What is needed to make a simple density-dependent response population model consistent with data for eastern North Pacific gray whales?[1]

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ABSTRACT

Census estimates indicate that the eastern North Pacific gray whale population showed an increase rate of some 3.2% per annum from 1968-1988. Further, historic records suggest that the population was 'commercially extinct' at the end of the 19th century. The standard HITTER-FITTER population model trajectories which pass through the 1987-88 census estimate of some 21,113, and utilise the customary historic commercial catch series, are inconsistent with both of these features; in particular, they generally show a decrease over the 1968-1988 period. The quantitative extent of various possible adjustment factors that would be needed to resolve these inconsistencies is examined. Depensation effects alone cannot account for the inconsistencies, while a model used to incorporate an additional response delay in recovery from exploitation produces unrealistic population oscillations. Other adjustment factors can, however, produce a 1968-1988 annual population increase rate of 2% or more, and all also correspond to a depletion of the population in 1900 to less than 25% of its size at the onset of commercial whaling in 1846. These are: an increase in the carrying capacity from 1846-1988 of at least 2.5 times; an underestimation of the historic commercial catch from 1846-1900 of at least 60%; or annual aboriginal catch levels prior to the commercial fishery at least three times those estimated by the 1990 Special Meeting of the Scientific Committee (IWC, 1993). These limits weaken if the adjustment factors are considered in combination rather than separately. The results appear insensitive to values assumed for the biological parameters of the population model (natural mortality, age at first parturition, age at recruitment and MSY level). However, they are sensitive to assumptions concerning data inputs, *viz* the accuracy of the 1987-88 census estimate used, and a 2:1 female:male ratio assumed for the commercial catches for which this information is not available. All trajectories which reflect a 1968-88 annual increase rate of 2% or more correspond to MSYR values (in terms of a 5+ exploitable population) of at least 4%. Fits of the population model to the series of gray whale census estimates are mis-specified, unless either or both of the historic commercial and aboriginal catches have been substantially underestimated (or carrying capacity has increased). The precision of these fits, conditional on fixed levels for such underestimation, is quite high, with coefficients of variation of about 10% for historic population sizes and about 20% for MSYR. There are indications that even if allowance was made for the uncertainty about these levels of underestimation, MSYR would remain relatively robustly estimated to be some 5% (or about 4% if expressed in terms of uniform selectivity on the 1+ population).

KEYWORDS: GRAY WHALE; NORTH PACIFIC; ASSESSMENT; WHALING-HISTORICAL; WHALING-ABORIGINAL; MSY

INTRODUCTION

The problem of reconciling the commercial catch history for the eastern North Pacific gray whale (*Eschrictius robustus*) population with the population increase rate deduced from censuses carried out at Monterey from 1967-68 to 1979-80 when using a simple density dependent response population model is well known (Reilly, 1981; Cooke, 1986; Lankester and Beddington, 1986).

Fig. 1 captures the essence of the problem. It shows population model trajectories for this stock for a number of choices for the maximum sustainable yield rate (MSYR) parameter (expressed in terms of the 'exploitable' component of the population throughout this paper except where indicated otherwise). All of these trajectories are constrained to pass through ('hit') a total (1+) population size of 21,113 in 1988, which corresponds to the 1987-88 census estimate (Breiwick *et al.*, 1988)[2]. Further details concerning the calculation of these trajectories are given in the following section of the paper. Note first that for this 'standard model', the average annual growth rate over the 1968-1988 period for every one of the trajectories shown is *negative*. This is in contrast to the *positive* growth rate of 2.5% per annum over the 1968-1980 period indicated by the census estimates reported in Reilly *et al*. (1983) and to the estimate of 3.2% (SE = 0.5%) per annum for the 1968-1988 period (IWC, 1993). Further, Fig. 1 (and Table 3) show that none of these trajectories indicates substantial depletion of the population by the commercial catches over the latter half of the 19th century. This hardly seems consistent with the history of a population 'commercially extinct' by the end of that period (Reilly, 1981), unless a large part of the stock ceased to frequent the lagoons in Baja California where much of the commercial whaling took place (Lankester and Beddington, 1986).

All the authors referenced above suggest factors that could resolve these inconsistencies. Lankester and Beddington (1986) allude to possible increases in carrying capacity or the lack of an immediate start to recovery after the cessation of whaling. Cooke (1986) intimates that the latter effect might have been a consequence of the disruptive influence of intensive whaling temporarily depressing the breeding rate (equivalent here to the depensation effect referred to below). Cooke himself adds the possibilities of under-recorded historical catches, an overestimate of the recent growth rate of the population, the population being held at a low level by aboriginal whaling prior to the onset of commercial whaling in 1846, and the recent population increase not constituting

[1] Originally presented as paper SC/A90/G10, updated to take account of data revisions agreed at the 1990 Special Meeting of the Scientific Committee on the Assessment of Gray Whales (IWC, 1993).
[2] A more recent reanalysis (Buckland *et al.*, 1993) published after this paper was finalised, provides an estimate for the 1987-88 census of 20,869 and an alternative 'modelled' estimate of 21,296. This does not affect the conclusions of this paper.

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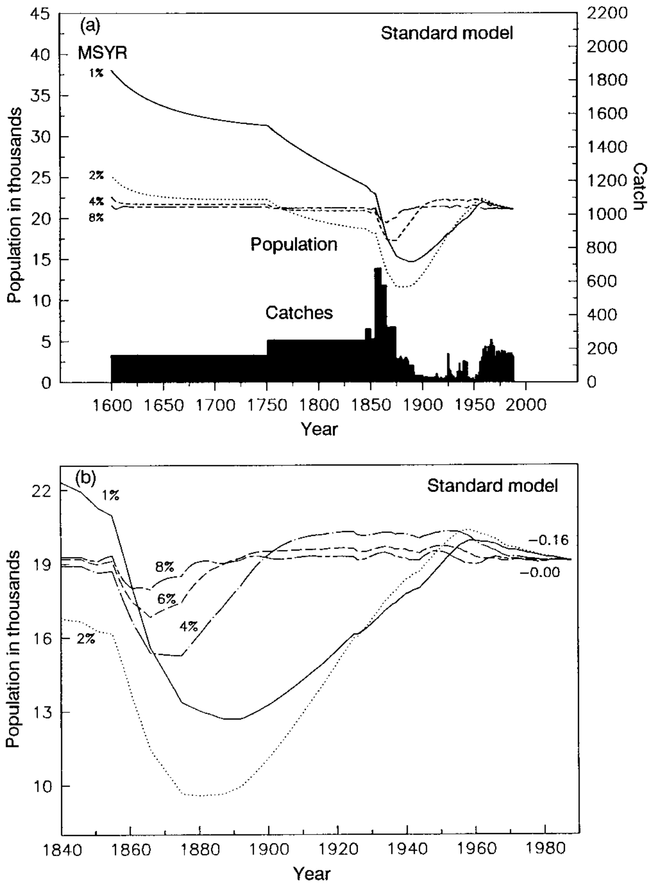


Fig. 1. The standard population model results, which incorporate the aboriginal catches of Table 2(b), for various MSYR values (1%, 2%, 4%, 6% and 8% as indicated in the Figure) for trajectories which hit a 1988 total population size of 21,113. In (a), the annual catches are also shown (on a different scale). A magnification of the population trajectories in (a) is shown in (b); the figures on the right hand extremities of the trajectories give the percentage annual increase ('Slope') of the total population from 1968-1988 as estimated from a linear regression fit to the logarithms of the model estimates of population size over this period.

a simple density-dependent response to previous exploitation. Reilly (1981) also considers the implications of earlier aboriginal whaling.

Only one of these possibilities appears to have been investigated quantitatively to any real extent. Lankester and Beddington (1986) considered the consequences of a constant annual aboriginal catch level (C_{abo}) prior to 1846, and concluded that this did not appear to influence the resultant population trajectory markedly (in particular, the trajectory still showed a decline over recent years). However, the case they illustrate (their fig. 3) has $C_{abo} = 250$ only. In contrast, Reilly (1981) provides results (his fig. 3) which indicate that a recent population increase is compatible with a population model if C_{abo} had increased to 600 by the year 1800, and comments that he is 'aware of nothing in the literature to clearly refute or substantiate' this possibility.

Clearly the factors mentioned, and indeed other possibilities, may well be able to reconcile the inconsistencies mentioned above. The important question though, is how *large* such factors would have to be to provide the requisite reconciliation; this must then be followed by the second question of whether there is any independent evidence for factors of that magnitude. The purpose of this paper is to attempt to answer the first of these questions, so that the second may be addressed by taking account of other evidence relating to those factors, including that presented in IWC (1993).

