An examination of assessment models for the eastern North Pacific gray whale based on inertial dynamics

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ABSTRACT

Bayesian assessments of the eastern North Pacific stock of gray whales are conducted using the standard BALEEN II model and the inertia model developed by Witting (2000; 2001; 2003). The analyses confirm the increase in gray whale population size since 1968, but indicate that catches up to 256 animals per annum will lead to population decline if the inertia model is correct. However, analyses based on the standard BALEEN II model with a starting year of 1930 or 1968 fit the calf count data better than the inertia model, and indicate a population at its (current) equilibrium level and that the current catches are sustainable. The results of both the BALEEN II model and the inertia model are sensitive to the choice of the functional form used to represent density-dependence and those of the inertia model to the starting year for the analyses.

KEYWORDS: GRAY WHALE; POPULATION ASSESSMENT; TRENDS; MODELLING; WHALING-ABORIGINAL

INTRODUCTION

The eastern North Pacific (ENP) stock of gray whales (*Eschrichtius robustus*) was reduced substantially due to the impact of large and unsustainable harvesting during the late 19th Century (Fig. 1). No direct estimates of historical population size nor of the population size following the large historical commercial removals are available, although Townsend (1886) believed the stock to be only 160 individuals. Following the cessation of commercial harvesting, and under low aboriginal harvests, the population began to recover and surveys during the 1990s placed the population between 20,000 and 30,000 animals. The two most recent estimates of abundance (in 2001 and 2002) are, however, lower (18,200 and 16,900) prompting hypotheses that the population may have reached (or even exceeded) its (current) equilibrium level in the absence of harvest.

Given the lack of information on abundance prior to the commencement of the surveys at Granite Canyon in 1967, the only way to determine historical population sizes is through the use of population dynamics models. The models commonly used to assess whale populations assume that some population component (usually the birth rate/infant survival rate) is subject to density-dependent regulation. However, the inability of simple density-dependent population dynamics models to reconcile the catch history and abundance estimates for the ENP gray whales is well-known (Reilly, 1981; 1984; Cooke, 1986; Lankester and Beddington, 1986; Butterworth *et al.*, 2002). The inconsistency between these data sources arises because the stock must be relatively productive given the trend in population size inferred from the surveys off California. However, this implies that the stock should have recovered to its pre-exploitation level given the relatively low catches over the past 80-100 years. Reasons advocated to explain this inconsistency include large changes over time in carrying capacity and that the historical catches have been substantially under-estimated (Butterworth *et al.*, 2002).

Recent (Bayesian) assessments of this stock (Punt and Butterworth, 2002; Wade, 2002) have adopted a different approach to dealing with this inconsistency; they have not attempted to model the entire exploitation history but have instead started the population projections in a more recent year. The philosophy underlying these Bayesian assessments is to place a prior distribution on the abundance in a particular year (in general 1930) and to assume that the population had a stable age-structure at the start of that year. The population is then projected forwards to 2002 and the likelihood for the projection is calculated. The assumption that the population had a stable age-structure in 1930 is not unreasonable given the low catches for many of the years prior to 1930 (Fig. 1). The results are, in any case, insensitive to the first year considered in the analysis within a fairly wide range (Punt and Butterworth, 2002). The *Evaluation Trials* developed for the ENP gray whales (IWC, 2002; 2003) are based on a similar approach to assessing this stock.

Witting (2000) introduced the concept of inertial dynamics to discussions of large whales. An 'inertia model' involves the intrinsic values for some of the model parameters (e.g. the birth rate) differing among individuals and being determined from the state of the population (i.e. its size relative to some reference level) when they were born. The values for these parameters do not change over time. This concept leads to time-varying carrying capacity and the possibility of cyclic dynamics. Witting (2001; 2003) extended the concept of an inertia model by incorporating inertial dynamics into the BALEEN II model (de la Mare, 1989; Punt, 1999) and conducting Bayesian assessments of the ENP gray whales. These assessments were simultaneously able to both start the population projections prior to 1930 and provide adequate fits to the abundance data. They suggested, however, a much lower current replacement yield than indicated by previous assessments, essentially because they predicted a reduction in carrying capacity in the future. The analyses of Witting (2001) suggest a marked decline in abundance in the future, even in

the absence of exploitation, although those of Witting (2003), which were based on a different data set, were less pessimistic.

Even ignoring inertial dynamics, the assumptions on which the analyses conducted by Witting (2001; 2003) are based differ somewhat from those underlying the most recent assessments of the ENP gray whales (Punt and Butterworth, 2002; Wade, 2002). This paper therefore develops an approach to including inertial dynamics into the model (BALEEN II) on which most recent assessments of the ENP gray whales are based (i.e. the conventional BALEEN II model is a special case of this extended model).

The analyses by Witting (2001; 2003) imply marked changes over time in birth rate. Therefore, consideration is given to validating the results of the alternative models using the data on calf counts (e.g. Poole, 1984; Perryman *et al.*, 2002). No attempt is made in this paper to fit the population dynamics model to the calf count data.

METHODS
Extensions of the BALEEN II model
The BALEEN II model and the extensions thereof needed to start the population projections for a year other than that in which the population was last equal to its pre-exploitation size with the corresponding age-structure are described in detail by Punt (1999). The key extension needed to include inertial dynamics in the BALEEN II model is (after Witting, 2001; 2003) to allow the age-specific birth rate/infant survival rate to be 'intrinsic' and related to the conditions when an animal was born (i.e. each cohort has a different 'intrinsic' birth rate/infant survival rate). The equation that defines the number of 0-year-olds (of both sexes) at the start of year *t*, B_t, is given by:

$$B_t = \sum_{a=a_m+1}^{x} \tilde{\gamma}_{t,a} \beta_a (R_{t,a}^f + U_{t,a}^f) \qquad (1)$$

where:

$R_{t,a}^s$ is the number of recruited animals of sex *s* (f= female/m=male) and age *a* at the start of year *t*;

$U_{t,a}^s$ is the number of unrecruited animals of sex *s* and age *a* at the start of year *t*;

a_m+1 is the lowest age that a female can reach first parturition;

β_a is the fraction of females of age *a* which have reached the age at first parturition;

$\tilde{\gamma}_{t,a}$ is the birth rate for females of age *a* during year *t*:

$$\tilde{\gamma}_{t,a} = \begin{cases} 0 & \text{if } f_t \gamma_{t,a} < 0 \\ f_t \gamma_{t,a} & \text{if } 0 \leq f_t \gamma_{t,a} \leq f_{max} \\ f_{max} & \text{if } f_t \gamma_{t,a} > f_{max} \end{cases} \qquad (2)$$

$\gamma_{t,a}$ is the 'intrinsic' birth rate for females of age *a* during year *t*;

f_{max} is the maximum possible birth rate;

f_t is the impact during year *t* of density-dependence on the birth rate/infant survival rate for those age-classes for which all females have reached the age at first parturition, multiplied by the birth rate at pre-exploitation equilibrium, either:

$$f_t = \begin{cases} f_0 e^{\kappa(1-D_t/D_{-\infty})} & \text{exponential} \\ \max(0, f_0[1 + A\{1 - (D_t/D_{-\infty})^z\}]) \\ \qquad\qquad\qquad \text{Pella-Tomlinson} \end{cases} \qquad (3)$$

A is the resilience parameter for the Pella-Tomlinson model;

z is the density-dependence parameter for the Pella-Tomlinson model;

κ is the resilience parameter for the exponential model;

f_0 is the birth rate at pre-exploitation equilibrium;

x is the maximum age-class (treated as a plus-group and taken to be age 15);

D_t is the size, at the start of year *t*, of the component of the population to which density dependence is functionally related – density-dependence is assumed to be functionally related to the number of females that have reached the age at first parturition, P_t^M, for the calculations of this paper for consistency with the assumptions underlying previous assessments of the ENP gray whales), and

$D_{-\infty}$ is the value of D_t at pre-exploitation equilibrium.

