{1+,t2}\right) \tag{14}$$

where:

$N_{1+,t}^{\text{obs}}$ is the survey estimate of 1+ abundance for year *t*;

$N_{1+,t}$ is the model estimate of 1+ abundance for year *t*; and

Σ^{-1} is the inverse of the variance-covariance matrix for the logarithms of the abundance estimates (excluding 1993).

Calf estimates

The residuals about the model fit to the estimate of the proportion of calves in the population were also assumed to be independent and identically normally distributed. This approach led to the following component of the negative log-likelihood function:

$$L_3 = 0.5\sum_{t}\frac{1}{\sigma_t^2}\left(p_{0,t}^{\text{obs}} - p_{0,t}\right)^2 \tag{15}$$

where:

$p_{0,t}^{\text{obs}}$ is the survey estimate of the proportion of calves in the population in year *t*;

σ_t is the standard deviation of $p_{0,t}^{\text{obs}}$, and;

$p_{0,t}$ is the model estimate of the proportion of calves in the population in year *t*:

$$p_{0,t} = N_{0,t}\left[\sum_{a=0}^{x} N_{a,t}\right]^{-1} \tag{16}$$

Environmental impact on birth rates

In addition to being subject to process error, the deviations of birth rates about the deterministic relationship each year were also allowed to be related to an environmental index I_t (in this case, the fraction of open water covering the eastern Beaufort Sea in September). It was assumed that I_t was measured subject to observation error (or there was some error in the relationship between the process error deviations and the environmental index). Consequently, I_t was treated as a state variable, like the model prediction of population size. Hence, the measurements of the environmental index were treated as data and were consequently included as a component of the likelihood function when the model was fit. The expected environmental index in a given year was assumed to be related to process error residuals for that year, such that the observed index was normally distributed about its expectation:

$$I_t^{obs} = \beta\varepsilon_t + \gamma_t \tag{17}$$

where:

I_t^{obs} is the observed value of the environmental index in year *t*;

β is a scaling parameter for the influence of the environment on the process error residuals;

γ_t is the difference between the observed and model-predicted amount of sea ice in year *t*, such that $\gamma_t \sim N(0;\sigma_I^2)$, and;

σ_I is the standard deviation of the residual error for the environmental index:

$$\sigma_I = |\beta|\,\sigma_I^* \tag{18}$$

This formulation takes a fixed input value for σ_I^* (Table 3) and scales the expected standard deviation of the fits to the environmental index by the estimated absolute value for β. Eqn. 18 leads to the desired effect of the process error deviations being more correlated with the environmental index at smaller values of σ_I.

The timing of the potential effect of sea-ice variability was allowed to be related to deviations from expected birth rates as opposed to the year prior to birth rates (i.e. a potential effect on ovulation rates). Given the estimation framework here, positive values of β correspond with less sea-ice (more open water) on the feeding grounds having a beneficial effect on birth rates (i.e., positive process error deviations).

Given these assumptions, the contribution of the environmental index to the likelihood function is:

$$L_4 = \sum_t \left[\ln(\sigma_I) + \frac{1}{2\sigma_I^2}\left(I_t^{obs} - I_t\right)^2 \right] \tag{19}$$

σ_I^* was assumed to be 0.30 for the base case scenarios, following Brandon and Punt (2009), (i.e., this value led to a reasonable balance between not over-fitting the environmental index, while still allowing for a relatively strong signal in the process error deviations for their ENP gray whale model). Analyses were also conducted for σ_I^* = 0.10 and 1.00 to assess the sensitivity of the results to the value assumed for σ_I^* (Table 3).

Parameterization and scenarios

Rather than treating all of the survival rates by age as estimable parameters, two survival rates were considered: (i) juvenile survival S_{juv} and, (ii) the survival rate for animals aged 4 and older S_{4+}. The assumed value for the age-at-transition to adult survival corresponds to the median of the prior adopted in previous assessments. Juvenile survival was not treated as an estimable parameter. Instead, the difference, Δ, between adult and juvenile survival was estimated. This also allowed the constraint that adult survival cannot be less than juvenile survival to be enforced.