To this end, this paper considers the quantitative consequences of five possible adjustments to the 'standard model' (and associated datasets). These are depensation and additional time-lags in the density-dependent response (either of which could delay recovery after the cessation of commercial whaling in the late 19th century), an increase in carrying capacity, underestimation of historic commercial catches and aboriginal catches prior to the commercial fishery. These possibilities are investigated using the HITTER-FITTER (or BALEEN II) population model (de la Mare, 1989) commonly applied in assessments conducted for the IWC Scientific Committee; the associated parameter estimation procedure is a development of an approach of matching the slope of a time-series of a relative abundance index while also hitting an estimate of absolute abundance, which was pioneered by Holt (1985; 1986). Sensitivity of the results to the input data and to choices for the values of the biological parameters for this model is explored to a limited extent. Similarly, there is a limited investigation of the consequences of combinations of the adjustment factors listed above. Finally, the population model is 'fit' to the series of census estimates up to 1987-88 for some of these combinations, and bootstrap confidence intervals are calculated for one of these 'fits' to indicate the precision of the values of the model parameters estimated in this process.

DATA AND METHODOLOGY

Data

The census estimates used for the final 'fits' of the population model, taken from Buckland and Breiwick (2002), are listed in Table 1. Breiwick (pers. comm.) advises that the fraction of cow-calf pairs in the census data is very

Table 1

Gray whale estimates, with standard errors in parentheses.

Year	Relative estimate	Absolute estimate
1967-68	9,871 (667)	13,012 (893)
1968-69	9,289 (350)	12,244 (484)
1969-70	9,693 (381)	12,777 (525)
1970-71	8,474 (603)	11,170 (806)
1971-72	7,466 (323)	9,841 (442)
1972-73	12,868 (477)	16,962 (660)
1973-74	11,241 (429)	14,817 (592)
1974-75	9,964 (392)	13,134 (540)
1975-76	11,236 (506)	14,811 (690)
1976-77	12,100 (371)	15,950 (524)
1977-78	12,993 (716)	17,127 (966)
1978-79	10,090 (361)	13,300 (501)
1979-80	12,579 (500)	16,581 (668)
1984-85	16,646 (728)	21,942 (994)
1985-86	15,514 (520)	20,450 (727)
1987-88	16,017 (486)	21,113 (688)

Data source: see Buckland and Breiwick (2002), table 8; the absolute estimates above are the 'adjusted abundance estimates' of that table, i.e. the relative estimates scaled so that the absolute estimate for 1987-88 equals the 21,113 abundance estimate of Breiwick *et al.* (1988).

The values listed above, which were used for the calculations of this paper, were taken from an earlier version of Buckland and Breiwick (2002). There are minor changes to these values in the final version of that paper published in this volume, but the effect of these on the results reported in this paper is negligible.

small, so that these estimates of abundance have been taken to refer to age classes 1+ when comparing to the output from the population model.

As discussed in IWC (1993), the analysis by Breiwick *et al*. (1988) of data from the 1987-88 census is considered to provide the most reliable estimate of *absolute* abundance. Estimates of absolute abundance for other years were obtained by scaling a relative abundance series to this value, as detailed in Buckland and Breiwick (2002) and IWC (1993).

A sex-differentiated catch series is required for application of the HITTER-FITTER model to calculate population trajectories. What will be termed the 'commercial catch' data (actually, these are augmented by some small aboriginal catches which had been identified prior to the 1990 Special Meeting on gray whales (IWC, 1993)) are listed in Table 2(a), which also details the sources for these data and further assumptions which have been made in their compilation. An earlier version of this Table has now been amended to incorporate the modifications to the commercial catch data considered appropriate in IWC (1993). It has also been extended (Table 2(b)) to show the specifications of aboriginal catch levels until 1930 given in IWC (1993) and appropriate additions to the known aboriginal catch data from 1931-1943.

It is conventional in the case of this gray whale population to label the time of the various census estimates in the form of, for example, '1967-68'. For the rest of this paper, such an estimate will be labelled by the latter of the two years, i.e. '1968' for the example given, and will be taken to correspond to the number of whales aged 1 and above provided by the population model for the 'beginning of the year'.

Population model

The HITTER-FITTER population model used is described in de la Mare (1989), Punt and Butterworth (1991) and Punt (1999), so that the details will not be repeated here. However, to aid in the explanation of certain subsequent model adjustments, it is useful to provide a simplified generic form of the basic population dynamics model (this

Table 2

Annual gray whale catches used for the population model. Data sources for commercial catches: Total catch: 1846 -1854 = IWC (1993), Annex E; 1855-1962 = Lankester and Beddington (1986); 1963-1988 = C. Allison (IWC document dated 16/1/90); Sex ratio of catch: 1965-1970 = Lankester and Beddington (1986); 1972-1976 = Lankester and Beddington (1986); 1977-1988 = C. Allison (IWC document dated 16/1/90). Notes: (1) struck and lost whales are included in the totals; (2) the sex ratio of unknown sex or lost animals is assumed to be the same as that of animals of known sex in the catch that year; (3) for years for which no sex ratio information is indicated above, a ratio of 2:1 female:male is used (as in Lankester and Beddington, 1986); Reilly (1981) argues for a similar female preponderance (60%) in the 19th century catches. Data source for aboriginal catches: Total catch and assumed 1:1 sex ratio = IWC (1993), Annex E.

Year	Male	Female	Total	Year	Male	Female	Total	Year	Male	Female	Total	Year	Male	Female	Total
(a) Commercial catches															
1846	23	45	68	1885	21	41	62	1924	5	11	16	1963	60	120	180
1847	23	45	68	1886	17	33	50	1925	50	99	149	1964	70	140	210
1848	23	45	68	1887	7	13	20	1926	19	38	57	1965	68	108	176
1849	23	45	68	1888	7	13	20	1927	16	32	48	1966	123	97	220
1850	23	45	68	1889	7	13	20	1928	9	18	27	1967	94	156	250
1851	23	45	68	1890	7	13	20	1929	6	12	18	1968	67	134	201
1852	23	45	68	1891	7	13	20	1930	5	10	15	1969	59	155	214
1853	23	45	68	1892	7	13	20	1931	5	11	16	1970	26	125	151
1854	23	45	68	1893	0	0	0	1932	5	10	15	1971	51	102	153
1855	162	324	486	1894	0	0	0	1933	3	7	10	1972	22	160	182
1856	162	324	486	1895	0	0	0	1934	18	36	54	1973	97	81	178
1857	162	324	486	1896	0	0	0	1935	11	23	34	1974	94	90	184
1858	162	324	486	1897	0	0	0	1936	34	68	102	1975	58	113	171
1859	162	324	486	1898	0	0	0	1937	5	9	14	1976	69	96	165
1860	162	324	486	1899	0	0	0	1938	18	36	54	1977	86	101	187
1861	162	324	486	1900	0	0	0	1939	10	19	29	1978	93	91	184
1862	162	324	486	1901	0	0	0	1940	35	70	105	1979	56	127	183
1863	162	324	486	1902	0	0	0	1941	19	38	57	1980	53	128	181
1864	162	324	486	1903	0	0	0	1942	34	67	101	1981	36	100	136
1865	162	324	486	1904	0	0	0	1943	33	66	99	1982	56	112	168
1866	79	159	238	1905	0	0	0	1944	0	0	0	1983	46	125	171
1867	79	159	238	1906	0	0	0	1945	10	20	30	1984	59	110	169
1868	79	159	238	1907	0	0	0	1946	7	15	22	1985	54	116	170
1869	79	159	238	1908	0	0	0	1947	3	6	9	1986	45	126	171
1870	79	159	238	1909	0	0	0	1948	6	13	19	1987	47	112	159
1871	79	159	238	1910	0	0	0	1949	9	17	26	1988	43	108	151
1872	79	159	238	1911	0	0	0	1950	4	7	11				
1873	79	159	238	1912	0	0	0	1951	4	9	13	**(b) Aboriginal catches**			
1874	79	159	238	1913	0	1	1	1952	15	29	44	1600-1750	80	80	160
1875	17	33	50	1914	6	13	19	1953	13	25	38	1751-1850	130	130	260
1876	17	33	50	1915	0	0	0	1954	13	26	39	1851-1860	95	95	190
1877	17	33	50	1916	0	0	0	1955	20	39	59	1861-1880	45	45	90
1878	17	33	50	1917	0	0	0	1956	41	81	122	1881-1891	40	40	80
1879	21	42	63	1918	3	5	8	1957	33	65	98	1892-1900	20	20	40
1880	17	34	51	1919	1	1	2	1958	49	99	148	1901-1915	15	15	30
1881	17	33	50	1920	1	1	2	1959	65	131	196	1916-1930	10	10	20
1882	17	33	50	1921	1	1	2	1960	58	115	173	1931-1939	5	5	10
1883	19	39	58	1922	2	3	5	1961	71	141	212	1940-1943	10	10	20
1884	23	45	68	1923	5	11	16	1962	49	98	147				

simplified form assumes equivalence of the components of the population which are exploitable and past the age at first parturition):

$$P_{t+1} = (P_t - C_t)e^{-M} + (1 - e^{-M})P_{t-t_m+1}[1 + A\{1 - (P_{t-t_m+1}/P_0)^z\}] \tag{1}$$

where:

- P_t is the exploitable population size at the beginning of year t;
- C_t is the catch taken in year t;
- M is the natural mortality rate;
- t_m is the age at first parturition;
- A is the resilience parameter (related to MSYR);
- z is the density-dependent exponent (related to the MSY level, MSYL, expressed in terms of the exploitable population size); and
- P_0 is the equilibrium exploitable population size in the absence of exploitation.

