

Assessment of the eastern stock of North Pacific gray whales: incorporating calf production, sea-ice and strandings data

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ABSTRACT

A stochastic population dynamics modelling framework that incorporated a hypothesized relationship between an environmental variable and process error in life history parameters was developed for a cetacean population. A method was adopted that integrated an index of sea-ice, which has been hypothesized to pertain to calf production, into the stock assessment for the eastern North Pacific stock of gray whales. In addition to stochastic birth rates, the framework also allowed for stochasticity in survival rates, and was fit to an index of strandings to capture the dynamics observed during the mortality event of 1999 and 2000. Sensitivity tests were performed to evaluate the consequences of various assumptions. The results of this framework were compared to those based on a deterministic model that was only fit to the abundance data. These alternatives were each able to fit the abundance data well, but led to different interpretations with regards to current depletion and other quantities of interest. The framework developed here can be used as an operating model with which to test the gray whale *SLA*, given climate forecasts and hypotheses regarding environmental impacts on population dynamics.

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

INTRODUCTION

Management of cetacean populations involves determining risk-adverse strategies that account for, among other factors, natural variability in the environment, and impacts of climate change on ecosystems (IWC, 1994; Tynan and DeMaster, 1997). Stock assessment methods that incorporate relationships between environmental factors and population processes offer the potential to improve management in several ways: (1) to increase the precision of parameter estimates for population dynamics models and hence catch or by-catch related quotas (Maunder and Watters, 2003); (2) to provide a tool to evaluate the performance of existing (e.g., *Strike Limit Algorithms* (SLA) that form part of an Aboriginal Whaling Management Procedure (AWMP)), and alternative, management strategies given forecasts of future climate (e.g. A'mar *et al.*, *in press*); (3) to increase the understanding of factors that might affect the recovery (or otherwise) of different stocks and the vulnerability of species or stocks for which little is known; and (4) to identify priorities for future research and management guidelines (IWC 1997).

The Eastern North Pacific (ENP) stock of gray whales is currently subject to aboriginal hunting, with strike limits based on the AWMP gray whale SLA (IWC 2004, 2005). The life history of this stock follows a typical baleen whale migration between low and high latitudes (Lockyer, 1984). Measurements of weight and girth support the hypothesis that whales on the northbound leg of the migration have lower fat reserves than their counterparts on the southbound migration, due to fasting during the winter

migration (Rice and Wolman, 1971; Perryman and Lynn, 2002). In general, the majority of animals in the population probably derive most of their annual caloric intake from rich benthic prey communities of the northern Bering and southern Chukchi Seas during the summer feeding season. Furthermore, observations from individuals killed off the coast of California during the 1960's suggest that pregnant females are the first to migrate northward to the feeding grounds after breeding (Rice and Wolman, 1971). Given these factors, it has been hypothesized that a relationship exists between the amount of sea-ice covering the early season feeding grounds (possibly acting as a physical barrier to forage habitat for pregnant females arriving early in the feeding season) and calf production the following year (Perryman *et al.*, 2002).

This paper provides the first attempt to integrate available estimates of abundance, calf production, strandings and an environmental index (which is potentially related to calf production) for ENP gray whales in a population dynamics modelling framework. This is one of the most well studied stocks of whales, and therefore provides an ideal candidate to illustrate the results of a method which integrates an environmental time series into a population dynamics modelling framework for cetaceans. The approach for incorporating a relationship between the environmental data and demographic stochasticity is similar in some respects to that of Maunder and Watters (2003), but differs in that the observations of sea-ice are treated as data and included as a component of the likelihood function (for a short discussion of different ways for treating environmental data, see Maunder (2006)). This allows the use of an environmental index with missing years to be incorporated in the analysis. The same approach has been used to assess bigeye tuna (*T. obesus*) in the eastern Pacific (Harley and Maunder, 2004) and is currently being adopted for assessment of sablefish (*A. fimbria*) off the US west coast (following, Schirripa and Colbert (2006)).

Unlike previous assessments of this stock (e.g. Brandon *et al.*, 2007), the population dynamics model accounts for three female stages: immature, mature receptive (fertile), and mature with calf, and allows for stochastic birth and survival rates. Mature females alternate between calving and receptive stages, with the number of calving females in a given year determined by the stochastic birth rate and the number of receptive females the previous year. This underlying population dynamics model is therefore similar to that of Cooke *et al.* (2007), except that it is age-structured rather than being individual-based. This assessment also attempts to take into account the unusual mortality event observed during 1999 and 2000, when anomalously high numbers of individuals were reported dead along the west coast of North America (Gulland *et al.*, 2005).

Results from the application of this approach are compared with those from the deterministic version of the same model, which is not fit to recent calf estimates and does not take potential environmental forcing into account. The results of alternative scenarios are also presented for the methods proposed here. These scenarios correspond to different assumptions regarding the weights assigned to different data sources or different levels of inherent demographic stochasticity and allow an evaluation of the sensitivity of the results to key assumptions with respect to these concerns.

METHODS

Population dynamics model

The analyses were based on a sex- and age-based population dynamics model with an annual time-step. The model included stochastic birth and survival rates, and explicitly considered the transition between receptive 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 cows with calves by year N_t^c , and the number of receptive females by year N_t^r (the age-structure of receptive 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 rate¹ according to the Pella-Tomlinson model:

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

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 and survival 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:

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

where:

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

¹ This is really the rate at which receptive females successfully conceive and then survive with calf to make it past central California on the northbound migration. 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 50% of mature females having a calf in any given year, due the nature of the population dynamics model.

- ε_t is the process error deviation in year t , such that $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$;
- σ_ε is a measure of the extent of variability in the process error, and;
- $\varepsilon_{add-1,t}$ allows for additional process error in birth rate for 1999 and 2000 (in other years, this parameter was set equal to zero).

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 (see Appendix A for the derivation). This transformation leads to a realized standard deviation (taken across years) of the process error deviations that is less than σ_ε (Punt, 2008). Therefore, the realized standard deviation σ_ε was also calculated for comparison.

Survival rates were also allowed to vary annually with the same process error residuals as birth rates (i.e. the deviations in birth and survival rates are assumed to be perfectly correlated). It was assumed that these rates were independent of sex and perfectly correlated between ages in a given year, such that:

$$S_{a,t}^* = \left[1 + \exp(-(\Phi^{-1}(S_a) \sqrt{2.76 + \sigma_\varepsilon^2} + \varepsilon_t + \varepsilon_{add-2,t})) \right]^{-1} \quad (3)$$

where:

- $S_{a,t}^*$ is the realized age-specific survival rate during year t ;
- S_a is the deterministic survival rate from age a to $a+1$; and
- $\varepsilon_{add-2,t}$ is a parameter which allows for additional process error in survival rates in 1999 and 2000 (in other years, this parameter was set equal to zero).

Preliminary analyses indicated that the distributional assumption for the process error deviations did not allow the model to fit the relatively extreme observations of calving and strandings data during '99 and '00. Thus, the ε_{add-1} and ε_{add-2} parameters were introduced into Eqns. 2 and 3 for those years, in order to try and capture the extreme nature of the population dynamics during the mortality event of '99 and '00. For all but one of the scenarios considered below, ε_{add-1} and ε_{add-2} were equal (Table 2).

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:

$$N_{a,t+1}^i = \begin{cases} 0.5N_{t+1}^c & \text{if } a = 0 \\ N_{a-1,t}^i S_{a-1,t}^* (1 - E_t^{fem} V_{a-1}) & \text{if } 1 \leq a \leq 6 \end{cases} \quad (4)$$

where

- E_t^{fem} is the exploitation rate during year t on females:

$$E_t^{fem} = C_t^{fem} / \left(N_t^r + N_t^c + \sum_a V_a N_{a,t}^i \right) \quad (5)$$

V_a is the selectivity on animals of age a , assumed to be constant with regard to sex and time, and uniform on ages 5+, following the approach of previous assessments (IWC, 1993):

$$V_a = \begin{cases} 0 & \text{if } a < 5 \\ 1 & \text{if } a \geq 5 \end{cases} \quad (6)$$

C_t^{fem} 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 6 (i.e. all females reached the age at first estrous at age 6). The plus-group age (denoted as age x) was set to be 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 7 yr, which is equivalent to the median of the prior distribution for this life history parameter adopted in previous assessments (IWC, 1993; Wade, 2002).

