Testing the *Gray Whale* Strike Limit Algorithm (*SLA*): allowing environmental variability to influence population dynamics

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ABSTRACT

The performance of the *Gray Whale SLA* is evaluated based on an operating model conditioned on available information for the eastern North Pacific stock of gray whales including: survey estimates of 1+ abundance; calf counts; strandings data; and the extent of sea-ice in the feeding grounds in the Bering Sea in the early season. Multiple scenarios are considered in the analyses to explore the impact of different sources of environmental variation, including scenarios in which future environmental forcing and episodic events are driven by the relationships between reproductive success and survival to sea ice. A variety of sources of uncertainty are considered, including parameter uncertainty, the uncertainty about the relationship between the extent of sea-ice and population dynamics, and observation error. The impact of these sources of uncertainty on the performance of the *Gray Whale SLA* is small. For all scenarios considered in the simulations, application of the *SLA* results in the stock being at or near carrying capacity at the end of a 92 year projection period for which sea-ice cover forecasts are available, while still satisfying the needs of aboriginal whalers.

KEYWORDS: BIRTH RATE; CLIMATE CHANGE; ICE; MANAGEMENT PROCEDURE; MODELLING; MORTALITY RATE; WHALING–ABORIGINAL; GRAY WHALE

INTRODUCTION

The IWC has established a procedure (an '*Implementation*') to provide scientific advice on catch limits for different whale stocks (e.g. IWC, 2012). The eastern North Pacific (ENP) population of gray whales is currently subject to aboriginal hunting, with recommended strike limits based on the *Gray Whale Strike Limit Algorithm* (*Gray Whale SLA*) under the Aboriginal Subsistence Whaling Management Procedure (AWMP) of the IWC (IWC, 2003). *Implementation Reviews* are scheduled under the AWMP every five years. The goal of *Implementation Reviews* is to evaluate new information that has become available since the last *Implementation Review* (or the original *Implementation*), *inter alia* to determine whether the current state of nature is outside the realm of plausibility envisioned during the simulation testing of the original *SLA*. If this is the case, additional simulation trials may be conducted to assess whether the anticipated performance of the *SLA* adopted remains reasonable, and if not, what changes to the *SLA* are needed.

New or updated sources of information pertaining to the population dynamics of ENP gray whales have become available in recent years, including: (1) new abundance estimates (Rugh *et. al.,* 2008); (2) new estimates of calf production during 1994–2008 from the northbound migration at Point Piedras Blancas, California (Perryman *et al.*, 2002; Perryman, unpublished data); and (3) the number of stranded animals on the coasts of California, Oregon and Washington states, for which a combined annual count is available for 1975–2006 (Brownell *et al.*, 2007). The last data source potentially contains information on the magnitude of the mortality event during 1999/2000 (Gulland *et al.*, 2005). In addition to these data sets, it has been hypothesised that observed variability in the calf counts is a function of the amount of sea-ice covering the feeding

grounds in the Bering Sea in the early season (Perryman *et al.*, 2002).

Accordingly, in this paper the performance of the *Gray Whale SLA* is tested given scenarios when future population dynamics are subject to environmental forcing and episodic events, using an operating model that integrates these sources of new information and the hypothesis of environmental forcing on the population dynamics (Brandon and Punt, 2009). A forecast of relevant sea-ice conditions based on global climate model output (Overland and Wang, 2007) is used to modify the future stochastic birth and survival rates generated when testing the *SLA*, given the estimated relationships of calf production and strandings data to observed variations in recent sea-ice. This technique involves the incorporation of climate-model-based forecasts into the operating model. The same basic framework is also being used to test the performance of alternative management approaches in other fisheries (e.g. Gulf of Alaska and Eastern Bering Sea walleye pollock, *Theragra chalcogramma*; A'mar *et al.*, 2009; Ianelli *et al.*, 2011).