The dynamics of the 'intrinsic' birth rate are given by:

$$\gamma_{t+1,a} = \begin{cases} g_{t+1} \dfrac{1}{P_{t+1}^M} \sum\limits_{a=a_m+1}^{x} \gamma_{t+1,a} \beta_a (R_{t+1,a}^f + U_{t+1,a}^f) & \text{if } a = 1 \\ \gamma_{t,a-1} & \text{if } 2 \leq a \leq x-1 \\ \dfrac{1}{R_{t+1,x}^f} \begin{pmatrix} \gamma_{t,x} R_{r,t,x}^f (1-F_{r,t,x}^f) S_x^f \\ + \gamma_{t,x-1} R_{r,t,x-1}^f (1-F_{r,t,x-1}^f) S_{x-1}^f \end{pmatrix} & \text{if } a = x \end{cases} \qquad (4)$$

where:

$F_{r,t,x}^s$ is the exploitation rate on 'recruited' animals of sex *s* and age *a* during year *t* (see Punt (1999) for details);

S_a^s is the (density-independent) survival rate for animals of sex *s* and age *a*;

P_t^M is the number of females that have reached the age at first parturition:

$$P_t^M = \sum_{a=a_m+1}^{x} \beta_a (R_{t,a}^f + U_{t,a}^f) \qquad (5)$$

g_t is the impact of density-dependence on the 'intrinsic' birth rate (governed by one of the following functional forms and constrained to be less than 5):

$$g_t = \begin{cases} e^{\phi\kappa(1-D_t/D_{-\infty})} & \text{exponential} \\ \max(0, 1 + A\phi\{1 - (D_t/D_{-\infty})^z\}) & \text{Pella-Tomlinson} \end{cases} \qquad (6)$$

ϕ determines the magnitude of 'inertial' dynamics.

The values for the $\gamma_{t,a}$ for the first year of the population projection, y_1, are set equal to 1. The function *g* determines the extent of inertial dynamics. The model outlined above collapses to the standard density-dependent population dynamics model (i.e. BALEEN II) if ϕ is set equal to 0, i.e. $\gamma_{t,a} = 1$ for all *t* and *a*.

Data and likelihood function
Fig. 1 plots the historical commercial and aboriginal catches. The sex-ratio of the commercial and recent aboriginal catch is known to be biased towards females. However, as no information is available about the sex-ratio of the historical (pre-1944) aboriginal catches, a 50:50 sex-ratio is assumed for these catches for consistency with previous analyses (e.g. IWC, 2002; 2003).
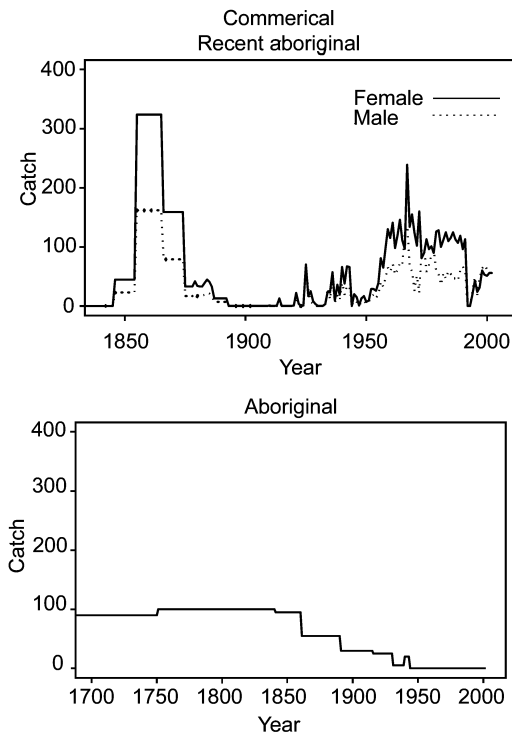
Fig. 1. The commercial and recent aboriginal (post-1943) catches (upper panel) and the historical (pre-1944) aboriginal catches (lower panel). The sex-ratio of the historical aboriginal catches is assumed to be 50:50.

The data used to estimate the values for the 'free' parameters of the model are the estimates of 1+ abundance from the surveys conducted at Granite Canyon, California. The sampling coefficients of variation for these estimates are known to underestimate the actual extent of observation error variability, so, following Wade (2002), these coefficients of variation are inflated by an 'additional variance' term. For consistency with the approach used to condition the AWMP *Evaluation Trials* (IWC, 2003) for the ENP gray whales, the 1+ abundance estimates are assumed to be independently and identically log-normally distributed. This assumption leads to the following likelihood function (ignoring constants independent of the model parameters):

$$L = \prod_{t} \frac{1}{\sqrt{\sigma_t^2 + E(CV_{\text{add},t}^2)}} \exp\left(-\frac{(\ell n P_t^{\text{obs}} - \ell n \hat{P}_t^{1+})^2}{2(\sigma_t^2 + E(CV_{\text{add},t}^2))}\right) \quad (7)$$

where:

P_t^{obs} is the shore-count-based estimate of the (1+) abundance at the start of year t (the data point for year t is the survey that straddled years t-1 and t);

$\hat{P}_t^{1+}$ is the model-estimate of the (1+) abundance at the start of year t;

σ_t is the standard deviation of the logarithm of P_t^{obs} (approximated by its coefficient of variation);

$E(CV_{\text{add},t}^2)$ is the square of the model-predicted CV of the additional variation for year t:

$$E(CV_{\text{add},t}^2) = CV_{\text{add}}^2 \frac{0.1 + 0.013 \tilde{K}_{1+} / \hat{P}_t^{1+}}{0.1 + 0.013 \tilde{K}_{1+} / \hat{P}_{1968}^{1+}}$$

CV_{add}^2 is the additional variation associated with the estimate of 1+ abundance for 1968; and

$\tilde{K}_{1+}$ the current equilibrium level for the 1+ component of the population[1].

The square of the total *CV* for the abundance estimate for year t is therefore modelled as the sum of two components: the square of the *CV* of the estimation error associated with the sampling variation (σ_t^2), and the square of the *CV* associated with the additional variance ($CV_{\text{add},t}^2$). The size of the latter component is assumed to be density-dependent with the extent of density-dependence modelled as for the AWMP *Evaluation Trials* (IWC, 2003). The value for CV_{add} for 1968 is treated as an estimable parameter of the model. Data are also available on the extent of variation due to school size estimation error. However, these data are only available since the 1995/96 survey and consequently are ignored for the purposes of the analyses of this paper. IWC (2003) includes these data when conditioning the AWMP *Evaluation Trials* for the ENP gray whales. This is because the performance of alternative *Strike Limit Algorithms*[2] for the ENP gray whales may be sensitive to the source of the additional variation in the abundance estimates.

Note that this approach to constructing the likelihood function implies that, although information on calf counts is available (e.g. Poole, 1984; Perryman *et al.*, 2002), these data are not used when fitting the model. Rather the calf count data are used to independently validate some of the predictions of the model.