The number of receptive females and cows with calves are given by:

$$N_{t+1}^r = S_{1+,t}^* \left[(1 - b_t^*) (N_{6,t}^i + N_t^r) + N_t^c \right] (1 - E_t^{fem} V_{5+}) \quad (7)$$

$$N_{t+1}^c = S_{1+,t}^* b_t^* (N_{6,t}^i + N_t^r) (1 - E_t^{fem} V_{5+}) \quad (8)$$

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:

$$N_{a,t+1}^{male} = \begin{cases} 0.5 N_{t+1}^c & \text{if } a = 0 \\ N_{a-1,t}^{male} S_{a-1,t}^* (1 - E_t^{male} V_{a-1}) & \text{if } 1 \leq a < x \\ S_{1+,t}^* (1 - E_t^{male} V_{5+}) (N_{6,t}^{male} + N_{x,t}^{male}) & \text{if } a = x \end{cases} \quad (9)$$

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 1930, under the assumption of a stable-age-distribution given some level of hunting mortality in 1930. A numbers-per-female-calf approach was taken to solve for the numbers-at-age in 1930 given values for the life-history parameters of the model, the depletion of the 1+ component in 1930, and the hunting mortality rate in 1930, E_{init} . The number of females per calf is given by:

$$NPR_a^{(E)} = \begin{cases} 0.50 & \text{if } a = 0 \\ NPR_{a-1}^{(E)} S_{a-1} (1 - E_{init} V_{a-1}) & \text{if } 1 \leq a < x \\ NPR_x^{(E)} S_{1+} (1 - E_{init} V_{5+}) / (1 - S_{1+} (1 - E_{init} V_{5+})) & \text{if } a = x \end{cases} \quad (11)$$

The birth rate at unexploited equilibrium b_{eq} is the inverse of the number of receptive females per-recruit 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-recruit was $NPR_x^{(E=0)}$. Given this, and that the number of calves is 1, b_{eq} is the reciprocal of the number of receptive females $NPR_x^{(E=0)} - 1$, i.e.

$$b_{eq} = (NPR_x^{(E=0)} - 1)^{-1} \quad (12)$$

The numbers-per-recruit approach of Punt (1999) was modified to take account of hunting mortality in 1930. This involved calculating b_{1930} using Eqn. 1 given b_{eq} , b_{max} and the depletion of the 1+ component in 1930, and using Newton's method (Press *et al.*, 1992) to solve for the value of E_{init} such that:

$$1 = b_{1930} (NPR_x^{(E=E_{init})} - 1) \quad (13)$$

The age- and sex-structure at the start of the 1930 was then calculated by scaling the numbers-per-calf by K_{1+} . The numbers at age of each sex in 1930 was then the total numbers-at-age divided by two.

Data and likelihood function

Four sources of data were considered when fitting the full model: (1) estimates of population size during 1967-2006 (starting year of survey) from the southbound migration at Granite Canyon, California (Rugh *et al.*, 2005; Rugh *et al.*, 2008); (2) estimates of calf production during 1994-2008² from the northbound migration at Point

² The two early estimates of calf production during 1980-1981 (Poole, 1984) were not used in these analyses, as they are not currently used when testing the *AWMP*.

Piedras Blancas, California (Perryman *et al.*, 2002; Perryman, *unpublished data*), (3) the number of stranded animals on the coasts of California, Oregon and Washington state, for which a combined annual count is available during 1975-2006 (Brownell Jr. *et al.*, 2007)³; and (4) estimated sea-ice area covering the Bering Sea, averaged over March and April during 1953-2006 as calculated by the Hadley Center for their sea ice and sea surface temperature data set version 1 ('HadISST') (Fig. 2, left panel; Rayner *et al.*, 2003).

The HadISST ice index was used here because it represents a good compromise between a shorter high resolution and a longer less precise environmental index. Observations from satellites are attractive because they provide a fine level of resolution, but are only available from 1978 to present. On the other hand, historical predictions from atmospheric circulation models are available since at least 1900, but were not found to match available observations of sea-ice acceptably well for the purposes of these analyses (for example, see Overland and Wang, 2007, Fig. 5).

The HadISST index is compromise between length and resolution. It is a compilation of several sources of data including the 'Walsh' charts of sea-ice extent prior to 1978 (Walsh, 1978), and satellite observations for recent decades. This index provides a long time series, calibrated by recent satellite observations. Finally, one of the major goals of these analyses is not only to estimate the parameters of the model, but also to use those results to form the basis of an operating model with which to test the *Gray Whale SLA* given predictions of future sea-ice. Since the primary purpose of the HadISST index is to form the basis for forcing atmospheric circulation models during simulations of future climate, and because we plan on using the results from such simulations of future climate when testing the *Gray Whale SLA*, the HadISST is the sea-ice index most consistent with the objectives of this research.

Catches by sex are available from 1930-2006 (Fig. 2, right panel). Selectivity-at-age resulting in the observed catches was treated as known. 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 catches during 2007 and 2008 were assumed equal to those in 2006.

The total negative of the logarithm of the likelihood function is the sum of the contributions for each data source. Additionally, penalties were added to the likelihood function to impose a normal prior with standard deviation σ_{ϵ} on the process error deviates and to ensure that 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 (Equations 2 and 3). Instead, a default value for σ_{ϵ} of 0.50 was used following preliminary analyses which suggested that this value was consistent with observed inter-annual variability in the data. Analyses were also conducted in which $\sigma_{\epsilon} = 0.30$ and 0.70 to assess the sensitivity of the results to the value assumed for σ_{ϵ} .

³ Data on strandings are collected in other locations (e.g. Mexico and Alaska), but the stranding network effort in California, Oregon and Washington has been more consistent through the years

Abundance estimates

The abundance estimates are based on survey seasons which span two calendar years. Hence, they are referred to here by the year during which the survey started (e.g., the 1967-68 abundance estimate is referred to as “1967”). In this way, the abundance of the population was considered to be surveyed after births and deaths in a given year. An additional variance term $CV_{\text{add-1}}$ was incorporated into the likelihood component for the abundance estimates following Wade (2002) and Butterworth *et al.* (1993). The residuals of the model fit to the abundance estimates were assumed to be independent between years and log-normally distributed. Moreover, it was assumed that the surveys provide estimates of the number of animals aged 1 and older. These assumptions led to the following component of the negative log-likelihood function⁴:

$$L_1 = \sum_t 0.5 \left(\ln(\sigma_t^2 + CV_{\text{add-1}}^2) + \frac{1}{\sigma_t^2 + CV_{\text{add-1}}^2} \left(\ln N_{1+,t}^{\text{obs}} - \ln N_{1+,t} \right)^2 \right) \quad (14)$$

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 ;
- $CV_{\text{add-1}}$ is the extent of additional error about the abundance estimates, and;
- σ_t is the standard deviation of the logarithm of $N_{1+,t}^{\text{obs}}$ (approximated by the CV of the untransformed abundance estimate).

Calf estimates

The residuals about the model fit to the calf estimates were also assumed to be independent and identically log-normally distributed. Following previous approaches which fit the calf estimates using a deterministic model of population dynamics (Wade, 1997; Wade and Perryman, 2002), the reported observation error about the calf estimates was assumed here to be subject to some additional observation error as was the case for the abundance estimates. This approach led to the following component of the negative log-likelihood function:

$$L_2 = \sum_t 0.5 \left[\ln(\sigma_t^2 + CV_{\text{add-2}}^2) + \frac{1}{\sigma_t^2 + CV_{\text{add-2}}^2} \left(\ln N_{0,t}^{\text{obs}} - \ln N_{0,t} \right)^2 \right] \quad (15)$$

where:

- $N_{0,t}^{\text{obs}}$ is the survey estimate of calf production in year t ;
- $N_{0,t}$ is the model estimate of calf production in year t ;
- $CV_{\text{add-2}}$ is the extent of additional error about the calf estimates, and;
- σ_t is the standard deviation of the logarithm of $N_{0,t}^{\text{obs}}$ (approximated by the CV of the untransformed calf production estimate).

⁴ The Likelihood components were calculated ignoring constants independent of the parameters of the model.

Stranding counts

The residuals about the model fit to the indices of number of stranded animals were assumed to be independent and identically log-normally distributed, leading to the following component of the negative log-likelihood function:

$$L_3 = \sum_t 0.5 \left[\ln(\sigma_M^2) + \frac{1}{\sigma_M^2} (\ln M_t^{obs} - \ln(\hat{q} \hat{M}_t))^2 \right] \quad (16)$$

where:

M_t^{obs} is the observed number of stranded animals (based on data for California, Oregon and Washington);

\hat{M}_t is the model-estimate of the number of animals dying due to natural causes:

$$\hat{M}_t = (1 - S_{x,t}^*) [N_t^r + N_t^c] + \sum_a (1 - S_{a,t}^*) [N_{a,t}^i + N_{a,t}^{male}] \quad (17)$$

\hat{q} is the constant of proportionality between the indices of stranded animals and \hat{M}_t .