Two points should be noted at this stage to avoid possible confusion.

(1) De la Mare (1989) *defines* the age at maturity for females as identical to the age at first parturition (t_m above); the HITTER-FITTER output of a female 'age at maturity' is thus actually referring to an 'age at first parturition'. This may differ from usage by other authors, who intend female 'age at maturity' to mean 'age at first parturition less the gestation period'. Reilly (1984) states that the gestation period for gray whales is most likely to be somewhat greater than 12 months, and Rice (1990) reports an estimate of 418 days.

(2) P_0 above applies to the exploitable component of the population (both sexes combined). In this paper, K is used for the corresponding value for the '*total*' population, N^{tot}, comprising all whales aged 1 and above. For model adjustments where an increase in carrying capacity is considered, this strictly refers to an increase in P_0 in equation (1); however, K will increase by the same proportion (if other parameters remain unchanged), so that the multiplicative increase factor has been labelled μ_K.

The 'base case' choice of parameter values for the trajectories calculated for this paper is as follows:

MSYL = 0.6 (related to choice of z, after other parameters have been fixed);
t_m = 8 yr (knife-edge and pertinent only to females);
M = 0.04 yr^{-1} (age and sex invariant); and
t_r = 5 yr (knife-edge and sex invariant)
where t_r is the age at recruitment.

These choices were made to relate to the ranges of parameter values examined by Lankester and Beddington (1986). Obviously cases could be made for other choices. Reilly (1984) reports a median age at sexual maturity of 8 years, with a minimum of 5 and a maximum of 11; in addition he estimates $M = 0.055$ yr^{-1} for females using age structure data, but this estimate also depends on his estimates of recent population growth rate and fishing mortality. However, the results of applications of the HITTER-FITTER model are generally not greatly sensitive to variations in these parameters, as indeed is demonstrated for a particular case later in this paper. For this reason, IWC (1993) decided to maintain this 'base case' choice for the calculation of population trajectories, although providing some additional estimates of biological parameters.

It has been conventional to apply and report results of the HITTER-FITTER package on the basis that density-dependence (the term multiplying the parameter A in equation (1)) is related to the exploitable component of the population, and MSYR is expressed in terms of this same component. Subsequent to the 1990 Special Meeting, it was discovered that the calculations of a previous version of this paper, and the results listed in tables 3 and 4 of the Special Meeting report (IWC, 1993) had used a version of the package whose code had been amended so that MSYL and MSYR related to the component of the population past the age at first parturition, rather than the exploitable component. The results that follow have been recalculated on the conventional basis.

HITTER model applications

The great majority of the results reported in this paper relate to population trajectories for given values of MSYR, which are constrained to pass through ('hit') a particular population estimate. The estimate chosen was the 1988 census estimate (i.e. 21,113), because this was regarded as the most reliable *absolute* abundance estimate (IWC, 1993). Thus, all the trajectories for such analyses have N^{tot}_{1988} = 21,113. For applications ignoring the aboriginal catches of Table 2(b), the population is assumed to be at its unexploited equilibrium level (with the associated equilibrium age structure) at the beginning of 1846. When earlier aboriginal catches are also taken into account, these assumptions apply to the year in which those catches are assumed to commence.

The value of MSYR (corresponding to the exploitable component of the population) was varied to ascertain the effect on the trajectories. The HITTER-FITTER program effects this variation internally, essentially by changing the value of the resilience parameter, A, of the model. (The density-dependent exponent, z, also needs to be changed slightly in this process, to maintain a fixed MSYL.) For most calculations, only two readily interpretable summary statistics have been reported:

(i) 'Slope'– the average annual increase of population size from 1968-1988 as estimated from a linear regression fit to the logarithms of the model output for N^{tot} over those years; and
(ii) the ratio $N^{tot}_{1900} / N^{tot}_{1846}$

The first of these statistics can be related to the population growth rate estimate of 3.2% per annum (IWC, 1993) obtained from the results of the censuses listed in Table 1; the second assists in assessing the consistency of the particular trajectory with the commercial extinction of the population at the turn of the century.

Model/dataset adjustments

Depensation

Depensation is the phenomenon of a decrease in the *per capita* growth rate of a resource when population size is reduced below a certain level. If commercial whaling in the 19th century did deplete the population to a level at which depensation was operative, this could account for what may have been a slow initial recovery rate of the stock.

Depensation was modelled by adjusting the final term in equation (1):

$$A\{1 - (P_{t-t_m+1}/P_0)^z\} \quad \rightarrow \quad A\{1 - P_{t-t_m+1}/P_0)^z\} f(P_{t-t_m+1}) \tag{2}$$

where $f(P_t) = \begin{cases} f_0 + (1-f_0)(P_t/P^*) & P_t < P^* \\ 1 & P_t \geq P^* \end{cases}$

Although, strictly, there will be a small domain of P below P^* for which the *per capita* growth rate still increases as P is reduced, for convenience, P^* will be referred to as the 'depensation level'.

Additional response time-lag

This was modelled in the same manner as suggested by IWC (1990):

$$A\{1 - P_{t-t_m+1}/P_0)^z\} \qquad\qquad A\{1-(P_{t-t_m+1-T}/P_0)^z\} \tag{3}$$

where T is the 'additional time-lag'. The introduction of such a parameter might be a way of mimicking the effect of population sub-structure (such as 'herds' within a stock) in an aggregated model representation such as equation (1).

Increase in carrying capacity

For this adjustment, equation (1) was modified as follows:

$$[P_{t-t_m+1}/P_0]^z \quad \rightarrow \quad [P_{t-t_m+1}/P_0(t)]^z \tag{4}$$

where:

$$P_0(t) = \begin{cases} P_0(1846) & t \leq 1846 \\ P_0(1846)+(t-1846)[\{P_0(1988) - P_0(1846)\}/(1988-1846)] & t > 1846 \end{cases}$$

$P_0(1988) = \mu_K P_0(1846)$

i.e. carrying capacity increases linearly over the period 1846-1988 by a multiplicative factor μ_K.

Underestimation of historic commercial catches

The commercial catch data in Table 2(a) are not equally reliable throughout the complete period detailed. For 1846-1874 they are based on oil yields and struck-but-lost inferences, while from 1875-1943 only scarce data are available (Reilly, 1981). It is therefore not impossible that the historic commercial catch data listed are underestimates (see also IWC, 1993). This has been examined in this paper by the adjustment:

$$C_t \rightarrow \begin{cases} \mu_C C_t & 1846 < t < 1900 \\ C_t & t > 1900 \end{cases} \tag{5}$$

where μ_C is termed the historic catch multiplicative factor. The sex ratio assumed for the catches (see footnotes to Table 2(a)) is kept unchanged in this adjustment.

Aboriginal catches prior to the commercial fishery

Both Reilly (1981) and Lankester and Beddington (1986) attempt to show the effect of such catches. Reilly also takes account of a likely reduction in such catches subsequent to 1800.

The approach adopted here is as follows. First, the effect of adding the aboriginal catch estimates specified in IWC (1993) and listed in Table 2(b) has been examined. Then, to allow for the possibility that these may be underestimates, their values have been adjusted by:

$$C_{abo}(t) \quad \rightarrow \quad \mu_A C_{abo}(t) \qquad t \geq t_s \tag{6}$$

where:

$N_{t_s}^{tot} = K$

$t_s = 1600$ (see Table 2(b)); and

μ_A is termed the aboriginal catch multiplicative factor.

In addition to $t_s = 1600$, calculations have been carried out for $t_s = 1200$ and 1700, with the annual catch level of 160 from 1600-1750 specified in Table 2(b) then assumed to commence instead in year t_s. There is no intention here to suggest that the level of aboriginal catch was precisely constant over the period from t_s to 1750. Rather, since historic catch levels and the time of their inception are not well known, alternative values of t_s reflect variations in the assumptions of a population at carrying capacity and with equilibrium age-structure in 1600.