Parameterisation and parameter estimation
The 'free' parameters of the model depend on whether the birth rate/infant survival rate is 'intrinsic' or not and the functional form assumed to model density-dependence. For the conventional density-regulated model (BALEEN II), these parameters are: $\tilde{K}_{1+}$, S_0 – the calf survival rate, S_{1+} – the survival rate for animals aged one year and above, a_m – the age-at-maturity, P_{1968}^{1+} – the 1+ population size in 1968, CV_{add} – the additional variance parameter, and the parameters of density-dependence function (A – the resilience parameter and z – the degree of compensation for the Pella-Tomlinson model, and κ for the exponential model; see Equation 3). The parameters of the 'intrinsic' model are the same as those of the density-regulated model, except that the value of ϕ (see Equation 6) is an estimated parameter rather than being assumed to be equal to 0.

The age at recruitment is not estimated. Instead, all of the analyses of this paper assume knife-edged recruitment at age 5 (IWC, 1993; Butterworth *et al.*, 2002). A Bayesian approach is used to estimate the 'free' parameters of the model based on the prior distributions in Table 1 and the Sampling/Importance Resampling (SIR) algorithm (Rubin, 1988).

The SIR algorithm for drawing a set of equally likely vectors of model parameters from the posterior distribution is as follows (the population projections are assumed to start in year y_1):

(a) Draw values for the parameters S_{1+}, $f_{\max}$, a_m, $MSYR_{\text{mat}}$, $MSYL_{\text{mat}}$, $\tilde{K}_{1+}$, P_{1968}^{1+}, CV_{add}, κ, and ϕ from the priors in Table 1.

(b) If density-dependence is assumed to be governed by the Pella-Tomlinson model, the system of equations that

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[1] Unlike the norm for baleen whale assessments, when y_1, the first year considered in the analysis, is greater than 1846, $\tilde{K}$ is not necessarily equal to the pre-exploitation size of the resource, because (for example) this analysis does not preclude a change over time in the environmental carrying capacity. Rather, when $y_1 > 1846$, $\tilde{K}$ should be considered to be the *current* (and assumed future) environmental carrying capacity.
[2] Algorithms that produce limits on the number of strikes for a stock of whales subject to aboriginal harvest.

relate *MSYL*, *MSYR*, S_0, S_{1+}, f_{max}, a_m, *A* and *z* assuming that there is no inertial dynamics (Punt, 1999; Equations 18-21) are solved to find values for S_0, *A* and *z*.

(c) If density-dependence is assumed to be governed by the exponential model, the value of S_0 is chosen so that the relationship $f_0 = f_{max} / e^{\kappa(1+\phi)}$ is satisfied.

(d) If $y_1 > 1846$ (e.g. 1930), find the population size in year y_1 and the population rate of increase in this year, so that, if the population is projected from year y_1 to 1968, the total (1+) population size in 1968 equals the generated value for P_{1968}^{1+}.

(e) If $y_1 = 1600$ or 1846, find the value of $\tilde{K}_{1+}$ so that, if the population is projected from year y_1 to 1968, the total (1+) population size in 1968 equals the generated value for P_{1968}^{1+} (see Butterworth and Punt (1995) and Punt and Butterworth (1999) for full details of how $\tilde{K}_{1+}$ is calculated given a value for P_{1968}^{1+}).

(f) Compute the likelihood for the projection (see Equation 7).

(g) Steps (a)-(f) are repeated a very large number (typically 1,000,000) of times.

(h) 5,000 parameter vectors are selected randomly from those generated using steps (a)-(f), assigning a probability of selecting a particular vector proportional to its likelihood.

The above formulation implies that the year for which a prior on abundance is specified (1968) is not necessarily the same as the first year of the population projections (y_1). Analyses are conducted for four alternative starting years (i.e. y_1=1600, 1846, 1930 and 1968). Those analyses with starting years of 1600 and 1846 begin the population projection at pre-exploitation equilibrium while those analyses with starting years of 1930 and 1968 begin the population projections at a stable age-structure. *MSYR* and *MSYL* do not have their conventional definitions when there are inertial dynamics (i.e. $\phi \neq 0$). These parameters are included to provide a link with the previous assessments and because they provide a 'natural' way to place priors on the parameters *A* and *z* when density-dependence is governed by the Pella-Tomlinson model.

The prior distributions assumed for the bulk of the parameters (Table 1) are taken to be those on which the 1997 assessment of the ENP gray whales (IWC, 1998) was based. The prior distributions for the parameters that determine the extent of inertial dynamics (κ and ϕ) are taken to be uniform with bounds chosen to encompass the values supported by the data.

Differences from Witting (2003)

Although the population dynamics model underlying the analyses of this paper (Equations 1-6) is identical to that on which the analyses of Witting (2003) are based, there are several notable differences between the approach used for parameter estimation in this paper and that used by Witting (2003).

(1) The analyses of this paper are based on the 'backwards' approach to conducting Bayesian analyses (see step (e) above), i.e. a uniform prior is placed on the population size in a recent year (1968) instead of a uniform prior being placed on the equilibrium level, $\tilde{K}_{1+}$. The main reason for parameterising the model in this way (Butterworth and Punt, 1997) is that it avoids the priors for the parameters that determine productivity (*MSYR* for the BALEEN II model and ϕ and κ for the inertia model) being updated purely by the process of projecting the model forward (because combinations of low productivity and low *K* lead to extinction before 2002 and are consequently assigned zero likelihood). The process of sampling parameter vectors from the prior is also more efficient if the 'backwards' approach is adopted. This approach to conducting Bayesian assessments forms the basis for the trials used to evaluate *Strike Limit Algorithms* for the ENP gray whales and the Bering-Chukchi-Beaufort Seas stock of bowhead whales (IWC, 2002; 2003).

(2) A prior is placed on the maximum possible birth rate rather than on the survival rate for calves. In contrast, Witting (2003) places independent uniform priors on S_{1+} and S_0 and a U[0.3, 0.6] (or U[0.2,0.6] for a start year of 1600) prior on the maximum possible birth rate. The approach of this paper (through steps (b) and (c) above) implies that the maximum possible birth rate can be achieved at very low population size; this is not case with the approach taken by Witting (2003). This paper also imposes the constraint that S_0 be less than S_{1+}, a constraint not imposed by Witting (2003) who assumed independent priors for these two parameters.

(3) Witting (2003) restricts the number of population size cycles between the first year of the assessment and 2005 to one when the analysis starts in 1846 and to two when it starts in 1600 – no such restriction (which is equivalent to adding a new prior) is imposed here; rather the data are used to determine the relative likelihood of alternative parameter values (and hence number of cycles).

Table 1

The prior distributions.

Parameter	Prior distribution
Non-calf survival rate, S_{1+}	U[0.95, 0.999]
Age-at-maturity, a_m	U[5, 9][a]
$\tilde{K}_{1+}$ [b]	U[0, 70,000]
1968 abundance, P_{1968}^{1+}	$\ln P_{1968}^{1+} = N(\ln 12,921; 0.0746^2 + CV_{add}^2)$
$MSYL_{mat}$ (%)	U[40, 80]
$MSYR_{mat}$ (%)	U[0, 10]
Extent of density-dependence, κ	U[0, 4]
Extent of inertial dynamics, ϕ	U[0, 4]
Maximum birth rate, f_{max}	U[0.3, 0.6]
Additional variation (population estimates), CV_{add}	U[0, 0.35]

[a]Discrete uniform distribution; [b]The prior for $\tilde{K}_{1+}$ is ignored if the population projections start at pre-exploitation equilibrium (i.e. $y_1 \leq 1846$).