Standard summary statistics are provided for the trials investigated here, and these are compared to results from the *Evaluation Trials* provided by Punt and Breiwick (2008) to the extent possible. The analyses presented here should help to ensure that the anticipated performance of the current *Gray Whale SLA* remains satisfactory (or else provide insight into potential weaknesses), given the new information that has become available since the phase of testing and adoption reported in IWC (2005a).

METHODS
Operating model
The population dynamics model developed by Brandon and Punt (2009) (corresponding to their 'Full' scenario) was used as the operating model. This model is sex- and age-based,
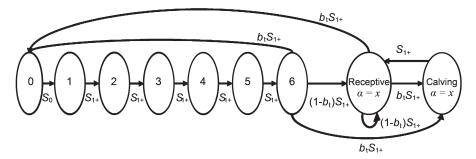
Fig. 1. Life cycle graph of the model used to track the number of females in each reproductive stage though time. This life cycle refers to the underlying deterministic model, with transition probabilities shown as functions of life history parameters. However, it should be noted that the birth and survival rates were modified to be stochastic in the all analyses except for 'H0'. The arrow from immature to calf arises because some immatures may mature and give birth (i.e. become pregnant at first estrous) during the projection interval from time t to $t+1$.

with an annual time-step. The dynamics include stochastic birth and survival rates, and explicitly consider the transition between receptive and calving stages for mature females (Fig. 1). For consistency, the notation of Brandon and Punt (2009) is adopted below.

Density dependence was assumed to act through the birth rate according to a Pella-Tomlinson function of 1+ depletion:

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

where b_{max} is the maximum birth rate (in the limit of zero population size); K_1 is the carrying capacity in terms of the 1+ component of the population (all animals aged 1 year and older)[1]; 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 a population size approximately 60% of K_1, the conventional value for MSYL assumed for whale populations, e.g. IWC, 2005a); and $N_{1+,t}$ is the size of the 1+ component of the population (both sexes combined) at the start of year t.

Selectivity was assumed to be knife-edged and uniform for ages 5+, catches were assumed to be taken at the start of the year, before natural mortality, and the population trajectories were initialised in 1930, under the assumption of a stable-age-distribution given some level of hunting mortality in 1930 (as in Brandon and Punt, 2009). Process error after 1930 ensures that the age-structure by the time data are available is non-equilibrium.

Deviations from expected birth and survival rates were allowed to be functions of sea-ice variability in the Bering Sea. Thus, the operating model is an adaptation of the hypothesis that the variability in calf production the following year may be related to the amount of sea-ice in the Bering Sea early during the feeding season (Perryman *et al.*, 2002). Birth rates were assumed to vary annually about the deterministic value given by Equation (1). Since this rate must lie between zero and one, its realisation in any one year was calculated using a logistic transformation:

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

Where Φ^{-1} is the inverse standard normal cumulative distribution function; ε_t is the process error deviation for year t, $\varepsilon_t \sim N(0; \sigma_\varepsilon^2)$, σ_ε is a measure of the extent of variability in process error and; allows for additional process error in the birth (and survival) rate during years with extraordinary dynamics, such as 1999 and 2000 (in other years before 2009, this parameter was set equal to zero; see below for how future catastrophic events are generated). This formulation of stochastic birth rates (e.g. the 2.76 factor) ensures that the expected birth rate in a given year equals the deterministic value from Equation (1) (see Appendix A of Brandon and Punt, 2009). The form of Equation (2) (and (3)) is such that 'positive' catastrophic events can lead to very high survival and birth rates (where the maximum birth rate is bounded by 0.99). However, it should be noted that Equation (2) only applies to receptive females and that a high birth rate in one year will result in a decrease in receptive females and hence a lower pregnancy rate the following year (Fig. 1).

Survival rates were also allowed to vary annually with the same process error deviations as birth rates to reflect the assumption that survival and birth rate covary. The effects of process error on survival and birth rate are assumed to be the same in the absence of data to distinguish these sources of process error. It was assumed that process error in survival rates were independent of sex and perfectly correlated between ages in a given year, so that:

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

where $S_{a,t}^*$ is the realised age-specific survival rate during year t; and S_a is the expected survival rate from age a to age $a+1$.