Three base-case scenarios were considered: (i) a deterministic version of the population dynamics model which was only fit to the abundance data; (ii) the stochastic model described above, which was fit to the sea-ice index, and; (iii) the same model, but excluding the sea-ice data. These scenarios were fit using maximum likelihood. Additionally, sensitivity runs were performed for the stochastic models with different values for σ_I^* or σ_ε as outlined above and in Table 3.

The estimable parameters of the model were: S_{4+}; Δ; $b_{\max}$; K_{1+}, the vector of process error residuals $\underline{\varepsilon}_t$ during 1979-2008, and β (except for those scenarios with no sea-ice, for which β was not applicable).

RESULTS

The three base case scenarios (corresponding with scenarios 0 through 2 in Table 3) were generally able to fit the abundance data well (Figs. 3 and 4). However, the deterministic model (which was only fit to the abundance data) was able to capture the trend in the abundance data slightly better than the stochastic models (which were also fit to the calf data). Further, the deterministic model estimated higher survival rates, a lower value for carrying capacity and a higher current depletion (i.e., the population was estimated to be closer to carrying capacity) than any of the stochastic scenarios (Table 4; Fig. 4). In addition, the deterministic scenario estimated that the stock was more severely depleted at the nadir of abundance, following the cessation of commercial whaling in the early 1900's (Fig. 4). While the deterministic model was not fit to the calf data, there are predictions of calf production for the deterministic model; these predictions were lower than all but the two lowest observations (Fig. 3). However, the maximum birth rate was estimated to be similar across all scenarios (range = 0.25 to 0.34). The two base case stochastic models (with and without sea-ice) were both able to provide reasonable fits to the calf data (Fig. 3) and likewise, these two scenarios resulted in virtually identical estimates for model parameters and derived values (Table 4).

The estimated parameter values and derived quantities resulting from the various sensitivity scenarios (corresponding to scenarios 3 - 8 in Table 3) were also very similar across these scenarios (Table 4; Fig. 4). However, the two scenarios which investigated the affect of a smaller value for the extent of process error σ_ε=0.30, led to estimates of juvenile survival which were larger than for the other stochastic scenarios and close to that for the deterministic model. Not surprisingly, the realized value for the extent of process error `σ_ε was smaller than the input value σ_ε for all of the stochastic scenarios, although this difference was generally small. β was estimated to be positive for all scenarios except that with σ_I^*=1.0 for those stochastic scenarios with sea-ice.

DISCUSSION

We developed a stochastic population dynamics modeling framework, which takes the reproductive life history stages of female bowhead whales into account and allows for the incorporation of an environmental index which may be related to deviations in birth rates. Development of this framework for the BCB bowheads is very preliminary and is primarily useful as a means of assessing model behavior and the potential sensitivity of

the framework to alternative assumed values for the extent of process error and the influence of an environmental index on deviations in birth rates.

The hypothesis that sea-ice in the eastern Beaufort Sea is related to calf production the following year is speculative. We have presumed this relationship to demonstrate how such hypotheses can be incorporated into a population dynamics modeling framework. The assumption that environmental conditions on the feeding grounds are potentially related to reproductive success follows a conceptual model, observations of body condition and examples of this phenomenon in other baleen whales. However, given the very long-lived and slow reproductive strategy of bowhead whales, reproductive success is likely to be correlated with environmental conditions (among other factors, such as density dependence) over a period of years as opposed to a single year. Therefore, future insight into such relationships would benefit from a meta-analysis of the time series of calf estimates and some other proxy of reproductive success through biological sampling of the catch. Potential relationships between the environment and bowhead population dynamics may become better understood as research continues along these avenues and time series of reproductive success increase in length.

This framework is flexible in its ability to incorporate a range of hypotheses for how environmental variability may impact population dynamics. Given relevant forecasts of environmental variability, it is possible to extend this framework to perform future projections of population dynamics conditioned on available data for calf production and abundance, and alternative hypotheses regarding how environmental variability might affect population dynamics. The ability to condition on all available data and relatively high resolution forecasts of environmental variability (i.e., future conditions on the feeding grounds) can provide an alternative set of trials with which to test the performance of the *Bowhead SLA* given forecasts of future climate change.

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Table 3
The scenarios considered in these analyses. Different data sets and parameter values are outlined.