Combinations of adjustments, and sensitivity tests

Naturally, numerous combinations of the adjustment factors listed above could be investigated. Only one of these has been analysed in this paper: the combination of underestimation of both the historic commercial and aboriginal catches. The reason for this choice is that it is possible to exercise some judgement regarding the reality of the magnitudes of these factors needed to resolve the fundamental inconsistencies between the population model analysis and the data, whereas there is no direct evidence to support (or to allow independent estimation of the possible magnitude of) a change in carrying capacity (IWC, 1993).

The possibilities for sensitivity tests to the numerous assumptions and parameter value choices for the implementation of the HITTER-FITTER model are even more voluminous. To keep these within reasonable bounds, only one instance of the combination of the two adjustments mentioned in the paragraph above has been investigated in this context: $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) for various values of MSYR, with trajectories 'hitting' a given value of N_{1988}^{tot}. Sensitivity tests have been carried out for two variations in the data input for the HITTER procedure: changes to N_{1988}^{tot} and changes to the sex ratio assumed for commercial catches for which this information is not available. Similar tests have been carried out for variations in the values assumed for the model parameters M, t_m, t_r and MSYL.

FITTER model applications

Naturally all the adjustments considered above could be investigated in a 'fitting' as well as a 'hitting' context. Again, to keep computations within reasonable bounds, only three cases have been analysed in this paper. These are a subset of those chosen for the sensitivity tests discussed above, *viz.* ($\mu_C = 1.5$; $\mu_A = 1.5$), ($\mu_C = 2$; $\mu_A = 2$) and ($\mu_C = 2.5$; $\mu_A = 2.5$). Table 8(a) indicates that a 1968-88 annual average growth rate of some 3.2% can be attained within the MSYR range investigated for the last of these cases, so that model mis-specification problems are less likely in this instance. Further, Table 8(b) shows that results consistent with commercial extinction of the population at the end of the 19th century can be obtained for all three cases.

The population estimates to which the model was 'fitted' are listed in Table 1. The fitting procedure needs to take cognisance of the manner in which the absolute abundance estimates (N_t^{tot}) of that Table were derived. These are of the form:

$$N_t^{tot} = b\, I_t \tag{7}$$

where:

I_t is the relative abundance estimate for year t; and
b is a scaling factor which was estimated for the 1988 census only.

The error structure assumed for model fitting purposes:

$$b\ I_t = N_t^{tot}\ e^{\varepsilon_t} \qquad \varepsilon_t \text{ from } N(0;\sigma^2) \tag{8}$$

where:

$\hat{N}_t^{tot}$ is the population model estimate of the number of whales aged 1 and above at the start of year t; and
$N(0;\sigma^2)$ is a normal distribution with mean 0 and variance σ^2.

The corresponding sum of squares functional minimised was therefore:

$$SS(K, MSYR, b) = (1/\sigma_1^2)\sum_{t=1968}^{1988}[\ln\ (bI_t) - \ln\ \hat{N}_t^{tot}]^2 + (1/\sigma_2^2)[\ln\ b_{obs} - \ln\ b]^2 \tag{9}$$

where b_{obs} is the estimate of b obtained independently from data from the 1988 census. The first term on the right hand side of equation (9) is taking account of the information on trend in abundance provided by the series of relative abundance estimates (I_t), while the second incorporates the information available on the absolute level of abundance.

The variance estimate (σ_1^2) used to weight the first term was obtained from the (bias-corrected) residuals about a quadratic fit to the ln I_t series, which yielded $\sigma_1 = 0.134$. The variance (σ_2^2) associated with the estimate b_{obs} followed from comparison of the two columns of Table 1, which indicates $b_{obs} = 1.318$, $\sigma_2 = 0.012$.

This procedure gives equal weights to each of the relative abundance estimates, despite their differing standard errors, SEs (and coefficients of variation CV). The reason for this is that these SE estimates correspond to the sampling contribution to the overall variance only, and are certainly not capturing most of the variability about the underlying trend (see discussion in Butterworth *et al.*, 2002). Note that this implies a CV for the 1988 absolute abundance estimate of $\sqrt{\sigma_1^2 + \sigma_2^2} = 0.135$; this corresponds to an SE of 2,840, which indicates rather lesser precision than does the SE estimate of 688 given in Table 1. Buckland *et al.* (1993) took into account more sources of variability and indeed found a larger value for this SE (913 or 1,288, depending on methodology).

Differentiating equation (9) partially with respect to b, and setting the result to zero, provides a closed form expression for the estimate of b:

$$\ln\ \hat{b} = \{n/\sigma_1^2 + 1/\sigma_2^2\}^{-1}\ [(1/\sigma_1^2)\sum_{t=1968}^{1988}\{\ln\ \hat{N}_t^{tot} - \ln I_t\} + (1/\sigma_2^2)\ \ln b_{obs}] \tag{10}$$

where n (= 16) is the number of censuses over the 1968-1988 period. In consequence, the non-linear minimisation search is over two parameters only: K and MSYR. The HITTER model applications discussed above are all of the form known as 'Hitting with fixed MSYR'. Given the series of census estimates, it becomes possible to estimate MSYR while still 'hitting' the 1988 census estimate. The non-linear minimisation search is then reduced to one parameter only.

A bootstrap technique was used to estimate SEs and confidence intervals (CIs) for the resultant fit. In place of the actual set of results from the censuses: $\{b_{obs};\ I_t: t = 1968,...,1988\}$, a large number of bootstrap sets was generated: $\{b_{obs}^S; I_t^S: t = 1968,...,1988\}$ where $S = 1,...,S_{max}$. The individual elements of these sets were generated as follows:

$$\begin{aligned} \ln\ I_t^S &= \ln(\hat{N}_t^{tot}/\hat{b}) + \epsilon_{1,t}^S \qquad \epsilon_{1,t}^S \text{ from } N(0;\sigma_1^2) \\ \ln\ b_{obs}^S &= \ln b + \epsilon_2^S \qquad \epsilon_2^S \text{ from } N(0;\sigma_2^2) \end{aligned} \tag{11}$$

The bootstrap distribution of a quantity of interest was then provided by minimising equation (9) for each of these alternative bootstrap data sets, which provides an estimate of the quantity for each set S. Bootstrap CIs were then obtained by ordering the resultant S_{max} estimates of the quantity, while an SE estimate was provided by the SD of these S_{max} estimates. For the results reported here, $S_{max} = 500$.

RESULTS AND DISCUSSION

The results of HITTER model applications for the various model/dataset adjustments considered are presented in a standard format in most cases. First, a table containing two matrices is given, the one providing values of 'Slope', and the other values of N_{1990}^{tot} / N_{1846}^{tot}. The rows in these tables correspond to MSYR values from 0% to 10%, and the columns to different values of the relevant adjustment factor.

'Slope' values relate to the corresponding estimate from the 1968-1988 censuses of an average annual growth rate of 3.2% over the period. As an aid for inspection of the tables, all 'Slope' values greater than 1.0% have been entered in italics. N_{1990}^{tot} / N_{1846}^{tot} entries of less than 0.30 are also entered in the same way, to draw attention to sets of parameter combinations which better reflect the commercial extinction of the population at the end of the 19th century.

Clearly it would be unreasonable to provide graphical representations of the trajectories for every parameter combination listed in the Tables described above. Figures have therefore been presented in two ways: first, the set of trajectories for a fixed MSYR for various adjustment factor values; and secondly, the set for a fixed adjustment factor value for various MSYRs. The fixed MSYR chosen was 5%, because this is usually the smallest MSYR value for which 'Slope' values of at least 3% can be achieved. Similarly, the fixed adjustment factor value normally chosen was the smallest for which a 'Slope' approaching 3% was possible. As an aid in relating the Tables and Figures, the Table entries for which Figures are provided (in most cases) are shown between dashed lines. Note that because the post-1840 period is of greater interest, the scale of the horizontal year axis has been reduced for the 1600-1840 period in many cases, to allow for better discrimination of the results for later years.

Aboriginal catches prior to the commercial fishery

Table 3(a) gives results for the application of the basic population model including only the 'commercial' catches of Table 2(a), i.e. corresponding to a resource at its carrying capacity level at the onset of commercial harvesting in 1846. None of these results is able to reflect a recent growth rate

Table 3

Results for the basic population model (and catch data of Table 2) for various values of MSYR for trajectories which hit a 1988 total population size (N^{tot}_{1988}) of 21,113. 'Slope' is the average annual increase of the total population from 1968 to 1988 as estimated from a linear regression fit to the logarithms of the model estimates of population size over this period. The unexploited equilibrium total population size $K = N^{tot}_{1846}$ for (a), which incorporates only the commercial catch data of Table 2(a); for (b), for which the aboriginal catches of Table 2(b) are included as well, $K = N^{tot}_{1600}$. The lowest size over 1846-1988 period is indicated by N^{tot}_{min}.

