An examination of certain of the assumptions made in the Bayesian approach used to assess the eastern North Pacific stock of gray whales (*Eschrichtius robustus*)[1]

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ABSTRACT

An assessment of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) is conducted using a variant of the Bayesian stock assessment method of Wade (2002). This variant is based on the BALEEN II population dynamics model and uses parameters whose values are more familiar to members of the International Whaling Commission's Scientific Committee. The sensitivity of the results to changes to some of the specifications used in the assessment is examined. The results are shown to be relatively insensitive to the first year considered in the analysis and the year for which a prior on absolute abundance is specified. An alternative Bayesian assessment method which involves projecting the population forward from pre-exploitation equilibrium in 1600 is also considered. As expected from previous assessments, results from this method are unable to mimic the recent trends in absolute abundance obtained from shore counts and are inconsistent with the fact that the fishery was commercially extinct by the end of the 19th Century. Allowing for underestimation of historical commercial and aboriginal catches provides improved consistency with recent trends in abundance but does not resolve these problems completely. The impact of process error (in the form of temporally correlated fluctuations in calf survival) on the dynamics of the population is found to be largely inconsequential in terms of resolving the inconsistency between historical catches and recent estimates of abundance.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; MODELLING; ABUNDANCE ESTIMATE

INTRODUCTION

Assessments of the eastern North Pacific stock of gray whales based on the assumption that the population was at its pre-exploitation equilibrium level in 1846 are unable to mimic the virtual doubling in abundance inferred from the survey estimates from 1967-1994. Various authors (e.g. Reilly, 1981; Cooke, 1986; Lankester and Beddington, 1986; Mathews, 1986; Butterworth *et al.*, 2002) have examined hypotheses related to why the fits of population models to the abundance data are poor. These include changes in environmental carrying capacity, the disruptive influence of intensive whaling on the breeding rate, underestimated historical commercial catches, an overestimate of the recent rate of population growth and inadequate allowance for historical aboriginal catches. However, none of these explanations in isolation seem particularly likely because the magnitude of the required difference from the 'conventional wisdom' of no such 'errors' is large. For example, Butterworth *et al.* (2002) found that only if the environmental carrying capacity was currently 250% (or more) than that in 1846 (and $MSYR_{\text{exp}} \geq 4\%$, where 5+ animals constitute the exploitable component of the population) is it possible to reconcile the catch history with the abundance data. They also showed that the requisite magnitude of the factors that they considered became smaller if more than one applied. Wade (2002) and Wade and DeMaster (1996) assessed the stock, but made no attempt to fit a population model to the entire period of exploitation, relying instead on the assumption of a stable age-structure at the start of 1968.

The assessments of Wade (2002) and Wade and DeMaster (1996) are based on the population model used by Breiwick *et al.* (1984) to assess the Bering-Chukchi-Beaufort Seas (B-C-B) stock of bowhead whales. This paper instead uses the BALEEN II population dynamics model (Punt, 1999). This population model has been used extensively in recent assessments of the bowhead stock (e.g. Givens *et al.*, 1993; Butterworth and Punt, 1995) and is parameterised in terms of MSYR and MSYL, parameters with whose values most members of the Scientific Committee are rather more familiar than those of the Breiwick *et al.* (1984) model (λ and z).

This paper first outlines the method used by Wade (2002) as applied here using the BALEEN II model (the base-case analysis). It then contrasts the results of this analysis with those of Wade (2002). The primary intent of the paper, however, is to consider the sensitivity of the results of this base-case analysis to variations in its specifications. In particular, sensitivity is examined to changing the year in which the population is assumed to have had a stable age-structure, changing the year for which a prior distribution for the (1+) population size is specified, allowing for underestimation of historical commercial and aboriginal catches, and incorporating 'process error' in the form of a stochastic term in the annual calf survival rate.

DATA AND METHODS

The base-case assessment

The philosophy underlying the Bayesian assessments of Wade (2002) and Wade and DeMaster (1996) is to place a prior distribution on the abundance in a particular year (1968 in those assessments) and to assume that the population had a stable age-structure at the start of that year. The population is then projected forwards from 1968 to 1996 and the likelihood for the projection is calculated. The only data included in the likelihood function are the estimates of abundance (Table 1). The catch data (commercial and

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aboriginal) used when projecting the population forwards over this period are listed in Tables 2 and 3. The posterior distributions for the quantities of interest to management are computed using the SIR algorithm (Rubin, 1987; Gelman *et al.*, 1995). A total of 500,000 iterations of this algorithm are used for the calculations of this paper to ensure that adequate numerical representations of the posterior distributions of interest are achieved.

A disadvantage, when working with an age-structured population model (such as BALEEN II), of initiating population trajectories in a year (here 1968) subsequent to the onset of exploitation is that it is then no longer possible to generate the starting age-structure under the assumption of unharvested equilibrium. Instead it becomes necessary to assume a stable age structure, which in turn involves specifying the effective 'rate of increase' (γ) that applies to each age-class. There are two components contributing to γ, one relating to the overall population rate of increase (γ^+)

Table 1

Estimates of absolute abundance with associated standard errors (SE) for the eastern North Pacific stock of gray whales based on shore counts (source: Wade, 2002).

Year	Estimate	SE
1967/68	13,012	893
1968/69	12,244	484
1969/70	12,777	525
1970/71	11,170	806
1971/72	9,841	442
1972/73	16,962	660
1973/74	14,817	592
1974/75	13,134	540
1975/76	14,811	690
1976/77	15,950	524
1977/78	17,127	966
1978/79	13,300	501
1979/80	16,581	668
1984/85	21,942	994
1985/86	20,450	727
1987/88	21,113	688
1992/93	17,674	1,029
1993/94	23,109	1,262
1995/96	22,571	1,174

Table 3

Historical (pre-1944) aboriginal catches from the eastern North Pacific stock of gray whales. The sex ratio of these catches is assumed to be 1:1 (source: IWC 1993).

Years	Annual catch (both sexes)
1600 - 1750	160
1871 - 1850	260
1851 - 1860	190
1861 - 1880	90
1881 - 1891	80
1892 - 1900	40
1901 - 1915	30
1916 - 1930	20
1931 - 1939	10
1940 - 1943	20

Table 2

Commercial and recent aboriginal (post 1943) catches from the eastern North Pacific stock of gray whales. Sources: 1846 -1854: IWC (1993); 1855-1961: Lankester and Beddington (1986); 1962-1991: C. Allison, pers. comm.; 1994: Blokhin (1995); 1995: Borodin (1996).

Year	Male	Female	Year	Male	Female	Year	Male	Female	Year	Male	Female
1846	23	45	1884	23	45	1922	2	3	1960	58	115
1847	23	45	1885	21	41	1923	5	11	1961	71	141
1848	23	45	1886	17	33	1924	5	11	1962	49	98
1849	23	45	1887	7	13	1925	50	99	1963	60	120
1850	23	45	1888	7	13	1926	19	38	1964	70	140
1851	23	45	1889	7	13	1927	16	32	1965	68	108
1852	23	45	1890	7	13	1928	9	18	1966	123	97
1853	23	45	1891	7	13	1929	6	12	1967	94	156
1854	23	45	1892	7	13	1930	5	10	1968	67	134
1855	162	324	1893	0	0	1931	5	11	1969	59	155
1856	162	324	1894	0	0	1932	5	10	1970	26	125
1857	162	324	1895	0	0	1933	3	7	1971	51	102
1858	162	324	1896	0	0	1934	18	36	1972	22	160
1859	162	324	1897	0	0	1935	11	23	1973	97	81
1860	162	324	1898	0	0	1936	34	68	1974	94	90
1861	162	324	1899	0	0	1937	5	9	1975	58	113
1862	162	324	1900	0	0	1938	18	36	1976	69	96
1863	162	324	1901	0	0	1939	10	19	1977	86	101
1864	162	324	1902	0	0	1940	35	70	1978	94	90
1865	162	324	1903	0	0	1941	19	38	1979	57	126
1866	79	159	1904	0	0	1942	34	67	1980	53	128
1867	79	159	1905	0	0	1943	33	66	1981	36	100
1868	79	159	1906	0	0	1944	0	0	1982	56	112
1869	79	159	1907	0	0	1945	10	20	1983	46	125
1870	79	159	1908	0	0	1946	7	15	1984	59	110
1871	79	159	1909	0	0	1947	3	6	1985	55	115
1872	79	159	1910	0	0	1948	6	13	1986	46	125
1873	79	159	1911	0	0	1949	9	17	1987	47	112
1874	79	159	1912	0	0	1950	4	7	1988	43	108
1875	17	33	1913	0	1	1951	4	9	1989	61	119
1876	17	33	1914	6	13	1952	15	29	1990	67	96
1877	17	33	1915	0	0	1953	13	25	1991	57	113
1878	17	33	1916	0	0	1954	13	26	1992	0	0
1879	21	42	1917	0	0	1955	20	39	1993	0	0
1880	17	34	1918	3	5	1956	41	81	1994	15	29
1881	17	33	1919	1	1	1957	33	65	1995	44	41
1882	17	33	1920	1	1	1958	49	99			
1883	19	39	1921	1	1	1959	65	131			

and the other to the exploitation rate. Under the assumption in this paper of knife-edge recruitment to the fishery at age five, only the γ^+ component applies to ages a of 4 or less. The number of animals of age a at the start of 1968 relative to the number of calves at that time, $N^*_{1968,a}$, is therefore given by the equation:

$$N^*_{1968,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^*_{1968,a-1}\, s_{a-1}(1-\gamma^+) & \text{if } a \le 5 \\ N^*_{1968,a-1}\, s_{a-1}(1-\gamma) & \text{if } 5 < a < x \\ N^*_{1968,x-1}\, s_{x-1}(1-\gamma)/(1-s_x(1-\gamma)) & \text{if } a = x \end{cases} \quad (1)$$

where:

s_a is the survival rate of animals of age a (assumed to be independent of sex);

N_0 is the number of calves in 1968[2]:

$$N_0 = \left(1-\left[1/(P_{mat}\,fec)-1\right]/A\right)^{1/z}\frac{\tilde{K}_{mat}}{P_{mat}} \quad (2)$$

P_{mat} is the number of mature animals per calf in 1968:

$$P_{mat} = \sum_{a=a_m+1}^{x} N^*_{1968,a} \quad (3)$$

A is the resilience parameter;

z is the degree of compensation;

a_m is the age-at-maturity (note that the summation in Equation (3) commences from age a_m+1 to allow for a one year gestation period);

$\tilde{K}_{mat}$ is the number of mature animals at the projected equilibrium in the absence of future catches[3];

fec reflects fecundity (the annual number of births per mature animal) at pre-exploitation equilibrium; and

x is the maximum age considered.