Scenario	Description	Abundance Data	Calf Data	Sea-Ice data	σ_ε	σ_I^*	Stochasticity
0	Deterministic	Yes	No	No	NA	NA	None (Deterministic)
1	Stochastic (sea-ice)	Yes	Yes	Yes	0.5	0.3	Environmental (sea-ice)
2	Stochastic (no sea-ice)	Yes	Yes	No	0.5	NA	Environmental (no sea-ice)
3	Stochastic (no sea-ice); σ_ε = 0.3	Yes	Yes	No	0.3	NA	Environmental (no sea-ice)
4	Stochastic (no sea-ice); σ_ε = 0.6	Yes	Yes	No	0.6	NA	Environmental (no sea-ice)
5	Stochastic (sea-ice); σ_ε = 0.3	Yes	Yes	Yes	0.3	0.3	Environmental (sea-ice)
6	Stochastic (sea-ice); σ_ε = 0.6	Yes	Yes	Yes	0.6	0.3	Environmental (sea-ice)
7	Stochastic (sea-ice); σ_I^* = 0.1	Yes	Yes	Yes	0.50	0.1	Environmental (sea-ice)
8	Stochastic (sea-ice); σ_I^* = 1.0	Yes	Yes	Yes	0.50	1.0	Environmental (sea-ice)

Table 4
Parameter estimates and other values of interest are shown for each scenario. S_{juv} is the survival rate for animals aged 0 to 3yrs (as determined by the difference in the survival rates Δ).

Scenario	Description	S_{4+}	S_{juv}	$b_{\max}$	β	$\grave{\sigma}_\varepsilon$	K_{1+}	$N_{1+,2009}/K_{1+}$
0	Deterministic	0.995	0.988	0.30	-	NA	10,933	0.94
1	Stochastic (sea-ice)	0.986	0.936	0.29	1.46	0.46	13,363	0.75
2	Stochastic (no sea-ice)	0.985	0.935	0.29	-	0.46	13,325	0.74
3	Stochastic (no sea-ice); σ_ε = 0.3	0.985	0.984	0.25	-	0.20	13,123	0.78
4	Stochastic (no sea-ice); σ_ε = 0.6	0.987	0.937	0.32	NA	0.54	12,588	0.79
5	Stochastic (sea-ice); σ_ε = 0.3	0.985	0.984	0.25	1.77	0.20	13,087	0.79
6	Stochastic (sea-ice); σ_ε = 0.6	0.986	0.936	0.34	1.26	0.59	12,517	0.82
7	Stochastic (sea-ice); σ_I^* = 0.1	0.989	0.939	0.25	1.94	0.47	13,230	0.78
8	Stochastic (sea-ice); σ_I^* = 1.0	0.986	0.936	0.27	-0.99	0.45	13,410	0.73