				N^{tot}_{min}/K	
MSYR (%)	Slope (%)	K	$N^{tot}_{1900}/N^{tot}_{1846}$	Estimate	Year occurs
(a) Commercial catches only (Table 2a)					
0	-0.90	40,869	0.73	0.52	1988
1	-0.45	27,568	0.78	0.74	1877
2	0.29	24,529	0.88	0.77	1875
3	-0.14	23,316	0.95	0.81	1875
4	-0.05	22,555	0.98	0.85	1866
5	-0.01	22,061	0.99	0.88	1866
6	-0.00	21,738	0.99	0.91	1866
8	-0.02	21,346	0.99	0.96	1860
10	0.02	21,261	0.99	0.97	1859
(b) Addition of aboriginal catches (Tables 2a and 2b)					
0	-0.89	96,491	0.64	0.22	1988
1	-0.12	38,032	0.64	0.39	1890
2	-0.16	25,127	0.70	0.46	1881
3	-0.14	23,320	0.95	0.66	1875
4	-0.05	22,555	1.02	0.77	1875
5	-0.01	22,061	1.03	0.82	1866
6	-0.00	21,739	1.02	0.87	1866
8	-0.02	21,345	1.00	0.93	1866
10	0.03	21,278	0.99	0.97	1860

('Slope') which exceeds 0.3% (let alone 3%) and the extent of the estimated reduction in abundance between 1846 and 1900 is scarcely compatible with commercial extinction.

The consequences of including the levels of (additional) aboriginal catch (principally prior to the commercial fishery) that were specified in IWC (1993)[3], are shown in Table 3(b) and Fig. 1. Although marginally greater proportional reduction over the 1846-1900 period is rendered possible by their inclusion, there are no qualitative differences from the results of Table 3(a), so that these levels of aboriginal catch alone are unable to resolve the conflicts between the population model and observations.

The model and data used to produce the results of Fig. 1 and Table 3(b) will henceforth be referred to as the 'standard model'. All further model fits reported in this paper *include* the aboriginal catches listed in Table 2(b).

Depensation

Table 3(b) (and Fig. 1) also provides results for the 'standard model' for the lowest depletion ($N^{tot}_{\min}/K$) over the back-projection period considered. Disregarding the unrealistic MSYR = 0% result (which is included only to provide values associated with a lower bound for MSYR), the lowest depletion shown by any of these trajectories is 0.39 and most other values are substantially higher than this.

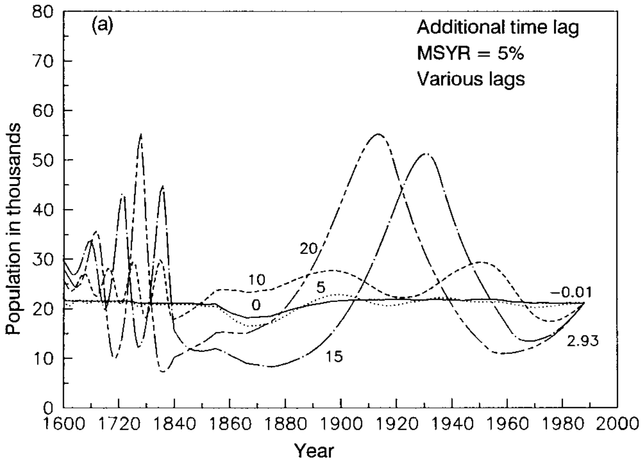
Thus, depensation can have an effect only if the depensation level P^* exceeds at least 0.39 P_0 (see equation 2). It hardly seems realistic to invoke depensation effects at population levels N^{tot} that are not considerably lower than the 0.6K conventionally assumed for MSYL. Accordingly depensation *alone* does not appear to be a candidate for resolving the inconsistencies related to the population model, although it could of course play a role in combination with some other adjustment factor.

[3] See Table 2(b).

Additional response time-lag

Results for the adjustment indicated by equation (3) are shown in Fig. 2. The larger of the values chosen for the additional time-lag T lead to marked oscillations in the population trajectories. Although these trajectories can produce 'Slope' values in the range indicated by the censuses, none correspond to a population which could be regarded as commercially extinct at the turn of the century.

Thus, none of these results appears to provide a reasonable representation of the gray whale population history, and the Table corresponding to Fig. 2 has accordingly been omitted. The manner in which the response time-lag is modelled in equation (3) therefore does not seem to hold any promise for resolving the inconsistencies in question.



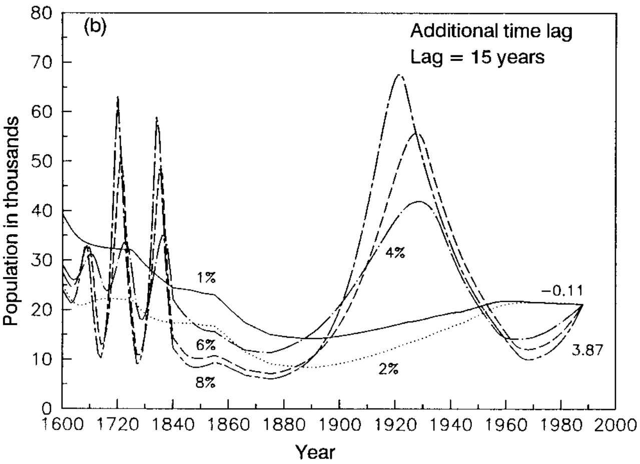


Fig. 2. The effect on population trajectories of introducing an additional time-lag into the density-dependent response term in the population model: (a) MSYR = 5%, additional time-lags from 0-20 years as indicated on each trajectory; (b) additional time-lag of 15 years, MSYR from 1% to 8%. (Note that the scale of the horizontal axis changes from 1840 in this and some following Figures.)

Table 4

Results of allowing carrying capacity to increase linearly over the period 1846-1988 by a multiplicative factor μ_K. Carrying capacity is constant prior to 1846. 'Slope' and 'N^{tot}' are as for Table 3. Fig. 3 shows the trajectories corresponding to the row and the column between dashed lines.

MSYR(%)	μ_K 1.0	1.5	2.0	2.5	3.0	4.0	5.0
(a) Slope							
0	-0.90	-0.90	-0.90	-0.90	-0.90	-0.90	-0.90
1	-0.45	0.01	0.06	0.08	0.09	0.10	0.10
2	-0.28	0.58	0.81	0.90	0.95	0.99	*1.01*
3	-0.14	0.63	*1.35*	*1.59*	*1.70*	*1.80*	*1.84*
4	-0.05	0.18	*1.72*	*2.18*	*2.38*	*2.54*	*2.61*
5	-0.01	0.23	*1.88*	*2.72*	*3.00*	*3.24*	*3.33*
6	-0.00	0.25	0.77	*3.22*	*3.60*	*3.89*	*4.01*
8	-0.02	0.23	0.36	*4.08*	*4.72*	*5.12*	*5.27*
10	0.02	0.26	0.38	0.44	*5.74*	*6.22*	*6.37*
(b) Total population in 1900 as a proportion of that in 1846							
0	0.73	0.64	0.64	0.64	0.64	0.64	0.64
1	0.77	0.61	0.60	0.60	0.60	0.60	0.60
2	0.88	0.49	0.45	0.44	0.44	0.43	0.43
3	0.95	0.39	0.32	0.31	0.30	0.30	0.30
4	0.98	0.73	*0.24*	*0.23*	*0.23*	*0.22*	*0.23*
5	0.99	1.09	*0.19*	*0.18*	*0.18*	*0.18*	*0.19*
6	0.99	1.20	*0.18*	*0.16*	*0.16*	*0.16*	*0.17*
8	0.99	1.19	1.38	*0.14*	*0.15*	*0.15*	*0.15*
10	1.00	1.17	1.36	1.27	*0.14*	*0.15*	*0.15*