Conditioning

The operating model was conditioned on available data, including: (1) estimates of population size during 1967–2006 (covering the years of surveys) from the southbound migration at Granite Canyon, California (Rugh *et al.*, 2005; 2008); (2) estimates of calf production during 1994–2008[2] from the northbound migration at Point Piedras Blancas,

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[1] Strictly, K_{1+} is only the carrying capacity in the deterministic case (no fluctuations in birth rate and no catastrophic events). It should be interpreted here as a parameter which relates to stochastic carrying capacity. The latter could be defined as the average long-term population size in the absence of catches.

[2] The two early estimates of calf production during 1980–1981 (Poole, 1984) were not used in these analyses.
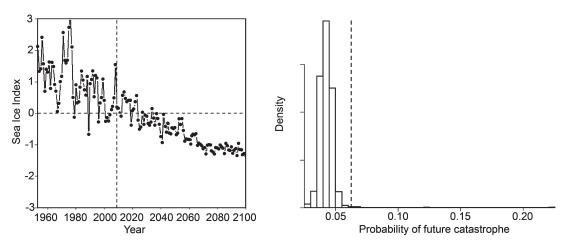
Fig. 2. Left panel: The standardised index for the March–April average sea-ice area covering the Bering Sea. The vertical dashed line denotes 2009 and the start of that portion of the time series which is based on the ensemble global climate model mean predictions provided by Overland and Wang (2007). Prior to 2009, the time series is based on the HadSST observations of sea-ice (Rayner *et al.*, 2003). The horizontal dashed line at zero is shown for reference; positive values indicate years with greater than average sea-ice over the entire time period and *vice versa*. Right panel: The distribution for the probability of a future catastrophe in any one year. This distribution is conditioned on the number of years for which the depletion of each trajectory is greater 0.40 during 1930–2008, divided by 2 (the number of years with observed catastrophes, corresponding to 1999 and 2000) (Brandon and Punt, 2009). The dashed vertical line denotes the probability as calculated from the strandings index (Brownell, *et al.*, 2007).

California (Perryman *et al.*, 2002; Perryman, unpublished data); (3) the number of stranded animals on the coasts of California, Oregon and Washington states, for which a combined annual count is available for 1975–2006 (Brownell *et al.*, 2007)[3]; and (4) estimated sea-ice area cover in the Bering Sea, averaged over March and April during 1953–2008, as calculated by the Hadley Center for their sea ice and sea surface temperature data set version 1 ('HadSST') (Rayner *et al.*, 2003) (see Fig. 2, left panel). The conditioning process involves fitting the operating model to the data and estimating posterior distributions from the basis for probabilistic projections of future population dynamics.

The deviations of birth and survival rates about the deterministic relationship each year were allowed to be related to an environmental index I_t (the amount of sea-ice covering the Bering Sea) during the conditioning. 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 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:

$$I_t^{obs} = \beta \varepsilon_t + \gamma_t \qquad (4)$$

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:

$$\sigma_I = |\beta| \sigma_I^* \qquad (5)$$

This formulation takes a fixed input value for (assumed to be 0.30 for these analyses, corresponding to the 'Full' model of Brandon and Punt, 2009) and scales the expected standard deviation of the fits to the environmental index by the estimated absolute value for β.

Future projections

Once the operating model was conditioned on the available data, it was possible to project simulated population trajectories into the future. Each forward projection was initialised in 2009, based on the estimated status of the simulated population and the parameter values (e.g. K_{1+}, b_{max} etc…) for a given trajectory from the joint Bayesian posterior distribution. The posterior was constructed using the MCMC algorithm during the conditioning phase (Brandon and Punt, 2009).