The value of x (the age at which the numbers-at-age are accumulated in a plus-group) is set equal to 15 for the analyses of this paper. This choice is based on computational convenience; given the assumptions of uniform selectivity harvesting above age five and a maximum age-at-first parturition of 10, any choice for x of 10 or larger would lead to identical results.

Given a specification for the relationship between γ and γ^+, and if N^g_{1968} is a value generated from the prior for the total (1+) abundance in 1968, the following equation is then solved for the 'rate of increase' effective in 1968, γ:

$$N^g_{1968} = N_0 \sum_{a=1}^{x} N^*_{1968,a} \quad (4)$$

The value of γ is restricted to lie between 0 and 1. This implies that the 1+ abundance at the start of 1968 is restricted to be smaller than the projected equilibrium level, $\tilde{K}_{1+}$. Any draws from the prior distribution for which it is not possible to satisfy Equation (4) are rejected and assigned zero likelihood. Given an increasing population, it follows that $0 < \gamma^+ < \gamma$, but it is not immediately clear how a prior distribution for the ratio γ^+/γ might be specified. One option would be to assign an 'uninformative' U[0, 1] prior. The approach taken in this paper is to set $\gamma^+ = 0$, i.e. equal to one of the extremes of its possible range. This choice was made primarily for computational convenience. Sensitivity of the results to the assumption of the other extreme ($\gamma^+ = \gamma$) is examined later in the paper.

The assumption of a stable age-structure at the start of 1968 is defensible only if the population was increasing geometrically at that time. If this is true, the value of γ obtained from solving Equation (4) should be consistent with the population increase and exploitation rates for the trajectory in question. This can be checked by comparing the posterior distribution for γ with the posterior distribution for the effective 'rate of increase' (γ^*) estimated directly from the population estimates generated by the population model. This effective 'rate of increase' is again defined as the sum of the actual rate of increase of the population and the exploitation rate:

$$\gamma^* = \gamma_1 + \gamma_2 \quad (5)$$

where:

γ_1 is the average annual increase of the exploitable (5+) population from 1968 to 1972 as estimated from a linear regression fit to the logarithms of the model estimates of (5+) population size over this period;

γ_2 is the exploitation rate over the period 1959-1968:

$$\gamma_2 = \sum_{y=1959}^{1968} C_y \Big/ \sum_{y=1959}^{1968} N^{exp}_{1968}(1-\gamma_1)^{1968-y} \quad (6)$$

C_y is the catch during year y; and

N^{exp}_y is the exploitable (5+) population size for year y.

The estimate of the exploitation rate is based on the years 1959-1968, and assumes that the population rate of increase from 1959-1968 is the same as that from 1968-1972. A period prior to 1968 is chosen because the age-structure of the population in 1968 would depend particularly on the size of the catches in the years immediately preceding. In principle, γ_1 should have been calculated for the same years as the exploitation rate. However, this is not possible because the population projections start only in 1968.

Fig. 1 presents the posterior distributions for γ and γ^* as well as the posterior distribution for the difference between γ and γ^*. The results in this Figure suggest little difference and hence that the assumption of a stable age-structure at the start of 1968 is not violated to any substantial extent.

The prior distributions assumed for the analyses are listed in Table 4. The distributions for the non-calf natural survival rate (s) which is assumed to be independent of age, the age-at-maturity (a_m), the projected equilibrium level ($\tilde{K}_{1+}$), and the maximum pregnancy rate (ρ_{max}) are taken from Wade (2002). The prior distribution for $MSYL_{mat}$ is selected (by analogy) as that used in the 1994 assessment of the B-C-B bowhead stock by the Scientific Committee (IWC, 1995). The prior distribution for $MSYR_{mat}$ is also not based on the choices made by Wade (2002), but is instead expanded to capture the whole range of values considered by Butterworth *et al.* (2002). The selection of uniform prior distributions is intended to reflect a lack of information about the parameters in question.

The analysis does not incorporate a prior distribution for the survival rate of calves (s_c) explicitly. Instead, following Wade (2002), an implicit prior distribution for this parameter is calculated from the priors for the five parameters s, a_m, ρ_{max}, $MSYL_{mat}$ and $MSYR_{mat}$. For any specific draw from the prior distributions for these five parameters, the value for s_c is selected so that the relationships imposed by the

[2] Equation (2) follows directly from the definition of fecundity (see Punt, 1999 for further details).

[3] Unlike the norm for baleen whale assessments, $\tilde{K}$ is not necessarily equal to the pre-exploitation size of the resource (hence the ~ notation), because (for example) this analysis does not preclude a change over time in the environmental carrying capacity. For this reason, we will refer to $\tilde{K}$, which corresponds to the *current* environmental carrying capacity, as the 'projected equilibrium level' for the remainder of this paper.

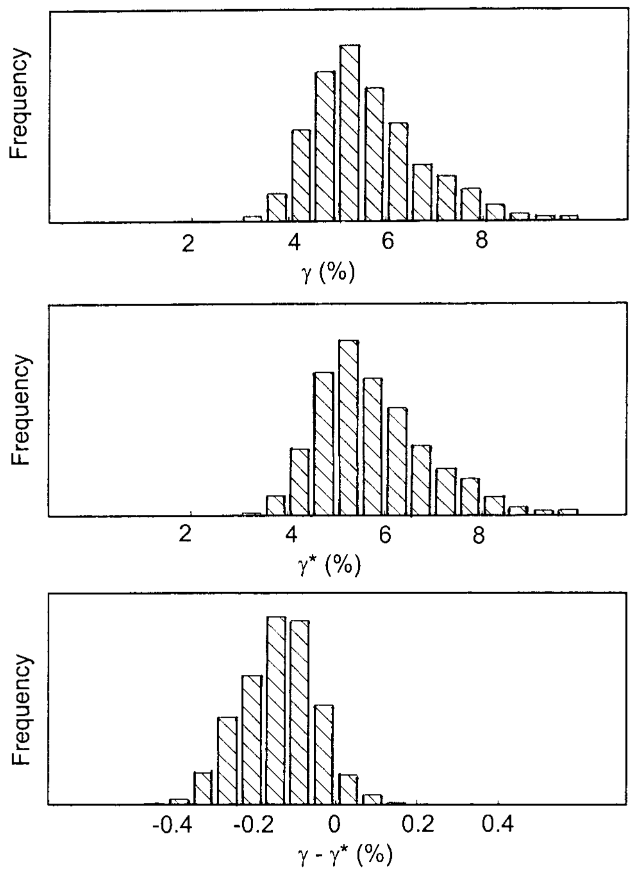

Fig. 1. Posterior distributions for γ, γ^* and $\gamma - \gamma^*$ for the base-case analysis (see text for definitions).

Table 4

The prior distributions used in this assessment of the eastern North Pacific stock of gray whales.

Parameter	Prior distribution
Non-calf survival rate, s	U[0.95; 0.999]
Age-at-maturity, a_m	U[5; 9]
$\tilde{K}_{1+}$	U[0; 70,000]
$MSYL_{mat}$	U[0.4; 0.8]
$MSYR_{mat}$ (%)	U[0; 10]
Maximum pregnancy rate, ρ_{max}	U[0.3; 0.6]
Additional variation, CV_{add}	U[0; 0.35]

population model among the six parameters are satisfied. If the resulting value for s_c is less than zero or greater than that of s, the values for s, a_m, ρ_{max} and $MSYL_{mat}$ are drawn again. Thus, the prior for s_c is forced to conform to the intuitive notion that the survival rate of calves must be lower than that for older animals (and must be larger than zero). The process introduces a correlation between survival rate and age-at-maturity, i.e. it updates these priors to some extent (Punt and Butterworth, 1999). However, the redrawing procedure deliberately leaves the original draw for $MSYR_{mat}$ unchanged, so that the associated uninformative prior is (intentionally) not updated until information on population trends is taken into account via the likelihood. A prior distribution for the age-at-recruitment is not specified. Instead, all of the analyses of this paper assume knife-edged recruitment at age five (IWC, 1993; Butterworth *et al.*, 2002). This assumption has little impact on the results, which hardly change if a value of four or six is used instead.

It is conventional to denote the shore-count-based estimates of abundance for these gray whales by the seasons during which the counts were conducted (e.g. 1968/69). However, in this paper, the estimates are labelled by the latter of the two years and they are assumed to be indices of the numbers at the start of that year – specifically 1+ abundance because the fraction of cow-calf pairs observed is very small (Shelden *et al.*, 1997). Following the example of Wade (2002), the 19 estimates in Table 1 are assumed to be independent estimates of absolute abundance. This treatment of the data differs from that of Butterworth *et al.* (2002), who assumed that the estimate of 21,113 for 1988 (Breiwick *et al.*, 1988) provided an estimate of absolute abundance while the remaining abundance estimates were indices of relative abundance.