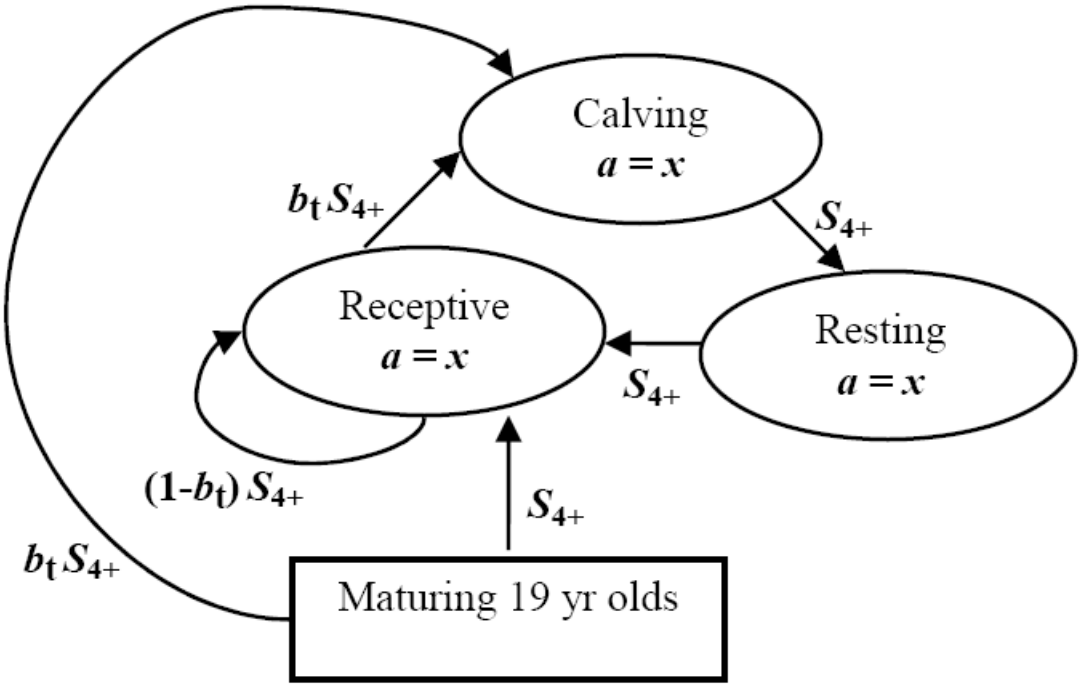

Figure 1. Life cycle graph of the model used to track the number of females in each reproductive stage though time. Note that the birth rates were modified to be stochastic for these analyses. The arrow from immature to calf arises because some juveniles may mature and give birth (i.e. become pregnant at first estrous) during the projection interval from time *t* to *t*+1. The number of calves available to be surveyed in a given year was assumed to equal the number of calving females.

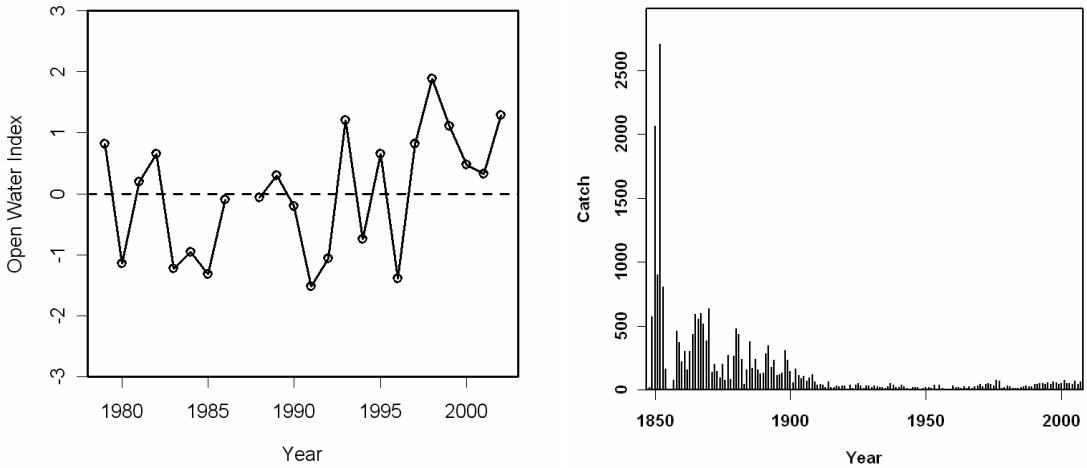

Figure 2. (Left panel) The standardized index of the fraction of open water in the eastern Beaufort Sea during September (Moore and Laidre, 2006). Note there is no data point available for 1987. Positive values represent years with greater than average open water over the time period considered. (Right panel) Catches by individuals: 1848-2007.