Future values for the sea-ice index were based on an ensemble mean forecast of sea-ice in the Bering Sea (March–April average) (Overland and Wang, 2007). The trials were based on a 92-year time horizon ($T = 92$), because the time series of forecasted sea-ice was only available until 2098. In a given year, the process error deviations about the expected birth and survival rates were a function of forecasted sea-ice according to:

$$\varepsilon_t = \left(I_t^{obs} / \beta \right) - \gamma_t \qquad (6)$$

where I_t^{obs} is the forecasted value of the sea-ice index for year t (Fig. 2, left panel); and $\gamma_t \sim N(0; \sigma_I^2)$

Future abundance estimates were assumed to become available every 10 years. Observation error was assumed to be log-normal:

$$N_{1+,t}^{obs} = N_{1+,t} e^{\phi_t} \qquad (7)$$

[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 over time.

where $I_{1+,t}^{obs}$ is the survey estimate of 1+ abundance for year t; $N_{1+,t}$ is the 'true' 1+ abundance at the start of year t; $\phi_t \sim N(0;\sigma^2)$; where $\sigma = \sqrt{\overline{CV}_{est}^2 + CV_{addA}^2}$; CV_{addA} is the extent of additional error about the abundance estimates (sampled from the joint posterior), and; $\overline{CV}_{est}$ is the expected (sampling) standard deviation of the logarithm of $N_{1+,t}^{obs}$:

$$\overline{CV}_{est} = \sqrt{\tfrac{1}{Y}\sum_{y=1}^{Y} CV_y^2} \qquad (8)$$

where y indexes years for which there are survey data up to 2008; CV_y is the sampling CV associated with the abundance estimate for year y; and Y is the total number of years with past surveys. The estimates of abundance and $\overline{CV}_{est}$ (as distinct from σ) were passed to the *SLA*. No attempt was made to account for further estimation error in the abundance estimates (i.e. mean school size estimation error calculations were ignored).

Need[4]

The annual need Q_t for year t was calculated according to the 'need envelope':

$$Q_t = Q_{2009} + \frac{t-2009}{91}\left(Q_{2098} - Q_{2009}\right) \qquad (9)$$

where Q_{2009} (= 150) is the present need; and Q_{2098} is the final need (in year 2098). The level of need supplied to the *SLA* was the total (block) need for the 5-year period for which the strike limits were to be set. Two values were assumed for final need (in year 2098), corresponding to the 'base case' ($Q_{2098} = 340$) and 'high need' ($Q_{2098} = 530$) trial levels used in previous testing of the *SLA* (IWC, 2003).

Trials

The set of trials is listed in Table 1. In addition to the two levels of final need, six scenarios were explored with respect to p^*, the future probability (if any) of catastrophic (otherwise known as 'episodic') events, and the nature of stochastic (or deterministic) population dynamics.

(1) (H0) Deterministic population dynamics with no future catastrophic events[5];

(2) (H1) Environmental stochasticity (as a function of sea-ice) with no future catastrophic events;

(3) (H2) Environmental stochasticity (as a function of sea-ice), with probability of future catastrophic events conditioned on the stranding index (0.0625, the proportion of years for which an episodic event was observed, divided by the total number of years in the strandings index (2yr/32yr) (Brownell *et al.*, 2007));

(4) (H3) Environmental stochasticity (as a function of sea-ice) with the probability of future catastrophic events conditioned on the percentage of times they occurred during the fitting process when 1+ depletion was greater than 0.40 (Eqn. 9; Fig. 2 right);

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[4] This is the number of whales a country or the Commission specifies is required to satisfy cultural and subsistence 'needs' before taking the conservation situation into account

[5] The two deterministic trials are most comparable with the base case operating models in IWC (2004).

(5) (H4) As for H3, but the environmental stochasticity was independent of the sea-ice index, i.e. simply $\varepsilon_t \sim N(0,\sigma_\varepsilon^2)$; and

(6) (H5) As for H4 but with no future catastrophes.