An empirical estimate for the observation error of the stranding counts does not exist (Brownell Jr. *et al.*, 2007). Therefore, reasonable alternative values were chosen ($\sigma_M = 0.10$ or 0.20) to assess the sensitivity of the results to the value assumed for this parameter. A value for σ_M of 0.20 implies that the lower 95% limits for the stranding estimates for '99/'00 do not overlap with the upper 95% limits for the standings estimates for any other years, and it is therefore an upper limit for this parameter which would be consistent with those years representing an unusual mortality event.

The value for \hat{q} was set to its maximum likelihood estimate. This is equivalent to integrating over the prior for this parameter when its prior distribution is uniform in log-space (Walters and Ludwig; 1994). The counts of stranding animals were only made along a portion of the migratory route, and further it seems unlikely that all animals that die will wash ashore or that all of those that do will be counted. Hence it was reasonable to assume that \hat{q} was less than 1.0. Additionally, an underlying assumption of this method is that \hat{q} was constant through time. This is unlikely to be strictly true. But given that, gray whales migrate (and die) close to the coast, observation effort has been relatively constant through time for the stranding index considered here and that the mortality event of '99 and '00 is believed to have been caused by a substantial decrease in survival (as opposed to a higher fraction of carcasses washing ashore due to a change in wind, ocean currents or the like), minor violations of this assumption were unlikely to be consequential to the results.

Environmental impact on demographic rates

In addition to being subjected to process error, the deviations of birth and survival rates about the deterministic relationship each year were also allowed to be related to an environmental index I_t (in this case, the amount of sea-ice covering the Bering Sea, averaged over March and April). 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:

$$I_t^{obs} = \beta \varepsilon_t + \gamma_t \quad (18)$$

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 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:

$$\sigma_I = |\beta| \sigma_I^* \quad (19)$$

This formulation takes a fixed input value for σ_I^* (Table 2) and scales the expected standard deviation of the fits to the environmental index by the estimated absolute value for β . This differs from the approach of Brandon *et al.* (2007), who treated σ_I as an estimated parameter. It was found through preliminary analyses that this was no longer a tractable approach given the framework considered here. Likewise, simply fixing σ_I to a given fixed input parameter (ignoring Eqn. 19) was found through preliminary analyses to lead to estimates of the process error deviations ε_t which became increasingly small with smaller assumed values of σ_I . Eqn. 19 leads to the desired effect of the process error deviations being more correlated with the environmental index at smaller values of σ_I .

Perryman *et al.* (2002) investigated two different time lags (corresponding with the potential effect of sea-ice on ovulation or pregnancy rates) and concluded that a relationship between sea-ice and reproductive success would most likely result from an effect on existing pregnancy rates. Therefore, 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, negative values of β correspond with larger values of the sea-ice index having detrimental affects on birth and survival rates (negative process error deviations).

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

$$L_4 = \sum_t \left[\ln(\sigma_I) + \frac{1}{2\sigma_I^2} (I_t^{obs} - I_t)^2 \right] \quad (20)$$

σ_I^* was assumed to be 0.30 for the base case scenario, because preliminary analyses indicated that this value provided a conservative weight for the environmental index during the model fitting (i.e., it 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). Analyses were also conducted with $\sigma_I^* = 0.10$ and 1.00 to investigate the sensitivity of the results to alternative values. Likewise, two scenarios were considered in which the model was fit only to data for sea-ice pertaining to those years for which it would have had an effect on recent calf production (1993 – 2008). In these scenarios an alternative index of sea-ice was fit based on an updated version of the index used by Perryman *et al.* (2002) (Fig. 2, left panel; Perryman, *unpublished data*). This was done to assess the impact of the length of the time-series of environmental data on the results, as well as that given an alternative index of sea-ice.

Parameterization and scenarios

The estimable parameters of the population dynamics model are listed in Table 1. Rather than treating all of the survival rates by age as estimable parameters, two survival rates were considered: (i) calf survival S_0 and, (ii) the survival rate for animals aged 1 and older S_{1+} . Moreover, calf survival was not treated as an estimable parameter. Instead, the difference, Δ , between adult and calf survival was estimated. This also allowed the constraint that adult survival cannot be less than calf survival to be enforced. The values for ε_{add-1} and ε_{add-2} were assumed to be the same for the most of the analyses, although one of the scenarios investigated estimating these parameters separately (Table 2). All but one of the scenarios in which the calf data were used to fit the model involved setting the level of additional observation error equal to that for the abundance data (i.e. only one CV_{add} was estimated, such that $CV_{add-2} = CV_{add-1}$).

Table 2 outlines the full set of scenarios. The two base case scenarios were: (i) the stochastic model described above (“Full” in Table 2), and; (ii) a deterministic version fit only to abundance data following the approach of previous assessments (e.g., Wade, 2002) (“Deterministic” in Table 2). Additionally, several alternative scenarios were considered for the full stochastic model, to investigate the affects of certain assumptions and data sources on the results. These alternative scenarios involved estimating the maximum likelihood values for the parameters (MLE), while the two base cases involved parameter estimation in using a Bayesian as well as a maximum likelihood framework, to facilitate comparison with previous assessments and to form a basis for evaluating the performance of the gray whale SLA. A parallel set of scenarios was considered which ignored the calf estimates from 1998-2001. This was done to assess the ability of the model to fit the mortality event when the process error deviations were not conditioned on the calf data during those years.

Parameter estimation

The models were developed using AD Model Builder (ADMB, Otter Research, <http://otter-rsch.com/admodel.htm>). ADMB uses automatic differentiation (Griewank and

Corliss, 1991) to efficiently estimate the variance-covariance matrix of model parameters with respect to the likelihood function. Additionally, it allows for Bayesian estimation by sampling from the posterior distribution using Markov Chain Monte Carlo (MCMC), as implemented by the Metropolis-Hastings algorithm (Hastings, 1970; Gelman *et al.*, 2004). The proposal (or “jump”) function used by ADMB for the MCMC algorithm is multivariate normal with a variance-covariance matrix based on that estimated for the model parameters.

The Bayesian Output Analysis Program (BOA) for MCMC was used to diagnose the convergence of the MCMC algorithm (Smith, 2007). The Heidelberger and Welch (1983) stationarity and half-width tests, the Geweke (1992) and the Raftery and Lewis (1992) convergence diagnostics were inspected for signs of non-convergence and used as guidelines for determining an appropriate burn-in and thinning interval for the chain.

RESULTS

The MCMC algorithm was run for 50 million iterations, saving every 25,000th sample after a 20% burn-in, leading to a final sample size of 1,600 draws from the posterior. This process resulted in diagnostics for the chain that gave no sign of not having converged, as indicated by the plots in Figure 3.

The model was able to fit the abundance and calf data reasonably well for all scenarios (see Fig. 4 for three examples for calf data; Fig. 5 upper panels for abundance data for all scenarios). The results were consistent with this stock being at or near carrying capacity, although estimates of carrying capacity differed among scenarios (Fig. 6, left panels; Tables 3 and 4). The scenarios that did not take the strandings data into account (the deterministic and ‘No Strandings Data’ scenarios), or did not place much weight on the strandings data (the $\sigma_M = 0.20$ scenario) estimated carrying capacity to be in the low 20,000s, and that the population size has been constant at this level since the late-1980s or early 1990s (Fig. 4, upper right panel; Fig. 5, lower panels). The inability of certain scenarios to fit the 1999-2000 mortality event is indicated by values of ε_{add-1} that are closer zero in Tables 3 and 4. The estimates of maximum birth rate and survival rates were similar among the scenarios that were unable to fit the 1999-2000 mortality event, with higher maximum birth rates and somewhat lower survival rates than for the remaining scenarios (Tables 3 and 4). The “Full” scenario estimated life history parameters more precisely than the “Deterministic” scenario, and also estimated lower maximum birth rates and higher survival rates (Fig. 7).

The scenarios which estimated both CV_{add-1} (abundance) and CV_{add-2} (calf) resulted in estimates for CV_{add-1} which were generally equal to those for the other scenarios. However, CV_{add-2} was estimated to be equal to zero. The model was able to fit the strandings data during the 1999-2000 mortality event when the calf data during the 1999-2000 mortality event were ignored ($\varepsilon_{add-1} = -2.04$). However, the fit to the mortality event was generally poorer ($\varepsilon_{add-1} = -0.87$) when those calf data were included, although not as poor as for the scenarios mentioned above.

