Population status of the eastern North Pacific stock of gray whales in 2009

ANDRE E. PUNT+ AND PAUL R. WADE*

Contact e-mail: aepunt@u.washington.edu

ABSTRACT

An age- and sex-structured population dynamics model is fitted using Bayesian methods to data on the catches and abundance estimates for the Eastern North Pacific (ENP) stock of gray whales. The prior distributions used for these analyses incorporate revised estimates of abundance for ENP gray whales and account explicitly for the drop in abundance caused by the 1999–2000 mortality event. A series of analyses are conducted to evaluate the sensitivity of the results to different assumptions. The model fits the available data adequately, but, as in previous assessments, the measures of uncertainty associated with the survey-based abundance estimates are found to be negatively biased. The data support the inclusion of the 1999–2000 mortality event in the model, and accounting for this event leads to greater uncertainty regarding the current status of the resource. The baseline analysis estimates the ENP gray whale population to be above the maximum sustainable yield level (MSYL) with high probability (0.884). The posterior mean for the ratio of 2009 (1+) abundance to MSYL is 1.29 (with a posterior median of 1.37 and a 90% probability interval of 0.68–1.51). These results are consistent across all the model runs conducted. The baseline model also estimates the 2009 ENP gray whale population size (posterior mean of 20,366) to be at 85% of its carrying capacity (posterior mean of 25,808), and this is also consistent across all the model runs. The baseline model estimate of the maximum rate of increase, λ_{max}, is 1.062 which, while high, is nevertheless within the range of estimates obtained for other baleen whales.

KEYWORDS: ASESSMENT; GRAY WHALES; WHALING – ABORIGINAL

INTRODUCTION

The eastern North Pacific (ENP) gray whale (*Eschrichtius robustus*) population has been hunted extensively by both commercial and aboriginal whalers. Indigenous peoples of both North America and Russia have hunted gray whales in some locations for centuries and possibly for 2000 years or more (Krupnik, 1984; O'Leary, 1984). The winter breeding grounds of the ENP gray whale (lagoons and adjacent ocean areas in Baja California, Mexico) were discovered by Yankee whalers in the early 19th century, and two commercial whaling vessels first hunted gray whales (in Magdalena Bay) in the winter of 1845–46 (Henderson, 1984). This began a period of intense hunting with large catches of ENP gray whales by Yankee whalers from 1846 until 1873 which decimated the population. Whaling ships and shore-based whalers continued to catch gray whales for the next two decades which drove the population to apparent commercial extinction by 1893. In the 20th century, modern commercial pelagic whaling of ENP gray whales began in 1910 and ended in 1946 when gray whales received full protection under the International Convention for the Regulation of Whaling (Reeves, 1984). Aboriginal catches of ENP gray whales along the Chukotka Peninsula of Russia have continued since 1946 until the present.

From 1846 to 1900 recorded commercial kills numbered nearly 9,000 gray whales, and it is roughly estimated that about 6,500 gray whales were killed by aboriginal hunters during this same period, for a total of more than 15,500 whales caught (Table 1). Since 1900, about 11,500 additional ENP gray whales have been killed by commercial and aboriginal whalers for a total since 1846 of more than 27,000 whales caught (Table 1). The magnitude of the catches, particularly for the period of high exploitation during the 1800s, gives some information on the likely pre-exploitation population size. For example, Jones *et al.* (1984) state that 'most whaling historians and biologists believe the pre-exploitation stock size was between 15,000 and 24,000 animals'.

ENP gray whales migrate along the west coast of North America, and the US National Marine Fisheries Service (NMFS) has taken advantage of this nearshore migration pattern to conduct shore-based counts of the population in central California during December–February from 1967–68 to 2006–07. These survey data have been used to estimate the abundance of the ENP gray whale stock over the survey period (Buckland *et al.*, 1993; Hobbs *et al.*, 2004; Laake *et al.*, 1994; Reilly, 1981; Rugh *et al.*, 2008a; 2005). The resulting sequence of abundance estimates has also been used to estimate the population's growth rate (Buckland and Breiwick, 2002; Buckland *et al.*, 1993), as well as its status relative to the maximum sustainable yield level (MSYL)[1] and carrying capacity (*K*) (Cooke, 1986; Lankester and Beddington, 1986; Punt and Butterworth, 2002; Reilly, 1981; Wade, 2002). However, attempts to model the gray whale population from 1846 until the present, accounting for the catch record and assuming that the stock was at its carrying capacity in 1846, have run into difficulties because the catch history cannot be reconciled with a population that increased at the observed rate from 1967/68 to 1979/80 (Cooke, 1986; Lankester and Beddington, 1986; Reilly, 1981). The

[1] MSYL expressed in terms of 1+ component of the population.

+ *School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA.*
* *National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way, NE Seattle, WA 98115-6489, USA.*

Table 1a

Historical (pre-1944) aboriginal catches from the eastern North Pacific stock of gray whales (C. Allison, IWC Secretariat, pers. comm.).

Years	Annual kill
1600–1675	182
1676–1750	183
1751–1840	197.5
1841–1846	193.5
1847–1850	192.5
1851–1860	187
1861–1875	111
1876–1880	110
1881–1890	108
1891–1900	62
1901–1904	61
1905–1915	57
1916–1928	52
1929–1930	47
1931–1939	10
1940–1943	20

explanation for this is simple; if one assumes a relatively low maximum growth rate, the ENP gray whales would not have been able to increase between 1967/68 and 1979/80 because of the catches during that time, and if one assumes a high maximum growth rate, the population would not be increasing then because it would have already returned to carrying capacity. Butterworth *et al.* (2002) investigated the inability to fit a standard population dynamics model to the data for the ENP gray whales extensively and concluded that the catch history and the observed rate of increase could be reconciled in one of three different ways, which were not mutually exclusive: (1) a 2.5X increase in *K* between 1846 and 1988, (2) a 1.7X increase or more in the commercial catch between 1846 and 1900, and (3) a 3X increase or more in aboriginal catch levels prior to 1846 compared to what was previously assumed (Butterworth *et al.*, 2002).

Given these difficulties, recent gray whale assessments have been conducted by modelling the population since 1930 or later, rather than trying to model the population since 1846 (e.g. Punt and Butterworth, 2002; Wade, 2002). These analyses differed from the earlier assessments by not assuming that the population size in 1846 was *K*. Instead, *K* is essentially estimated by the recent trend in abundance, where a growing population implies that *K* has likely not yet been reached, and a roughly stable population implies the population is at or near *K*. Based on abundance surveys through 1995–96, point estimates of *K* from these analyses ranged from 24,000 to 32,000, but these estimates were relatively imprecise because they had broad probability intervals (Punt and Butterworth, 2002; Wade, 2002). In particular, the results did not exclude the possibility that *K* could be much larger than this range. However, these analyses did suggest that the population was probably close to *K* and at or above its MSYL. For example, Wade (2002) estimated a probability of 0.72 that the population was above $MSYL^{1+}$ in 1996. Punt and Butterworth (2002) also conducted analyses projecting the population from the year 1600 under various assumptions that historic commercial and aboriginal catches were underestimated (as in Butterworth *et al.*, 2002). Those analyses resulted in point estimates of *K* that ranged between 15,000 and 19,000. In those analyses, it was estimated the population was at a very high fraction of *K* in 1996 and had a very high probability of being above $MSYL^{1+}$.

Recently, Rugh *et al.* (2008b) evaluated the accuracy of various components of the shore-based survey method, with a focus on pod size estimation. They found that the correction factors that had been used to compensate for bias in pod size estimates were calculated differently for different sets of years. In particular, the correction factors estimated by Laake *et al.* (1994) were substantially larger than those estimated by Reilly (1981). Also, the estimates for the surveys prior to 1987 in the trend analysis were scaled based on the abundance estimate from 1987–88. This meant that the first 16 abundance estimates used one set of correction factors, and the more recent 7 abundance estimates used different (and larger) correction factors which would influence the estimated trend and population trajectory. In addition, there were other subtle differences in the analysis methods used for the sequence of abundance estimates. Thus, a revaluation of the analysis techniques and of the abundance estimates was warranted to apply a more uniform approach throughout the years. Laake *et al.* (In press) derived a better, more consistent, approach to abundance estimation, and incorporated it into an analysis to re-estimate abundance for all 23 shore-based surveys. These new revised abundance estimates led to the present re-assessment of the ENP gray whale population.

The population is assessed by fitting an age- and sex-structured population model to these revised abundance estimates, using methods similar to those of Wade (2002) and Punt and Butterworth (2002); recent abundance estimates from 1997/98, 2000/01, 2001/02, and 2006/07 that were not available in previous assessments are also used. As in Punt and Butterworth (2002), sensitivity tests are performed to examine various assumptions or modelling decisions.

The analyses also incorporate new information about the biology of the ENP gray whales from recent studies. In particular, it is now recognised that the population experienced an unusual mortality event in 1999 and 2000. An unusually high number of gray whales were stranded along the west coast of North America in those years (Gulland *et al.*, 2005; Moore *et al.*, 2001). Over 60% of the dead whales were adults, and more adults and subadults stranded in 1999 and 2000 relative to the years prior to the mortality event (1996–98), when calf strandings were more common. Many of the stranded whales were emaciated, and aerial photogrammetry documented that migrating gray whales were skinnier in girth in 1999 relative to previous years (Perryman and Lynn, 2002; W. Perryman, SWFSC, pers. comm.). In addition, calf production in 1999 and 2000 was less than one third of that in the previous years (1996–98). In 2001 and 2002, strandings of gray whales along the coast decreased to levels that were below their pre-1999 level (Gulland *et al.*, 2005) and average calf production in 2002–2004 returned to the level seen in pre-1999 years (Table 2). A US Working Group on Marine Mammal Unusual Mortality Events (Gulland *et al.*, 2005) concluded that the emaciated condition of many of the stranded whales supported the idea that starvation could have been a significant contributing factor to the higher number of strandings in 1999 and 2000. Perryman *et al.* (2002) found a

Table 1b

Commercial and recent aboriginal (post-1943) catches from the eastern North Pacific stock of gray whales (C. Allison, IWC Secretariat, pers. comm.).