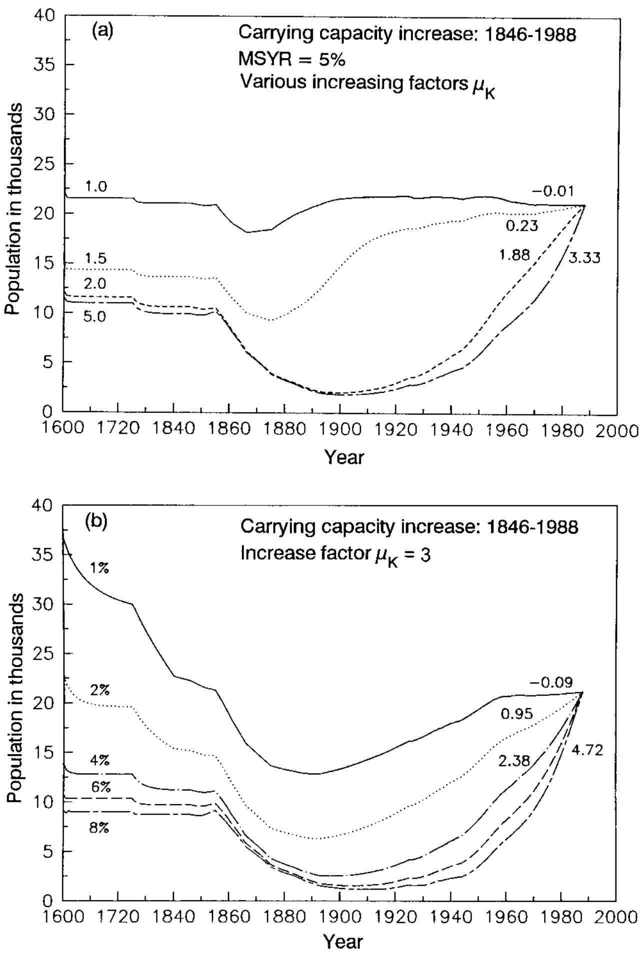


Fig. 3. The effect on population trajectories of a linear increase in carrying capacity over the period 1846-1988 by a multiplicative factor μ_K: (a) MSYR = 5%, μ_K = 1.0, 1.5, 2.0 and 5.0; (b) μ_K = 3.0, MSYR from 1% to 8%.

Increase in carrying capacity

Table 4 and Fig. 3 show the results of the adjustment of equation (4), which corresponds to a linear increase in carrying capacity over 1846-1988. Introduction of this factor can remove the inconsistencies, as typically $\mu_K > 2$ and MSYR $\geqslant$ 3% provide 'Slope' values exceeding 1%. Note that a saturation effect comes into play for high μ_K : once μ_K exceeds 3, little change is evident in the resultant population trajectories.

Thus, this particular analysis provides a simple answer to the first question of how large an adjustment factor needs to be to remove the inconsistencies: the multiplicative increase in carrying capacity must be at least 2 and probably about 3. However, this alone cannot be regarded as an entirely satisfactory resolution of the problem, given that there is no independent evidence for an effect of this size (IWC, 1993).

Naturally, increases in K differing from the linear trend examined could be envisaged. Specific choices are problematic in the absence of independent evidence relating to the probable periods of greatest change. However, as a first approximation, μ_K will still remain meaningful as typical of the magnitude of adjustment factor necessary.

Underestimation of historic commercial catches

Results for a multiplicative increase (by μ_C) of the commercial catches between 1846 and 1900 (see equation 5) are given in Table 5 and Fig. 4. Once again the inconsistencies can be removed - in this instance 'Slope' values exceeding 1% are obtained provided $\mu_C \geqslant 2.25$ and MSYR $\geqslant$ 3%. A saturation effect is evident for $\mu_C > 3$, larger values having little effect on the post-1900 sections of the population trajectories.

To achieve a 'Slope' of at least 2% from historic commercial catch underestimation *alone* requires $\mu_C \geqslant 2.5$ (i.e. at least 60% underestimation). IWC (1993) discussed problems associated with the data and methods used to

Table 5

Results of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor μ_C. 'Slope' and 'N^{tot}' are as for Table 3. Fig. 4 shows the trajectories corresponding to the row and the column between dashed lines.

MSYR (%)	μ_C 1.0	2.0	2.25	2.5	3.0	4.0	5.0
(a) Slope							
0	-0.90	-0.90	-0.90	-0.90	-0.91	-0.91	-0.92
1	-0.45	-0.04	-0.03	-0.01	0.00	0.03	0.04
2	-0.28	0.47	0.56	0.64	0.74	0.84	0.89
3	-0.14	0.69	0.99	*1.18*	*1.41*	*1.61*	*1.70*
4	-0.05	0.41	*1.32*	*1.70*	*2.07*	*2.35*	*2.46*
5	-0.01	-0.01	*1.50*	*2.21*	*2.71*	*3.06*	*3.19*
6	-0.00	-0.00	0.00	*2.67*	*3.34*	*3.74*	*3.87*
8	-0.02	-0.02	-0.02	0.01	*4.53*	*5.00*	*5.14*
10	0.02	0.02	0.02	0.05	*5.64*	*6.13*	*6.29*
(b) Total population in 1900 as a proportion of that in 1846							
0	0.73	0.53	0.51	0.49	0.45	0.40	0.35
1	0.77	0.44	0.41	0.39	0.34	*0.28*	*0.25*
2	0.88	0.33	*0.29*	*0.27*	*0.23*	*0.19*	*0.17*
3	0.95	*0.24*	*0.21*	*0.19*	*0.17*	*0.14*	*0.13*
4	0.98	*0.20*	*0.16*	*0.15*	*0.13*	*0.12*	*0.11*
5	0.99	0.47	*0.14*	*0.13*	*0.12*	*0.11*	*0.10*
6	0.99	0.81	*0.17*	*0.12*	*0.11*	*0.10*	*0.10*
8	0.99	1.00	0.96	*0.13*	*0.11*	*0.10*	*0.10*
10	1.00	0.98	0.97	1.01	*0.11*	*0.11*	*0.11*

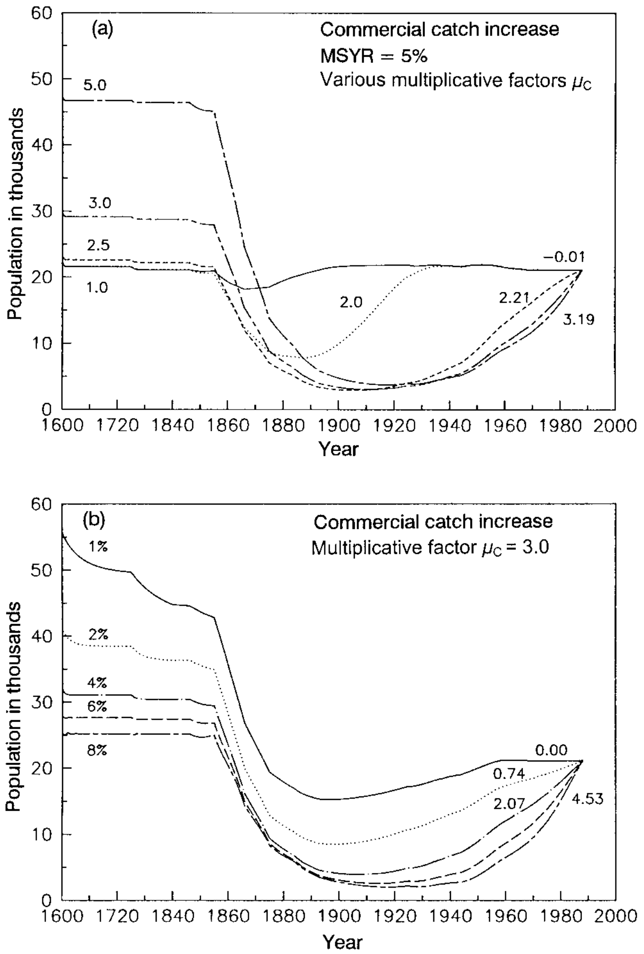


Fig. 4. The effect on population trajectories of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor μ_C: (a) MSYR = 5%, μ_C = 1.0, 2.0, 2.5, 3.0 and 5.0; (b) μ_C = 3.0, MSYR from 1% to 8%.

estimate the 19th century commercial catches and the extent to which these might have been underestimated. Readers are invited to use those comments as a basis for judging whether underestimation by as much as 60% is a realistic possibility.

Underestimation of aboriginal catches

Results for such catches over the period commencing in 1600 are shown in Table 6 and Fig. 5. Table 7 shows that the effect of changing the period considered for such catches to 1200-1845 or 1700-1845, for the case $\mu_A = 3$, makes no difference to the results of interest. It should be noted that some of the aboriginal catch levels considered are greater than the associated MSY for the resource, as is evident from inspection of Fig. 5a.

From Table 6, it is clear that $\mu_A \geqslant 2$ is needed to achieve a 'Slope' of at least 1%, and $\mu_A \geqslant 3$ for a 'Slope' exceeding 2%. For $\mu_A > 3$, a saturation effect is evident, with minimal change in the post-1900 trajectories.