The remaining scenarios were able to capture at least some of additional mortality during 1999 and 2000, and estimated that the population has since recovered following that event to numbers that equal or possibly exceed those in 1998, but do not necessarily equal carrying capacity (Fig. 4, left and middle panels). Those scenarios which were able

to fit the 1999-2000 mortality event also resulted in less precise (and slightly lower) estimates of current depletion (Fig. 6, right panels). There was essentially no support for carrying capacity being greater than 40,000 or that the stock size is at less than 70% of carrying capacity for any of the scenarios (Fig. 5, lower panels; Fig. 6, right panels; Tables 3 and 4).

The “Full” model was able to capture the variability in the calf production estimates quite well (Fig. 4; left panels). The “Deterministic” model was consistent with the average observed calf production in recent years - even though this model did not fit the calf data – albeit with much more uncertainty around this estimate than the “Full” model (Fig. 4; right panels). None of the scenarios considered were fitted to the 1980 and 1981 calf counts. However, there are model-predictions corresponding to those counts. In general, the predicted numbers of calves in 1980 and 1981 exceeded the observations, more so for the “Deterministic” model (although the observed values were within the 95% probability intervals for this model) (Fig. 4).

The “Full” model fit the data nearly equally well irrespective of whether the calf counts for 1999-2001 were fitted or not (Fig. 4 left and centre panels). However, the estimates of ε_{add-1} were quite different between these scenarios (Tables 3 and 4, second row last two columns). The scenario which ignored the calf counts for 1999-2001 estimated a larger value for ε_{add-1} and was better able to fit the strandings data during the years of the mortality event (Fig. 4, middle and bottom rows; Tables 3 and 4).

When all of the calf data were included in the analyses and both ε_{add-1} (birth) and ε_{add-2} (survival) were estimated separately, the model was able to fit the calf and strandings data during the 1999-2000 mortality event and estimated a value for ε_{add-2} that was roughly twice that of ε_{add-1} (Table 3). The additional process error for birth rates was estimated to be small for this scenario when the calf counts for 1999-2001 were ignored (Table 4), which resulted in the model essentially predicting zero calf production during 1999-2001. This was a somewhat surprising result, for which we propose a possible explanation below.

The parameter which related the sea-ice index to the process error deviations β was estimated to be negative for all scenarios (Tables 3 and 4). Setting $\sigma_i^*=0.30$ allowed the model to fit all but the most extreme years of the sea-ice index (e.g., Fig. 4, left and middle panels). Consequently, birth and survival rates were lower (i.e. lower calf production and higher numbers of strandings) than expected during years for which the sea-ice index was large. This result was most evident during those years before the first stranding and calf estimates. For example, calf production and survival were estimated to have been less than otherwise expected during the heavy sea-ice years of the 1970's because of negative process error deviations during those years (Fig. 4).

Varying the value of σ_i^* did not greatly affect the ability of the model to fit the data other than the sea-ice index itself. The environmental signal in the process error deviations became more pronounced, especially for those years before the stranding and calf data were available, by giving the sea-ice data more weight (i.e., the $\sigma_i^*=0.10$ scenario in Tables 3 and 4). Likewise, the process error deviations were close to zero prior to there being strandings and calf data when the sea-ice data were substantially

down-weighted (i.e., the $\sigma_I^*=1.00$ scenarios in Tables 3 and 4). The estimated survival rates also decreased as the value for σ_I^* was increased (Tables 3 and 4).

There was essentially no difference between the results for the two scenarios which only fit to recent sea-ice data from 1993-2008 (“Recent Ice” and “Perryman *et al.* Ice” in Tables 3 and 4). However, the estimated values for ε_{add-1} were more negative for those scenarios which ignored the calf counts for 1999-2001, leading again to better fits to the strandings data and higher estimates of the numbers of animals which died during those years (“Natural Mortality ’99 + ’00” in Table 4). It followed that the estimates of current depletion were lower for those scenarios which were only fit to the recent ice data and also ignored the ’99 – ’01 calf estimates (Table 4).

The realized standard deviation of the process error residuals (σ_ε) was similar across all stochastic scenarios and generally equal to about 0.20; with the notable exceptions of those scenarios for which the input value for σ_ε was varied (Tables 3 and 4). Not surprisingly, varying the value for σ_ε had a direct result on the realized standard deviations of the process error residuals. Additionally, the realized standard deviations were less than the value for σ_ε . For the Full model, the point estimates for σ_ε were 0.07, 0.21 and 0.33, given $\sigma_\varepsilon = 0.30, 0.50$ and 0.70 respectively. The scenarios with $\sigma_\varepsilon = 0.30$ exhibited fairly deterministic dynamics (with the exception of the impact on the ε_{add-1} during the 1999-2000 mortality event). These scenarios also led to estimated values for $CV_{add-1} = 0.18$, which was the largest of any of the scenarios considered in these analyses (Tables 3 and 4). The effect of increasing the standard deviation of the process errors was similar to that of decreasing the value for σ_I^* (or similarly, only fitting to the sea-ice data for 1993-2008), and vice-versa. That is, the estimated effects of sea-ice became more exaggerated for higher values of σ_ε or lower values for σ_I^* (or longer time series of sea-ice), especially during those years before calf and strandings data became available.

DISCUSSION

We incorporated an environmental index into a population dynamics modeling framework, and allowed for a hypothesized relationship between sea-ice and gray whale population dynamics when fitting to observations of abundance, sea-ice, strandings and calf production. The incorporation of such a relationship could potentially improve our understanding of cetacean population dynamics and help to determine whether existing management strategies are robust to climate-induced forcing of the population dynamics. However, it should be noted that the goal of this investigation was not to provide evidence for or against a certain hypothesis about how environmental conditions may affect population dynamics. Rather, the primary aim was to develop a tool by which alternative hypotheses may be explicitly taken into account within a population dynamics modeling framework, ultimately providing a means through which the robustness of management procedures may be evaluated, given such hypotheses and forecasts of future climate change.

The framework allowed for the deviations in birth and survival rates to be related to an index of sea-ice in the Bering Sea, following a plausible hypothesis about how this environmental index might be related to the population dynamics of ENP gray whales. The observations of calf production and stranding numbers were taken as direct measures of the variability in birth and survival rates, whereas the environmental index was used as a proxy measure. The sea-ice index provided information about birth and survival rates during years when direct observations of calf production and strandings were not available while the effect of sea-ice on the population dynamics was calibrated during the years for which calf count, strandings and sea-ice data were all available. However, something extraordinary clearly occurred during 1999 and 2000 (at least in terms of survival rates, as exemplified by the stranding counts; Fig. 4) and the ability of the different model configurations to fit the 1999-2000 mortality event had a large influence on the results. Specifically, the results were more optimistic in terms of recent depletion levels if the 1999-2000 mortality event was ignored. The recovery of the stock was attributed to higher calf production during the period of increasing abundance estimates, as opposed to higher survival rates, whereas recovery was explained through higher survival rates and lower calf production when the data on the 1999-2000 mortality event were used to fit the model.

It was not possible to fit the strandings data for the 1999-2000 mortality event without allowing for some additional process error in the survival rates during those years given the assumptions made regarding the nature of the process error deviations. The approach taken here for modeling this additional process error was relatively unsophisticated and could be improved upon in future work. For example, Ward *et al.* (2007) estimate the probability of an unusual or ‘catastrophic’ event by adopting a mixture distribution approach to process error. That is, they estimate if a given year was a catastrophic year, and, depending on that assessment, draw the process error for that year from one of two (regular and catastrophic) distributions (in effect we have assumed an underlying mixture distribution with a step function for 1999 and 2000, where those years are given probability of 1.0 for catastrophe, and other years assigned zero probability). An estimate of the probability of a mortality event would be of great interest when running future projections and testing the gray whale *SLA*, whereas the approach taken here is more limited in its predictive ability of future catastrophic events.

Observations of recent variability in calf production and the amount of sea-ice covering the early season feeding grounds suggest that there exists some relationship between sea-ice and calf production in gray whales. However, it is possible that this relationship (if it exists) is something that has developed or strengthened within the last two decades. For example, the two early (1980s) calf production estimates are nearly equal (Fig. 4), yet occurred during years of disparate ice conditions (Fig. 2). We have assumed that the relationship between calf production and sea-ice is stationary (and specifically independent of population density), and one result of this assumption was that the model predicts lower than expected calf production during much of the 1960s and 1970s, when there were higher levels of sea-ice in the Bering Sea. Consequently, the estimates of survival were higher for the stochastic than for the deterministic configurations of the model (Fig. 7), which allowed the stochastic model to mimic for the observed trend in the abundance data.