Wade (2002) highlights the point that the coefficients of variation for the shore-count-based estimates of abundance are clearly negatively biased, although the reason for this is not fully understood. To account for this, Wade (2002) followed the example of Butterworth *et al.* (1993) by introducing an extra parameter to account for 'additional variation'. This practice is followed here so that the likelihood function (excluding multiplicative constants) is therefore[4]:

$$L = \prod_y \frac{1}{\sqrt{\sigma_y^2 + CV_{add}^2}} \exp\left(-\frac{(\ell n N_y^{obs} - \ell n \hat{N}_y)^2}{2(\sigma_y^2 + CV_{add}^2)} \right) \quad (7)$$

where:

N_y^{obs} is the shore-count-based estimate of the (1+) abundance at the start of year y;

$\hat{N}_y$ is the model-estimate of the (1+) abundance at the start of year y;

σ_y is the standard deviation of the logarithm of N_y^{obs} (approximated here by its coefficient of variation); and

CV_{add}^2 is the additional variation.

Following the example of Wade (2002), a U[0, 0.35] prior for CV_{add} is assumed for the analyses of this paper.

The prior distribution for the (1+) abundance at the start of 1968 is taken to be the same as the sampling distribution for the survey estimate for 1967/68[5] (Wade, 2002) and this estimate is consequently omitted from Equation (7). This is equivalent to including all of the shore-count-based estimates of abundance in the likelihood function and placing a U[0, ∞) prior on the (1+) abundance at the start of 1968 (Punt and Butterworth, 1999).

Sensitivity tests: underestimation of historical commercial and aboriginal catches

IWC (1993) examines the implications of the possibilities that the early (1846-1900) commercial catches and the historical aboriginal catches may have been underestimated. The latter possibility is handled in this paper by multiplying the values in Table 3 by a quantity μ_A, and similarly the possibility that the commercial catches prior to 1901 are underestimated by multiplying them by a quantity μ_C.

The bulk of the analyses ignore the possibility that the historical catches are underestimated (i.e. $\mu_C = \mu_A = 1$).

[4] The assumption of a log-normal distribution for the observation errors is based on the suggestion of Buckland (1992).

[5] The *CV* for the prior distribution for this abundance estimate includes a contribution from the additional variation.

However, five sensitivity tests examine the implications of placing prior distributions on μ_C and μ_A:

(a) $\mu_C \sim U[1,2]$ and $\mu_A \sim U[1,2]$
(b) $\mu_C = 1$ and $\mu_A \sim U[1,3]$
(c) $\mu_C \sim U[1,3]$ and $\mu_A = 1$
(d) $\mu_C = 1$ and $\mu_A \sim U[1,5]$
(e) $\mu_C \sim U[1,5]$ and $\mu_A = 1$

The basis for the prior distributions for the first sensitivity test is the selection of values considered by IWC (1993), while the other four sets of prior distributions examine the impact of uncertainty in one of these contributions to the historical catches only. The upper bounds of the priors are larger for these sensitivity tests and were chosen to incorporate the values identified by Butterworth *et al.* (2002) as being sufficient to allow the population model to fit the observed abundance estimates adequately, and to check sensitivity to the choice of the value for this bound.

The population projections for these sensitivity tests start in 1600 and assume that the population was at its pre-exploitation equilibrium level (K) at that time. An analysis which is based on the assumption that the population was at its pre-exploitation equilibrium level at the start of 1600 but assumes that $\mu_C = \mu_A = 1$ (abbreviation 'original') was conducted to assess the extent to which underestimation of historical catches can improve the fit to the abundance data.

Sensitivity tests: initial conditions

The base-case analysis involves projecting the population forwards from the start of 1968 and placing a prior distribution on the abundance in that year. The choice of the year 1968 by Wade (2002) is based on computational convenience. The sensitivity of the results to alternative choices for the year for which a prior distribution on (1+) abundance is specified, y_{prior}, and the first year considered in the analysis, y_1[6], can be explored as follows.

(a) The 1+ abundance at the start of year y_{prior} is generated from its prior distribution. If y_{prior} is one of the years for which a shore-count-based estimate of abundance is available, this prior distribution is taken to be the sampling distribution for the survey in that year and the corresponding abundance estimate is omitted from the likelihood function.
(b) The abundance at the start of year y_1 is chosen so that if the population model is projected from year y_1 to year y_{prior}, the 1+ abundance in year y_{prior} is equal to the value generated at step (a).

Two sets of sensitivity tests are conducted to explore the impact of different choices for the years y_1 and y_{prior}. The first set involves fixing y_1 to the base-case choice of 1968 and examining the implications of different choices for y_{prior} in the range [1968, 1996][7]. The abbreviations for these sensitivity tests are 'y_{prior} = 19??'. The second set of sensitivity tests involves fixing y_{prior} at 1968 and examining the implications of different choices for y_1 (abbreviation 'y_1 = 19??').

Sensitivity tests: process error

The base-case analysis assumes that the population dynamics are deterministic. To examine whether the inability to fit the abundance data is caused by periods of better/worse calf survival (the population parameter considered most likely to be impacted by process error, S. Reilly, pers. comm.), sensitivity tests are conducted in which the annual number of calves is multiplied by the factor $e^{\varepsilon_y - \sigma_r^2/2}$ where $\varepsilon_y \sim N(0;\sigma_r^2)$. To mimic extended periods of better/worse calf survival, the same multiplicative factor is applied to the births during each decade of the projection[8]. The sensitivity of the results to the choice of the parameter σ_r is examined by considering values of 0 (base-case), 0.05, 0.1 and 0.2.

[6] Although these years need not be the same, year y_1 must, of course, be earlier than year y_{prior}. The age-structure at the start of year y_1 is assumed to be stable.
[7] If y_{prior} is set equal to 1996, the analysis is analogous to the 'backwards' method of Butterworth and Punt (1995).

RESULTS AND DISCUSSION

Management-related quantities

The results are summarised by the values of nine management-related quantities:

(a) $MSYR_{mat}$: the Maximum Sustainable Yield Rate (in terms of harvesting of the mature component of the population) expressed as a percentage;
(b) $\tilde{K}_{1+}$: the projected equilibrium level for the 1+ component of the population;
(c) $N^f_{96} / \tilde{K}_{mat}$: the number of mature females at the start of 1996 expressed as a fraction of that corresponding to the projected equilibrium level;
(d) $N^f_{96} / MSYL_{mat}$: the number of mature females at the start of 1996 expressed as a fraction of that at which MSY is achieved;
(e) *Slope*: the average annual increase of the total (1+) population from 1968-1996 as estimated from a linear regression fit to the logarithms of the model estimates of (1+) population size over this period;
(f) RY (1996): the 1996 replacement yield;
(g) RY^* (1996):

$$RY^*(1996) = \begin{cases} RY(1996) & \text{if } N_{96} / MSYL_{mat} < 1 \\ MSY & \text{otherwise} \end{cases} \quad (8)$$

where MSY is defined in terms of harvesting of the exploitable component of the population, and N is the number of mature animals of both sexes;
(h) CV_{add}: the additional variation expressed as a coefficient of variation; and
(i) $N^f_{00} / \tilde{K}_{mat}$: the number of mature females at the start of 1900 expressed as a fraction of that corresponding to the projected equilibrium level[9].

The depletion of the mature female component of the population at the start of 1900 is used to assess the extent of consistency with the perception (Reilly, 1981) that the population was commercially extinct by the end of the 19th century.

The base-case analysis

Table 5 contrasts the post-model-pre-data and posterior distributions for base-case analysis. In addition to quantities (a)-(h) above, results are presented for the calf and non-calf survival rates (s_c and s respectively), the maximum pregnancy rate, ρ_{max}, $MSYL_{mat}$, $MSYR$ for harvesting on the exploitable component of the population, $MSYR_{exp}$, and the ratios of the 1996 1+ abundance to $\tilde{K}_{1+}$ and to $MSYL_{1+}$. Where possible, the estimates obtained by Wade (2002) are

[8] These multiplicative process error terms are also applied to the age-structure for the first year of the projection, with different values applying to the cohorts from each decade.
[9] Computed only for those analyses for which $y_1 \leq 1900$.

included in this table. Table 5 also provides the posterior distribution for the 'original' analysis that involves projecting the population from pre-exploitation equilibrium in 1600 and ignores any possible underestimation of historical catches.

Table 5 gives results for the base-case assumption that $\gamma^+ = 0$ (see Equation (2) and following discussion), and also for the other extreme of the possible range for an increasing population: $\gamma^+ = \gamma$. The two sets of results are virtually identical. This strongly suggests that the assumption $\gamma^+ = 0$ made for this paper (rather than making allowance for the fact that its value actually lies between 0 and γ) does not introduce a bias of any quantitative consequence for the results presented.

Of the fourteen quantities in Table 5, only four (*Slope*, *RY* (1996), *RY** (1996) and CV_{add}) are updated markedly by the data (Fig. 2). Of the remaining eleven, the lower 2.5 percentiles of the distributions for $N^f_{96} / \tilde{K}_{mat}$, $N^f_{96} / MSYL_{mat}$, $MSYR_{mat}$, $N^{1+}_{96} / \tilde{K}_{1+}$, $N^{1+}_{96} / MSYL_{1+}$, $MSYR_{exp}$ and $\tilde{K}_{1+}$ are increased by including the abundance estimates in the analysis. The probability that the mature population size is larger than $MSYL_{mat}$ is slightly above 50% at 0.53. However, the posterior distribution for this quantity is very wide (Fig. 3). The status of the resource relative to its projected equilibrium level is also very uncertain (Fig. 3). There is a 0.15 probability that the resource has reached this level in terms of the mature component of the population. The negative value of the lower 2.5 percentile for *RY**(1996) for the post-model-pre-data distribution is a consequence of transient age-structure effects.