Year	Male	Female	Year	Male	Female	Year	Male	Female	Year	Male	Female
1846	23	45	1889	7	13	1932	3	7	1975	58	113
1847	23	45	1890	7	13	1933	36	69	1976	69	96
1848	23	45	1891	7	13	1934	64	92	1977	86	101
1849	23	45	1892	7	13	1935	48	96	1978	94	90
1850	23	45	1893	0	0	1936	74	114	1979	57	126
1851	23	45	1894	0	0	1937	5	9	1980	53	129
1852	23	45	1895	0	0	1938	18	36	1981	36	100
1853	23	45	1896	0	0	1939	10	19	1982	56	112
1854	23	45	1897	0	0	1940	39	66	1983	46	125
1855	162	324	1898	0	0	1941	19	38	1984	59	110
1856	162	324	1899	0	0	1942	34	67	1985	55	115
1857	162	324	1900	0	0	1943	33	66	1986	46	125
1858	162	324	1901	0	0	1944	0	0	1987	47	112
1859	162	324	1902	0	0	1945	10	20	1988	43	108
1860	162	324	1903	0	0	1946	7	15	1989	61	119
1861	162	324	1904	0	0	1947	0	1	1990	67	95
1862	162	324	1905	0	0	1948	6	13	1991	69	100
1863	162	324	1906	0	0	1949	9	17	1992	0	0
1864	162	324	1907	0	0	1950	4	7	1993	0	0
1865	162	324	1908	0	0	1951	5	9	1994	21	23
1866	79	159	1909	0	0	1952	15	29	1995	48	44
1867	79	159	1910	0	1	1953	19	29	1996	18	25
1868	79	159	1911	0	1	1954	13	26	1997	48	31
1869	79	159	1912	0	0	1955	20	39	1998	64	61
1870	79	159	1913	0	1	1956	41	81	1999	69	55
1871	79	159	1914	6	13	1957	32	64	2000	63	52
1872	79	159	1915	0	0	1958	49	99	2001	62	50
1873	79	159	1916	0	0	1959	66	130	2002	80	51
1874	79	159	1917	0	0	1960	52	104	2003	71	57
1875	17	33	1918	0	0	1961	69	139	2004	43	68
1876	17	33	1919	0	0	1962	53	98	2005	49	75
1877	17	33	1920	1	1	1963	60	120	2006	57	77
1878	17	33	1921	13	25	1964	81	138	2007	50	82
1879	21	42	1922	6	4	1965	71	110	2008	64	66
1880	17	34	1923	0	0	1966	100	120			
1881	17	33	1924	1	0	1967	151	223			
1882	17	33	1925	70	64	1968	92	109			
1883	19	39	1926	25	17	1969	93	121			
1884	23	45	1927	7	25	1970	70	81			
1885	21	41	1928	4	8	1971	62	91			
1886	17	33	1929	0	3	1972	66	116			
1887	7	13	1930	0	0	1973	98	80			
1888	7	13	1931	0	0	1974	94	90			

significant positive correlation between an index of the amount of ice-free area in gray whale feeding areas in the Bering Sea and their estimates of calf production for the following spring for the years 1994 to 2000; the suggested mechanism is that longer periods of time in open water provides greater feeding opportunities for gray whales. Whether or not heavy ice cover was ultimately the mechanism that caused the 1999–2000 event, it is clear that ENP gray whales were substantially affected in those years; whales were on average skinnier, they had a lower survival rate (particularly of adults) and calf production was dramatically lower. Given that this event may have affected the status of the ENP gray whale population relative to K, an additional model parameter ('catastrophic mortality') has been specified in the model that allowed for lower survival in the years 1999 and 2000 to investigate this effect.

METHODS

Available data

A variety of data sources are available to assess the status of the ENP stock of gray whales. These data sources are used when developing the prior distributions for the parameters of the population dynamics model, when pre-specifying the values for some of the parameters of this model, and when constructing the likelihood function. Table 1 lists the time-series of removals. It should be noted that the catches for the years prior to 1930 are subject to considerable uncertainty, and evaluating these catches remains an active area of research. However, the uncertainty associated with these early catches is inconsequential for this paper because the population projections do not start before 1930.

The key source of information on the abundance of the ENP gray whales is data collected from the southbound surveys that have been conducted since 1967/68 near Carmel, California (Laake *et al.*, In press; Table 2). Information on trends in calf numbers are also available from surveys of calves during the northbound migration (Perryman *et al.*, 2002; W. Perryman, pers. comm.; Table 2). The calf abundance data are not included in the baseline analyses, but are considered in one of the tests of sensitivity.

Analysis methods

The population dynamics model

An age- and sex-structured population dynamics model is used that assumes that all whaling takes place at the start of

Table 2

Baseline estimates of 1+ abundance (and associated standard errors of the logs) from southbound surveys (Laake *et al.*, In press), the estimates of 1+ abundance used in previous assessments, two alternative series of abundance estimates ('Hi' and 'Lo', see footnote 7 for details), and estimates of calf numbers from northbound surveys (W. Perryman, SWFSC, pers. comm.).

1+ abundance								1+ abundance				
	Laake *et al.* (In press)		Unrevised estimates		Calf counts				Lo series		Hi series	
Year	Estimate	CV	Estimate	CV	Year	Estimate	SE	Year	Estimate	SE	Estimate	SE
1967/68	13,426	0.094	13,776	0.078	1994	945	68.2	1967/68	12,961	0.094	14,298	0.095
1968/69	14,548	0.080	12,869	0.055	1995	619	67.2	1968/69	14,043	0.080	15,493	0.081
1969/70	14,553	0.083	13,431	0.056	1996	1,146	70.7	1969/70	14,049	0.082	15,498	0.084
1970/71	12,771	0.081	11,416	0.052	1997	1,431	82.0	1970/71	12,328	0.081	13,601	0.082
1971/72	11,079	0.092	10,406	0.059	1998	1,388	92.0	1971/72	10,695	0.092	11,799	0.093
1972/73	17,365	0.079	16,098	0.052	1999	427	41.1	1972/73	16,763	0.079	18,493	0.080
1973/74	17,375	0.082	15,960	0.055	2000	279	34.8	1973/74	16,772	0.081	18,503	0.083
1974/75	15,290	0.084	13,812	0.056	2001	256	28.6	1974/75	14,760	0.084	16,283	0.085
1975/76	17,564	0.086	15,481	0.060	2002	842	78.6	1975/76	16,955	0.086	18,705	0.087
1976/77	18,377	0.080	16,317	0.050	2003	774	73.6	1976/77	17,739	0.079	19,570	0.081
1977/78	19,538	0.088	17,996	0.069	2004	1,528	96.0	1977/78	18,860	0.088	20,806	0.089
1978/79	15,384	0.080	13,971	0.054	2005	945	86.9	1978/79	14,850	0.080	16,383	0.081
1979/80	19,763	0.083	17,447	0.056	2006	1,020	103.3	1979/80	19,077	0.082	21,046	0.083
1984/85	23,499	0.089	22,862	0.060	2007	404	51.2	1984/85	22,684	0.089	25,025	0.090
1985/86	22,921	0.081	21,444	0.052	2008	553	53.0	1985/86	22,126	0.081	24,409	0.082
1987/88	26,916	0.058	22,250	0.050	2009	312	41.9	1987/88	25,661	0.057	28,692	0.056
1992/93	15,762	0.067	18,844	0.063				1992/93	14,785	0.065	17,879	0.072
1993/94	20,103	0.055	24,638	0.060				1993/94	19,468	0.057	21,124	0.056
1995/96	20,944	0.061	24,065	0.058				1995/96	20,636	0.063	22,314	0.063
1997/98	21,135	0.068	29,758	0.105				1997/98	20,426	0.063	22,378	0.065
2000/01	16,369	0.061	19,448	0.097				2000/01	16,051	0.063	17,145	0.062
2001/02	16,033	0.069	18,178	0.098				2001/02	15,162	0.066	16,883	0.067
2006/07	19,126	0.071	20,110	0.088				2006/07	18,775	0.071	20,129	0.072

the year, and that all animals are 'recruited' to the hunted population by age 5 (i.e. hunting only occurs on animals age 5 and older) (Punt, 1999; Punt and Butterworth, 2002). The dynamics of the population are assumed to be governed by the equations:

$$N^s_{t+1,a} = \begin{cases} 0.5P^M_{t+1} f_{t+1} & \text{if } a = 0 \\ N^s_{t,a-1}(1 - F^s_{t,a-1})S_{a-1}\tilde{S}_t & \text{if } 1 \le a \le x-1 \\ N^s_{t,x}(1 - F^s_{t,x})S_x\tilde{S}_t + N^s_{t,x-1}(1 - F^s_{t,x-1})S_{x-1}\tilde{S} & \text{if } a = x \end{cases} \quad (1)$$

where

$N^s_{t,a}$ is the number of animals of age a and sex s (m/f) at the start of year t,

S_a is the annual survival rate of animals of age a in the absence of catastrophic mortality events (assumed to be the same for males and females),

$\tilde{S}_t$ is the amount of catastrophic mortality (represented in the form of a survival rate) during year t (catastrophic events are assumed to occur at the start of the year before mortality due to whaling and natural causes; in general $\tilde{S}_t = 1$, i.e. there is no catastrophic mortality),

$F^s_{t,a}$ is the exploitation rate on animals of sex s and age a during year t,

P^M_t is the number of females that have reached the age at first parturition by the start of year t,

$$P^M_t = \sum_{a=a_m+1}^{x} N^f_{t,a} \quad (2)$$

a_m is the age-of-maturity,

f_t is pregnancy rate (number of calves of both sexes per 'mature' female) during year t (note that Equation (1) assumes an equal male : female sex ratio at birth), and

x is the maximum age-class, which for convenience is lumped across older age-classes (i.e. individuals stay in this age-class until they die).