Combinations

Results for combinations of the last two adjustment factors above are reported in Table 8 and Fig. 6. The primary objective of investigating this combination is to assess to what extent the separate requirements of $\mu_C \geqslant 2.5$ and $\mu_A \geqslant 3$ to achieve a 'Slope' of at least 2% might be relaxed.

Table 6

Results for multiples of μ_A of the annual aboriginal catch (C_{abo}) given in Table 2(b). 'Slope' and 'N^{tot}' are as for Table 3. Fig 5 shows the trajectories corresponding to the row and column between dashed lines.

MSYR (%)	μ_A 1.0	2.0	2.25	2.5	3.0	5.0	10.0
(a) Slope							
0	-0.90	-0.90	-0.90	-0.90	-0.90	-0.90	-0.90
1	-0.45	0.04	0.05	0.07	0.08	0.10	0.11
2	-0.28	0.72	0.80	0.85	0.91	*1.00*	*1.03*
3	-0.14	*1.09*	*1.31*	*1.45*	*1.61*	*1.81*	*1.89*
4	-0.05	0.53	*1.45*	*1.82*	*2.17*	*2.56*	*2.69*
5	-0.01	-0.01	-0.01	*1.67*	*2.58*	*3.24*	*3.44*
6	-0.00	-0.00	-0.00	-0.00	*2.69*	*3.86*	*4.14*
8	-0.02	-0.02	-0.02	-0.02	-0.02	*4.96*	*5.44*
10	0.02	0.03	0.03	0.03	0.04	*5.83*	*7.22*
(b) Total population in 1900 as a proportion of that in 1846							
0	0.73	0.58	0.56	0.55	0.53	0.45	0.35
1	0.77	0.52	0.50	0.48	0.45	0.37	*0.28*
2	0.88	0.40	0.38	0.36	0.34	*0.28*	*0.23*
3	0.95	0.30	*0.28*	*0.27*	*0.25*	*0.22*	*0.19*
4	0.98	*0.27*	*0.23*	*0.22*	*0.21*	*0.19*	*0.17*
5	0.99	1.13	1.03	*0.19*	*0.18*	*0.17*	*0.16*
6	0.99	1.09	1.13	1.20	*0.17*	*0.16*	*0.16*
8	0.99	1.02	1.03	1.05	1.10	*0.16*	*0.15*
10	1.00	0.99	0.99	0.99	1.01	*0.16*	*0.15*

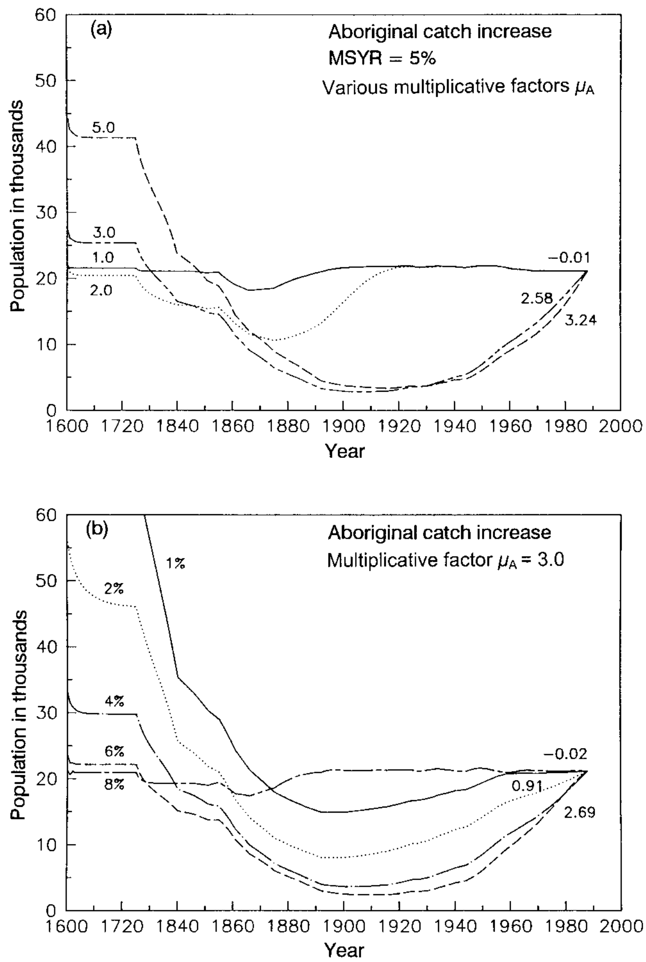


Fig. 5. The effect on population trajectories of increasing the aboriginal catches (C_{abo}) of Table 2(b) over the period from 1600 by a multiplicative factor μ_A: (a) MSYR = 5%, μ_A = 1.0, 2.0, 3.0 and 5.0; (b) μ_A = 3.0, MSYR from 1% to 8%.

Table 7

Comparison of results for a change from 1600 of the year in which an aboriginal catch commences (see Table 2 (b)). Results are shown for the case μ_A =3, so that the commencing level of annual catch is 480 whales. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR	Year C_{abo} commences			MSYR	Year C_{abo} commences		
(%)	1200	1600	1700	(%)	1200	1600	1700
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.90	-0.90	-0.90	0	0.53	0.53	0.53
1	0.08	0.08	0.07	1	0.45	0.45	0.45
2	0.91	0.91	0.91	2	0.34	0.34	0.34
3	*1.61*	*1.61*	*1.61*	3	*0.25*	*0.25*	*0.25*
4	*2.17*	*2.17*	*2.17*	4	*0.21*	*0.21*	*0.21*
5	*2.58*	*2.58*	*2.58*	5	*0.18*	*0.18*	*0.18*
6	*2.69*	*2.69*	*2.69*	6	*0.17*	*0.17*	*0.17*
8	-0.02	-0.02	-0.02	8	1.10	1.10	1.10
10	0.04	0.04	0.04	10	1.01	1.01	1.01

Table 8

Results for the combined effects of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor μ_A and aboriginal catches of Table 2(b) by a multiplicative factor μ_A. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR	μ_A			MSYR	μ_A		
(%)	1.5	2.0	2.5	(%)	1.5	2.0	2.5
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
μ_C (1846-1900) = 1.5							
0	-0.90	-0.90	-0.90	0	0.55	0.53	0.50
1	0.00	0.04	0.07	1	0.48	0.45	0.42
2	0.57	0.76	0.86	2	0.36	0.33	0.31
3	0.66	*1.24*	*1.49*	3	*0.29*	*0.25*	*0.23*
4	-0.05	*1.34*	*1.95*	4	0.54	*0.20*	*0.19*
5	-0.01	-0.01	*2.14*	5	0.91	0.47	*0.17*
6	-0.00	-0.00	-0.00	6	1.02	0.99	*0.24*
8	-0.02	-0.02	-0.02	8	1.00	1.02	1.05
10	0.03	0.03	0.04	10	0.98	0.99	0.99
μ_C (1846-1900) = 2.0							
0	-0.90	-0.90	-0.90	0	0.51	0.49	0.47
1	0.02	0.05	0.06	1	0.42	0.40	0.38
2	0.67	0.80	0.87	2	0.30	*0.29*	*0.27*
3	*1.11*	*1.38*	*1.54*	3	*0.22*	*0.21*	*0.21*
4	*1.38*	*1.82*	*2.09*	4	*0.17*	*0.17*	*0.17*
5	*1.33*	*2.16*	*2.56*	5	*0.15*	*0.15*	*0.15*
6	-0.00	*2.31*	*2.94*	6	0.43	*0.13*	*0.14*
8	-0.02	-0.02	-0.01	8	1.00	0.93	0.32
10	0.02	0.03	0.04	10	0.97	0.98	0.99
μ_C (1846-1900) = 2.5							
0	-0.90	-0.90	-0.90	0	0.47	0.45	0.44
1	0.02	0.05	0.06	1	0.37	0.36	0.34
2	0.75	0.83	0.89	2	*0.26*	*0.25*	*0.25*
3	*1.36*	*1.49*	*1.59*	3	*0.19*	*0.19*	*0.19*
4	*1.93*	*2.10*	*2.23*	4	*0.15*	*0.15*	*0.15*
5	*2.48*	*2.68*	*2.83*	5	*0.13*	*0.13*	*0.14*
6	*3.01*	*3.24*	*3.40*	6	*0.12*	*0.12*	*0.13*
8	*3.98*	*4.29*	*4.50*	8	*0.12*	*0.12*	*0.12*
10	-0.02	0.05	*5.50*	10	0.82	*0.14*	*0.12*