A depletion level of 0.40 during the conditioning phase was used for calculating the probability of future episodic events for scenarios H3 and H4 because the population almost always recovers to 40% of carrying capacity by when the catastrophes occur. The probability of future catastrophes p^* conditioned on the percentage of times they occurred during the fitting process when 1+ depletion was greater than 0.40 was then:

$$p^* = 2\left[\left(\sum_{t=1930}^{2008} I(N_{1+,t}/K > 0.4)\right)^{-1}\right] \qquad (10)$$

where $I()$ is the indicator function. Hence, a future year was determined to be either normal ($\varepsilon_{add} = 0$) or catastrophic by drawing a random variate from a Bernoulli distribution with probability p^* for these scenarios if the 1+ depletion was greater than 0.40. Future catastrophic years were modelled through the inclusion of the estimated ε_{add} parameter into Eqn. 2 and 3 for birth and survival rates during those years (Fig. 2, right).

No attempt was made to model correlation between years with catastrophes, i.e. the probability of a catastrophe occurring did not depend on the whether or not there was one the previous year.

Performance statistics

The performance statistics were calculated based on future block quotas returned from the standalone version of the 'GUP2' *SLA* (IWC, 2005b; Punt and Breiwick, 2008). All performance statistics were computed in terms of the age 1+ component of the population following the standard methods and notation of the AWMP (IWC, 2003). Specifically, four performance statistics were calculated:

(1) (D1) Final depletion: $N_{1+,2098}/K_{1+}$;

(2) (D8) Rescaled final population size: $N_{1+,2098}/N_{1+,2098}^*$, where $N_{1+,2098}$ is the 1+ population size in 2098, under a scenario of zero future catches;

(3) (D10) Relative increase: $N_{1+,2098}/N_{1+,2009}$; and

(4) (N9) Average need satisfaction: $\dfrac{1}{T}\sum_{t=2009}^{2098}\dfrac{C_t}{Q_t}$

where T is the number of years in the projection period; and C_t is the catch during year t, which is determined by the *SLA* through the 5-year block quota system.

RESULTS

1,601 simulations were run for each scenario, corresponding to the number of samples from the posterior provided by Brandon and Punt (2009). In general, the *Gray Whale SLA* was able to satisfy need and maintain a population size near carrying capacity for all of scenarios examined in these analyses. For example, all of the scenarios with base need had an average need satisfaction of 100% and the lowest median final 1+ depletion was 0.874 (Table 2). Not

Table 1

The scenarios considered. The trials are denoted by an 'H' followed with the trial number and then 'BN' or 'HN' for base or high final need. Descriptions are given for each scenario in terms of the stochastic or deterministic nature of the population dynamics and the probability of future catastrophes.

Trial	Description	σ_ε	Final need	Probability of future catastrophe	Future stochasticity
H0:BN	Deterministic + no future catastrophes	N/A	340	0	None (deterministic)
H1:BN	Environmental stochasticity + no future catastrophes	0.5	340	0	Environmental
H2:BN	Environmental stochasticity + p(future catastrophe) = 0.0625	0.5	340	0.0625	Environmental
H3:BN	Environmental stochasticity + p(future catastrophe) = p^*	0.5	340	p^* (Eqn. 10)	Environmental
H4:BN	Stochasticity (no sea-ice) + p(future catastrophe) = p^*	0.5	340	p^* (Eqn. 10)	Environmental (no sea-ice)
H5:BN	Stochasticity (no sea-ice) + no future catastrophes	0.5	340	0	Environmental (no sea-ice)
H0:HN	Deterministic + no future catastrophes	N/A	530	0	None (deterministic)
H1:HN	Environmental stochasticity + no future catastrophes	0.5	530	0	Environmental
H2:HN	Environmental stochasticity + p(future catastrophe) = 0.0625	0.5	530	0.0625	Environmental
H3:HN	Environmental stochasticity + p(future catastrophe) = p^*	0.5	530	p^* (Eqn. 10)	Environmental
H4:HN	Stochasticity (no sea-ice) + p(future catastrophe) = p^*	0.5	530	p^* (Eqn. 10)	Environmental (no sea-ice)
H5:HN	Stochasticity (no sea-ice) + no future catastrophes	0.5	530	0	Environmental (no sea-ice)

surprisingly, those scenarios based on higher final need resulted in lower final depletion levels and lower average need satisfaction. However, the differences were not large (e.g. the lowest median 1+ depletion for the high need scenarios was 0.817). Moreover, none of the scenarios resulted in a lower 5th percentile for the final 1+ depletion less than 0.60. The relative increase statistic (D10) was close to 1 for all scenarios. The increase in population size is somewhat constrained because even under decreases in ice cover, Eqn. 1 still imposes an upper bound on abundance.