(4) The priors for some of the remaining parameters are slightly different and there are some slight differences in how the model is parameterised (e.g. Witting (2003) defines the function g as $\exp(\phi\kappa(D_t - D_{-\infty}))$ rather than as $\exp(\phi\kappa(1 - D_t/D_{-\infty}))$).

Apart from (3) the differences between the approach of this paper and that of Witting (2003) relate to how the model is implemented within a Bayesian estimation framework. Maximum likelihood results do not depend on how the model is parameterised nor on the priors for the model parameters so the two approaches should be fully comparable had the analyses been based on maximum likelihood rather than Bayesian techniques.

RESULTS AND DISCUSSION

Management related quantities

The results are summarised by the posterior medians, means and 90% credibility intervals for the following management-related quantities:

(a) $MSYR_{mat}$ — the Maximum Sustainable Yield rate (in terms of harvesting of the mature component of the population and expressed as a percentage);

(b) $\tilde{K}_{1+}$ – the equilibrium level for the 1+ component of the population;

(c) $P^{1+}_{2002} / \tilde{K}_{1+}$ – the number of 1+ animals at the start of 2002, expressed as a percentage of that corresponding to the equilibrium level;

(d) $P^{1+}_{2002} / MSYL_{1+}$ the number of 1+ animals at the start of 2002, expressed as a percentage of that at which MSY is achieved;

(e) *Slope* – the average annual increase of the total (1+) population from 1968 to 1988 as estimated from a linear regression fit to the logarithms of the model estimates of (1+) population size over this period – this statistic is used to assess the extent to which model is able to mimic the abundance data – a log-regression through the actual abundance estimates for 1968-88 leads to a value for *Slope* of 0.032;

(f) RY_{2002} – the replacement yield during 2002;

(g) λ_{max} – the maximum rate of increase (given a stable age-structure); and

(h) κ and ϕ - the parameters of the inertia model.

The values for the quantities related to MSY are meaningless for the analyses that allow for inertial dynamics. Therefore, 100-year population projections under (constant) future annual catches of 0, 128, and 256 (split equally among males and females) were conducted and the results summarised by the 5th, mean, median and 95th percentiles of $P^{1+}_{2102} / \tilde{K}_{1+}$.

Sensitivity to alternative population dynamics models

Table 2 provides the values for the management-related quantities for assessments of the ENP gray whales using the standard BALEEN II model (the 'basic' model) and the inertia model, when the inertial dynamics are based on the exponential formulation (see Equations 3 and 4). Two variants of each model based on varying the first year of the historical projection period (y_1) are considered. The choices y_1=1930 and 1968 for the standard BALEEN II model were made for consistency with the most recent assessments conducted by the Scientific Committee of the International Whaling Commission (IWC, 1998; Punt and Butterworth,

2002; Wade, 2002) The choice y_1=1846 for the inertia model was made because Witting (2001) initiated his historical projections in this year while the choice y_1=1600 reflects the first year for which estimates of aboriginal removals have been postulated (Fig. 1). Witting (2003) also presented results for analyses that begun both in 1846 and in 1600. The posterior medians and 90% credibility intervals for the time-trajectories of total (1+) population size and calf numbers for period 1950-2025[3] from the four baseline analyses are shown in Fig. 2. This figure also displays the estimates of absolute abundance and the calf counts[4].

All four baseline analyses are able to mimic the change in population size over the period 1968-98 adequately (Fig. 2), although the posterior distribution for the rate of change in population size from 1968-88 obtained from the inertia model with y_1=1846 is shifted to noticeably lower values compared with the posterior distributions obtained from the other three baseline analyses (Table 2; column *Slope*). None of the four analyses is able to mimic the calf counts particularly successfully, although the two analyses based on the BALEEN II model perform better at this than the two analyses based on the inertia model (Fig. 2). Specifically, the BALEEN II models mimic the calf counts better than the inertia model (in terms of the posterior medians) for all years except 1996-98 and achieve a lower mean square error than the inertia model.

It is not straightforward to compare the results of the analyses based on the standard BALEEN II model with those based on the inertia model because many of the standard BALEEN II model outputs refer to Maximum Sustainable Yield, MSY, in some way (e.g. $MSYR$) whereas the inertia model does not include MSY[5]. However, it is possible to compare the posterior distributions for the biological parameters, the current population size, the 2002 replacement yield, and the future time-trajectories of population size. The analyses based on the standard BALEEN II model indicate that the population is currently at its (estimated) equilibrium population size and consequently the current replacement yield is negative. In contrast, the analyses based on the inertia model suggest a higher current population size that is substantially in excess of its pre-exploitation (1600 or 1846) population size, and a positive current replacement yield. The posterior distributions for λ_{max} are, however, remarkably similar among the four baseline analyses.

Fig. 3 explores the consequences of annual catches from 2003 of 0 and 256 for each of the four baseline analyses in terms of the time-trajectories of 1+ population size from year y_1 to 2200. Except for the inertia model: y_1=1600 analysis, all of the analyses suggest that under a regime of zero catches in the future, the 1+ population will stabilise close to its current population size (Fig. 3; Table 2). In contrast, the inertia model: y_1=1600 analysis predicts a continuing decline in 1+ population size even with zero future catches. Projections to 2102 indicate that annual catches of up to a level of 256 will not have a substantial impact on the population size if the standard BALEEN II model is correct (Table 2). This is perhaps not surprising given that MSY is estimated to be larger than 600 for the two analyses based on this model. The projections based on the inertia model do predict future declines in population size

[3] The projections beyond 2002 are based on a catch of zero.

[4] The calf counts are displayed in Fig. 2 even though the analyses on which the population trajectories are based ignore these data when fitting the population dynamics model.