Modeling the interaction between population density and the effects of environmental variability on vital rates, and the probability of mortality events is beyond the scope of this paper. However, as populations increase in density, the impact of density-independent factors on population dynamics probably become more pronounced (e.g., Durant *et al.*, 2005) and accounting for density-dependent mortality events may have implications for management strategies (e.g., Wilcox and Eldred, 2003). Therefore, if the framework presented here is used to test management strategies, we recommend identifying a plausible set of scenarios for how such environmental affects and the probability of mortality events might change with population density. It seems unlikely that it will be possible to estimate such relationships given the amount of data available for most cetaceans, but the framework presented here could be modified to examine different assumptions along these lines (e.g., modifying σ_i^* as a fixed function of depletion).

It is interesting to note that the scenario which estimated both ε_{add-1} and ε_{add-2} , but ignored the 1999-2001 calf counts, resulted in an estimated value of the additional process error for birth rates which led to essentially no calf production during those years. One possible explanation for this behavior is that by doing so, the model estimated an increase in the number of receptive females during those years (as previously calving females recruited into the receptive stage) such that, when birth rates were allowed to have returned to ‘normal’ following the 1999-2000 mortality event, the model was better able to fit subsequent estimate(s) of calf production.

The assumption that the birth and survival process errors were perfectly correlated was rather simplistic. In reality, there is likely to be some correlation, but it may be imperfect and non-linear (Eberhardt 1977; Gaillard *et al.*, 2000). The assumption made here was fairly inconsequential during normal stranding years, because the variability in strandings between years is generally low. However, the consequence of this assumption during the 1999-2000 mortality event was substantial. Ignoring the calf data during the mortality event or estimating both ε_{add-1} and ε_{add-2} provided better fits to the observed strandings during this event. These scenarios illustrated the constraint placed on the ability of the model to simultaneously fit the calf and strandings data during the mortality event, when the additional process error during those years was assumed to be the same for birth and survival rates. While the fits were not dramatically different between the two “Full” scenarios (using or ignoring the calf counts for 1999 and 2000), the differences between the estimates of ε_{add-1} (roughly twice as large when ignoring the calf counts) could have implications for projections of population dynamics if future mortality events are conditioned on those estimates of ε_{add-1} .

A forecast of future sea-ice conditions will be needed to perform projections of future population dynamics within this framework and hence test the gray whale *SLA*. Overland and Wang (2007) have provided one such forecast, based on an ensemble mean from a suite of models considered by the Intergovernmental Panel on Climate Change. We plan on including that forecast as input for population projections in the next stage of this research, using the framework presented here as an operating model while testing the gray whale *SLA*.

Future work may extend this framework to other cetacean stocks. Several alternative candidates exist for which a relationship between environmental conditions and population dynamics has been recognized, for example: northeast Atlantic fin whales (Lockyer, 1986); sperm whales off the Galapagos Islands (Whitehead, 1997); and north and south Atlantic right whales (Green *et al.*, 2003; Leaper *et al.*, 2006). In addition, recent observations suggest a possible relationship between body condition and sea-ice for animals taken in the aboriginal hunt for the Bering-Chuckchi-Beaufort Seas stock of bowhead whale (George *et al.*, 2009). Such information, combined with an index of calf production for this stock (Koski *et al.*, 2007), could eventually be included in a framework similar to that presented here, and then applied to testing of the bowhead *SLA* given relevant climate forecasts.

In conclusion, the framework developed here provides a tool for testing management strategies, given a hypothesis about how environmental factors influence population dynamics and climate forecasts. The results indicated that including the environmental index and fitting to the mortality event lead to somewhat different interpretations of the population dynamics of the ENP gray whale when compared to those provided by a deterministic model. Using this framework to test the gray whale *SLA* should help to ensure that management is robust to a plausible range of scenarios for how future climate might impact this, and other cetacean populations.

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Table 1

The parameters and their assumed prior distributions. The abbreviations for prior distributions include: U [uniform] and N [normal]. Footnotes below describe the sources and reasoning behind these parameter values and distributions.

Parameter	Prior distribution
Maximum non-calf survival rate, S_{1+}	U[0.950, 0.999] ^a
Maximum birth rate, b_{\max}	U[0.01, 0.99]
Difference between non-calf and calf survival, $\Delta=S_{1+} - S_0$	U[0.01, 0.25] ^b
Carrying capacity, K_{1+}	U[15 000, 70 000] ^b
Depletion in 1930, $N_{1+,1930} / K_{1+}$	U[0.050, 0.50] ^b
Process error residuals, ε_t	N[0, σ_ε^2]
Additional process error during '99/'00 mortality event, ε_{add-1} and ε_{add-2}	U[-4.0, 4.0] ^b
Influence of sea-ice on calf production, β	U[-400, 400] ^b

a. Equal to the prior distribution used in recent assessments (IWC, 1998).

b. Preliminary analyses provided no support for values outside this range.

Table 2

The scenarios considered in these analyses. Different data sets, parameter values and estimation techniques are outlined. The scenarios labeled ‘Deterministic’ and ‘Full’ refer to the base cases, for which a Bayesian estimation framework was adopted as well as maximum likelihood estimation (MLE). A further set of parallel runs were performed for the Full model, but not fitting the calf estimates from ’99 – ’01 (see Table 4 for results). The remaining scenarios are variations of the ‘Full’ base case (see Table 3 for results). ‘NA’ signifies a variable that is not applicable to a certain scenario (e.g., σ_I^* is not applicable when the sea-ice data are not considered).

	Abundance Data	Calf Data	Ice Data	Strandings data	CV_{add-1} (abundance)	CV_{add-2} (calf)	σ_ε	σ_M	σ_I^*	$\varepsilon_{add-1,t}$	$\varepsilon_{add-2,t}$	$\underline{\varepsilon}_t$	Bayesian or MLE
Deterministic	Yes	No	No	No	Estimated	NA	NA	NA	NA	NA	NA	NA	Both
Full	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	Both
Drop ’99–’01 Calf Data	Yes	Drop ’99–’01	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	Both
$\sigma_M = 0.20$	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.20	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
Recent Ice	Yes	Yes	’93-’08	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
Perryman <i>et al.</i> Ice	Yes	Yes	’93-’08	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
$\sigma_I^* = 0.10$	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.10	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
$\sigma_I^* = 1.00$	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	1.00	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
$\sigma_\varepsilon = 0.30$	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.30	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
$\sigma_\varepsilon = 0.70$	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.70	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
CV_{add-1} & CV_{add-2}	Yes	Yes	Yes	Yes	Estimated	Estimated	0.50	0.10	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE
ε_{add-1} & ε_{add-2}	Yes	Yes	Yes	Yes	Estimated	$= CV_{add-1}$	0.50	0.10	0.30	Estimated	Estimated	Estimated	MLE
No Strandings data	Yes	Yes	Yes	No	Estimated	$= CV_{add-1}$	0.50	NA	0.30	Estimated	$= \varepsilon_{add-1,t}$	Estimated	MLE

Table 3

Results for the scenarios based on the Full model that uses all of the available data. The estimates correspond to the mode of the posteriors for the Bayesian analyses, and MLEs are shown for the ML analyses: \tilde{S} is the median stochastic survival rate over all years; $\sigma_{\mathcal{E}}$ is the standard deviation of the realized process errors (after the transformation in Eqns. 2 and 3), and; the combined natural mortality during '99-'00, corresponding to the total number of whales estimated to have died during the mortality event is also shown. The asterisk on CV_{add-2} (calf) indicates that this parameter was estimated to be zero.