Density dependence on fecundity can be modelled by writing the pregnancy rate, f_t, as follows:

$$f_t = \max\left(f_{eq}\left[1 + A\left\{1 - \left(\overline{S}_{t-2}P^{1+}_{t-2} / K^{1+}\right)^z\right\}\right], 0\right). \quad (3)$$

Where f_{eq} is the pregnancy rate at the pre-exploitation equilibrium, $f(F = 0)$[2]:

$$f(F) = 2\left\{\sum_{a=a_m+1}^{x} \tilde{N}^f_a(F)\right\}^{-1} \quad (4)$$

A is the resilience parameter:

$$A = \frac{f_{max} - f_{eq}}{f_{eq}} \quad (5)$$

f_{max} is the maximum (theoretical) pregnancy rate,

z is the degree of compensation,

P^{1+}_t is number of animals aged 1 and older at the start of year t:

$$P^{1+}_t = \sum_s \sum_{a=1}^{x} N^s_{t,a} \quad (6)$$

K^{1+} is the (current) pre-exploitation equilibrium size (carrying capacity) in terms of animals aged 1 and older, and

$\tilde{N}^s_a(F)$ is the number of animals of sex s and age a when the exploitation rate is fixed at F, expressed as a fraction of the

[2]The pregnancy rate at the pre-exploitation equilibrium can be considered to be the equilibrium pregnancy rate when the exploitation rate, F, is fixed at zero.

number of calves of the same sex s (see appendix 1 of Punt (1999) for details).

Although these equations are written formally as if only the pregnancy rate component of 'fecundity' as defined here is density-dependent, exactly the same equations follow if some or all of this dependence occurs in the infant survival rate (Punt, 1999). Catastrophic mortality is assumed to occur before density-dependence because many of the deaths in 1999 and 2000 occurred before mating was likely to have occurred. Non-catastrophic natural mortality does not appear in Equation 3 because it cancels out. The time-lag in Equation 3 is specified to match the reproductive cycle of gray whales; mature female gray whales mate and become pregnant in early winter, have a gestation period of slightly longer than one year, and give birth at the start of the next year (on average in January) (Rice and Wolman, 1971; Shelden *et al.*, 2004). Their body condition at the end of the summer feeding season will help determine their probability of becoming pregnant the following winter and producing a calf a year later. Therefore, the density-dependent effect on calf production is assumed to be determined by the population size during the feeding season two time-steps prior (approximately 1.5 years earlier).

Following past assessments of the ENP stock of gray whales (e.g. Butterworth *et al.*, 2002; Punt *et al.*, 2004; Punt and Butterworth, 2002), the catch (by sex) is assumed to be taken uniformly from the animals aged five and older, that is:

$$F^s_{t,a} = C^s_t \Big/ \sum_{a=5}^{\pi} N^s_{t,a} \qquad (7)$$

Where C^s_t is the catch of animals of sex s during year t.

The population is assumed to have had a stable age-structure at the start of the projection period (year t_{INIT}).

$$N^s_{t_{INIT},a} = N^{Tot}_{t_{INIT}} \tilde{N}^s_a(F_{INIT}) \Big/ \sum_{s'} \sum_{a'=0}^{\pi} \tilde{N}^{s'}_{a'}(F_{INIT}) \qquad (8)$$

Where $N^{Tot}_{t_{INIT}}$ is the size of the total (0+) component of the population at the start of year t_{INIT}. The value of F_{INIT} is selected numerically so that:

$$N^{Tot}_{t_{INIT},a} = 0.5 N_0(F_{INIT}) \Big/ \sum_{s} \sum_{a=0}^{\pi} N^s_a(F_{INIT}) \qquad (9)$$

Where $N_0(F_{INIT})$ is the number of calves (of both sexes) at the start of the year when $F = F_{INIT}$:

$$N_0(F_{INIT}) = \left(1 - \frac{1}{A}\left[\frac{f(F_{INIT})}{f_{\max}} - 1\right]\right)^{1/z} \frac{K^{1+}}{\tilde{P}^{1+}(F_{INIT})} \qquad (10)$$

$\tilde{P}^{1+}(F)$ is the size of the 1+ component of the population as a function of F, expressed as a fraction of the number of calves (of both sexes).

Parameter estimation

Catastrophic mortality is assumed to be zero (i.e. $\tilde{S}_y = 1$) except for 1999 and 2000 when it is assumed to be equal to a parameter $\tilde{S}$. This assumption reflects the large number of dead whales observed stranded along the coasts of Oregon and Washington during 1999 and 2000 relative to numbers stranding there annually historically (Brownell *et al.*, 2007; Gulland *et al.*, 2005).

The parameters of the population dynamics model are a_m; $\tilde{S}$; K^{1+}; the 1+ population size at the start of 1968, P^{1+}_{1968}[3]; MSYL^{1+} (the maximum sustained yield level for the 1+ population, which is the population size at which maximum sustained yield (MSY) is achieved when hunting takes place uniformly on animals aged 1 and older, relative to K^{1+}); MSYR^{1+} (the ratio of MSY to MSYL^{1+}); $f_{\max}$; and the non-calf survival rate, S_{1+}. The analysis does not incorporate a prior distribution for the survival rate of calves (S_0) explicitly. Instead, following Wade (2002), an implicit prior distribution for this parameter is calculated from the priors for the five parameters a_m, $f_{\max}$, S_{1+}, MSYR^{1+} and MSYL^{1+}. For any specific draw from the prior distributions for these five parameters, the value for S_0 is selected so that the relationships imposed by the population model among the six parameters are satisfied. If the resulting value for S_0 is less than zero or greater than that of S_{1+}, the values for S_{1+}, a_m, $f_{\max}$, MSYR^{1+} and MSYL^{1+} are drawn again[4]. Thus, the prior for S_0 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 (Caughley, 1966).

Under the assumption that the logarithms of the estimates of abundance based on the southbound surveys are normally distributed, the contribution of these estimates to the negative of the logarithm of the likelihood function (ignoring constants independent of the model parameters) is:

$$-\ell nL = 0.5\ell n\left|\mathbf{V} + \Omega\right| + 0.5\sum_i \sum_j (\ell n N^{obs}_i - \ell n \hat{P}^{1+}_i)[\mathbf{V} + \Omega)^{-1}]_{i,j}(\ell n N^{obs}_j - \ell n \hat{P}^{1+}_j), \qquad (11)$$

Where N^{obs}_i is the ith estimate of abundance[5],

$\hat{P}_i$ is the model-estimate corresponding to N^{obs}_i,

$\mathbf{V}$ is the variance-covariance matrix for the abundance estimates, and

Ω is a diagonal matrix with elements CV^2_{add} (this matrix captures sources of uncertainty not captured elsewhere; termed 'additional variance' in Wade (2002)).

A Bayesian approach is used to estimate the 'free' parameters of the model based on the prior distributions in Table 3 and the sampling/importance resampling (SIR) algorithm (Rubin, 1988).

(a) Draw values for the parameters S_{1+}, a_m, $f_{\max}$, MSYR^{1+}, MSYL^{1+}, K^{1+}, P^{1+}_{1968}, $\tilde{S}$, and CV_{add} from the priors in Table 3.

(b) Solve the system of equations that relate S_0, S_{1+}, a_m, $f_{\max}$, MSYR^{1+}, MSYL^{1+}, A and z (Punt, 1999; Eqs. 18–21) to find values for S_0, A, and z, and find the population size in year t_{INIT} and the population rate of increase in this year, so that, if the population is projected from year t_{INIT}

[3]The 1968 population size is taken to be a measure of initial abundance so that the analyses based on different starting years are comparable in terms of their prior specifications.

[4]The implications of different treatments of how to handle situations in which the calculated value for S_0 is outside of plausible bounds is examined by Brandon *et al.* (2007).

[5]The abundance estimate for year $y/y+1$ is assumed to pertain to abundance at the start of year $y+1$.

to 1968, the total (1+) population size in 1968 equals the generated value for P^{1+}_{1968}.

(c) Compute the likelihood for the projection (see Equation 11).

(d) Repeat steps (a)–(c) a very large number (typically 5 million) of times.

(e) Select 5,000 parameter vectors randomly from those generated using steps (a)–(d), 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 projection (t_{INIT}, baseline value 1930). Starting the population projection before the first year for which data on abundance are available allows most of the impact of any transient population dynamics caused by the assumption of a stable age-structure to be eliminated. Therefore, the model population should mimic the real population more closely by allowing the sex- and age-selectivity of the catches to correctly influence the sex- and age-distribution of the population once the trajectory reaches years where it is compared to the data (i.e. 1967/68 and beyond).

Table 3
The parameters and their assumed prior distributions.

Parameter	Prior distribution
Non-calf survival rate, S_{1+}	U[0.950, 0.999][a]
Age-at-maturity, a_m	U[6,12][b]
Maximum pregnancy rate, f_{max}	U[0.3, 0.6][a]
Carrying capacity, K^{1+}	U[10,000, 70,000][c]
Population size in 1968, P^{1+}_{1968}	U[5,000, 20,000][c]
Maximum Sustainable Yield Level, $MSYL^{1+}$	U[0.4, 0.8][a]
Maximum Sustainable Yield Rate, $MSYR^{1+}$	U[0, 0.1][a]
Catastrophic mortality, $\tilde{S}$	U[0.2, 1.0][c]
Additional variance, 1+ abundance estimates, CV_{add}	U[0, 0.35][a,c]
Additional variance, calf counts, CV_{add-2}	U[0.2, 0.8][c,d]
Constant of proportionality, ℓnq	U[$-\infty$, ∞][b,e]

[a]Equal to the prior distribution used in the most recent assessments (Punt *et al.*, 2004); [b]Bradford *et al.* (2010); [c]preliminary analyses provided no evidence of posterior support for values outside this range; [d]not used in the baseline analysis; [e]the non-informative prior for a scale parameter (Butterworth and Punt, 1996).

Output statistics

The results are summarised by the posterior medians, means and 90% credibility intervals for $MSYR^{1+}$, $MSYL^{1+}$, S_{1+}, S_0, $\tilde{S}$, and K^{1+} and the following management-related quantities:

(a) P^{1+}_{2009} is the number of 1+ animals at the start of 2009;

(b) P^{1+}_{2009} / K^{1+} is the depletion level, or the number of 1+ animals at the start of 2009, expressed as a percentage of that corresponding to the equilibrium level;

(c) P^{1+}_{2009} / $MSYL^{1+}$ is the MSYL *ratio*, the number of 1+ animals at the start of 2009, expressed as a percentage of that at which MSY is achieved; and

(d) λ_{max} is the maximum rate of increase (given a stable age-structure and the assumption of no maximum age; Breiwick *et al.*, 1984)

P^{1+}_{2009} / K^{1+} is termed the *depletion level* because it provides a measure of how depleted the population is relative to the carrying capacity, as the equilibrium level in a density-dependent model is equivalent to carrying capacity. P^{1+}_{2009} / $MSYL^{1+}$ is referred to as the MSYL *ratio* because it provides a measure of whether the population is above $MSYL^{1+}$ Note that λ_{max} can be equated to r_{max} (e.g. as in Wade, 1998) through the equation $r_{max} = \lambda_{max} - 1.0$.