[5] The outputs that depend on MSY are consequently omitted from Table 2.
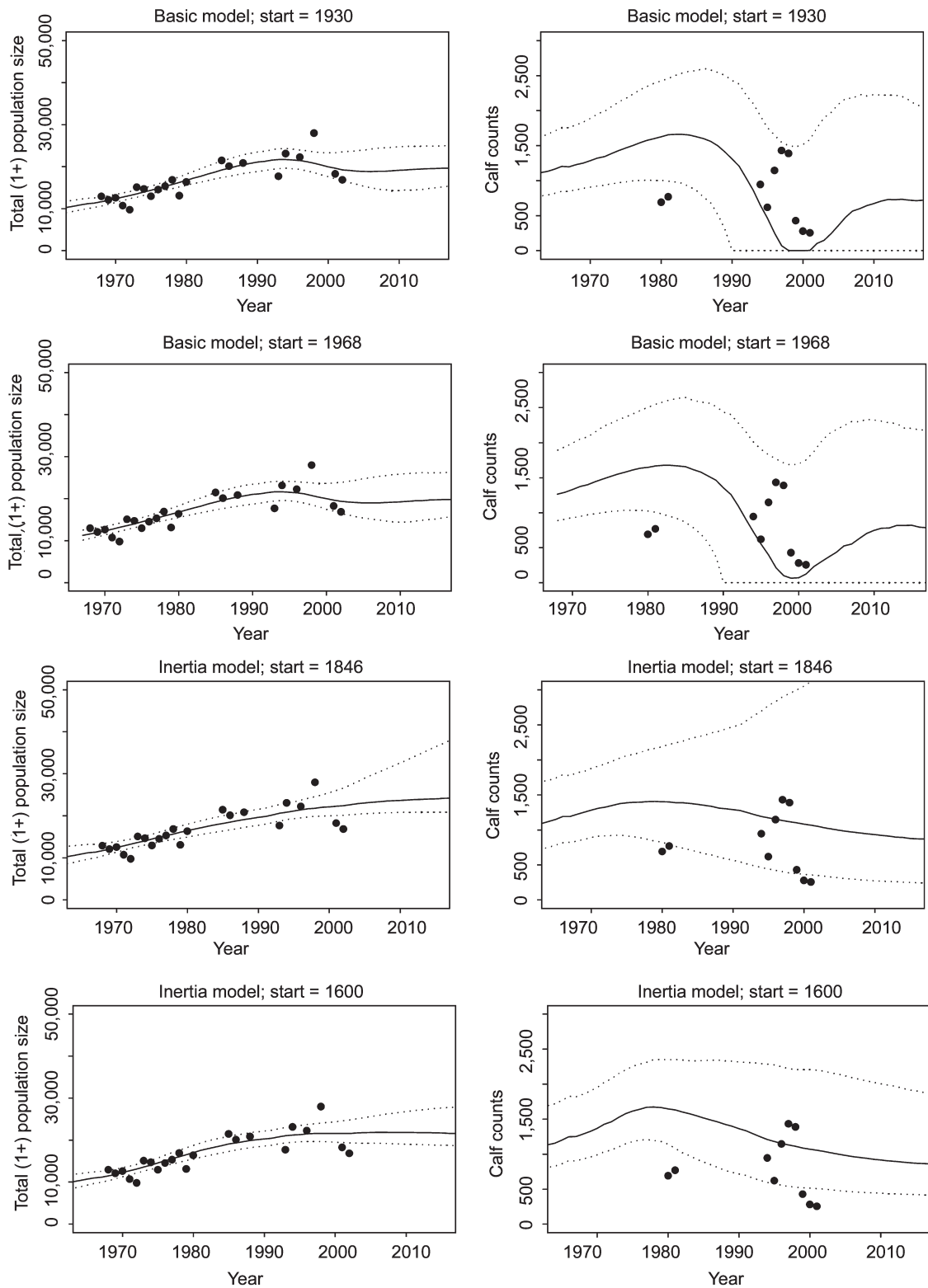
Fig. 2. Posterior distributions (medians and 90% intervals) for the time-trajectories (1965-2015) of 1+ population size and calf numbers for the four baseline analyses. The dots indicate the data points available for use in the analyses. The projections beyond 2002 assume zero catches.

for annual catches of 256 but the population still exceeds its pre-exploitation size substantially in 2102 (Table 2). Projections beyond 2102 are more pessimistic for the inertia model:y_1=1846 analysis which predicts population collapse in over 5% of cases.

The posterior median for $\tilde{K}_{1+}$ is largest for the analyses based on the standard BALEEN II model, lower for the inertia model:y_1=1846 analysis and lowest for the inertia model:y_1=1600 analysis. The latter result is perhaps

unexpected given that the total historical catch is highest for the y_1=1600 analysis. The reason for the differences in $\tilde{K}_{1+}$ between the two analyses based on the inertia model relate to differences in the estimates of ϕ and κ (Table 2) which lead to there being two cycles for the y_1=1600 analysis but to only one cycle for the y_1=1846 analysis (Fig. 3). The posterior for the replacement yield for 2002 from the y_1=1846 analysis assigns more probability to high values than that for the y_1=1600 analysis.

Table 2

Estimates of twelve management-related quantities for the eastern north Pacific stock of gray whales. The point estimates given are posterior medians, followed by posterior means in round parenthesis. Posterior 90% credibility intervals are given in square parenthesis.