The distribution of probabilities of future catastrophes for the 'H3' and 'H4' scenarios is shown in Fig. 2 (right panel). The probability of future catastrophe ranged between 0.025 and 0.222 for those scenarios, with a median of 0.043, which was less than that when conditioned on the stranding index. However, the average difference between these two

approaches was relatively small, as evidenced by the nearly identical results for these two assumptions (Table 2; Fig. 3).

The predicted area of sea-ice on the Bering Sea feeding grounds is forecast to decrease dramatically, with less than 50% of the average observed area of sea-ice in March–April during future decades (Fig. 2, left panel; Overland and Wang, 2007). The scenarios H1, H2, and H3 with population dynamics that are a function of this sea-ice index resulted in the most optimistic outcomes (Table 2), with some final depletion levels slightly greater than 1.0. On the other hand, the two scenarios that modelled generic environmental stochasticity independent of sea-ice (H4 and H5) resulted in the most pessimistic final depletion levels of any of the scenarios investigated (Table 2). Likewise, the trend in process error deviations was very different between these two sets of scenarios. Those scenarios which modelled

Table 2

The medians, and upper and lower 5th percentiles of the performance statistics for each scenario. See text for the definitions for each of the performance statistics.

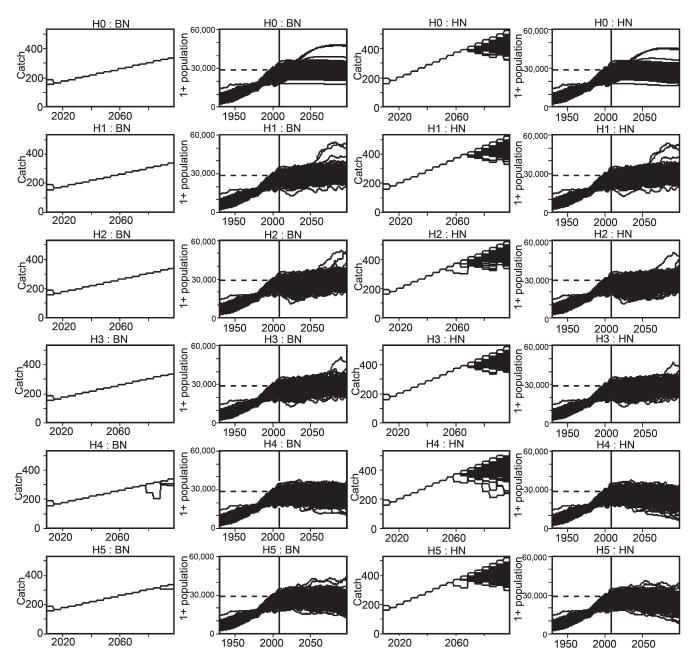| Trial	Description	D1: Final 1+ depletion			D8: Rescaled 1+ depletion			D10: 1+ relative increase			N9: Avg. need satisfaction		
		5%	Median	95%	5%	Median	95%	5%	Median	95%	5%	Median	95%
H0:BN	Deterministic + no future catastrophes	0.908	0.933	0.950	0.875	0.918	0.948	0.947	0.986	1.095	1.000	1.000	1.000
H1:BN	Environmental stochasticity + no future catastrophes	0.940	0.981	1.030	0.910	0.965	1.019	0.973	1.041	1.179	1.000	1.000	1.000
H2:BN	Environmental stochasticity + p(future catastrophe) = 0.0625	0.914	0.974	1.026	0.886	0.959	1.016	0.954	1.032	1.158	1.000	1.000	1.000
H3:BN	Environmental stochasticity + p(future catastrophe) = p^*	0.922	0.976	1.027	0.896	0.961	1.017	0.960	1.034	1.167	1.000	1.000	1.000
H4:BN	Stochasticity (no sea-ice) + p(future catastrophe) = p^*	0.745	0.874	0.953	0.731	0.861	0.945	0.807	0.932	1.050	1.000	1.000	1.000
H5:BN	Stochasticity (no sea-ice) + no future catastrophes	0.802	0.897	0.960	0.775	0.883	0.954	0.846	0.952	1.066	1.000	1.000	1.000
H0:HN	Deterministic + no future catastrophes	0.855	0.899	0.927	0.833	0.884	0.921	0.913	0.950	1.038	0.971	0.980	0.988
H1:HN	Environmental stochasticity + no future catastrophes	0.913	0.963	1.017	0.889	0.946	1.006	0.951	1.022	1.156	0.974	0.981	0.988
H2:HN	Environmental stochasticity + p(future catastrophe) = 0.0625	0.880	0.954	1.011	0.858	0.937	1.001	0.927	1.011	1.132	0.973	0.981	0.988
H3:HN	Environmental stochasticity + p(future catastrophe) = p^*	0.894	0.957	1.013	0.868	0.941	1.002	0.932	1.015	1.138	0.973	0.981	0.988
H4:HN	Stochasticity (no sea-ice) + p(future catastrophe) = p^*	0.657	0.817	0.917	0.649	0.805	0.909	0.725	0.873	0.989	0.959	0.979	0.987
H5:HN	Stochasticity (no sea-ice) + no future catastrophes	0.722	0.847	0.927	0.707	0.834	0.921	0.776	0.901	1.013	0.964	0.980	0.988