Fig. 4 shows the fits achieved by the base-case and 'original' analyses to the abundance estimates. The slope of a linear regression of the logarithms of the abundance estimates against time where each data point is weighted by the inverse of its (sampling) variance is 0.0253 yr^{-1}, but this drops to 0.0241 when additional variation with a *CV* of 0.14 (the median of the base-case posterior for CV_{add}) is taken into account. The median of the posterior distribution for the '*slope*' statistic for the base-case analysis is 0.0242 which is almost the same as the latter figure. The median of the posterior for the '*slope*' statistic for the 'original' analysis (0.0177) is much smaller than either of these values.

It is not straightforward to compare the base-case results with those of Wade (2002) because the two sets of analyses are based on different population models, use different sets of parameters and make different assumptions regarding prior distributions. The posterior distribution for the calf survival rate (s_c) differs the most between the two sets of analyses (Table 5). The reason for this is that Wade (2002) defined s_c differently – as the geometric average survival rate from birth to maturity rather than the survival rate in the first year of life.

Table 5

Posterior and post-model-pre-data distributions for 15 management-related quantities for the eastern North Pacific stock of gray whales. The point estimates given are distribution medians, followed by distribution means in round parentheses. 95% credibility intervals are given in square parentheses. Results are shown for the base-case analysis, the analysis conducted by Wade (2002), and an analysis that considers the entire period 1600-1995 and assumes no underestimation of historic commercial and aboriginal catches ('Original').

	Base-case			Wade (2002)	Original
Quantity	Posterior distribution, $\gamma^+=0$	Posterior distribution, $\gamma^+=\gamma$	Post-model-pre-data distribution	Posterior distribution	Posterior distribution
$MSYR_{mat}$ (%)	5.2 (5.4) [2.9; 9.1]	5.2 (5.4) [3.0; 9.0]	4.9 (4.9) [0.3; 9.7]		7.9 (7.9) [5.5; 9.8]
$\tilde{K}_{1+}$ *	31,327 (35,427) [16,240; 67,722]	31,199 (35,392) [16,207; 67,768]	39,815 (40,273) [13,384; 68,460]	31,840 [19,890; 67,220]	14,684 (14,354) [10,685; 16,397]
$N^f_{96} / \tilde{K}_{mat}$ *	0.58 (0.64) [0.26; 1.18]	0.59 (0.64) [0.26; 1.17]	0.52 (0.56) [0.12; 1.15]		1.16 (1.17) [0.98; 1.35]
$N^f_{96} / MSYL_{mat}$	1.04 (1.09) [0.43; 1.90]	1.05 (1.09) [0.42; 1.90]	0.91 (0.96) [0.22; 1.89]		1.59 (1.60) [1.30; 1.92]
Slope (%)	2.42 (2.42) [1.63; 3.24]	2.42 (2.42) [1.62; 3.23]	1.99 (1.94) [-1.69; 5.56]		1.77 (1.75) [0.96; 2.67]
RY (1996)	545 (497) [-183; 852]	544 (496) [-186; 855]	390 (619) [-273; 2,435]	533 [118; 940]	-126 (-94) [-668; 474]
*RY** (1996)	651 (662) [446; 935]	650 (661) [447; 934]	609 (813) [-17; 2,715]		654 (658) [476; 847]
CV_{add}	0.14 (0.14) [0.09; 0.21]	0.13 (0.14) [0.09; 0.21]	0.17 (0.17) [0.01; 0.34]	0.14 [0.10; 0.22]	0.15 (0.15) [0.09; 0.23]
s_c	0.607 (0.626) [0.380; 0.944]	0.607 (0.625) [0.381; 0.940]	0.561 (0.593) [0.376; 0.930]	0.927 [0.802; 0.989]	0.688 (0.699) [0.421; 0.938]
s	0.973 (0.973) [0.952; 0.997]	0.973 (0.973) [0.952; 0.997]	0.969 (0.971) [0.951; 0.997]	0.984 [0.952; 0.999]	0.973 (0.972) [0.950; 0.997]
ρ_{max}	0.453 (0.451) [0.308; 0.591]	0.455 (0.453) [0.309; 0.597]	0.438 (0.440) [0.306; 0.590]	0.494 [0.316; 0.596]	0.462 (0.448) [0.307; 0.579]
$MSYL_{mat}$	0.578 (0.585) [0.421; 0.772]	0.581(0.588) [0.424; 0.776]	0.589 (0.588) [0.411; 0.774]		0.744 (0.732) [0.609; 0.797]
$MSYR_{exp}$ (%)	4.2 (4.4) [2.6; 6.9]	4.2 (4.4) [2.6; 7.0]	4.0 (4.0) [0.2; 8.1]	3.7 [2.4; 6.5]	5.4 (5.4) [3.9; 6.8]
$N^{1+}_{96} / \tilde{K}_{1+}$ *	0.76 (0.79) [0.35; 1.28]	0.77 (0.79) [0.35; 1.28]	0.69 (0.70) [0.15; 1.29]	0.73 [0.36; 1.01]	1.27 (1.29) [1.10; 1.75]
$N^{1+}_{96} / MSYL_{1+}$	1.08 (1.04) [0.47; 1.56]	1.09 (1.04) [0.46; 1.56]	0.96 (0.93) [0.26; 1.54]	1.29 [0.60; 1.73]	1.19 (1.19) [1.00; 1.47]

* K replaces $\tilde{K}$ for results under 'Original'.

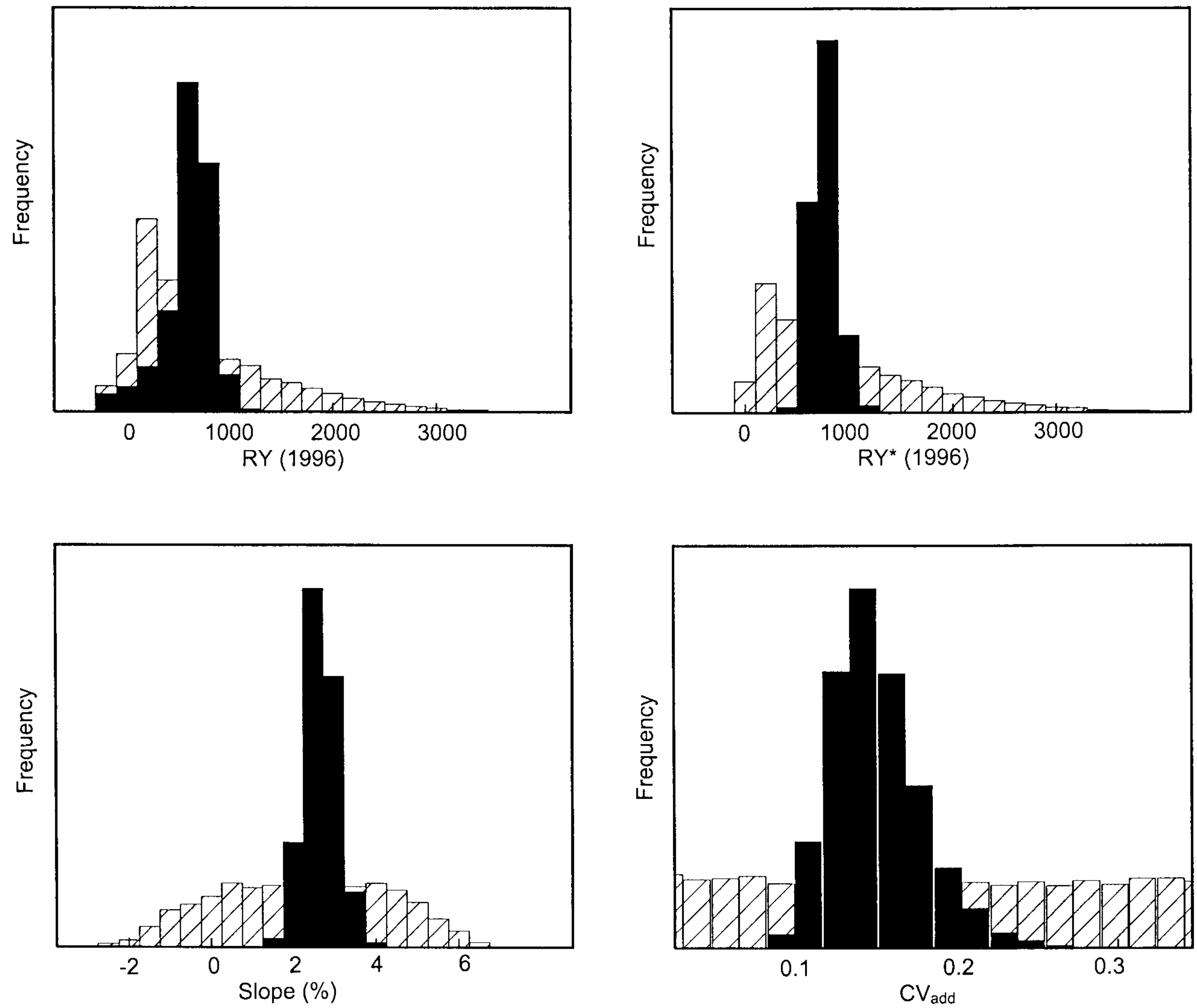

Fig. 2. Post-model-pre-data and posterior distributions (hashed and solid bars respectively) for the base-case analysis for four quantities of interest to management.