|	$MSYR_{mat}$ (%)	$\tilde{K}_{1+}$	$P^{1+}_{2002} / \tilde{K}_{1+}$ (%)	$P^{1+}_{2002} / MSYL_{1+}$ (%)	Slope	RY_{2002}	λ_{max}	κ	ϕ	$P^{1+}_{2102} / \tilde{K}_{1+}$ Catch=0	Catch=128	Catch=256
Basic model; y_1=1930												
Baseline	7.0 (7.0) [4.8; 9.2]	18,454 (19,355) [15,553; 24,900]	106 (106) [89; 123]	124 (125) [96; 158]	2.92 (2.91) [1.94; 3.82]	-193 (-191) [-685; 399]	1.057(1.059) [1.041; 1.085]			101 (103) [85; 121]	101 (103) [85; 121]	103 (104) [91; 124]
Exponential form		40,094 (42,375) [26,640; 65,103]	59 (59) [37; 82]	82 (86) [44; 143]	1.93 (1.94) [1.28; 2.59]	447 (449) [299; 612]	1.058(1.061) [1.041; 1.090]	1.524 (1.516) [0.148; 2.843]		100 (99) [95; 100]	92 (91) [85; 94]	83 (82) [74; 88]
No surveys since 2000	5.2 (5.3) [3.5; 7.5]	38,190 (39,973) [19,333; 66,363]	76 (79) [44; 117]	108 (107) [58; 155]	2.58 (2.60) [1.97; 3.34]	713 (639) [-73; 1,067]	1.049(1.053) [1.038; 1.083]			100 (101) [91; 108]	100 (100) [93; 110]	99 (99) [90; 111]
Post-model-pre-data	5.3 (5.3) [1.4; 9.3]	39,781 (40,353) [15,956; 66,730]	84 (78) [22; 121]	111 (103) [34; 155]	2.33 (2.31) [-.82; 5.26]	411 (577) [-358; 1,913]	1.051(1.051) [1.017; 1.085]			100 (97) [69; 110]	100 (92) [17; 112]	99 (86) [0; 116]
Basic model; y_1=1968	6.8 (6.8) [4.4; 9.1]	18,927 (20,002) [16,078; 26,735]	104 (103) [85; 121]	119 (120) [92; 154]	2.97 (2.99) [1.97; 3.97]	-195 (-189) [-685; 419]	1.054(1.057) [1.039; 1.082]			101 (101) [84; 118]	101 (102) [84; 121]	102 (104) [89; 124]
Inertia model; y_1=1846		14,835 (15,273) [13,187; 18,936]	151 (150) [125; 168]		2.56 (2.52) [1.43; 3.53]	255 (310) [135; 682]	1.061(1.059) [1.032; 1.085]	0.116 (0.369) [0.074; 2.065]	1.492 (1.611) [0.307; 3.216]	159 (162) [143; 190]	145 (147) [131; 171]	134 (135) [118; 155]
Inertia model; y_1=1600												
Baseline		10,079 (10,621) [8,573; 14,443]	214 (209) [152; 240]		2.94 (2.95) [2.00; 3.85]	131 (151) [-25; 404]	1.057(1.058) [1.040; 1.081]	0.239(0.326) [0.071; 0.911]	1.096 (1.180) [0.611; 1.988]	172 (169) [121; 197]	154 (151) [93; 180]	140 (136) [78; 169]
Pella-Tomlinson form		12,254 (12,311) [9,379; 15,100]	155 (156) [116; 208]		2.76 (2.75) [1.65; 3.75]	-290 (-309) [-738; 77]	1.049(1.050) [1.034; 1.069]			108 (112) [85; 152]	109 (112) [82; 148]	115 (115) [72; 157]
50:50 sex-ratio		10,502 (10,914) [8,873; 14,186]	207 (205) [167; 235]		3.00 (2.98) [2.10; 3.75]	155 (176) [20; 415]	1.052(1.051) [1.036; 1.066]	0.311 (0.414) [0.081; 1.005]	0.965 (1.026) [0.534; 1.719]	171 (165) [118; 196]	151 (145) [91; 179]	134 (127) [67; 169]
No surveys since 2000		12,976 (14,925) [9,688; 26,308]	202 (192) [113; 239]		2.62 (2.66) [1.96; 3.50]	498 (549) [97; 1,088]	1.047(1.048) [1.038; 1.062]	0.662 (1.078) [0.115; 3.360]	0.826 (0.891) [0.264; 1.789]	176 (183) [112; 284]	156 (159) [95; 243]	134 (137) [80; 204]
U[0.2, 0.6] prior on f_{max}		10,223 (11,125) [8,802; 17,298]	213 (204) [131; 236]		2.91 (2.86) [1.74; 3.78]	149 (182) [-2; 494]	1.055(1.056) [1.036; 1.079]	0.244 (0.355) [0.069; 1.013]	1.103 (1.181) [0.575; 2.055]	174 (172) [126; 202]	157 (153) [98; 182]	140 (137) [82; 170]
Post-model-pre-data		16,580 (18,203) [9,469; 30,305]	155 (160) [35; 295]		1.83 (1.75) [1.20; 4.66]	342 (492) [25; 1,458]	1.046(1.048) [1.014; 1.092]	1.230 (1.490) [0.075; 3.574]	0.541 (0.699) [0.149; 1.812]	172 (175) [92; 278]	148 (149) [45; 246]	126 (126) [0; 231]
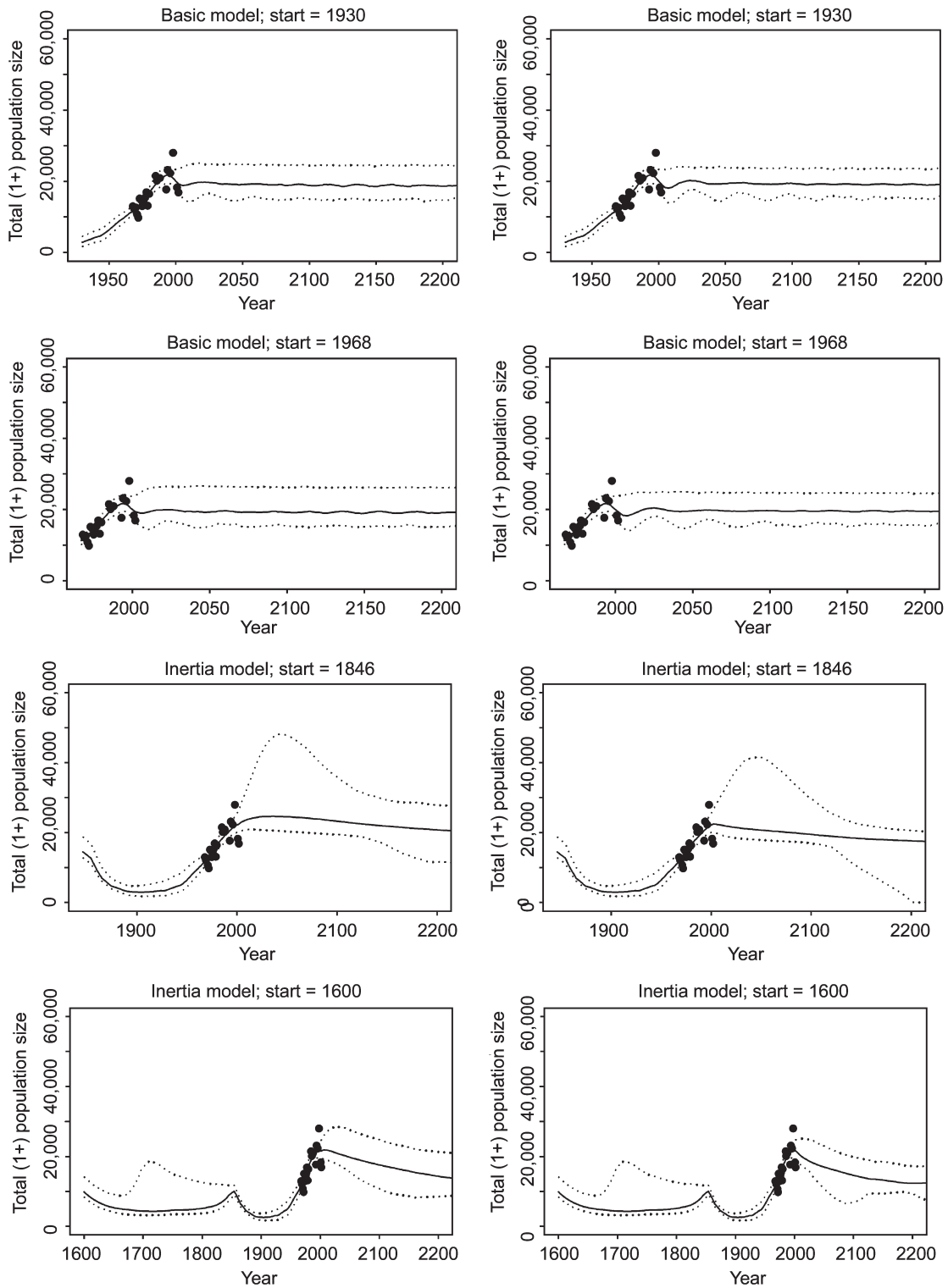
Fig. 3. Posterior distributions (medians and 90% intervals) for the time-trajectories (year y_1-2200) of 1+ population size for the four baseline analyses. The projections beyond 2002 assume zero catches (left panels) and 256 animals annually (right panels).

Table 2 provides results for some variants of the BALEEN II model when y_1 is set to 1930 and of the inertia model when y_1 is set to 1600. Changing the functional form used to model inertial dynamics from the exponential model to the Pella-Tomlinson model (Equations 3 and 5) lowers the current depletion (though it still exceeds 100%), suggests a negative rather than a positive current replacement yield, and indicates a much smaller impact of future catches of 256 on 1+ population size compared to that of future catches of zero (Table 2). The time-trajectory of the future population

size is more oscillatory for the Pella-Tomlinson model than for the exponential model (Fig. 4 top right panel), one consequence of which is that, even for a zero catch, there is a substantial drop in 1+ population size by 2102. The oscillatory behaviour of the Pella-Tomlinson model occurs because this functional form leads to zero calves when the number of mature animals exceeds $(1 + A\phi) / A\phi$ of that in 1600 (Equation 6). This effect is present in both the density-regulated and the inertia models but is more pronounced for the inertia model because the impact of inertial dynamics

can be to drive the population substantially in excess of the 1600 level. The fit of the model to the abundance data is, however, poorer for this model variant (the median for *Slope* in Table 2 is only 2.76% for the Pella-Tomlinson model compared to 2.94% for the baseline model and 3.22% for a log-regression through the data points for 1968-88).

The results for the standard BALEEN II model are also sensitive to the form assumed for the density-dependence function. For example, changing the density-dependence function for the basic model from the Pella-Tomlinson model to the exponential model (Table 2, row 'exponential form'; the value of the quantity *slope* for the exponential model is substantially less for this model than based on the data) leads to markedly poorer fits to the data. The poorer fit to the data may be a consequence of the reduction in the number of parameters governing density-dependence (two for the Pella-Tomlinson model compared to only one for the exponential model).

The posterior medians for the management-related quantities are not notably sensitive to assuming that the sex ratio of the historical harvest since 1944 is 50:50 rather than the actual sex ratio, which is biased towards females (Fig. 1). However, the probability of resource extirpation exceeds 5% for projections based on a future catch of 256 (Fig. 4, bottom left panel). This result is consistent with the maximum likelihood results obtained by Witting (2003) who predicted drastic reductions in population size after 2000 had the sex-ratio of the historical catches been 50:50. The results are insensitive to reducing the lower limit of the prior for f_{max} from 0.3 to 0.2.