Fig. 3. Time-trajectories of future catches (first and third columns) and population trajectories from 1930–2098 (second and fourth columns) for the twelve scenarios (Table 1). The left and right pairs of columns are respectively for a final need levels of 340 and 530 whales per year. The results for each simulation are plotted as an individual line (thus a single visible line for catches represents a series of years where future catches were identical across scenarios).

process error as a function of future sea-ice resulted in an increasing trend in the size of process error deviations, while those scenarios which modelled environmental stochasticity as an independent process led to no such trend (Fig. 4). However, in terms of the median average need satisfaction, there was essentially no difference amongst all the scenarios; the *SLA* was able to achieve high need satisfaction for all of those examined here (Table 2).

The results of the 'deterministic' trials (H0) were more optimistic than those of the corresponding trials on which the *Gray Whale SLA* was based (GE01 and GE14) (compare table 2 of Breiwick *et al.* (2009) with the results for the two H0 trials in Table 2 of this paper). However, the differences in the values for the performance statistics are slight, and qualitatively the results of trial H0 and GE01 are identical. The differences in results are attributable to a variety of

causes, including differences in the population dynamics models, in the data used to condition the operating model, and in the priors for the parameters of that model.

DISCUSSION

The approach taken here allows a forecast for an index of environmental variability to be incorporated into an operating model, which can be used to test management approaches given hypothesized interactions between the environment and population dynamics. These trials differ slightly from the standard set designed by the Standing Working Group of the AWMP during the original *Implementation* of the *Gray Whale SLA* (IWC, 2005a) in that they are conditioned on updated and newly available data, as well as a hypothesis regarding the effect of sea-ice on deviations in demographic rates. Hence, these analyses serve
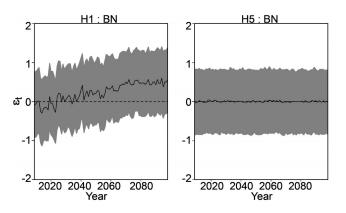
Fig. 4. The time-trajectories of future process error deviations for a case where these deviations are a function of future sea-ice (H1:BN; left panel) and where they are independent of the sea-ice index (H5: BN; right panel). The annual median is plotted as the solid line, the 90% probability interval envelope is shaded in gray, and the horizontal dashed line at zero is shown for reference.

to take account of new information that has become available since the original *Implementation*. The results provide evidence that the current state of nature is not outside the realm of plausibility envisioned during the simulation testing of the original *SLA*.