Sensitivity tests

Our baseline assessment includes the baseline estimates of 1+ abundance (Table 2) and allows for a catastrophic mortality event in 1999–2000. The sensitivity of the results of the analyses is explored to:

(a) varying the first year considered in the population projection (1940, 1950 and 1960);

(b) replacing the estimates of abundance for the southbound migration by the values used in the previous assessment (Table 2, 'Unrevised estimates');

(c) replacing the abundance estimates with the 'Lo' and 'Hi' series (Table 2)[6] ;

(d) ignoring the catastrophic event in 1999–2000 (abbreviation 'No event');

(e) basing the analysis on the generalised logistic equation (see Appendix 1 for details; abbreviation 'Gen Logist')[7];

(f) splitting the abundance series after 1987/88 (abbreviation 'Split series'), where the first abundance series is treated as a relative index of abundance scaled to absolute abundance through a constant of proportionality, and the second series is treated as an absolute index of abundance; and

(g) including the calf counts at Point Piedras Blancas, California (Perryman *et al.*, 2002; Perryman, pers. comm.) in the analysis (abbreviation 'With calf counts').

For the last sensitivity test, the contribution of the data on calf counts to the negative of the logarithm of the likelihood function (ignoring constants independent of the model parameters) is based on the assumption that the calf counts are relative indices of the total number of calves and are subject to both modelled and unmodelled sources of uncertainty:

$$-\ell nL = 0.5\sum_i \ell n(\sigma_i^2 + CV_{add-2}^2)$$

$$+0.5\sum_i \frac{(\ell nA_i^{obs} - \ell n(q(N_{i,0}^m + N_{i,0}^f)))^2}{\sigma_i^2 + CV_{add-2}^2} \qquad (12)$$

[6]The sequence of gray whale abundance estimates depends in part on the estimates of observer detection probability that were measured with the double observer data. Assessment of matches amongst the pods detected by the observers depends on the weighting parameters for distance and time measurements (Laake *et al.*, In press). The weighting parameters used for the baseline abundance estimates were selected such that 95% of the observations of the same pod would be correctly matched. Sensitivity is explored to matching weighting parameters that gave 98% and 90% (table A2; Laake *et al.*, In press).

[7]This sensitivity test is provided because the generalised logistic model has been the basis for some previous management advice for this stock (for example, Wade, 2002).

where

A_i^{obs} is the estimate of the number of calves during year i based on the surveys at Point Piedras Blancas;

q is the constant of proportionality between the calf counts and model estimates of the number of calves;

σ_i is the standard error of the logarithm of C_i^{obs} ; and

CV^2_{add-2} is the additional variance associated with the calf counts.

Prior distributions

The prior distributions (Table 3) are generally based on those used in recent International Whaling Commission (IWC) assessments of ENP gray whales. The prior distributions for S_{1+}, K^{1+}, $\tilde{S}$, CV_{add}, CV_{add_2}, and ℓnq were selected to be uniform over a sufficiently wide range so that there is effectively no posterior probability outside of that range.

The prior for the age-at-maturity differs from that used in previous assessments, Uniform[5,9], based on the review by Bradford *et al.* (2010) who could find no basis for that range in the literature. They concluded that the most relevant data set for age-at-maturity was that of Rice and Wolman (1971), corrected by Rice (1990) for the underestimation of whale ages by one year in the original study, resulting in a median age of 9, and lower and upper bounds of 6 and 12. Bradford *et al.* (2010) note that the only observation of the age-at-first-reproduction (AFR) in ENP gray whales (a known whale observed with a calf for the first time) was 7 years for a whale first seen as a calf in a lagoon in Mexico. In the western Pacific population of gray whales, there have been observations of AFR of 7 and 11 years for the only two whales whose first calving has been documented to date (Bradford *et al.*, unpublished ms). The prior for the maximum pregnancy rate, f_{max}, was set equal to the prior selected for recent assessments (Punt and Butterworth, 2002; Wade, 2002). This prior implies a minimum possible calving interval between 1.67 and 3.33 years.

The prior for the population size (in terms of animals aged 1 and older) in 1968 differs from that used in previous assessments. Rather than combining a uniform prior on 1968 population size with the abundance estimate for 1968 to create an informative prior for P^{1+}_{1968} as was the case in previous assessments, this assessment assumes a broad uniform prior for 1968 population size, and includes all of the estimates of abundance in the likelihood function. This is because the previous approach cannot be applied because all of the estimates of abundance are correlated (Laake *et al.*, In press).

The prior for $MSYR^{1+}$ is bounded below by the minimum possible value and above by a value which is above those supported by the data. This prior is broader than those considered in previous assessments because those assessments assigned a prior to $MSYR^{1+}$ when this parameter is expressed in terms of removals of mature animals only. The prior for $MSYL^{1+}$ has been assumed to be uniform from 0.4 to 0.8. The central value for this prior reflects the common assumption when conducting IWC assessments of whale stocks that maximum productivity occurs at about 60% of carrying capacity. The upper and lower bounds reflect values commonly used to bound MSYL for whale stocks (e.g. those used in the tests that evaluated the IWC's catch limit algorithm).

RESULTS

The baseline assessment estimates that ENP gray whales increased substantially from 1930 until 1999 when a substantial reduction in population size from close to carrying capacity (in terms of median parameter estimates) occurred (Fig. 1). This reduction was associated with an estimated decline in non-calf survival from 0.982 to 0.847 (posterior means, where 0.981 × 0.863 = 0.847) in each of 1999 and 2000. The population is estimated to have been

Table 4

Posterior distributions for the key model outputs (posterior mean, posterior median [in square parenthesis], and posterior 90% intervals) for the baseline analysis and the sensitivity tests.

	Baseline	t_{INIT}=1940	t_{INIT}=1950	t_{INIT}=1960	Unrevised estimates	No event	Gen logist	With calf counts
K^{1+}	25,808 [22,756]	25,450 [22,506]	24,681 [22,282]	24,396 [22,047]	41,046 [37,889]	21,640 [20,683]	21,146 [20,668]	27,716 [24,194]
	(19,752 49,639)	(19,537 49,109)	(19,454 43,887)	(19,212 43,307)	(24,214 66,564)	(18,301 25,762)	(18,229 24,292)	(20,387 51,775)
$MSYR^{1+}$	0.046 [0.048]	0.047 [0.048]	0.049 [0.049]	0.048 [0.049]	0.035 [0.034]	0.052 [0.053]	0.065 [0.066]	0.040 [0.040]
	(0.022 0.064)	(0.022 0.067)	(0.024 0.068)	(0.024 0.070)	(0.025 0.050)	(0.026 0.068)	(0.034 0.096)	(0.022 0.057)
$MSYL^{1+}$	0.656 [0.669]	0.664 [0.677]	0.677 [0.689]	0.691 [0.702]	0.611 [0.611]	0.672 [0.684]	0.630 [0.640]	0.632 [0.638]
	(0.532 0.725)	(0.535 0.741	(0.541 0.762)	(0.545 0.786)	(0.506 0.706)	(0.577 0.730)	(0.441 0.786)	(0.514 0.725)
P^{1+}_{2009} / K^{1+}	0.849 [0.919]	0.865 [0.933]	0.885 [0.946]	0.899 [0.959]	0.615 [0.598]	0.956 [0.977]	0.964 [0.976]	0.775 [0.816]
	(0.393 1.006)	(0.403 1.016)	(0.451 1.022)	(0.453 1.043)	(0.334 0.948)	(0.872 0.987)	(0.922 0.989)	(0.372 0.984)
$P^{1+}_{2009} / MYSL^{1+}$	1.288 [1.366]	1.295 [1.362]	1.302 [1.355]	1.296 [1.343]	1.002 [0.992]	1.423 [1.424]	1.541 [1.515]	1.217 [1.284]
	(0.681 1.508)	(0.701 1.522)	(0.775 1.516)	(0.786 1.513)	(0.580 1.459)	(1.303 1.583)	(1.252 2.091)	(0.681 1.494)
P^{1+}_{2009}	20,366 [20,447]	20,489 [20,511]	20,583 [20,648]	20,678 [20,705]	22,773 [22,701]	20,247 [20,127]	20,213 [20,090]	19,892 [19,863]
	(17,515 23,127)	(19,628 23,274)	(17,726 23,247)	(17,856 23,497)	(19,910 25,865)	(17,726 22,993)	(17,827 22,910)	(16,872 22,723)
λ_{max}	1.062 [1.063]	1.063 [1.063]	1.063 [1.062]	1.062 [1.060]	1.054 [1.052]	1.068 [1.069]	0.107 [0.088]	1.057 [1.057]
	(1.032 1.088)	(1.033 1.094)	(1.035 1.094)	(1.035 1.092)	(1.036 1.081)	(1.038 1.091)	(0.042 0.242)*	(1.033 1.080)
S_{1+}	0.981 [0.982]	0.981 [0.982]	0.980 [0.982]	0.980 [0.982]	0.978 [0.980]	0.983 [0.985]	N/A	0.972 [0.972]
	(0.957 0.997)	(0.957 0.997)	(0.957 0.997)	(0.957 0.997)	(0.956 0.997)	(0.960 0.998)		(0.954 0.993)
S_0	0.711 [0.732]	0.716 [0.734]	0.713 [0.727]	0.706 [0.720]	0.662 [0.666]	0.730 [0.747]	N/A	0.722 [0.751]
	(0.423 0.950)	(0.426 0.949)	(0.426 0.952)	(0.425 0.949)	(0.400 0.926)	(0.437 0.955)		(0.428 0.943)
$\tilde{S}$	0.863 [0.865]	0.866 [0.867]	0.868 [0.870]	0.870 [0.870]	0.814 [0.809]	1	N/A	0.847[0.840]
	(0.772 0.951)	(0.778 0.951)	(0.779 0.960)	(0.781 0.961)	(0.725 0.915)			(0.749 0.949)

*r rather λ_{max}

Cont.