The posterior distribution for the 1+ population size trajectory based on the post-model-pre-data distribution[6] (lower right panel of Fig. 4) is, as expected, much less precise than the corresponding posterior from the baseline analysis (upper left panel of Fig. 4).

Ignoring the two most recent total population size estimates has a marked impact on the results of assessments based on the standard BALEEN II model (Fig. 5; Table 2). Instead of the population being at (or above) its (current) equilibrium level, it is estimated to be only 80% of this level (posterior median). As a consequence of this, the replacement yield for the 'no surveys since 2000' analysis is markedly higher than those for the analyses that include these two data points (Table 2). Ignoring these two data points also increases the posterior median for $\tilde{K}_{1+}$ markedly. Previous analyses (e.g. Punt and Butterworth, 2002) have concluded that assessments which start the population projections after 1900 and that are based on data until 1998 provide essentially no information about the upper bound for $\tilde{K}_{1+}$. The two most recent data points provide such information and hence have a marked impact on the posterior distributions. These two estimates are therefore the first evidence from population counts that the population has reached its current 'carrying capacity'. In contrast, the calf count data suggest that evidence in this regard has been available for several years (Fig. 2).

Ignoring the 2001 and 2002 data points for the inertia model:y_1=1600 analysis (Fig. 6) again leads to higher values for the posterior median for $\tilde{K}_{1+}$ (but not to the extent evident for the standard BALEEN II model). However, the posterior distributions for current depletion and the consequences of future catches of 0, 128 and 256 whales per annum are affected much less.

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[6] The post-model-pre-data distribution is the joint distribution for the parameters that arises when the parameter combinations that are unfeasible (e.g. correspond to extinction prior to 1968) are excluded.

General discussion

The analyses of this paper confirm the conclusion of Witting (2001; 2003) that a model which incorporates inertial dynamics can reconcile the catches and population count data for the ENP gray whale population. Furthermore, the results confirm that assessments based on this model structure reveal the current population size to be larger than the pre-exploitation size, and that catches of less than 256 would cause some population decline, rather than just reducing the rate of (further) population increase, as suggested by past assessments based on the standard BALEEN II model. However, the future declines do not lead to the collapses suggested by Witting (2001), at least within the 300-year time-frame considered in the analyses of this paper. This is probably because, in common with the analyses of Witting (2003), the analyses of this paper are based on the actual catches by sex rather than on assuming a 50:50 sex ratio for the historical catches.

Although the inertia model is as effective as the standard BALEEN II model at replicating the absolute abundance data when the population projections for the standard model begin in 1930 or 1968, it is less able to mimic the changes over time in the calf counts (Fig. 2).

The results from the standard BALEEN II model and inertia model are both very sensitive to exactly how density-dependence (exponential or Pella-Tomlinson) is formulated, while the results from the inertia model are somewhat sensitive to the choice of the first year considered in the analysis (contrast the results for y_1=1846 and y_1=1600 in Table 2). 1600 was clearly not the first year in which aboriginal takes of gray whales occurred, raising the question of how to choose an appropriate first year for the application of an analysis based on the inertia model. In contrast, the results for the standard BALEEN II model are insensitive to a choice for y_1 between 1900 and 1968 (Punt and Butterworth, 2002).

The results for the baseline case of this paper for y_1=1846 are quite similar to those for the corresponding case in Table 3 of Witting (2003). However, the results for y_1=1600 are notably different (the posterior median for $\tilde{K}_{1+}$ is lower and that for the current depletion higher in this paper than in Witting (2003)). As noted above, there are some differences in exactly how the Bayesian estimation is implemented in the analyses and it appears that these differences have some notable impacts on the results for the choice y_1=1600.

The inertia model formally incorporates changes over time in carrying capacity into the population dynamics through Equation 6. This differs in concept from previous attempts to reconcile the catch and abundance data for the ENP gray whales by postulating changes in carrying capacity in which the extent of change was estimated as a free parameter of the model (e.g. Butterworth *et al.*, 2002). An untested (and possibly untestable even in the medium term) assumption of the inertia model is, however, that cycles have occurred prior to 1846 (e.g. Fig. 3, bottom right panel) and will occur in the future. This is because the only data to compare alternative formulations for how carrying capacity may have changed are the abundance data which exhibit an increasing trend over the period 1967-88. The inertia model predicts that carrying capacity is declining at present whereas predictions based on formulations of the standard BALEEN II model (e.g. Butterworth *et al.*, 2002; Punt and Butterworth, 2002; Wade, 2002) have been predicated on the assumption that carrying capacity will remain at its current level. Apart from the calf count information, there are no other data not already included in
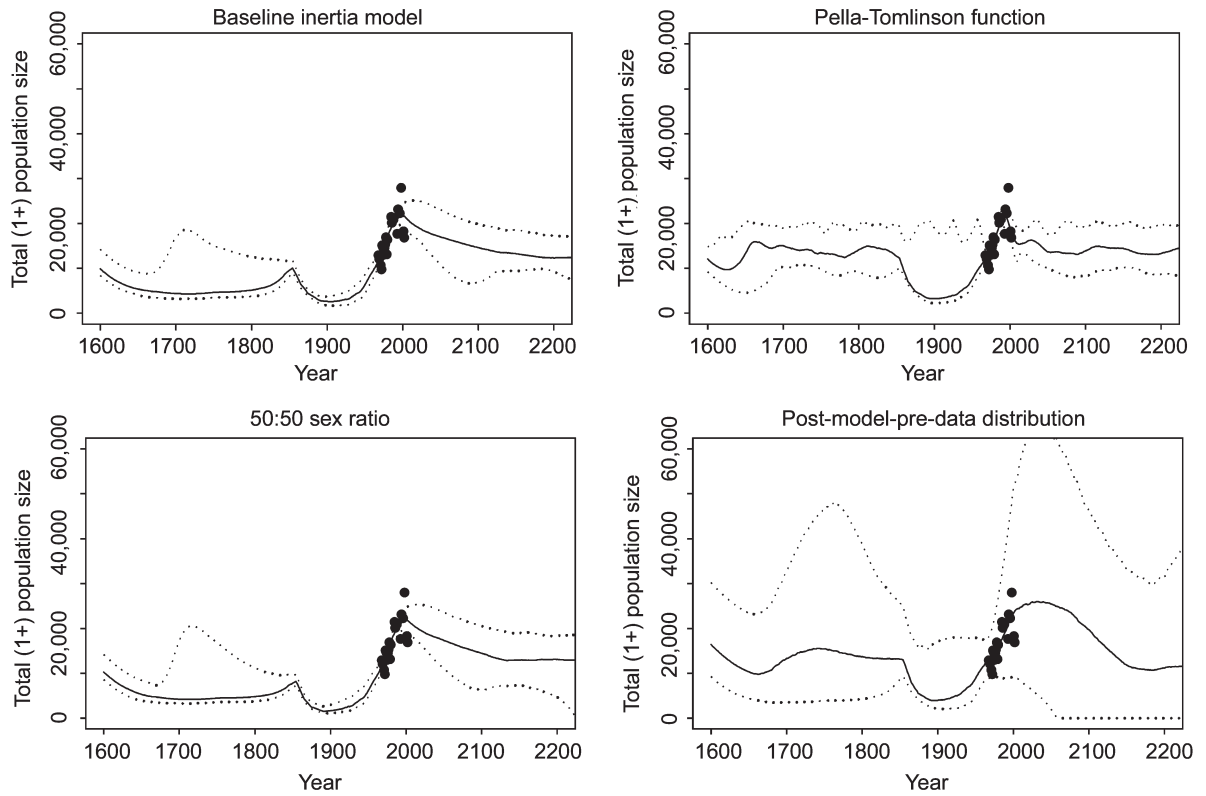
Fig. 4. Posterior distributions (medians and 90% intervals) for the time-trajectories (1600-2200) of 1+ population size for variants of the inertia model: y_1=1600 analysis. The projections beyond 2002 assume an annual catch of 256 animals.
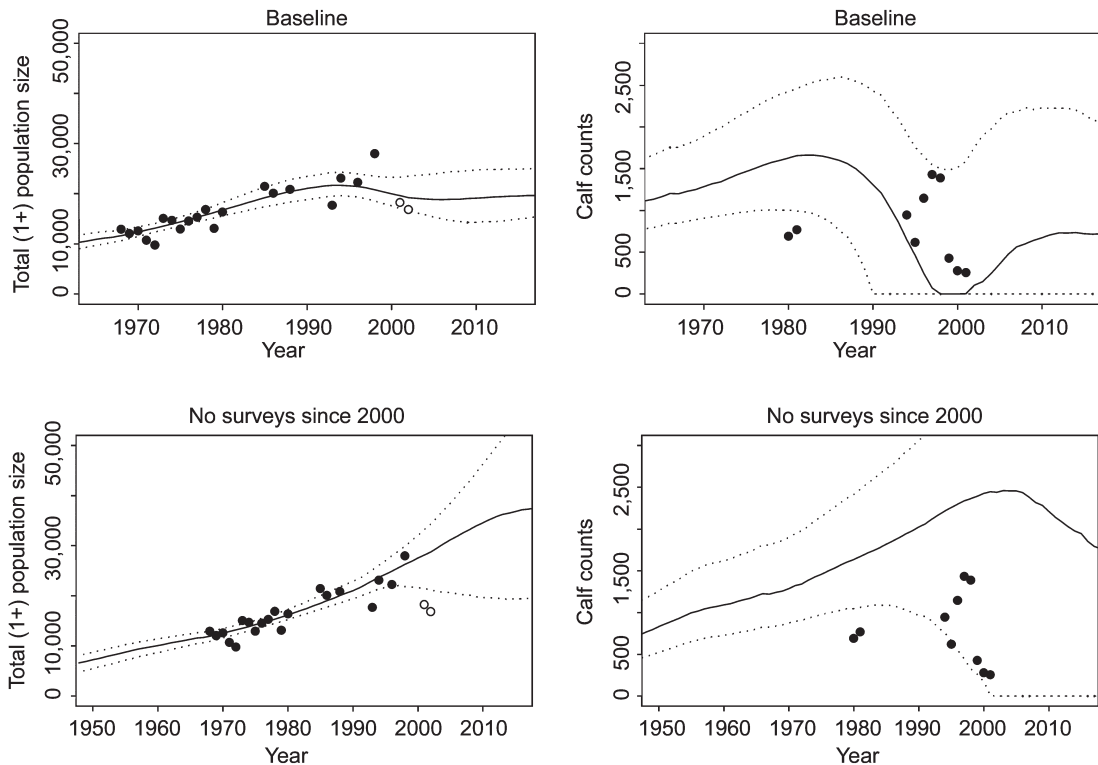