	$N_{1+, 2009} / K_{1+}$	K_{1+}	b_{max}	S_{1+}	\tilde{S}_{1+}^*	S_0	\tilde{S}_0^*	$\sigma_{\mathcal{E}}$	β	Natural Mortality '99 + '00	CV_{add-1} (abundance)	CV_{add-2} (calf)	$\mathcal{E}_{add-1,t}$ (birth)	$\mathcal{E}_{add-2,t}$ (survival)
Deterministic	0.981	22,621	0.990	0.964	NA	0.714	NA	NA	NA	2,414	0.11	NA	NA	NA
Full	0.979	26,773	0.32	0.989	0.981	0.979	0.971	0.21	-2.32	2,455	0.12	0.12	-1.01	-1.01
$\sigma_M = 0.20$	0.996	23,159	0.65	0.978	0.971	0.968	0.961	0.22	-2.25	2,072	0.09	0.09	-0.44	-0.44
Recent Ice	0.938	26,650	0.31	0.989	0.982	0.979	0.972	0.18	-2.28	2,575	0.11	0.11	-0.91	-0.91
Perryman <i>et al.</i> Ice	0.940	26,054	0.33	0.988	0.980	0.977	0.969	0.18	-2.11	2,679	0.09	0.09	-0.66	-0.66
$\sigma_I^* = 0.10$	0.980	29,784	0.25	0.995	0.989	0.960	0.954	0.23	-3.20	1,996	0.19	0.19	-1.20	-1.20
$\sigma_I^* = 1.00$	0.941	26,162	0.33	0.988	0.980	0.978	0.970	0.18	-0.93	2,688	0.10	0.10	-1.05	-1.05
$\sigma_{\mathcal{E}} = 0.30$	0.941	28,889	0.28	0.994	0.985	0.984	0.975	0.07	-2.97	2,538	0.18	0.18	-1.19	-1.19
$\sigma_{\mathcal{E}} = 0.70$	0.962	30,890	0.21	0.997	0.993	0.870	0.866	0.33	-1.85	1,314	0.14	0.14	-1.22	-1.22
CV_{add-1} & CV_{add-2}	0.988	26,578	0.36	0.987	0.980	0.977	0.970	0.22	-2.30	2,351	0.13	0.00*	-0.87	-0.87
\mathcal{E}_{add-1} & \mathcal{E}_{add-2}	0.940	29,632	0.22	0.999	0.995	0.773	0.770	0.23	-2.25	2,620	0.12	0.12	-0.99	-2.24
No Strandings data	0.992	22,454	0.99	0.980	0.972	0.742	0.735	0.23	-2.14	1,468	0.08	0.08	-0.06	-0.06

Table 4
As for table 3, except that calf estimates for 1999-2001 are ignored

	$N_{1+, 2009} / K_{1+}$	K_{1+}	b_{\max}	S_{1+}	\tilde{S}_{1+}^*	S_0	\tilde{S}_0^*	$\sigma_{\mathcal{E}}$	β	Natural Mortality '99 + '00	$CV_{\text{add-1}}$ (abundance)	$CV_{\text{add-2}}$ (calf)	$\mathcal{E}_{\text{add-1},t}$ (birth)	$\mathcal{E}_{\text{add-2},t}$ (survival)
Deterministic	0.981	22,621	0.990	0.964	NA	0.714	NA	NA	NA	2,414	0.11	NA	NA	NA
Full	0.923	31,094	0.22	0.999	0.995	0.812	0.794	0.16	-4.41	2,429	0.14	0.14	-2.09	-2.09
$\sigma_M = 0.20$	0.987	22,323	0.99	0.966	0.960	0.956	0.950	0.22	-2.15	1,978	0.09	0.09	-0.07	-0.07
Recent Ice	0.790	32,586	0.21	0.999	0.995	0.749	0.745	0.16	-2.85	3,484	0.13	0.13	-2.63	-2.63
Perryman <i>et al.</i> Ice	0.797	32,600	0.20	0.999	0.995	0.752	0.748	0.14	-3.32	3,278	0.14	0.14	-2.62	-2.62
$\sigma_I^* = 0.10$	0.963	31,760	0.21	0.999	0.995	0.869	0.866	0.25	-3.06	1,915	0.18	0.18	-1.83	-1.83
$\sigma_I^* = 1.00$	0.868	29,722	0.23	0.998	0.994	0.754	0.750	0.18	-0.93	3,319	0.11	0.11	-2.30	-2.30
$\sigma_{\mathcal{E}} = 0.30$	0.916	31,769	0.22	0.999	0.995	0.847	0.843	0.06	-2.98	2,441	0.18	0.18	-1.93	-1.93
$\sigma_{\mathcal{E}} = 0.70$	0.949	29,862	0.21	0.999	0.996	0.750	0.747	0.36	-1.75	2,303	0.13	0.13	-2.34	-2.34
$CV_{\text{add-1}}$ & $CV_{\text{add-2}}$	0.954	30,825	0.23	0.999	0.995	0.806	0.802	0.23	-2.23	2,293	0.15	0.00*	-2.04	-2.04
$\mathcal{E}_{\text{add-1}}$ & $\mathcal{E}_{\text{add-2}}$	0.938	30,387	0.22	0.999	0.995	0.813	0.809	0.22	-2.25	2,367	0.13	0.13	-3.99	-2.08
No Strandings data	0.987	22,323	0.99	0.966	0.960	0.956	0.950	0.22	-2.15	1,978	0.09	0.09	-0.07	-0.07

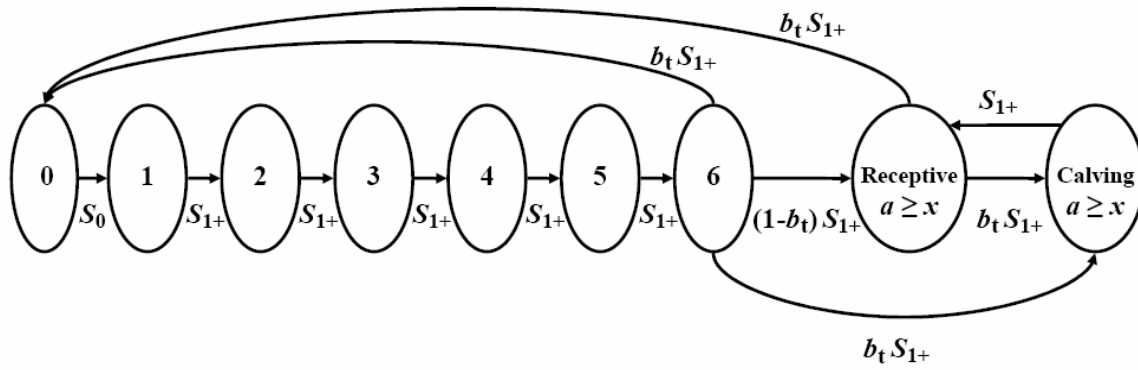


Figure 1. Life cycle graph of the model used to track the number of females in each reproductive stage through time. This life cycle refers to the underlying deterministic model, with transition probabilities shown as functions of life history parameters. However, it should be noted that the survival and birth rates were modified to be stochastic in the all analyses presented here (except ‘Deterministic’). 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 $t+1$.

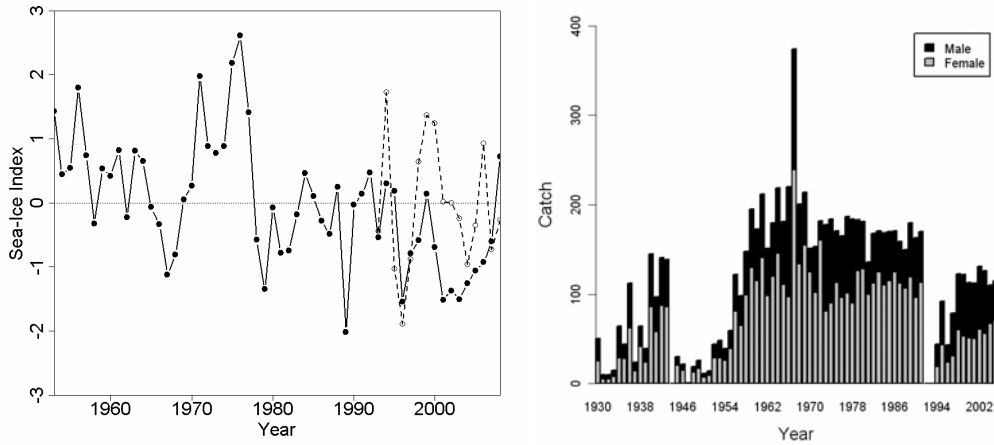


Figure 2. (Left panel) The standardized HadISST index for the March-April averaged sea-ice area covering the Bering Sea is shown by the solid line, and the Perryman *et al.* index is shown as the dashed line. Positive values represent years with greater than average spring ice over the time period considered. (Right panel) Catches by individuals and sex: 1930-2006.