Qualitatively, the results for the 'original' analysis differ markedly from those for the base-case analysis in that the resource is assessed to have a much lower pre-exploitation equilibrium level (K) than the projected equilibrium level ($\tilde{K}$) for the other analyses, and to be currently above K with high probability (Table 5). The 1996 replacement yield is consequently assessed to be negative with high probability. One unrealistic feature of the results for the 'original' analysis is that the population size is assessed to have been fairly large at the start of the 20^{th} century (Table 6); this would seem to be contradicted by the fact (Reilly, 1981) that the gray whale population was extinct in terms of commercial fishing potential at this time. Although the base-case and 'original' analyses differ in terms of assessments of current status, the posterior distributions for *RY** (1996) are fairly similar.

Sensitivity tests: underestimation of historical commercial and aboriginal catches

Allowance for underestimation of historical catches (Table 6) improves the fit to the abundance estimates (see '*slope*' posterior statistics). Of the five analyses which consider such underestimation, those which allow for underestimation of commercial catches alone lead to the most realistic results in terms of the size of the population in 1900, though only the analysis in which the prior for μ_C is U[1, 5] results in what might be considered to be commercial extinction at that time. The posterior distribution for $N^f_{00} / \tilde{K}_{mat}$ for this μ_C ~ U[1, 5] analysis is very skew. The median is 0.07 but the probability that $N^f_{00} / \tilde{K}_{mat} > 1$ exceeds 30%, so that the mean of this distribution (0.49) is much larger than the median. The posterior distributions for the '*slope*' statistic remain markedly different from that for the base-case analysis. Therefore, the introduction of priors for the extent of underestimation of historical catches as considered in this paper is insufficient to allow the population model to mimic the observed trend in the indices of absolute abundance.

Sensitivity tests: initial conditions

The fits to the abundance estimates (as measured by the median of the posterior distribution for the '*slope*' statistic) for the analyses which involve changing the value of y_{prior}, the year for which a prior on absolute abundance is specified, from its base-case choice of 1968 are generally as good as that for the base-case analysis (Table 7a). Some of the management-related quantities are sensitive to the choice of y_{prior}. For example, the assessments based on choices of 1972, 1993, 1994 and 1996 suggest a rather lower probability that the stock has recovered to its *MSY* level in terms of the mature component of the population and there is a decreasing trend in $MSYR_{mat}$ estimates with increasing y_{prior}. In contrast to the results for N^f_{96} / $MSYL_{mat}$ and *RY*

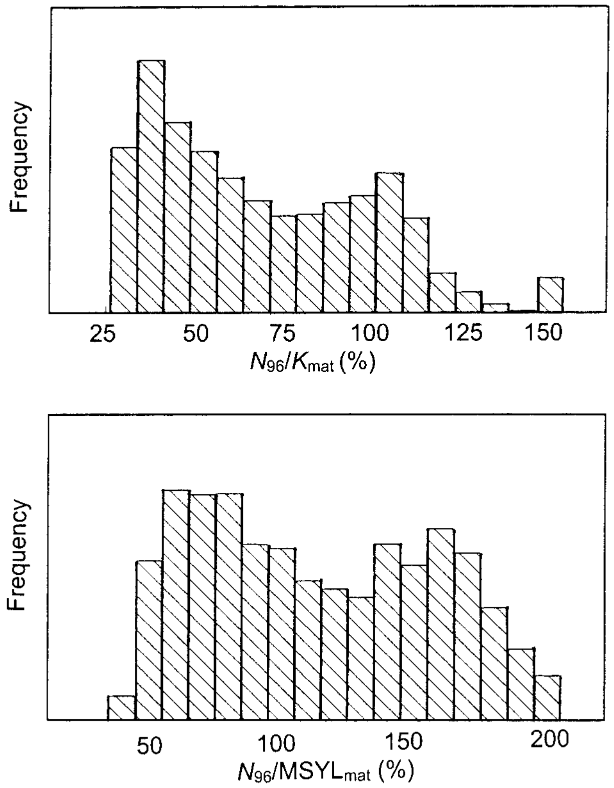

Fig. 3. Posterior distributions for $N^f_{96} / \tilde{K}_{mat}$ and $N^f_{96} / MSYL_{mat}$ from the base-case analysis.

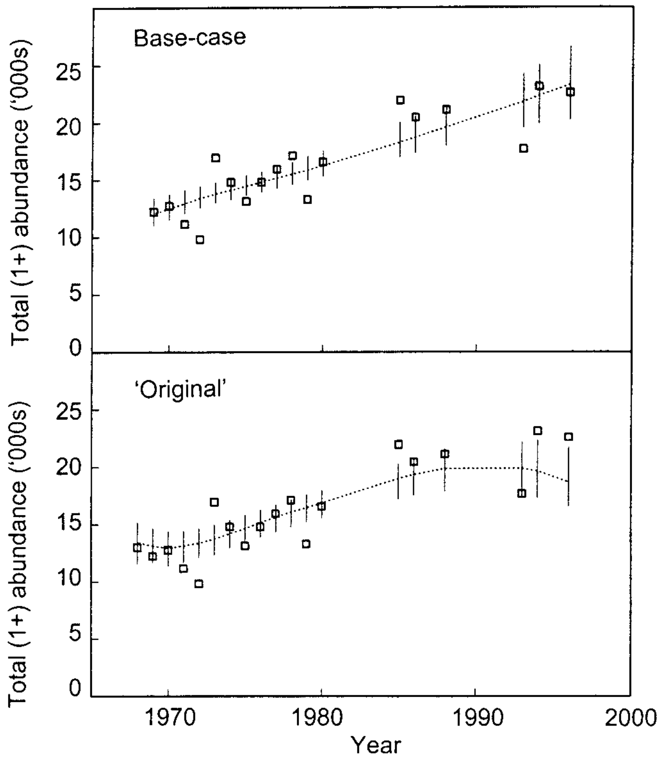

Fig. 4. Shore-count-based estimates of 1+ abundance for the eastern north Pacific stock of gray whales (open squares) along with posterior distributions of 1+ population size for the base-case and 'original' analyses. The dotted line joins the posterior medians and the bars represent posterior 95% credibility limits.

(1996), the posterior distribution for RY^* (1996) is not particularly sensitive to the choice of y_{prior}. The reasons for the sensitivity to the choice of y_{prior} are unclear, but are likely not related to the data used for assessment purposes because some of the patterns evident in Table 7a (for example, that for N^f_{96} / $MSYL_{mat}$) are also evident in statistics of the post-model-pre-data distributions (Table 7b).

Table 6

Estimates of eleven 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 parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that place prior distributions on the extent of under-reporting of historical catches.

Quantity	Base-case Posterior distribution	Original Posterior distribution	Priors for μ_A and μ_C: μ_A ~U[1, 2] μ_C ~ U[1, 2]	μ_A = 1 μ_C ~ U[1, 3]	μ_A ~U[1,3] μ_C = 1	μ_A = 1 μ_C ~ U[1, 5]	μ_A ~U[1,5] μ_C = 1
$MSYR_{mat}$ (%)	5.2 (5.4) [2.9; 9.1]	7.9 (7.9) [5.5; 9.8]	8.4 (8.1) [4.8; 9.9]	7.8 (7.5) [4.1; 9.8]	8.1 (8.0) [5.2; 9.9]	6.4 (6.5) [3.9; 9.8]	7.9 (7.9) [4.6; 9.9]
$\tilde{K}_{1+}$ *	31,327 (35,427) [16,240; 67,722]	14,684 (14,354) [10,685; 16,397]	15,613 (15,652) [11,088; 19,253]	15,553 (16,549) [10,611; 27,957]	15,286 (15,330) [11,452; 21,401]	18,525 (24,103) [12,971; 46,594]	15,301 (15,724) [11,280; 32,687]
$N^f_{96} / \tilde{K}_{mat}$ *	0.58 (0.64) [0.26; 1.18]	1.16 (1.17) [0.98; 1.35]	1.11 (1.12) [0.80; 1.36]	1.10 (1.06) [0.58; 1.38]	1.12 (1.13) [0.77; 1.37]	0.87 (0.84) [0.37; 1.30]	1.11 (1.11) [0.55; 1.38]
$N^f_{96} / MSYL_{mat}$	1.04 (1.09) [0.43; 1.90]	1.59 (1.60) [1.30; 1.92]	1.60 (1.59) [1.22; 1.89]	1.53 (1.49) [0.96; 1.89]	1.62 (1.60) [1.21; 1.91]	1.31 (1.25) [0.58; 1.77]	1.55 (1.56) [0.92; 1.91]
Slope (%)	2.42 (2.42) [1.63; 3.24]	1.77 (1.75) [0.96; 2.67]	1.94 (1.91) [1.13; 2.52]	1.91 (1.87) [1.01; 2.55]	1.86 (1.83) [1.11; 2.38]	1.99 (1.99) [1.22; 2.81]	1.91 (1.87) [1.08; 2.45]
RY (1996)	545 (497) [-183; 852]	-126 (-94) [-668; 474]	46 (-1) [-611; 510]	75 (57) [-590; 718]	-0 (-22) [-660; 469]	377 (254) [-574; 795]	35 (14) [-518; 532]
RY^* (1996)	651 (662) [446; 935]	654 (658) [476; 847]	674 (676) [469; 842]	678 (662) [437; 838]	648 (658) [490; 844]	641 (636) [420; 865]	645 (657) [498; 846]
$N^f_{00} / \tilde{K}_{mat}$ *	N/A	1.11 (1.06) [0.35; 1.35]	1.04 (0.79) [0.03; 1.32]	0.58 (0.65) [0.03; 1.37]	1.15 (1.08) [0.11; 1.31]	0.07 (0.49) [0.02; 1.36]	1.16 (1.06) [0.09; 1.40]
CV_{add}	0.14 (0.14) [0.09; 0.21]	0.15 (0.15) [0.09; 0.23]	0.14 (0.15) [0.10; 0.22]	0.14 (0.15) [0.10; 0.23]	0.14 (0.14) [0.10; 0.22]	0.14 (0.14) [0.09; 0.22]	0.14 (0.14) [0.10; 0.23]
μ_C	1	1	1.33 (1.39) [1.02; 1.92]	1.46 (1.61) [1.04; 2.80]	1	1.94 (2.39) [1.06; 4.69]	1
μ_A	1	1	1.51 (1.49) [1.01; 1.96]	1	1.82 (1.82) [1.08; 2.71]	1	1.87 (1.87) [1.05; 3.22]

* K replaces $\tilde{K}$ for results under 'Original' and 'Priors for μ_A and μ_C'.