Table 4 (continued).

	Baseline	Split series	Lo series	Hi series	Unrevised no event	Calf counts no event
K^{1+}	25,808 [22,756]	27,489 [22,870]	25,826 [22,030]	26,902 [24,181]	24,162 [23,044]	21,501 [20,887]
	(19,752 49,639)	(19,640 55,929)	(19,129 52,878)	(21,043 48,118)	(20,946 29,554)	(18,439 24,793)
$MSYR^{1+}$	0.046 [0.048]	0.046 [0.047]	0.046 [0.048]	0.046 [0.048]	0.047 [0.048]	0.049 [0.050]
	(0.022 0.064)	(0.024 0.062)	(0.021 0.064)	(0.023 0.063)	(0.032 0.061)	(0.028 0.065)
$MSYL^{1+}$	0.656 [0.669]	0.648 [0.663]	0.654 [0.670]	0.654 [0.664]	0.663 [0.673]	0.668 [0.676]
	(0.532 0.725)	(0.529 0.721)	(0.520 0.725)	(0.537 0.725)	(0.568 0.722)	(0.577 0.733)
P^{1+}_{2009} / K^{1+}	0.849 [0.919]	0.819 [0.908]	0.837 [0.917]	0.855 [0.913]	0.957 [0.975]	0.958 [0.974]
	(0.393 1.006)	(0.358 1.003)	(0.355 1.008)	(0.428 1.005)	(0.881 0.985)	(0.906 0.984)
$P^{1+}_{2009} / MYSL^{1+}$	1.288 [1.366]	1.253 [1.357]	1.270 [1.361]	1.301 [1.366]	1.446 [1.442]	1.438 [1.436]
	(0.681 1.508)	(0.642 1.502)	(0.632 1.504)	(0.748 1.512)	(1.344 1.608)	(1.314 1.607)
P^{1+}_{2009}	20,366 [20,447]	20,380 [20,372]	19,752 [19,817]	21,654 [21,594]	22,781 [22,456]	20,337 [20,283]
	(17,515 23,127)	(17,708 23,139)	(16,925 22,432)	(18,607 24,683)	(20,432 26,047)	(17,912 23,050)
λ_{max}	1.062 [1.063]	1.063 [1.064]	1.062 [1.063]	1.063 [1.064]	1.063 [1.062]	1.065 [1.065]
	(1.032 1.088)	(1.037 1.088)	(1.032 1.088)	(1.034 1.089)	(1.043 1.087)	(1.037 1.090)
S_{1+}	0.981 [0.982]	0.981 [0.982]	0.980 [0.982]	0.981 [0.982]	0.982 [0.984]	0.980 [0.982]
	(0.957 0.997)	(0.957 0.997)	(0.957 0.997)	(0.957 0.998)	(0.959 0.997)	(0.958 0.997)
S_0	0.711 [0.732]	0.711 [0.729]	0.710 [0.728]	0.708 [0.725]	0.705 [0.716]	0.720 [0.732]
	(0.423 0.950)	(0.420 0.949)	(0.420 0.949)	(0.425 0.949)	(0.420 0.950)	(0.426 0.954)
$\bar{S}$	0.863 [0.865]	0.860 [0.862]	0.862 [0.862]	0.855 [0.857]	1	1
	(0.772 0.951)	(0.763 0.958)	(0.775 0.950)	(0.772 0.939)		

increasing since 2000. The model fits the data well, although, as in previous IWC assessments, the analyses suggest that the coefficients of variation for the abundance estimates are underestimated (by 14% median estimate). The baseline assessment estimates that this stock is currently well above $MSYL^{1+}$ (posterior mean for P^{1+}_{2009} / $MSYL^{1+}$ of 1.29) (Table 4). The posterior probability that the stock is currently greater than $MSYL^{1+}$ is 0.884.

The posterior probability that the stock is currently above $MSYL^{1+}$ is less for the baseline analysis and for the analysis in which the original abundance estimates are used ('Unrevised estimates' in Table 4) than in some earlier assessments. The reasons for this are explored using the analyses in which no allowance is made for survival having dropped in 1999–2000 ('No Event' and 'Unrevised, No event' in Table 4, see also Fig. 2) because the previous assessments did not explicitly account for the mortality event. This comparison suggests that allowing for the possibility of a catastrophic mortality event in 1999–2000 has reduced the ability to constrain the upper bound for carrying capacity because the lower 5% limit for P^{1+}_{2009} / $MSYL^{1+}$ is notably higher for the analyses which ignore this event (Table 4). Bayes factors comparing the analyses which include a 1999–2000 catastrophic mortality event and those which do not provide support for estimating a parameter for the 1999/2000 event. For example, in the baseline analysis the *ln* (Bayes factor) value is 3.00 compared to the 'No event' model. This is interpreted as strong, but not definitive, support (Kass and Raftery, 1995) for including the catastrophic mortality parameter in the model.

The results are insensitive to changing the first year of the analysis (Table 4, Fig. 3). The key management-related results are also not sensitive to splitting the series in 1987–88, using the calf count estimates and using the 'Lo' and 'Hi' abundance estimates (Fig. 4). The results for the generalised logistic model are most comparable with the two 'No event' analyses because no account is taken of a catastrophic mortality event in 1999–2000 when fitting the generalised logistic model (see Appendix 1). While not entirely comparable, the qualitative conclusions from the generalised logistic model are identical to those from the age-structured model.

Fig. 5 shows the posterior distributions for the parameters for the baseline analysis. These posteriors show that the data update the priors for $MSYR^{1+}$ and $MSYL^{1+}$ to a substantial extent. The posterior for $MSYL^{1+}$ emphasises higher values for $MSYL^{1+}$, which is not unexpected given that the rate of

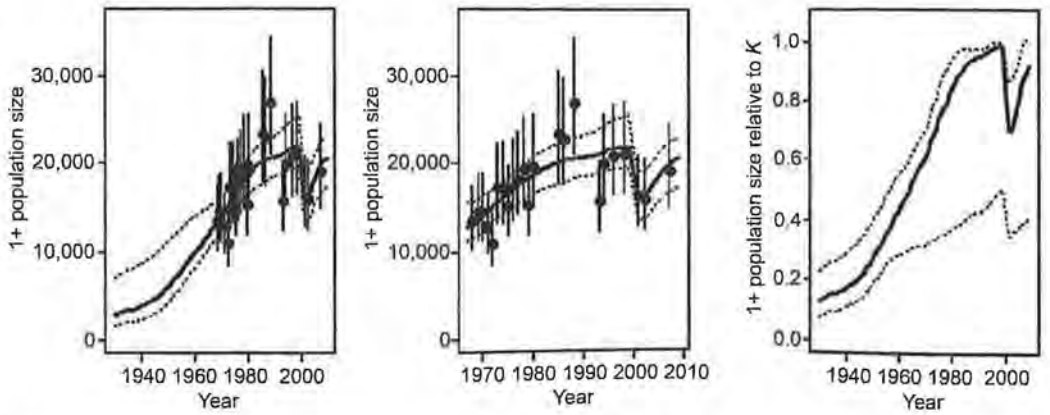

Fig. 1. Posterior distributions (medians and 90% credibility intervals) for the time-trajectories of 1+ population size (left and centre panels) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis.

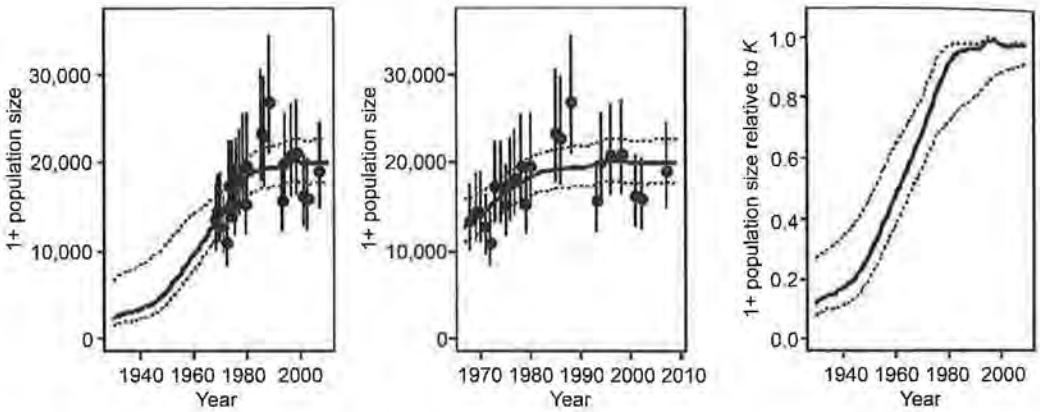

Fig. 2. Posterior distributions (medians and 90% credibility intervals) for the time-trajectories of 1+ population size (left and centre panels) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the 'No Event' analysis.

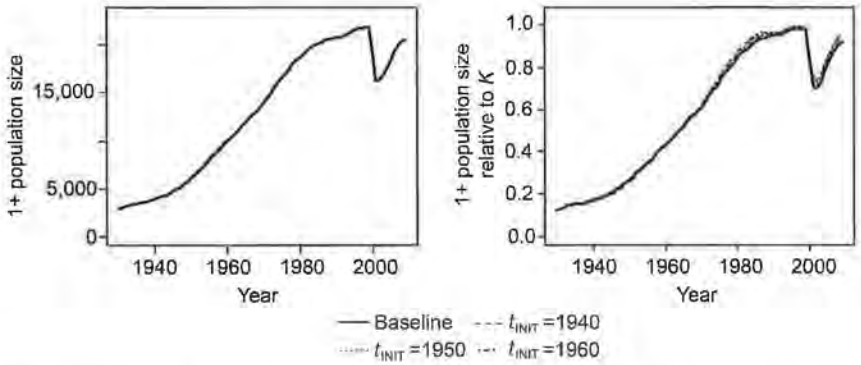

Fig. 3. Posterior median time-trajectories of 1+ population size (left panel) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis and the sensitivity tests which vary the value for t_{INIT}.