The magnitude of future additional mortality events was assigned in an *ad hoc* manner during the original *Implementation* of the *Gray Whale SLA*, i.e. future events were assumed to result in 20% declines in abundance (a likely large value, chosen to test the robustness of the *SLA*). In these analyses however, the operating model is conditioned in part on the strandings data, which allows the deviations in survival rates during the 1999/2000 mortality event and the resulting population size at the start of the future trajectories to be estimated directly. Likewise, the observed frequency and magnitude of those mortality events determined when conditioning are used to model the potential impact of future events. A set of several alternative trials was also preformed, to compare the results of the environmental forcing scenario to those for which future population dynamics were assumed to be deterministic, or to be subject to random environmental stochasticity (i.e. ignoring possible sea-ice impacts). For all of the scenarios considered here, the *Gray Whale SLA* was able to maintain stock size and satisfy need at higher levels. Therefore, there is no indication from these analyses that any revisions to the *SLA* are necessary.

While the *SLA* performed well under the scenarios considered in these analyses, there is still considerable uncertainty about how changes in sea-ice (or other environmental conditions) will affect future population dynamics. At present, the available information about the affects of environmental variability on cetacean population dynamics is largely correlative in nature, with the underlying mechanisms responsible for fluctuations in birth and survival rates not well understood. Although a plausible explanation has been hypothesised for ENP gray whales (i.e. that sea-ice may act as a physical barrier to prime feeding habitat), it is not straightforward to predict how other changes resulting from reductions in sea-ice will interact with the mechanisms that are currently influencing the dynamics of this population. Therefore, the conclusion that the *Gray Whale*

SLA is robust to predicted changes in sea-ice should be tempered by uncertainty regarding the underlying assumption that current ecological processes will remain unchanged in the future, especially when so many other fundamental changes in ecosystems are expected as a result of climate change. Indeed, this one is one of the reasons *Implementation Reviews* are mandatory.

The assumption that the population dynamics were related to sea-ice led to more optimistic results. This was essentially the result of extrapolating (based on those years for which calf production and strandings data exist) a recent relationship between the environment and population dynamics into the future, under the assumption that such an effect (if it exists) would be invariant over time and independent of population density, among other factors. While more optimistic results would have been expected given the nature of the relationship between calf production and sea-ice cover, the magnitude of the effect could not be determined *a priori*. In addition, it was possible that the impact of trends in birth rate and survival could have 'confused' the *SLA* and led to poorer performance (e.g. the models underlying the *SLA*s could have concluded that the stock was depleted rather than close to carrying capacity) and reduced the strike limit.

The operating model used here could be modified to take into account alternative hypotheses with respect to predicted changes in the relationship between future environmental variability and population dynamics. For example, it would be relatively straightforward to model a change-point in the relationship between deviations in demographic rates and sea-ice, such that a loss of sea-ice might be beneficial up to some future time, after which the continued loss of sea-ice results in negative effects on population dynamics (e.g. by changing the sign of β after some future year). The operating model could then be used to test the performance of the *SLA* under such scenarios. A disadvantage of this approach would be that there are no data to determine the magnitude of negative effects, so any results would be speculative.

One of the appealing attributes of the framework for incorporating environmental data is its flexibility. As continuing research provides more insight into the mechanisms underlying the impacts of environmental variability on the population dynamics of ENP gray whales, the basic operating model used here can provide a basis for integrating this new information into assessments and evaluating alternative management approaches. For example, alternative environmental data (e.g. an index of El Niño/Southern Oscillation, a sea-ice index on the Chukchi Seas feeding grounds, or some weighted combination of different indices) could be substituted during the model fitting process to take alternative hypothesised relationships between environmental variability and population dynamics into account. Likewise, the framework could, with some modification, be applied to other populations of cetaceans for which environmental fluctuations are hypothesised to be an important determinant of population dynamics. Therefore, this framework should help to ensure that management strategies are robust to hypothesised impacts of future environmental variability on cetacean population dynamics.

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