Table 7

Estimates of eight 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 parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that vary y_{prior}, the year for which a prior distribution on 1+ abundance is specified.

y_{prior}	$MSYR_{mat}$	$\tilde{K}_{1+}$	$N^f_{96} / \tilde{K}_{mat}$	$N^f_{96} / MSYL_{mat}$	*Slope* (%)	*RY* (1996)	*RY** (1996)	CV_{add}
(a) Posterior distributions								
1968	5.2 (5.4)	31,327 (35,427)	0.58 (0.64)	1.04 (1.09)	2.42 (2.42)	545 (497)	651 (662)	0.14 (0.14)
(Base-case)	[2.9; 9.1]	[16,240; 67,722]	[0.26; 1.18]	[0.43; 1.90]	[1.63; 3.24]	[-183; 852]	[446; 935]	[0.09; 0.21]
1969	5.2 (5.4)	30,317 (35,046)	0.61 (0.65)	1.07 (1.11)	2.42 (2.42)	543 (491)	654 (664)	0.14 (0.14)
	[3.0; 9.1]	[16,267; 67,704]	[0.26; 1.17]	[0.42; 1.92]	[1.59; 3.24]	[-223; 848]	[442; 935]	[0.09; 0.21]
1970	5.2 (5.4)	30,187 (35,236)	0.61 (0.64)	1.06 (1.10)	2.43 (2.42)	544 (492)	655 (665)	0.14 (0.14)
	[2.9; 9.1]	[16,374; 67,753]	[0.26; 1.17]	[0.42; 1.91]	[1.60; 3.24]	[-251; 858]	[446; 942]	[0.09; 0.21]
1971	5.2 (5.4)	32,189 (35,903)	0.57 (0.63)	1.01 (1.07)	2.41 (2.42)	548 (499)	653 (661)	0.13 (0.14)
	[3.0; 9.1]	[16,001; 67,540]	[0.26; 1.18]	[0.42; 1.89]	[1.61; 3.22]	[-226; 844]	[443; 934]	[0.09; 0.21]
1972	5.1 (5.3)	37,939 (39,332)	0.48 (0.57)	0.76 (0.93)	2.33 (2.34)	562 (521)	637 (644)	0.13 (0.13)
	[3.0; 8.8]	[16,395; 68,339]	[0.26; 1.13]	[0.38; 1.89]	[1.60; 3.18]	[-231; 843]	[437; 917]	[0.08; 0.20]
1973	5.0 (5.3)	33,034 (36,410)	0.55 (0.62)	0.98 (1.06)	2.39 (2.41)	551 (502)	642 (657)	0.13 (0.14)
	[3.0; 8.9]	[15,987; 67,812]	[0.26; 1.16]	[0.43; 1.88]	[1.63; 3.24]	[-186; 860]	[449; 940]	[0.09; 0.21]
1974	5.2 (5.4)	31,327 (35,672)	0.58 (0.63)	1.03 (1.08)	2.42 (2.42)	552 (501)	653 (662)	0.14 (0.14)
	[3.0; 9.0]	[16,272; 67,536]	[0.26; 1.17]	[0.42; 1.91]	[1.61; 3.22]	[-202; 851]	[444; 935]	[0.09; 0.21]
1975	5.2 (5.4)	31,807 (35,884)	0.57 (0.63)	1.00 (1.07)	2.43 (2.43)	549 (497)	656 (665)	0.14 (0.14)
	[3.0; 9.1]	[16,001; 67,901]	[0.26; 1.19]	[0.41; 1.89]	[1.61; 3.23]	[-223; 854]	[437; 941]	[0.09; 0.21]
1976	5.2 (5.4)	31,897 (35,815)	0.57 (0.63)	1.01 (1.08)	2.42 (2.43)	550 (496)	653 (665)	0.14 (0.14)
	[2.9; 9.1]	[16,115; 67,624]	[0.26; 1.19]	[0.42; 1.87]	[1.63; 3.24]	[-251; 852]	[444; 947]	[0.09; 0.21]
1977	5.1 (5.3)	32,529 (36,222)	0.56 (0.62)	0.99 (1.06)	2.42 (2.42)	551 (506)	650 (660)	0.14 (0.14)
	[2.9; 8.9]	[16,349; 67,695]	[0.26 1.17]	[0.42; 1.86]	[1.60; 3.23]	[-201; 859]	[445; 938]	[0.09; 0.21]
1978	5.1 (5.4)	31,883 (35,991)	0.57 (0.63)	1.01 (1.06)	2.44 (2.43)	557 (507)	655 (665)	0.14 (0.14)
	[3.0; 9.0]	[16,350; 67,877]	[0.26; 1.17]	[0.42; 1.87]	[1.64; 3.23]	[-201; 861]	[446; 938]	[0.09; 0.21]
1979	5.0 (5.3)	34,781 (37,218)	0.53 (0.60)	0.94 (1.03)	2.41 (2.41)	562 (520)	648 (660)	0.13 (0.14)
	[3.0; 8.9]	[16,329; 67,701]	[0.26; 1.18]	[0.42; 1.88]	[1.60; 3.23]	[-180; 866]	[441; 946]	[0.09; 0.21]
1980	5.1 (5.3)	32,842 (36,546)	0.55 (0.62)	0.97 (1.04)	2.42 (2.42)	559 (511)	654 (663)	0.14 (0.14)
	[2.9; 8.8]	[16,265; 67,753]	[0.26; 1.18]	[0.42; 1.85]	[1.62; 3.22]	[-211; 854]	[441; 937]	[0.09; 0.21]
1985	4.9 (5.1)	35,741 (38,150)	0.51 (0.58)	0.90 (0.99)	2.42 (2.42)	573 (533)	643 (654)	0.14 (0.14)
	[2.9; 8.6]	[16,719; 67,889]	[0.26; 1.15]	[0.42; 1.80]	[1.60; 3.20]	[-115; 857]	[435; 921]	[0.09; 0.21]
1986	5.0 (5.2)	35,973 (38,249)	0.51 (0.58)	0.90 (0.98)	2.43 (2.43)	574 (547)	648 (656)	0.14 (0.14)
	[2.9; 8.4]	[16,880; 68,055]	[0.26; 1.14]	[0.42; 1.80]	[1.62; 3.23]	[-60; 864]	[436; 917]	[0.09; 0.21]
1988	4.9 (5.0)	37,394 (39,426)	0.49 (0.55)	0.86 (0.94)	2.42 (2.42)	582 (572)	642 (648)	0.14 (0.14)
	[2.9; 8.0]	[17,577; 68,372]	[0.26; 1.07]	[0.41; 1.74]	[1.61; 3.23]	[190; 873]	[435; 910]	[0.09; 0.21]
1993	4.7 (4.8)	42,763 (43,716)	0.43 (0.47)	0.72 (0.80)	2.43 (2.43)	610 (625)	637 (651)	0.14 (0.14)
	[2.9; 7.3]	[20,742; 68,308]	[0.25; 0.87]	[0.39; 1.55]	[1.58; 3.29]	[377; 934]	[425; 949]	[0.09; 0.21]
1994	4.6 (4.7)	43,007 (43,528)	0.42 (0.48)	0.75 (0.83)	2.38 (2.39)	595 (604)	627 (635)	0.14 (0.14)
	[2.9; 6.9]	[19,827; 68,510]	[0.25; 0.91]	[0.40; 1.58]	[1.58; 3.20]	[377; 872]	[425; 888]	[0.09; 0.21]
1996	4.6 (4.7)	43,807 (44,378)	0.42 (0.46)	0.72 (0.80)	2.40 (2.40)	609 (615)	631 (639)	0.14 (0.14)
	[2.8; 7.0]	[21,376; 68,682]	[0.25; 0.85]	[0.40; 1.53]	[1.57; 3.24]	[382; 890]	[424; 901]	[0.09; 0.21]
(b) Post-model-pre-data distributions								
1968	4.9 (4.9)	39,815 (40,273)	0.52 (0.56)	0.91 (0.96)	1.99 (1.94)	390 (619)	609 (813)	0.17 (0.17)
(Base-case)	[0.3; 9.7]	[13,384; 68,460]	[0.12; 1.15]	[0.22; 1.89]	[-1.69; 5.56]	[-273; 2,435]	[-17; 2,715]	[0.01; 0.34]
1969	4.8 (4.9)	39,206 (39,648)	0.49 (0.54)	0.84 (0.91)	1.98 (1.93)	402 (629)	570 (783)	0.17 (0.17)
	[0.2; 9.7]	[12,157; 68,291]	[0.12; 1.14]	[0.21; 1.84]	[-1.85; 5.65]	[-205; 2,443]	[-19; 2,707]	[0.01; 0.34]
1970	5.0 (5.0)	39,026 (39,529)	0.51 (0.55)	0.88 (0.93)	2.02 (1.98)	412 (633)	595 (793)	0.18 (0.17)
	[0.2; 9.7]	[12,122; 68,259]	[0.13; 1.15]	[0.22; 1.84]	[-1.73; 5.61]	[-225; 2,415]	[-18; 2,636]	[0.01; 0.34]
1971	4.9 (4.9)	38,607 (39,048)	0.42 (0.48)	0.73 (0.81)	2.00 (1.90)	391 (596)	503 (696)	0.17 (0.17)
	[0.3; 9.7]	[11,838; 68,192]	[0.10; 1.11]	[0.17; 1.76]	[-2.03; 5.70]	[-41; 2,268]	[-21; 2,474]	[0.01; 0.34]
1972	4.9 (4.9)	38,154 (38,856)	0.35 (0.42)	0.61 (0.71)	1.97 (1.81)	372 (553)	447 (615)	0.17 (0.17)
	[0.2; 9.7]	[11,498; 68,303]	[0.08; 1.08]	[0.14; 1.68]	[-2.35; 5.60]	[-31; 2,049]	[-24; 2,180]	[0.01; 0.34]
1973	5.0 (5.0)	40,181 (40,436)	0.60 (0.63)	1.04 (1.07)	2.00 (2.03)	425 (659)	682 (878)	0.17 (0.17)
	[0.3; 9.7]	[12,477; 68,465]	[0.20; 1.18]	[0.35; 1.87]	[-1.16; 5.58]	[-357; 2,534]	[-7; 2,793]	[0.01; 0.34]
1974	4.9 (4.9)	39,583 (40,155)	0.52 (0.57)	0.90 (0.96)	2.09 (2.08)	438 (660)	621 (804)	0.17 (0.17)
	[0.3; 9.7]	[12,593; 68,428]	[0.17; 1.14]	[0.29; 1.82]	[-1.35; 5.70]	[-183; 2,432]	[-11; 2,613]	[0.01; 0.34]
1975	5.0 (4.9)	39,518 (39,926)	0.45 (0.50)	0.78 (0.86)	2.16 (2.07)	453 (636)	568 (730)	0.17 (0.17)
	[0.2; 9.7]	[11,994; 68,363]	[0.14; 1.10]	[0.24; 1.75]	[-1.54; 5.71]	[-40; 2,222]	[-17; 2,355]	[0.01; 0.34]
1976	4.9 (5.0)	39,733 (40,027)	0.50 (0.55)	0.87 (0.93)	2.15 (2.13)	468 (655)	604 (770)	0.17 (0.17)
	[0.3; 9.7]	[12,489; 68,385]	[0.17; 1.12]	[0.29; 1.77]	[-1.29; 5.70]	[-122; 2,294]	[-10; 2,450]	[0.01; 0.34]
1977	4.9 (4.9)	39,751 (40,336)	0.51 (0.56)	0.89 (0.95)	2.14 (2.13)	471 (670)	626 (790)	0.17 (0.17)
	[0.3; 9.7]	[12,496; 68,365]	[0.19; 1.13]	[0.32; 1.78]	[-1.20; 5.74]	[-122; 2,344]	[-7; 2,489]	[0.01; 0.34]
1978	4.9 (5.0)	40,391 (40,657)	0.53 (0.58)	0.93 (0.98)	2.18 (2.18)	486 (679)	649 (817)	0.17 (0.17)
	[0.3; 9.8]	[12,401; 68,290]	[0.20; 1.14]	[0.34; 1.80]	[-1.09; 5.73]	[-169; 2,332]	[-4; 2,534]	[0.01; 0.34]
1979	4.8 (4.9)	39,292 (39,687)	0.41 (0.47)	0.71 (0.80)	2.07 (2.04)	429 (592)	509 (659)	0.17 (0.17)
	[0.3; 9.7]	[12,073; 68,289]	[0.15; 1.09]	[0.25; 1.69]	[-1.41; 5.66]	[-29; 2,041]	[-12; 2,174]	[0.01; 0.34]
1980	4.9 (4.9)	40,573 (40,797)	0.48 (0.54)	0.84 (0.92)	2.22 (2.15)	495 (653)	609 (750)	0.17 (0.17)
	[0.3; 9.7]	[12,847; 68,290]	[0.19; 1.11]	[0.33; 1.77]	[-1.12; 5.66]	[-32; 2,182]	[-5; 2,317]	[0.01; 0.34]
1985	5.1 (5.2)	41,812 (41,548)	0.55 (0.59)	0.94 (1.00)	2.39 (2.33)	606 (747)	722 (852)	0.17 (0.17)
	[0.4; 9.7]	[12,254; 68,472]	[0.25; 1.09]	[0.42; 1.78]	[-0.94; 5.77]	[-18; 2,229]	[21; 2,368]	[0.01; 0.34]