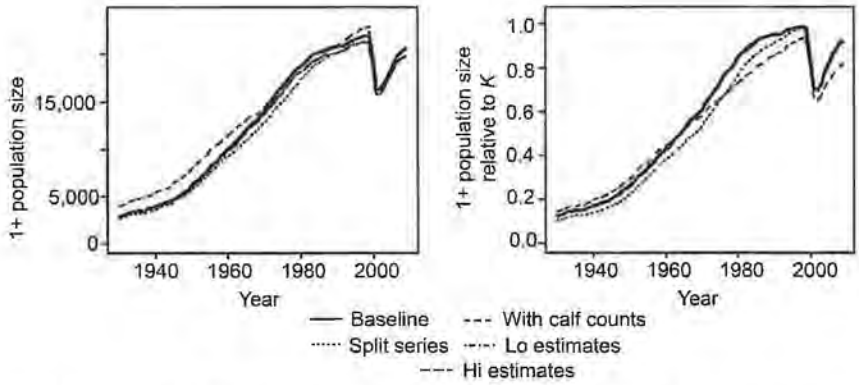

Fig. 4. Posterior median time-trajectories of 1+ population size (left panel) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis and a subset of the sensitivity tests.

increase for the ENP gray whales is assessed to have been high until just before this population (almost) reached its current carrying capacity. The posteriors for the age-at-maturity, maximum fecundity, and adult survival place greatest support on low, high, and high values, respectively. This is consistent with the fairly high growth rates and values for $MSYR^{1+}$. The posterior for the survival multiplier is also updated substantially, with both high (close to 1) and low values (below 0.7) assigned low posterior probability. Sensitivity tests in which the bounds for the priors were widened (results not shown) did not lead to outcomes which differed noticeably from the baseline assessments.

The maximum rate of increase, λ_{max}, is well-defined in all of the analyses. The posterior mean estimates of this quantity range from 1.057 to 1.068 and are fairly precisely determined (Table 4).

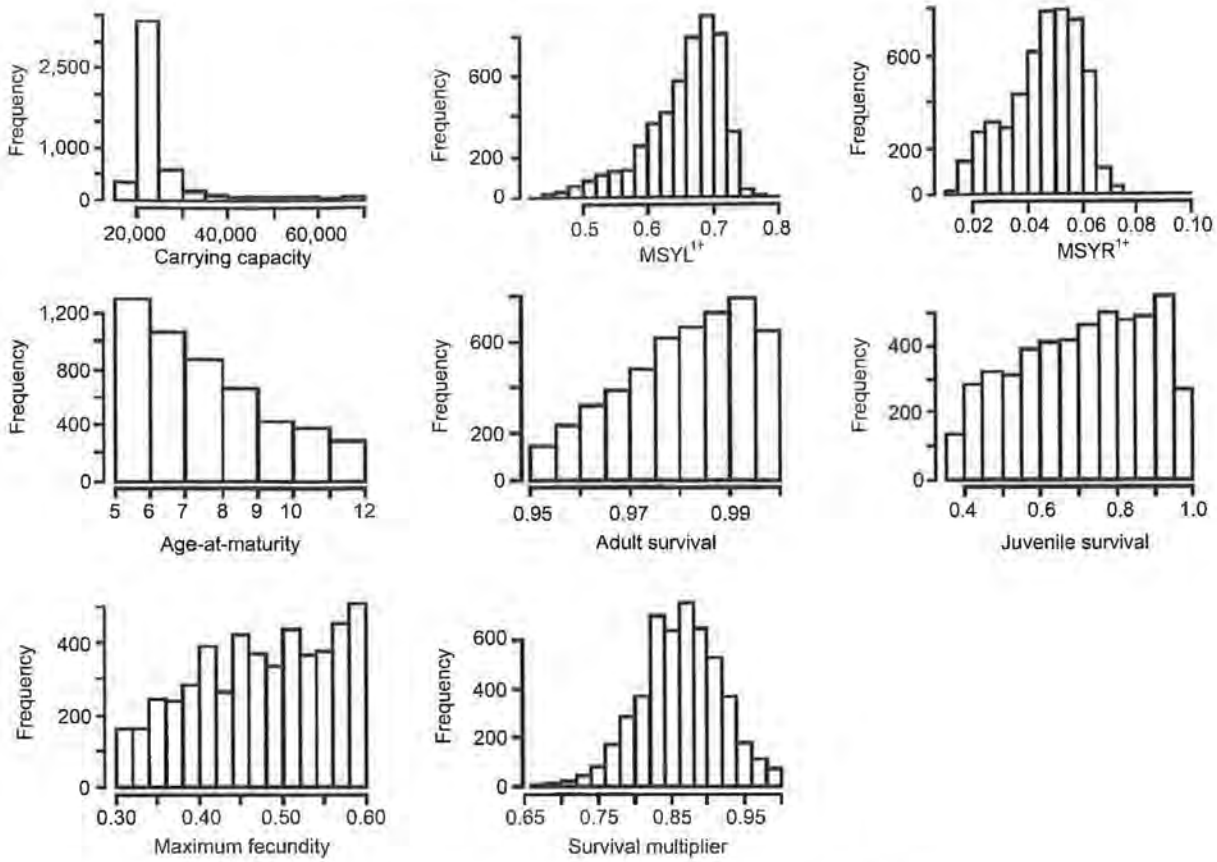

Fig. 5. Posterior distributions for the parameters of the baseline analysis.

DISCUSSION

The sensitivity tests were designed to examine the effect of various assumptions on the assessment results and to examine the effect of changes in the methods that have occurred, particularly related to abundance estimation. Overall, the results are consistent across most of the sensitivity tests with some exceptions. In particular, the baseline model fit to the unrevised abundance estimates had relatively different results from the other analyses. Leaving aside that analysis for the moment, the posterior medians for the parameters of interest were relatively consistent. Across all the other analyses, posterior means for K^{1+} ranged from 21,146 to 27,716, for the *depletion level* ranged from 0.76 to 0.96, and for the *MSYL ratio* ranged from 1.22 to 1.54. Therefore, as in previous assessments, the ENP gray whale population is estimated to be above $MSYL^{1+}$ and approaching or close to K. The estimates of *depletion level* and *MSYL ratio* in Wade (2002) and in Punt and Butterworth (2002) are very similar to the results presented here, although our current estimates of K are lower. The results in Wade and Perryman (2002) and Brandon (2009), which were the only previous assessments to use abundance estimates from the 1997/98 and subsequent surveys, gave higher and more precise estimates for *depletion level* and *MSYL ratio* than estimated here. However, in common with previous assessments, those results are superseded by this new assessment because it uses the revised abundance estimates of Laake *et al.* (In press).

The posterior means for the life history parameters were very consistent as well, with the posterior means for λ_{max} ranging from 1.057 to 1.068, non-calf survival ranging from 0.972 to 0.983, and calf survival ranging from 0.706 to 0.730. The parameter $MSYL^{1+}$ was updated to strongly emphasise higher values in the baseline analysis. There are theoretical arguments for why MSYL should be relatively higher in marine mammals than, say, marine fishes (Eberhardt and Siniff, 1977; Fowler, 1981; Taylor and DeMaster, 1993), but, in general, there has not been empirical data of sufficient quantity and quality to estimate this parameter well for marine mammals (Gerrodette and DeMaster, 1990; Goodman, 1988; Ragen, 1995). Empirical evidence that is available for large, long-lived mammals has shown convex nonlinear density-dependence in life history parameters such as age-specific birth and mortality rates (Fowler, 1987; 1994; Fowler *et al.*, 1980), which suggest MSYL > 0.5K. A relatively long time-series of abundance estimates has documented the recovery of harbour seal (*Phoca vitulina*) populations in Washington state, and Jeffries *et al.* (2003) estimated MSYL to be greater than 0.5K for these populations. In the ENP gray whale analysis here, values from 0.40 to 0.54 for $MSYL^{1+}$ have low probability in the posterior distribution (Fig. 5, Table 4) which is consistent with the conclusions of Taylor and Gerrodette (1993) that MSYL was likely to be greater than 0.5K. Thus, the posterior distribution for $MSYL^{1+}$ estimated here (posterior means for the baseline analysis of 0.656, range of posterior means 0.611– 0.691), suggests that the ENP gray whale population experienced a decrease in population growth only when it was relatively close to K^{1+}.

The results did not vary much for a large number of the sensitivity tests, providing assurance that the assumptions made for the baseline analysis did not have a substantial influence on the results. Changing the initial year from which the model was projected had little effect on the results, which is similar to the results seen in Punt and Butterworth (2002) for initial years ranging from 1930 to 1968, as used here. The results for the 'Lo' and 'Hi' series of abundance estimates are very similar to the baseline results, suggesting that assumptions made in calculating the abundance estimates do not have a strong influence on the results of the assessment. Additionally, splitting the abundance time series in 1987/88 did not have a substantial effect. This is particularly reassuring, because some changes in the field methods happened at that time, notably the use of a second independent observer during that and subsequent surveys (Laake *et al.*, In press). The generalised logistic model provided similar results to the 'No-event' analysis, with some small differences. This was similar to results seen in Wade (2002), where the quantitative values for some parameters were somewhat different for the generalised logistic, although the qualitative results are nearly identical in this case. That the quantitative results differ between the generalised logistic and our baseline analyses is to be expected because the analysis based on the generalised logistic did not account for the dynamics of sex- and age-structure, and also ignored time-lags in the dynamics.

The baseline analysis fits the abundance data better than in the 'No-event' analysis because it includes the catastrophic mortality event in 1999–2000 (Figs 1 and 2). Furthermore, the Bayes factor confirms that there is strong, but not definitive, evidence supporting the use of a model including the catastrophic mortality. The model estimates that 15.3% of the non-calf population died in each of the years with catastrophic mortality, compared to about 2% in a normal year. In that 2-year period, the model estimates of the population size relative to K^{1+} fell from being at 99% of K^{1+} in 1998 to 83% in 1999 and 71% in 2000, before increasing back up to 91% by 2009. In contrast, the 'No-event' analysis estimates the population had reached a level very close to K^{1+} by ~1995 and has remained there since, which clearly does not match the evidence regarding the biological effects on the population in 1999 and 2000. In the baseline analysis, the estimate of the number of whales that died in 1999 and 2000 was 3,303 (90% interval 1,235–7,988) and 2,835 (90% interval 1,162–6,389), respectively, for a combined total for the two years of 6,138 (90% interval 2,398–14,377). In comparison, the 'No-event' analysis estimates that the number of whales that died in 1999 was 587 and in 2000 it was 447. Comparing the number of strandings (from Mexico to Alaska) reported in Gulland *et al.* (2005) in the years around the mortality event to these estimates of total deaths from the baseline model indicates that only 3.9–13.0% of all ENP gray whales that die in a given year end up stranding and being reported.