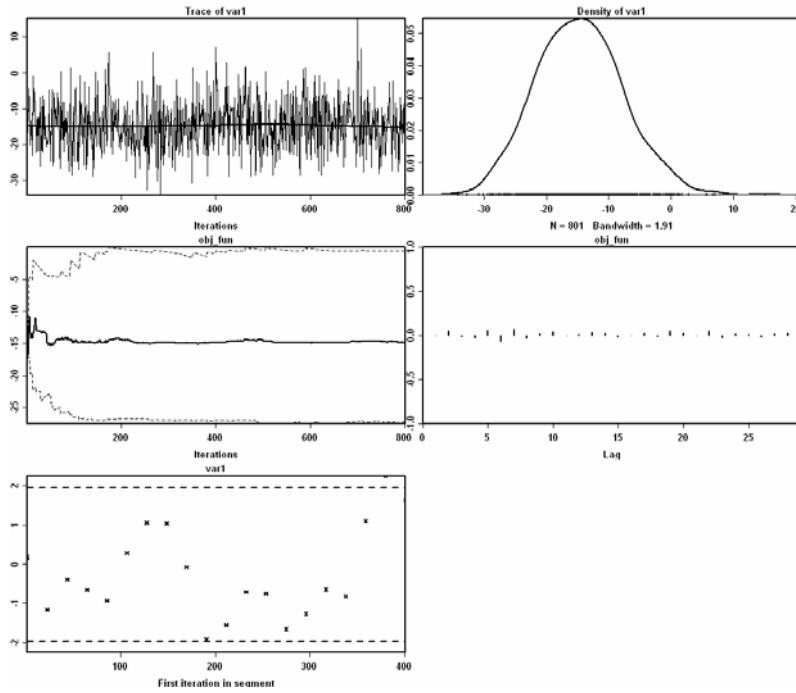


Fig. 3. Diagnostic plots for the negative log-likelihood function resulting from the MCMC chain for the Full model scenario (all data). Clockwise from upper left: trace, density, autocorrelation, Geweke's z-score, and the cumulative quantile plots showing the evolution of the median (solid line) and 95th percentiles of the chain.

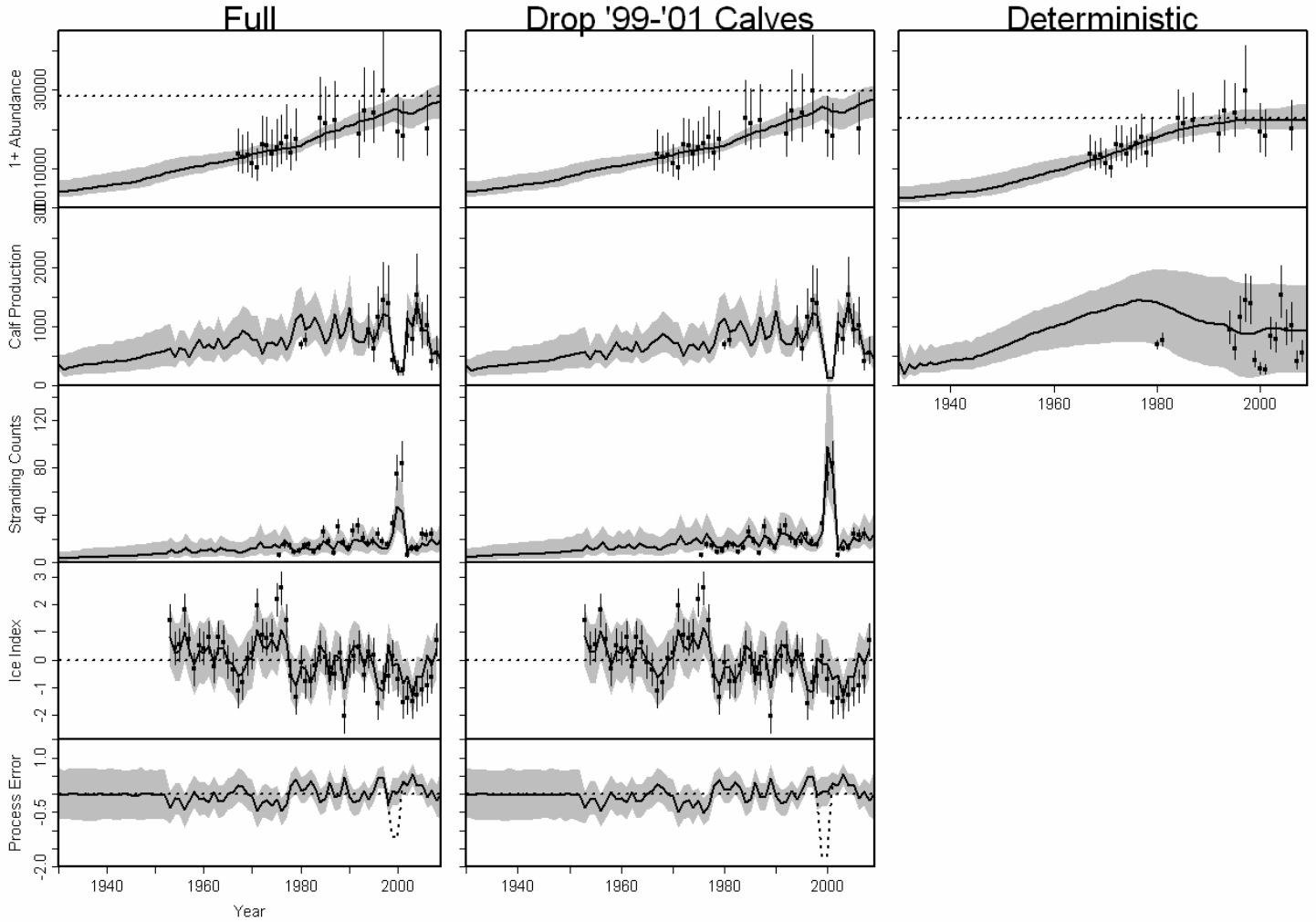


Fig. 4. Model fits are shown: left column is the Full model; middle column is that model, but ignoring the low calf estimates from '99-'01, and; right column is the Deterministic model. From top to bottom: model fit to the abundance estimates; model fit to the calf estimates; model fit to the strandings data; model fit to the sea-ice data; and estimated process error deviations. The abundance estimates are plotted with the 95% CIs associated with the mode of the posterior distribution for CV_{add-1} . The median of the posterior estimate for carrying capacity is plotted as a horizontal line with the the abundance fits. For all plots, the medians and 95% Bayesian credibility intervals are shown as solid lines and shaded areas respectively. The calf estimates for '80-'81 were not fit for the first two scenarios, nor were any of the recent calf estimates fit for the Deterministic model. However, they are plotted for reference. Horizontal dotted lines at zero are plotted in the fits to the sea-ice data and the process error deviation estimates for reference. And the median of the posterior for ϵ_{add-1} is represented by the more vertical dashed line on the bottom two plots.