cont...

Table 7 continued.

y_{prior}	$MSYR_{mat}$	$\tilde{K}_{1+}$	$N_{96}^f / \tilde{K}_{mat}$	N_{96}^f / $MSYL_{mat}$	*Slope* (%)	*RY* (1996)	*RY** (1996)	CV_{add}
(b) Post-model-pre-data distributions (continued)								
1986	5.0 (5.0)	41,187 (41,252)	0.50 (0.55)	0.87 (0.94)	2.37 (2.27)	576 (701)	666 (786)	0.17 (0.17)
	[0.3; 9.7]	[12,439; 68,492]	[0.23; 1.07]	[0.38; 1.76]	[-0.95; 5.72]	[-15; 2,085]	[12; 2,246]	[0.01; 0.34]
1988	5.1 (5.1)	41,600 (41,589)	0.49 (0.54)	0.84 (0.92)	2.43 (2.32)	603 (704)	683 (784)	0.17 (0.17)
	[0.4; 9.7]	[12,440; 68,583]	[0.23; 1.02]	[0.38; 1.73]	[-0.91; 5.70]	[-6; 1,996]	[23; 2,180]	[0.01; 0.34]
1993	4.8 (4.9)	41,132 (41,195)	0.37 (0.43)	0.64 (0.74)	2.07 (2.02)	468 (538)	499 (578)	0.17 (0.17)
	[0.3; 9.7]	[12,666; 68,505]	[0.16; 0.95]	[0.27; 1.61]	[-0.97; 5.23]	[-12; 1,657]	[3; 1,845]	[0.01; 0.34]
1994	5.2 (5.3)	42,031 (41,908)	0.45 (0.50)	0.77 (0.85)	2.43 (2.32)	604 (665)	663 (733)	0.18 (0.18)
	[0.6; 9.7]	[12,220; 68,524]	[0.20; 1.00]	[0.34; 1.71]	[-0.89; 5.48]	[-7; 1,857]	[39; 2,009]	[0.01; 0.34]
1996	5.1 (5.2)	42,318 (42,128)	0.41 (0.47)	0.70 (0.80)	2.32 (2.20)	557 (603)	610 (670)	0.17 (0.17)
	[0.6; 9.7]	[12,388; 68,549]	[0.18; 1.00]	[0.31; 1.71]	[-0.91; 5.25]	[-6; 1,723]	[38; 1,905]	[0.01; 0.34]

The results for the analyses that involve changing the first year considered in the projection (y_1) are given in Table 8. The assumption of a stable age-structure at the start of year y_1 becomes less defensible as y_1 is reduced. However, the influence of violations of this assumption on the dynamics of the population during the period for which abundance estimates are available also decreases as y_1 is reduced. Butterworth *et al.* (1995) assessed the Cape fur seal population off southern Africa using an approach similar to that applied here, and selected y_1 so that the impact of transient age-structure effects on the period for which abundance estimates are available is slight.

The fits to the abundance data (as measured by the median of the posterior distribution for the '*slope*' statistic) are worst for $y_1 = 1900$ and $y_1 = 1890$, although the median of the posterior for '*slope*' is nevertheless closer to the base-case value than for the 'original' analysis. The posterior distributions for the depletion of the mature population in 1900 for the three analyses which set y_1 to 1900 or earlier are much more consistent with perceptions of a stock highly depleted at that time. For example, the posterior for $N_{00}^f / \tilde{K}_{mat}$ for the $y_1 = 1880$ analysis has a median of 0.03 and 95% credibility interval [0.01, 0.07].

The results are generally insensitive to decreasing y_1 from 1968 to any year after 1930. For a choice of y_1 between 1890 and 1910, the assessment becomes slightly more pessimistic than the base-case analysis (lower $MSYR_{mat}$, lower *RY** (1996) and a more depleted resource). However, the results for $y_1 = 1880$ are closer to those for $y_1 = 1920$ than to those for $y_1 = 1890$.

The results in Tables 7 and 8 indicate that although the base-case choices for y_1 and y_{prior} were selected primarily for computational convenience, the results of the assessment are not markedly sensitive to them. This conclusion applies particularly to the posterior for *RY** (1996), the median of which varies within a narrow range for all of the choices for y_1 and y_{prior} examined.