The baseline analysis is more conservative regarding status relative to K^{1+} than the 'No-event' analysis. On the other hand, it can be argued that the 'No-event' analysis provides a more accurate estimation of current average K^{1+}. In other words, the baseline analysis does a better job of modelling the actual time-course of the population by including the mortality event, but it might provide an overestimate of the average recent K^{1+} by essentially considering high abundance estimates to be near K^{1+}, but lower abundance estimates to be lower than K^{1+}. The different interpretations hinge on whether K^{1+} is viewed as relatively fixed, with the 1999–2000 mortality event considered to be unrelated to density-dependence (and therefore K^{1+}), or whether K^{1+} is viewed as something that can vary from year to year, with the 1999–2000 years viewed as an event when K^{1+} itself was low. As populations increase in density, the impact of density-independent factors on population dynamics probably becomes more pronounced (Durant *et al.*, 2005; Wilcox and Eldred, 2003). The actual carrying capacity of the environment, in terms of prey available for the ENP gray whale population, is likely to vary from year to year to a greater or lesser extent due to oceanographic conditions affecting primarily benthic production. In terms of the model, the parameter K^{1+} that is being estimated is interpreted as the average carrying capacity in recent years. In the baseline analysis, the estimated K^{1+} is approximately (though not exactly) the average recent K^{1+} for the years before 1999–2000, whereas in the 'No-event' analysis, the estimate of average recent K^{1+} includes all the recent years, including 1999–2000, and is lower. This is clear from the results, where the baseline estimate of K^{1+} is 25,808 (90% interval 19,752–49,639), whereas the 'No-event' estimate of K^{1+} is substantially lower, 21,640 (90% interval 18,301–25,762).

The analysis using the original unrevised estimates is not a sensitivity test in the usual sense. Those results are provided simply to aid in interpretation of the results of the other analyses relative to past results using the unrevised estimates. For example, no previous analyses other than Brandon (2009) had used the 2006/07 abundance estimate, so this sensitivity test provides a comparison in which both analyses use that estimate. In the 'No-event' model, the analyses using the original and revised abundance estimates are nearly identical for estimates of *depletion level* and *MSYL ratio*. K^{1+} was estimated to be higher in the analysis that used the original abundance estimates, but even though K^{1+} is lower using the revised abundance estimates, overall the entire time-series is shifted such that the estimates of status relative to K^{1+} are unchanged.

In contrast, in the baseline model, the original abundance estimates give a fairly different result from any other analysis. From the discussion of how correction factors for the abundance estimates were calculated in different years in Laake *et al.* (In press), it is clear that the revised abundance estimates should be more accurate, and there were shifts of certain sequences of abundance estimates relative to one another that influence the results. For example, the three estimates from 1993/94 to 1997/98 are the three highest estimates in the original time-series, whereas the three estimates from 1984/85 to 1987/88 are the three highest estimates in the revised time-series. This has an effect on the baseline analysis results because the model is trying to fit the drop in abundance that occurred after the 1997/98 abundance estimate. That drop is substantially larger in the unrevised data set than it is in the revised data set, and therefore the results for the baseline model differ somewhat between the revised and unrevised data sets.

The only previous assessment that modelled the 1999–2000 mortality event was that of Brandon (2009), whose point estimates of total natural mortality in those years ranged from 1,300 to 5,200, depending upon a variety of assumptions he explored, lower than the 6,138 estimated here in the baseline model. The difference presumably arises because Brandon (2009) modelled mortality as a function of a sea-ice index for the Bering Sea, following the relationship found between calf production and sea-ice (Perryman *et al.*, 2002). This constrains the dynamics of the mortality in Brandon (2009) to reflect the dynamics of the index to some extent. In contrast, the 1999–2000 mortality was unconstrained in the baseline analysis here and is essentially estimated by what value fit the drop in abundance estimates best. Brandon (2009) noted this difficulty in his analysis, stating it was not possible in his analysis to fit the strandings data for the 1999–2000 mortality event without allowing for some additional process error in the survival rates during those years.

λ_{max} is estimated to be 1.062 (90% interval 1.032–1.088) in the baseline analysis. This is similar to, but a little lower than, the estimate from Wade (2002) of 1.072 (90% interval 1.039–1.126) and the estimates from Wade and Perryman (2002). The posterior for λ_{max} from the 'No-event' analysis is very similar to this, as is that from the 'No-event' analysis using the unrevised abundance estimates, indicating the lower estimates of λ_{max} seen here are not due entirely to the revision of the abundance estimates but are instead partly due to the additional four abundance estimates used here (1997/98 to 2006/07) that were not available at the time the Wade (2002) analysis was conducted. To get an estimate of λ_{max} of 1.062, the posterior distribution favoured a low age-of-maturity, a high maximum fecundity, and a high adult survival. λ_{max} appears to be well-defined, as the posterior medians from most of the sensitivity tests are very similar. It should be noted that these are theoretical estimates of the population growth rate at a very low population size, based upon the density-dependent assumptions of the population model; the ENP gray whale has not been observed to actually grow this rapidly because the population was estimated to be approaching *K* by the time its growth rate was monitored; consequently, the observed population growth rate was less than its theoretical maximum.

The small and endangered western North Pacific population of gray whales has been estimated to have an annual population increase that is between 2.5% and 3.2% per year, but there is concern that this growth rate is low because of possible Allee effects and from ongoing human-caused mortality (Bradford *et al.*, 2008). Best (1993) summarised the growth rates of eight severely depleted baleen whale populations (other than gray whales) and the values ranged from 3.1% to 14.4%. Some of these estimates were not very precise, and Zerbini *et al.* (2010) suggested that the higher rates are implausible given life-history constraints for (at least) humpback whales (*Megaptera novaeangliae*). In more recent studies of other species, a number of estimates of trend have been similar to the estimates of λ_{max} reported here. In a simulation study based on empirical estimates of life history parameters for humpback whales, Zerbini *et al.* (2010) estimated maximum rates of increase of 7.5%/year (95% CI 5.1–9.8%) using one approach and 8.7%/year (95% CI 6.1–11.0%) using a second approach. Calambokidis *et al.* (2008) calculated point estimates of 4.9% to 6.7% for the North Pacific humpback whale population using data from a recently completed North Pacific study of humpback whale abundance. Zerbini *et al.* (2006) used line transect data from sequential surveys to estimate an annual rate of increase for humpback whales in shelf waters of the northern Gulf of Alaska from 1987 to 2003 of 6.6% per year (95% CI 5.2–8.6%), and for fin whales of 4.8% (95% CI 4.1–5.4%). On the other hand, Mizroch *et al.* (2004) estimated a rate of increase for North Pacific humpback whales in Hawaii using mark-recapture methods for the years 1980–1996 of 10% per year, but the confidence limits were wide (95% CI 3–16%). Other unpublished estimates are available spanning essentially a similar range as originally reported by Best (1993) (i.e. see IWC, 2010)). In summary, the estimates of λ_{max} reported here are similar to trend estimates seen in other species, but there are also lower and higher values that have been recorded.

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REFERENCES

Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. *ICES J. Mar. Sci.* 50(3): 169–86.

Bradford, A.L., Weller, D.W., Lang, A.R., Tsidulko, G.A., Burdin, A.M. and Brownell, R.L., Jr. 2010. Comparing age at first reproduction information from western gray whales to age at sexual maturity estimates of eastern gray whales. Paper SC/62/BRG2 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 6pp. [Paper available from the Office of this Journal]

Bradford, A.L., Weller, D.W., Wade, P.R., Burdin, A.M. and Brownell, R.L. 2008. Population abundance and growth rate of western gray whales *Eschrichtius robustus*. *Endangered Species Research* 6: 1–14.

Brandon, J.R. 2009. Quantifying uncertainty and incorporating environmental stochasticity in stock assessments of marine mammals. PhD thesis, University of Washington, Washington. 161pp.

Brandon, J.R., Breiwick, J.M., Punt, A.E. and Wade, P.R. 2007. Constructing a coherant joint prior while respecting biological realism: application to marine mammal stock assessments. *ICES J. Mar. Sci.* 64: 1085–100.

Breiwick, J.M., Eberhardt, L.L. and Braham, H.W. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). *Can. J. Fish. Aquat. Sci.* 41(3): 484–96.

Brownell, R.L., Makeyev, C.A.F. and Rowles, T.K. 2007. Stranding trends for eastern gray whales, *Eschrichtius robustus*: 1975–2006. Paper SC/59/BRG40 presented to the IWC Scientific Committee, May 2007, Anchorage, Alaska (unpublished). 11pp. [Paper available from the Office of this Journal].

Buckland, S.T. and Breiwick, J.M. 2002. Estimated trends in abundance of eastern Pacific gray whales from shore counts (1967/68 to 1995/96). *J. Cetacean Res. Manage.* 4(1): 41–48.

Buckland, S.T., Breiwick, J.M., Cattanach, K.L. and Laake, J.L. 1993. Estimated population size of the California gray whale. *Mar. Mammal Sci.* 9(3): 235–49.

Butterworth, D.S., Korrubel, J.L. and Punt, A.E. 2002. What is needed to make a simple density-dependent response population model consistent with data for the eastern North Pacific gray whales? *J. Cetacean Res. Manage.* 4(1): 63–76.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, US Department of Commerce Western Administrative Center, Seattle, Washington. [Available at *http://www.cascadiaresearch.org/SPLASH/SPLASH-contract-report-May08.pdf*].

Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47(6): 906–18.

Cooke, J.G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. *Rep. int. Whal. Commn* 36: 363–66.

Durant, J.M., Hjermann, D.O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. and Stenseth, N.C. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8: 952–58.