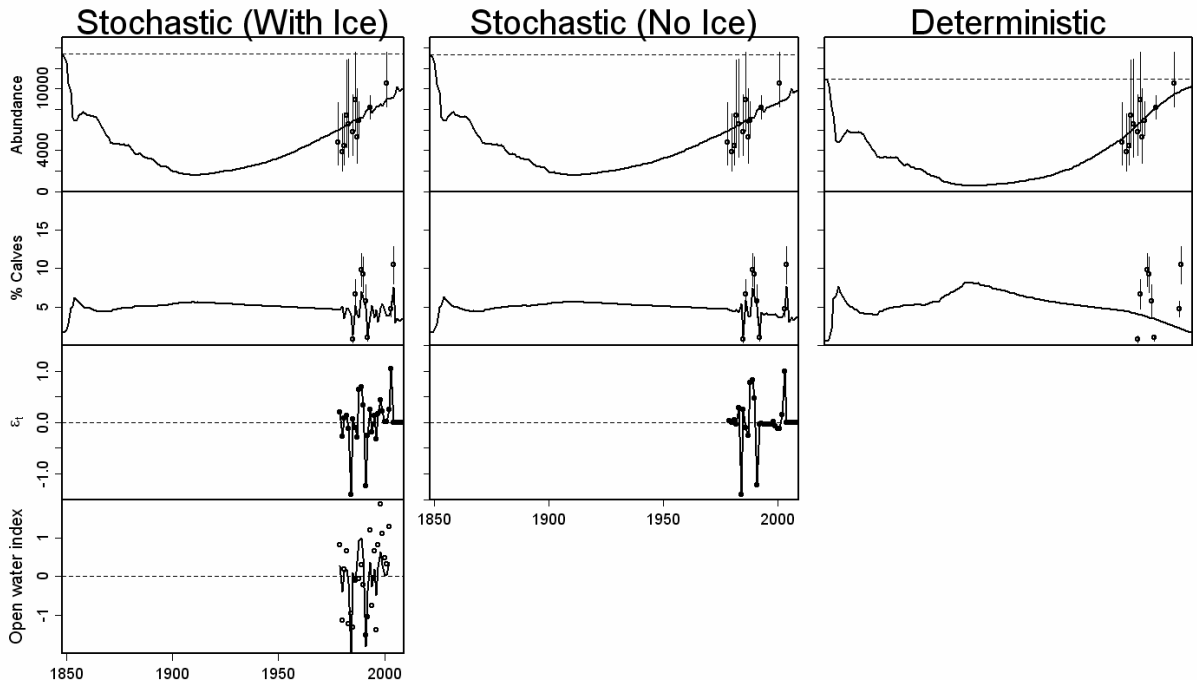

Figure 3. Plots showing model fits for the three base case scenarios. The dashed line on the abundance plots shows the estimated carrying capacity. Those on the other plots are plotted at zero for reference. The deterministic model was not fit to the calf data, but the model predictions are plotted with the data for reference.

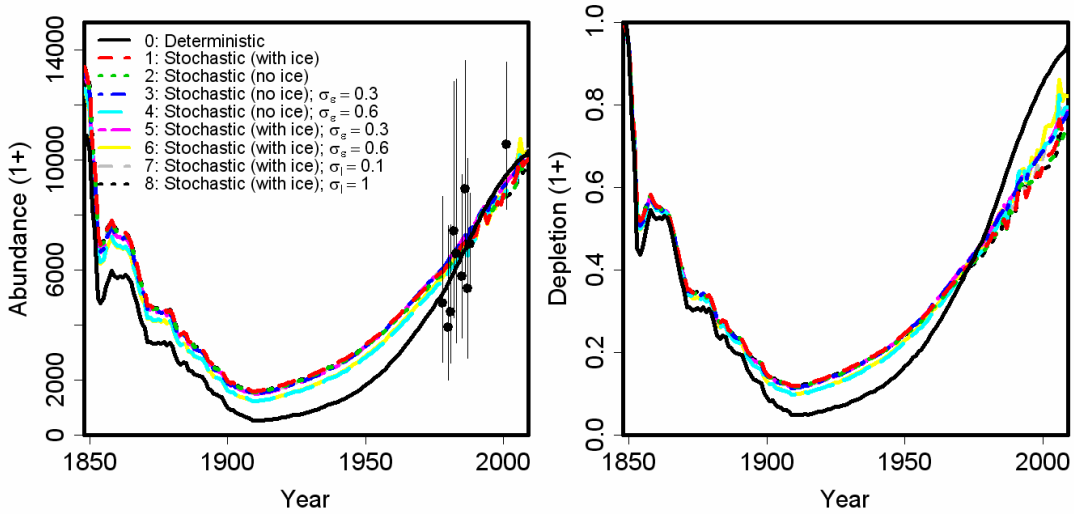

Figure 4. Plots showing 1+ abundance (left panel) and 1+ depletion (right panel) for the stochastic models (dashed lines) and the deterministic model (solid line, both panels).