Sensitivity tests: process error

Table 9 lists the results for the analyses which allow for process error. Results are shown for variants of the base-case and the 'original' analyses. For the analyses based on $y_1 = y_{prior} = 1968$, the posterior distributions for '*slope*' and CV_{add} are relatively insensitive to the value assumed for σ_r. However, the results in terms of the other quantities generally become a little less optimistic and more variable as the value of σ_r is increased from 0 to 0.2. The increase in variability is most notable for *RY* (1996) and *RY** (1996). For the computations based on the 'original' analysis with $y_1 = 1600$, the results frequently become more optimistic (in terms of resource productivity levels and population increase rates) and variable as σ_r is increased. Despite some

Table 8

Estimates of eight 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 parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that vary y_1, the first year considered in the analysis.

y_1	$MSYR_{mat}$	$\tilde{K}_{1+}$	$N_{96}^f / \tilde{K}_{mat}$	$N_{96}^f / MSYL_{mat}$	*Slope* (%)	*RY* (1996)	*RY** (1996)	CV_{add}
1968	5.2 (5.4)	31,327 (35,427)	0.58 (0.64)	1.04 (1.09)	2.42 (2.42)	545 (497)	651 (662)	0.14 (0.14)
(Base-case)	[2.9; 9.1]	[16,240; 67,722]	[0.26; 1.18]	[0.43; 1.90]	[1.63; 3.24]	[-183; 852]	[446; 935]	[0.09; 0.21]
1960	5.3 (5.5)	30,234 (34,951)	0.60 (0.64)	1.07 (1.10)	2.41 (2.41)	548 (496)	660 (669)	0.14 (0.14)
	[3.0; 9.2]	[15,836; 67,490]	[0.26; 1.18]	[0.43; 1.89]	[1.60; 3.24]	[-222; 862]	[449; 944]	[0.09; 0.21]
1950	5.3 (5.6)	29,504 (34,411)	0.61 (0.65)	1.11 (1.12)	2.42 (2.41)	546 (499)	665 (670)	0.14 (0.14)
	[3.1; 9.3]	[15,728; 67,551]	[0.26; 1.16]	[0.43; 1.92]	[1.60; 3.21]	[-165; 850]	[454; 919]	[0.09; 0.21]
1940	5.3 (5.6)	29,706 (34,364)	0.60 (0.64)	1.11 (1.14)	2.40 (2.40)	544 (499)	661 (665)	0.13 (0.14)
	[3.1; 9.2]	[15,935; 67,378]	[0.25; 1.15]	[0.45; 1.92]	[1.58; 3.19]	[-148; 847]	[450; 913]	[0.09; 0.21]
1930	5.2 (5.5)	30,392 (34,924)	0.59 (0.63)	1.10 (1.12)	2.39 (2.38)	545 (507)	654 (658)	0.14 (0.14)
	[3.0; 9.2]	[16,191; 67,640]	[0.25; 1.11]	[0.46; 1.88]	[1.57; 3.19]	[-77; 836]	[446; 896]	[0.09; 0.21]
1920	5.1 (5.3)	32,871 (36,267)	0.54 (0.60)	1.03 (1.07)	2.38 (2.38)	560 (531)	648 (653)	0.13 (0.14)
	[3.0; 8.7]	[16,116; 67,865]	[0.25; 1.09]	[0.45; 1.77]	[1.57; 3.17]	[28; 851]	[449; 884]	[0.09; 0.21]
1910	4.7 (4.8)	38,836 (40,293)	0.46 (0.52)	0.85 (0.92)	2.31 (2.30)	575 (569)	624 (629)	0.14 (0.14)
	[2.8; 7.3]	[17,341; 68,243]	[0.24; 1.02]	[0.45; 1.61]	[1.53; 3.02]	[238; 836]	[430; 857]	[0.09; 0.21]
1900	4.3 (4.4)	44,872 (44,544)	0.38 (0.44)	0.71 (0.78)	2.19 (2.17)	564 (566)	591 (594)	0.14 (0.14)
	[2.7; 6.3]	[19,654; 69,026]	[0.24; 0.87]	[0.43; 1.39]	[1.37; 2.81]	[331; 798]	[395; 805]	[0.09; 0.21]
1890	4.3 (4.4)	45,853 (45,136)	0.38 (0.44)	0.69 (0.76)	2.17 (2.14)	563 (562)	586 (588)	0.14 (0.14)
	[2.7; 6.3]	[19,333; 68,999]	[0.24; 0.88]	[0.43; 1.38]	[1.39; 2.75]	[328; 778]	[399; 793]	[0.09; 0.21]
1880	5.1 (5.3)	32,712 (36,384)	0.54 (0.60)	1.04 (1.08)	2.38 (2.38)	554 (526)	648 (653)	0.13 (0.14)
	[2.9; 9.1]	[16,116; 68,099]	[0.25; 1.09]	[0.46; 1.83]	[1.56; 3.18]	[-2; 855]	[446; 891]	[0.09; 0.21]

Table 9

Estimates of eight 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 parentheses. Posterior 95% credibility intervals are given in square parentheses. Results are shown for analyses that allow for process error in calf survival rate.

Specification	$MSYR_{mat}$	$\tilde{K}_{1+}$	$N^f_{96} / \tilde{K}_{mat}$	$N^f_{96} / MSYL_{mat}$	*Slope* (%)	*RY* (1996)	*RY** (1996)	CV_{add}
$y_1 = y_{prior}$=1968								
Base-case	5.2 (5.4)	31,327 (35,427)	0.58 (0.64)	1.04 (1.09)	2.42 (2.42)	545 (497)	651 (662)	0.14 (0.14)
	[2.9; 9.1]	[16,240; 67,722]	[0.26; 1.18]	[0.43; 1.90]	[1.63; 3.24]	[-183; 852]	[446; 935]	[0.09; 0.21]
σ_r=0.05	5.2 (5.4)	31,299 (35,589)	0.59 (0.64)	1.04 (1.09)	2.42 (2.42)	537 (496)	651 (659)	0.14 (0.14)
	[2.9; 9.1]	[16,247; 67,697]	[0.26; 1.16]	[0.43; 1.90]	[1.62; 3.24]	[-201; 888]	[419; 953]	[0.09; 0.21]
σ_r=0.1	5.2 (5.4)	31,213 (35,489)	0.59 (0.64)	1.05 (1.09)	2.41 (2.42)	516 (486)	647 (653)	0.13 (0.14)
	[2.8; 9.2]	[16,074; 67,247]	[0.26; 1.18]	[0.43; 1.90]	[1.60; 3.25]	[-193; 929]	[346; 984]	[0.09; 0.21]
σ_r=0.2	5.0 (5.2)	34,285 (36,950)	0.54 (0.61)	0.96 (1.05)	2.41 (2.41)	464 (458)	613 (621)	0.13 (0.14)
	[2.6; 9.3]	[16,276; 67,729]	[0.26; 1.19]	[0.42; 1.95]	[1.59; 3.22]	[-214; 1,041]	[172; 1,068]	[0.09; 0.21]
y_1=1600								
Original	7.9 (7.9)	14,684 (14,354)	1.16 (1.17)	1.59 (1.60)	1.77 (1.75)	-126 (-94)	654 (658)	0.15 (0.15)
	[5.5; 9.8]	[10,685; 16,397]	[0.98; 1.35]	[1.30; 1.92]	[0.96; 2.67]	[-668; 474]	[476; 847]	[0.09; 0.23]
σ_r=0.05	7.8 (8.0)	14,942 (14,800)	1.13 (1.16)	1.62 (1.62)	1.77 (1.78)	-34 (-66)	666 (664)	0.13 (0.14)
	[5.6; 9.8]	[11,186; 17,448]	[0.99; 1.36]	[1.30; 1.96]	[1.05; 2.37]	[-539; 434]	[490; 826]	[0.10; 0.22]
σ_r=0.1	8.2 (8.1)	15,103 (14,871)	1.12 (1.16)	1.63 (1.63)	2.02 (2.00)	78 (34)	665 (669)	0.13 (0.14)
	[5.6; 9.8]	[11,322; 17,128]	[1.01; 1.42]	[1.36; 1.95]	[1.22; 2.63]	[-612; 525]	[490; 849]	[0.09; 0.21]
σ_r=0.2	8.0 (7.7)	14,848 (14,906)	1.21 (1.18)	1.67 (1.68)	1.95 (1.96)	-242 (-157)	631 (636)	0.14 (0.14)
	[3.8; 9.7]	[11,495; 17,627]	[0.90; 1.42]	[1.26; 2.11]	[1.06; 2.59]	[-656; 502]	[326; 849]	[0.09; 0.22]

improvement, these analyses nevertheless remain unable to fit the shore-count-based abundance estimates adequately. This indicates that process error effects alone are not sufficient to resolve the discrepancy between the historical catches and the trend in the abundance estimates.

CONCLUDING REMARKS

The results of this paper confirm previous analyses that suggested that population models based on the assumption that the eastern North Pacific stock of gray whales was at pre-exploitation equilibrium in 1600 (or 1846) cannot mimic the size of and trends in recent shore-count-based estimates of abundance. The method proposed by Wade (2002) sidesteps this problem by starting the population projection from a stable age-structure in 1968. This paper indicates that the results of such an assessment approach are not sensitive to the choice of 1968 either as the year for which a prior for abundance is specified, or that from which projections commence. *RY** is among the most robust quantities that can be estimated from the data; the median of the posterior distribution for this quantity varies within a relatively narrow range for most of the analyses of this paper.

The 95% credibility intervals for the additional CV parameter (CV_{add}) have lower 2.5 percentiles well in excess of zero and therefore confirm that the inclusion of the term in Equation (7) for additional variance is justified. Wade and DeMaster (1996) showed using Bayes factors that models that included the possibility of additional variance provided more satisfactory fits to the abundance data.

Neither allowing for underestimation of historical commercial and aboriginal catches nor including the possibility of decade-long deviations from expectancy in pregnancy rate permit the model to mimic the observed data adequately. This result differs from the conclusions of Butterworth *et al.* (2002) who found that making allowance for under-estimation of historical removals could resolve this problem. This discrepancy is probably a consequence of the fact that the current assessment is based on a Bayesian rather than a maximum-likelihood estimation approach conditional on certain choices for the values of the biological parameters (i.e. some choices for these parameters do allow the model to fit the abundance data, but the bulk of them do not).

It is noteworthy that the posterior distributions for some of the model outputs (e.g. *MSYL*) are not notably different from their priors. This suggests that even this dataset (arguably one of the best for any marine mammal population) is unable to provide much information about some of the quantities of interest to management. The posterior distributions for $N^f_{96} / \tilde{K}_{mat}$ and $N^f_{96} / MSYL_{mat}$ are relatively imprecise. This is somewhat unexpected from the results of other Bayesian assessments (e.g. those for a standard approach for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Punt and Butterworth, 1999)). It seems likely that this imprecision is a consequence of dropping the assumption that the population was at its pre-exploitation equilibrium level at the start of the population projections.

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