Eberhardt, L.L. and Siniff, D.B. 1977. Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Can.* 34(2): 183–90.

Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology* 62: 602–10.

Fowler, C.W. 1987. A review of density dependence in populations of large mammals. pp.401–41. *In*: Genoways, H. (eds). *Current Mammalogy*. Plenum Press, New York. 519pp.

Fowler, C.W. 1994. Further consideration of nonlinearity in density dependence among large mammals. *Rep. int. Whal. Commn* 44: 385–91.

Fowler, C.W., Bunderson, W.T., Cherry, M.B., Ryel, R.J. and Steel, B.B. 1980. Comparative population dynamics of large mammals: a search for management criteria, Report to US Marine Mammal Commission, Springfield, VA. 330pp. Contract No. MM7AC013, Available Natl. Tech. Inf. Serv., as PB80-178627.

Gerrodette, T. and DeMaster, D.P. 1990. Quantitative determination of optimum sustainable population level. *Mar. Mammal Sci.* 6(1): 1–16.

Goodman, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. *Mar. Mammal Sci.* 4: 183–95.

Gulland, F.M.D., Pérez-Cortés, H., Urbán, J.R., Rojas-Bracho, L., Ylitalo, G., Weir, J., Norman, S.A., Muto, M.M., Rugh, D.J., Kreuder, C. and Rowles, T. 2005. Eastern North Pacific gray whale (*Eschrichtius robustus*) unusual mortality event, 1999–2000. *NOAA Tech. Mem. NMFS-AFSC*- 150: 34pp. [Available at: *www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-150.pdf*].

Henderson, D.A. 1984. Nineteenth century gray whaling: grounds, catches and kills, practices and depletion of the whale population. pp.159–86. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale*. Eschrictius robustus. Academic Press, Inc., Orlando, Florida. xxiv+600pp.

Hobbs, R.C., Rugh, D.J., Waite, J.M., Breiwick, J.M. and DeMaster, D.P. 2004. Abundance of gray whales in the 1995/96 southbound migration in the eastern North Pacific. *J. Cetacean Res. Manage.* 6(2): 115–20.

International Whaling Commission. 2010. Report of the Intersessional Workshop on MSYR for Baleen Whales, 6–8 February 2009, Seattle. *J. Cetacean Res. Manage. (Suppl.)* 11(2):493–508.

Jeffries, S.J., Huber, H.R., Calambokidis, J. and Laake, J. 2003. Trends and status of harbor seals in Washington State: 1978–1999. *J. Wildl. Manage.* 67: 208–19.

Jones, M.L., Swartz, S.L. and Leatherwood, S. 1984. *The Gray Whale, Eschrichtius robustus*. Academic Press Inc., Orlando, Florida. xxiv+600pp.

Kass, R.E. and Raftery, A.E. 1995. Bayes factors. *J. Am. Stat. Assoc.* 90: 773–95.

Krupnik, I. 1984. Gray whales and the aborigines of the Pacific Northwest: the history of aboriginal whaling. pp.103–20. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale, Eschrichtius robustus*. Academic Press Inc., Orlando, Florida. xxiv+600pp.

Laake, J.L., Punt, A.E., Hobbs, R., Ferguson, M., Rugh, D. and Breiwick, J. In press. Gray whale southbound migration surveys 1967–2006: an integrated re-analysis. *J. Cetacean Res. Manage* 12(3): In press.

Laake, J.L., Rugh, D.J., Lerczak, J.A. and Buckland, S.T. 1994. Preliminary estimates of population size of gray whales from the 1992/93 and 1993/94 shore-based surveys. Paper SC/46/AS7 presented to the IWC Scientific Committee, May 1994, Puerto Vallarta, Mexico (unpublished). 13pp. [Paper available from the Office of this Journal].

Lankester, K. and Beddington, J.R. 1986. An age structured population model applied to the gray whale (*Eschrichtius robustus*). *Rep. int. Whal. Commn* 36: 353–58.

Mizroch, S.A., Herman, L.M., Straley, J.M., Glockner-Ferrari, D.A., Jurasz, C., Darling, J., Cerchio, S., Gabriele, C.M., Salden, D.R. and von Ziegesar, O. 2004. Estimating the adult survival rate of central north Pacific humpback whales (*Megaptera novaeangliae*). *J. Mammal.* 85(5): 963–72.

Moore, S., Urbán R, J., Perryman, W., Gulland, F., Perez-Cortes, H., Rojas-Bracho, L. and Rowles, T. 2001. Are gray whales hitting 'K' hard? *Mar. Mammal Sci.* 17(4): 954–58.

O'Leary, B.L. 1984. Aboriginal whaling from the Aleutian Islands to Washington State. pp.79–102. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale, Eschrichtius robustus*. Academic Press Inc., Orlando, Florida. xxiv+600pp.

Perryman, W.L., Donahue, M.A., Perkins, P.C. and Reilly, S.B. 2002. Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar. Mammal Sci.* 18(1): 121–44.

Perryman, W.L. and Lynn, M.S. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *J. Cetacean Res. Manage.* 4(2): 155–64.

Punt, A.E. 1999. Report of the Scientific Committee. Annex R. A full description of the standard BALEEN II model and some variants thereof. *J. Cetacean Res. Manage. (Suppl.)* 1: 267–76.

Punt, A.E., Allison, C. and Fay, G. 2004. An examination of assessment models for the eastern North Pacific gray whale based on inertial dynamics. *J. Cetacean Res. Manage.* 6(2): 121–32.

Punt, A.E. and Butterworth, D.S. 1996. Further remarks on the Bayesian approach for assessing the Bering-Chukchi-Beaufort Seas stock of bowhead whales. *Rep. int. Whal. Commn* 46: 481–91.

Punt, A.E. and Butterworth, D.S. 2002. 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*). *J. Cetacean Res. Manage.* 4(1): 99–110.

Ragen, T.J. 1995. Maximum net productivity level estimation for the northern fur seal (*Callorhinus ursinus*) population of St. Paul island, Alaska. *Mar. Mammal Sci.* 11: 275–300. [AFSC Processed Report 92–08, Natl. Mar. Mammal Lab., Northwest and Alaska Fish. Cent. Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115. 66pp.].

Reeves, R.R. 1984. Modern commercial pelagic whaling for gray whales. pp.187–200. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale, Eschrichtius robustus*. Academic Press Inc., Orlando Florida. xxiv+600pp.

Reilly, S.B. 1981. Population assessment and population dynamics of the California gray whale (*Eschrichtius robustus*). PhD. Thesis, University of Washington. 265pp.

Rice, D.W. 1990. Life history parameters of the gray whale: a review of published estimates. Paper SC/A90/G22 presented to the special meeting of the Scientific Committee on the Assessment of Gray whales, Seattle, April 1990 (unpublished). 6pp. [Paper available from the Office of this Journal].

Rice, D.W. and Wolman, A.A. 1971. *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*. American Society of Mammalogists, Special Publication No. 3, Stillwater, Oklahoma. viii+142pp.

Rubin, D.B. 1988. Using the SIR algorithm to simulate posterior distributions. pp.395–402. *In*: Bernardo, J.M., DeGroot, M.H., Lindley, D.V. and Smith, A.F.M. (eds). *Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987*. Clarendon Press, Oxford. 805pp.

Rugh, D., Breiwick, J., Muto, M.M., Hobbs, R., Shelden, K., D'vincent, C., Laursen, I.M., Reif, S., Maher, S. and Nilson, S. 2008a. Report of the 2006–2007 census of the eastern North Pacific stock of gray whales. *AFSC Processed Report* 2008–03: 157pp. Alaska Fisheries Science Center, NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Rugh, D.J., Hobbs, R.C., Lerczak, J.A. and Breiwick, J.M. 2005. Estimates of abundance of the Eastern North Pacific stock of gray whales 1997 to 2002. *J. Cetacean Res. Manage.* 7(1): 1–12.

Rugh, D.J., Muto, M.M., Hobbs, R.C. and Lerczak, J.A. 2008b. An assessment of shore-based counts of gray whales. *Mar. Mammal Sci.* 24(4): 864–80.

Shelden, K.E.W., Rugh, D.J. and Schulman-Janiger, A. 2004. Gray whales born north of Mexico: indicatory of recovery or consequence of regime shift? *Ecol. Appl.* 14(6): 1789–805.

Taylor, B.L. and DeMaster, D.P. 1993. Implications of nonlinear density dependence. *Mar. Mammal Sci.* 9(4): 360–71.

Taylor, B.L. and Gerrodette, T. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conserv. Biol.* 7(3): 489–500.

Wade, P.R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Mar. Mammal Sci.* 14(1): 1–37.

Wade, P.R. 2002. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967–1996. *J. Cetacean Res. Manage.* 4(1): 85–98.

Wade, P.R. and Perryman, W. 2002. An assessment of the eastern gray whale population in 2002. Paper SC/54/BRG7 presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan (unpublished). 16pp. [Paper available from the Office of this Journal].

Wilcox, C. and Eldred, B. 2003. The effect of density-dependent catastrophes on population persistence time. *J. Appl. Ecol.* 40: 859–71.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010. Plausible maximum rates of increase in humpback whales. *Mar. Biol.* 157: 1225–36.

Zerbini, A.N., Wade, P.R. and Waite, J.M. 2006. Abundance and distribution of fin, humpback and minke whales from the Kenai Fjords to the Central Aleutian Islands, Alaska: Summer 2001–2002. *Deep-Sea Res. I* 53: 1772–90.

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Appendix 1

ANALYSES BASED ON THE GENERALISED LOGISTIC EQUATION

The dynamics of the population are assumed to be governed by the generalized logistic model:

$$N_{y+1} = N_y + rN_y(1-(N_y / K)^z) - C_y \qquad \text{(App.1)}$$

where N_y is the number of animals at the start of year y;

r is the intrinsic rate of growth;

z is the extent of compensation;

K is the (current) carrying capacity; and

C_y is the catch (in numbers) during year y.

The parameters of Equation (App.1) are r, z, and K while the data available to estimate these parameters are the estimates of abundance and their associated variance-covariance matrix. The analysis is based on the same likelihood function (Eqn (11) of the main text) and priors as the baseline analysis using the age- and sex-structured model.