Fig. 5. Posterior distributions (medians and 90% intervals) for the time-trajectories (1965-2015) of 1+ population size and calf numbers for the baseline basic model: y_1=1930 analysis and a variant thereof that ignores the data from the surveys since 2000. The dots indicate the data points available for use in the analyses. Note that the 2001 and 2002 abundance estimates (the open circles in the left panels) were not included in the 'no surveys since 2000' analysis.
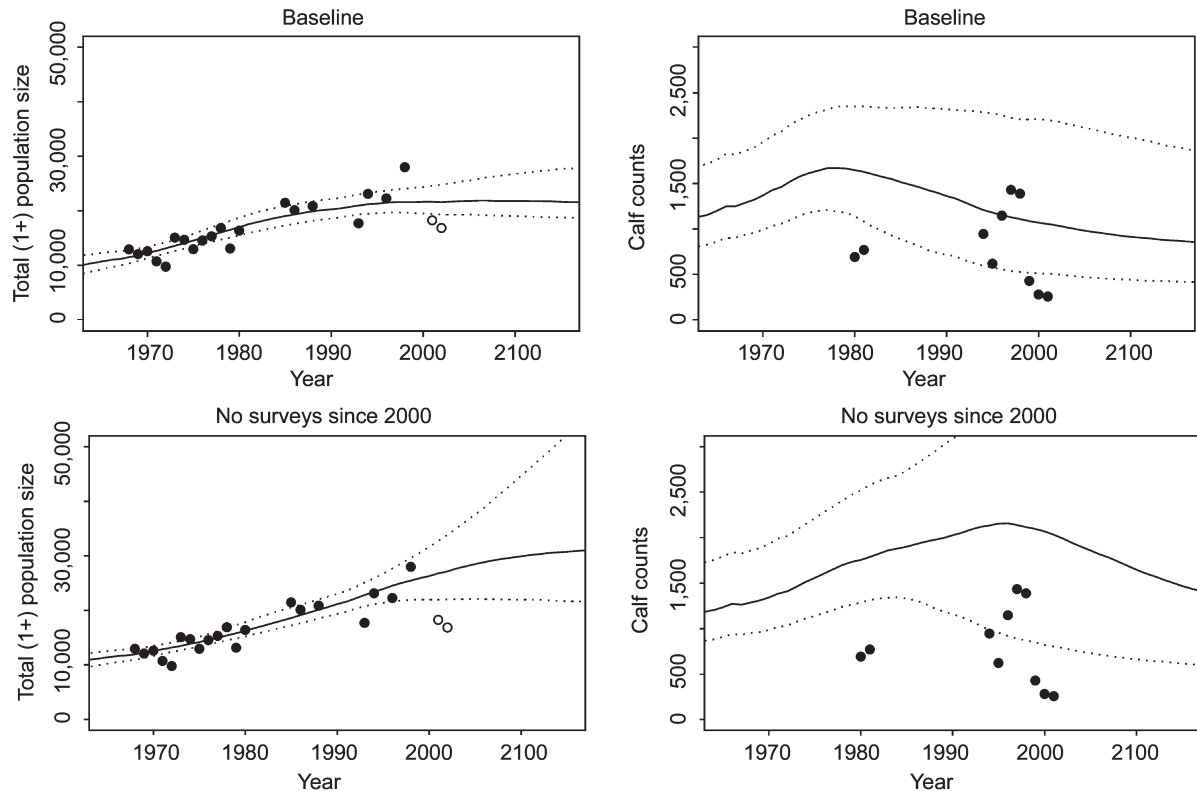
Fig. 6. Posterior distributions (medians and 90% intervals) for the time-trajectories (1915-2015) of 1+ population size and calf numbers for the inertia model: y_1=1600 analysis and a variant thereof that ignores the data from the surveys since 2000. The dots indicate the data points available for use in the analyses. Note that the 2001 and 2002 abundance estimates (the open circles in the left panels) were not included in the 'no surveys since 2000' analysis.

the analyses to distinguish between these two approaches to making future predictions.

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