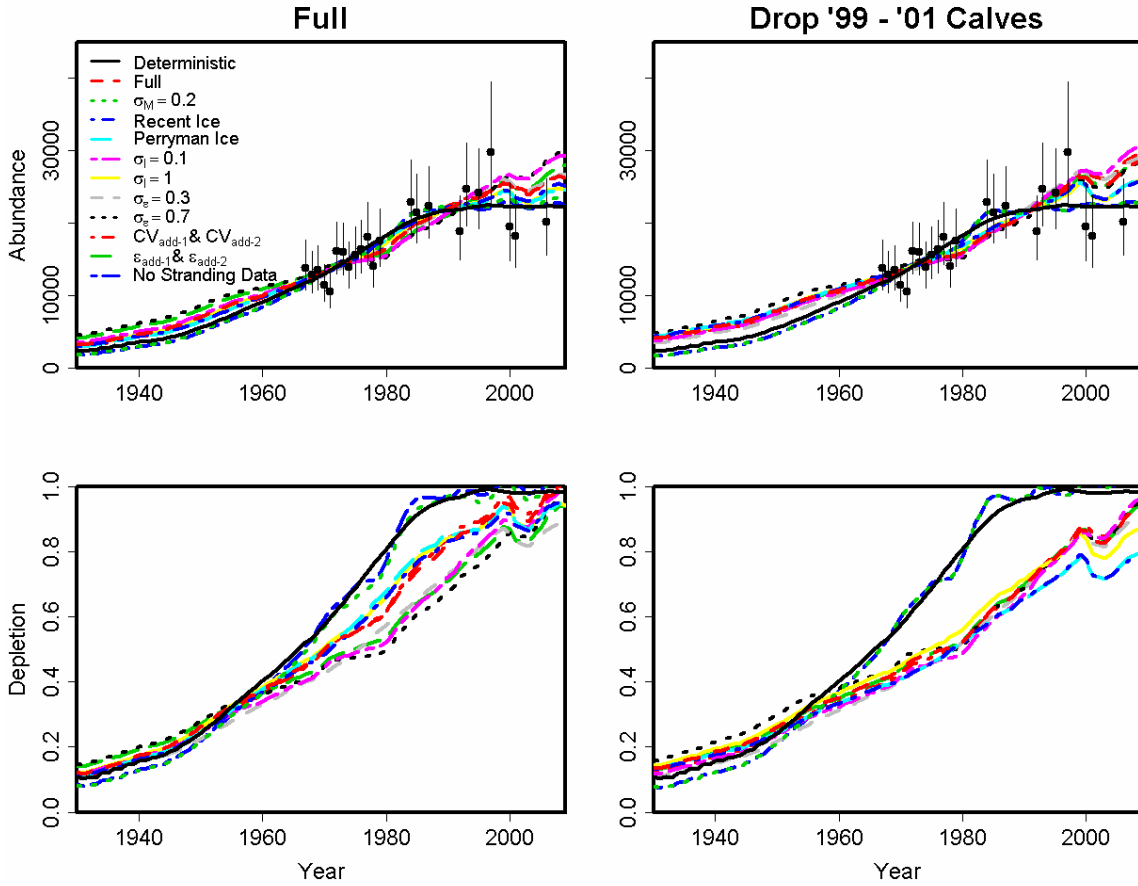


Fig. 5. Fits to the abundance data based on the maximum likelihood estimates for each scenario (upper panels) and the estimated depletion through time (bottom panels) are shown. The scenarios which fit all calf data are shown on the left, while those that ignored the '99-'01 data are shown on the right. The deterministic scenario is plotted as the solid black line. 95% CIs are plotted for the abundance estimates assuming a value for $CV_{add-1} = 0.10$.

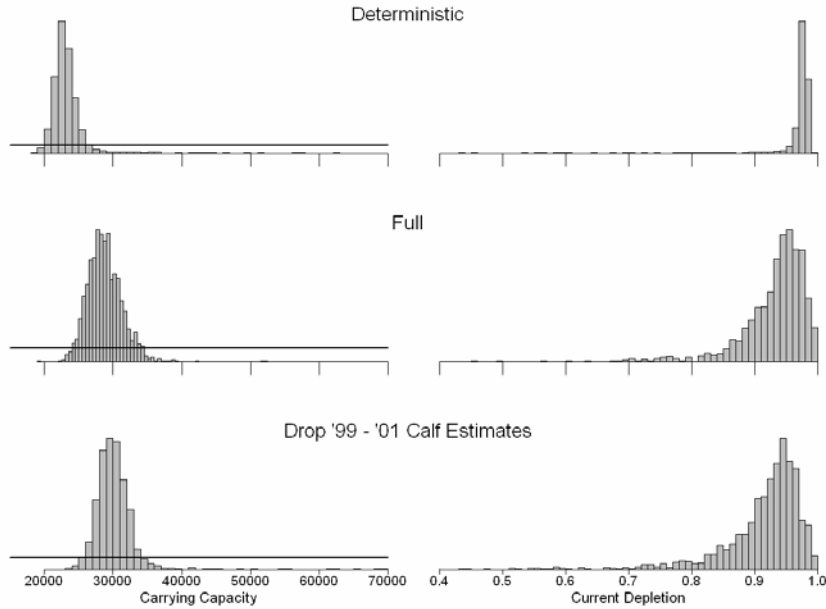


Fig. 6. Histograms are shown comparing marginal posterior densities (bars). Estimates of carrying capacity (plots on left side) and current depletion (right side) are shown. The upper row shows the samples from the posterior for the deterministic model, and the lower two rows shows samples from the posteriors for the stochastic model with (middle plots) and without the calf estimates from '99-'01 (lower plots) with environmental forcing. The uniform prior for carrying capacity is shown as a solid line.

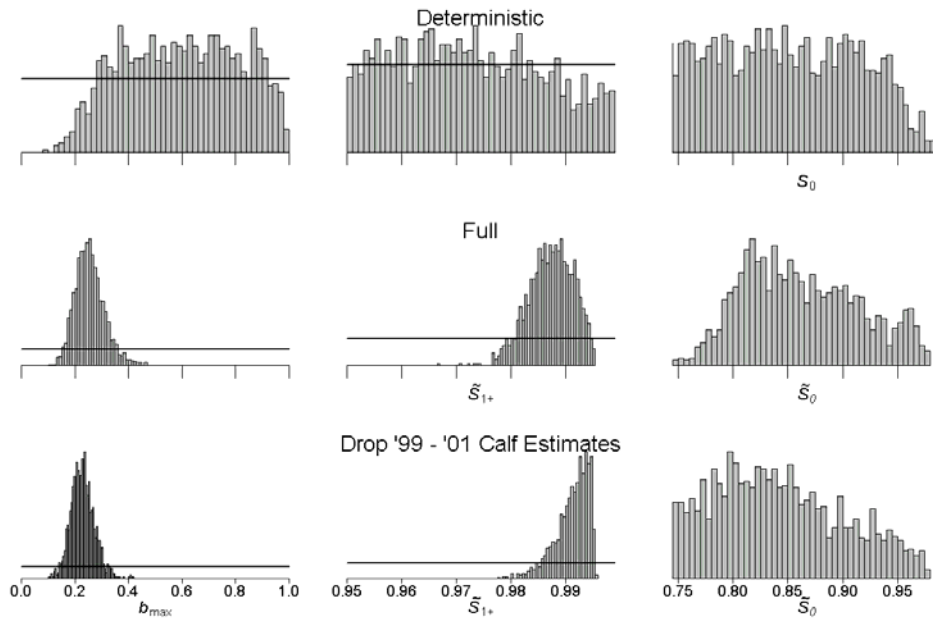


Fig. 7. Histograms are shown comparing marginal posterior densities (bars). Estimates of the maximum birth rate (in the limit of vanishing population size) (left column), survival rate of non-calves S_{1+} (middle column), and calf survival S_0 (right column) are shown. The upper row shows the samples from the posterior for the deterministic model, and the lower two rows shows samples from the posteriors for the Full model with (middle row) and without the calf estimates from '99-'01 (bottom row). The survival rates for the Full model are shown as the medians through time, in order to provide a better comparison with those estimates from the deterministic model. The uniform priors are shown as solid lines.

APPENDIX A: DERIVATION OF EQNS. 2 AND 3

In a given year, the realized stochastic birth rate can be written as a logistic function of a parameter related to the expected birth rate μ_t and process error ε_t that year:

$$b_t^* = [1 + \exp(-(\mu_t + \varepsilon_t))]^{-1} \quad \text{where:} \quad \varepsilon_t \sim N(0, \sigma_\varepsilon^2) \quad \text{A.1}$$

Further, let $\mu_t^* = \mu_t + \varepsilon_t$ where $\mu_t^* \sim N(\mu_t, \sigma_\varepsilon^2)$. Now, given a random variable generated from some underlying distribution $X \sim f(x)$ and a function of this random variable $Z = h(X)$, the expectation of the function can be written:

$$E[Z] = \int_{-\infty}^{\infty} h(x)f(x)dx \quad \text{A.2}$$

It is necessary to define the expectation of the stochastic birth rates as equal to the deterministic value from the Pella-Tomlinson model (Eqn. 1), i.e. $E[b_t^*] = b_t$ to model density dependence acting solely through the stochastic birth rate. Proceeding from the form of the expectation above, while noting that $b_t^* = h(\mu_t^*) = [1 + \exp(-\mu_t^*)]^{-1}$ and likewise, given its additive nature, that $\mu_t^* \sim N(\mu_t, \sigma_\varepsilon^2)$, substitute for $h(x)$ and $f(x)$ in equation A.2 and write the analytical expectation of the stochastic birth rates (Punt, 2008):

$$E[b_t^*] = \int_{-\infty}^{\infty} [1 + \exp(-\mu_t^*)]^{-1} \left[\frac{1}{\sigma_\varepsilon \sqrt{2\pi}} \exp\left(-\frac{(\mu_t^* - \mu_t)^2}{2\sigma_\varepsilon^2}\right) \right] d\mu_t^* \quad \text{A.3}$$

It was found through numerical methods that, the integral on the right side is well approximated by:

$$\approx \Phi\left(\frac{\mu_t}{\sqrt{2.76 + \sigma_\varepsilon^2}}\right) \quad \text{A.4}$$

where:

Φ is the standard normal cumulative distribution function.

2.76 is a value found through numerical minimization, which satisfies this expectation.

Setting the expectation of the stochastic birth rates equal to the deterministic density dependent rate:

$$\Phi\left(\frac{\mu_t}{\sqrt{2.76 + \sigma_\varepsilon^2}}\right) = b_t \quad \text{A.5}$$

And finally, rearranging to solve this equation for μ_t and substituting back into equation A.1 yields Eqns. 2 and 3. Of course, for those years with added process error, the stochastic expectation will not necessarily be equal to the deterministic value.