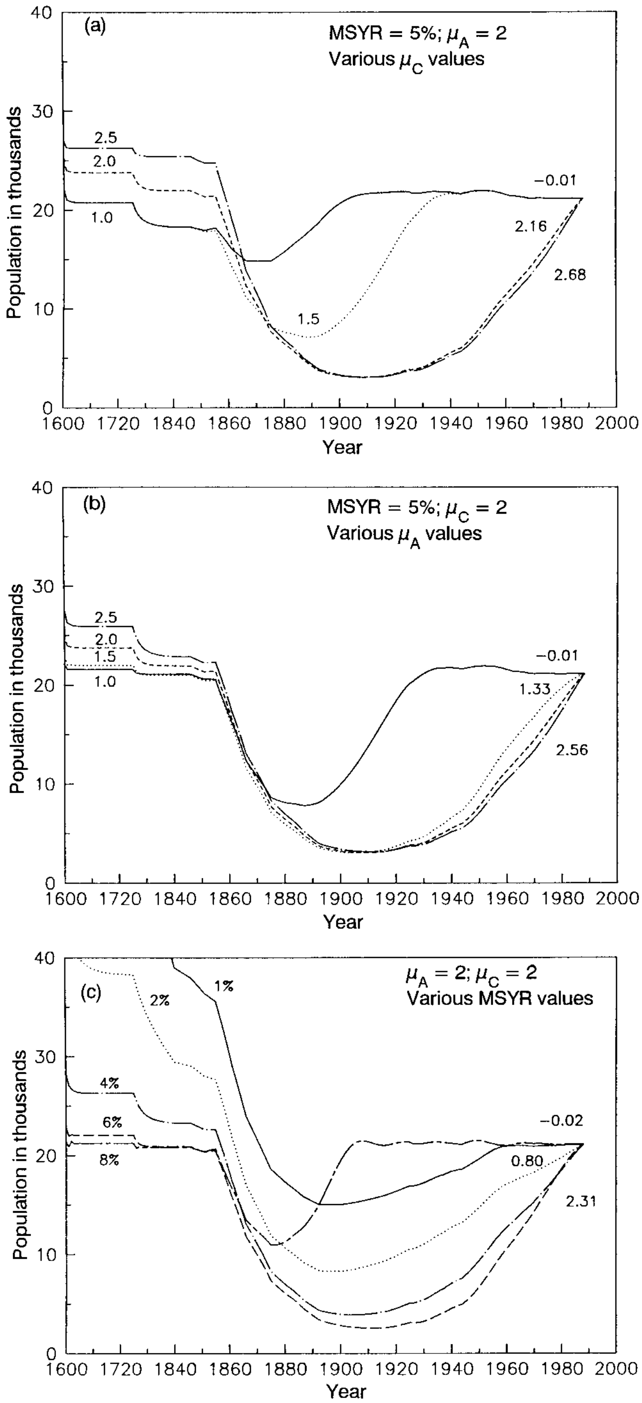


Fig. 6. The combined effects on population trajectories of increasing all historic commercial catches over the period 1846-1900 by a multiplicative factor μ_C, and also multiplying the aboriginal catches by a factor μ_A: (a) MSYR = 5%, μ_A = 2.0, μ_C from 1.0 to 2.5; (b) MSYR = 5%, μ_C = 2.0, ; μ_A from 1.0 to 2.5; (c) μ_C = 2.0, μ_A = 2.0, MSYR from 1% to 8%.

Table 8 shows that underestimation of the historic commercial catch is the dominant of the two factors. To achieve a 'Slope' of 2%, μ_A can be reduced to 2.5 if μ_C = 1.5. Similarly, relaxing the requirement that $\mu_C \geqslant$ 2.5 requires that $\mu_A \geqslant 2$.

The sensitivity tests that follow have been carried out for the (μ_C = 2; μ_A = 2) combination. These are provided for illustrative purposes and do not imply any reason for especially preferring this case as a representation of reality.

Sensitivity tests

The results of sensitivity tests to variations in the data input and the chosen model parameter values for the case μ_C = 2 (for 1846-1900) and μ_A = 2 (for 1600+) are shown in Tables 9-14. These reflect variations in N^{tot}_{1988}, the assumed female:male catch ratio in the earlier commercial catches, M, t_m, t_r and MSYL, respectively.

Table 9

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of N_{1988}^{tot} which the trajectory hits. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	N_{1988}^{tot} 19,113	21,113*	23,113	MSYR (%)	N_{1988}^{tot} 19,113	21,113*	23,113
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.99	-0.90	-0.83	0	0.47	0.49	0.50
1	-0.04	0.05	0.12	1	0.38	0.40	0.41
2	0.73	0.80	0.84	2	*0.27*	*0.29*	0.30
3	*1.36*	*1.38*	*1.35*	3	*0.20*	*0.21*	*0.22*
4	*1.90*	*1.82*	*1.64*	4	*0.16*	*0.17*	*0.18*
5	*2.38*	*2.16*	*1.54*	5	*0.14*	*0.15*	*0.15*
6	*2.82*	*2.31*	-0.00	6	*0.13*	*0.13*	0.53
8	*3.49*	-0.02	-0.02	8	*0.13*	0.93	1.02
10	0.05	0.03	0.03	10	1.01	0.98	0.98

* Used for previous calculations.

Table 10

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value assumed for the female:male sex ratio in the catches for years for which this information is not available for commercial catches (see Table 2(a)). 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	Female:male ratio in catches 1:1	2:1*	4:1	MSYR (%)	Female:male ratio in catches 1:1	2:1*	4:1
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.75	-0.90	-1.05	0	0.50	0.49	0.48
1	-0.25	0.05	-0.16	1	0.40	0.40	0.40
2	*1.04*	0.80	0.56	2	*0.27*	*0.29*	0.30
3	*1.59*	*1.38*	*1.13*	3	*0.18*	*0.21*	*0.23*
4	*1.80*	*1.82*	*1.64*	4	*0.13*	*0.17*	*0.19*
5	0.03	*2.16*	*2.13*	5	0.43	*0.15*	*0.17*
6	0.02	*2.31*	*2.60*	6	1.08	*0.13*	*0.16*
8	-0.01	-0.02	*3.47*	8	1.03	0.93	*0.15*
10	0.01	0.03	*4.23*	10	0.98	0.98	*0.16*

* Used for previous calculations.

Table 11

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of natural mortality M. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	M(yr^{-1}) 0.02	0.04*	0.06	MSYR (%)	M(yr^{-1}) 0.02	0.04*	0.06
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.89	-0.90	-0.93	0	0.50	0.49	0.47
1	0.08	0.05	-0.03	1	0.42	0.40	0.38
2	0.82	0.80	0.71	2	0.33	*0.29*	*0.27*
3	*1.36*	*1.38*	*1.30*	3	*0.26*	*0.21*	*0.19*
4	*1.74*	*1.82*	*1.77*	4	*0.23*	*0.17*	*0.14*
5	*1.97*	*2.16*	*2.16*	5	*0.21*	*0.15*	*0.12*
6	*1.64*	*2.31*	*2.45*	6	*0.21*	*0.13*	*0.10*
8	-0.03	-0.02	-0.00	8	1.01	0.93	0.58
10	0.00	0.03	0.01	10	0.97	0.98	0.99

* Used for previous calculations.

By and large, the results indicate insensitivity to these changes, except occasionally for the larger of the MSYR values listed. The only major exceptions to this are the cases of changed N_{1988}^{tot} values and female:male catch ratios (Tables 9 and 10). The inconsistencies between the population model and the other evidence become more difficult to resolve (in the sense of necessitating larger values of μ_C or μ_A, say) for a higher value of N_{1988}^{tot}, or for a smaller fraction of females in the catches. The results of the latter sensitivity test are also shown in Fig. 7 and serve to emphasise that it is the catch of *females* in particular that drives the model.

These tests suggest that the factors which are of most importance for further investigation involve the sex ratio of the catches and the accuracy of the 1988 census estimate (N_{1988}^{tot}) which the trajectories 'hit'. Improving estimates for M, t_m, t_r and MSYL is of much less consequence.

Table 12

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the age at first parturition t_m. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	t_m(yr) 5	8*	11	MSYR (%)	t_m(yr) 5	8*	11
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.88	-0.90	-0.91	0	0.49	0.49	0.48
1	0.04	0.05	0.05	1	0.41	0.40	0.39
2	0.77	0.80	0.82	2	0.30	*0.29*	*0.28*
3	*1.32*	*1.38*	*1.41*	3	*0.23*	*0.21*	*0.20*
4	*1.72*	*1.82*	*1.86*	4	*0.19*	*0.17*	*0.16*
5	*2.00*	*2.16*	*2.16*	5	*0.16*	*0.15*	*0.14*
6	*2.05*	*2.31*	*2.17*	6	*0.15*	*0.13*	*0.13*
8	-0.01	-0.02	0.07	8	0.95	0.93	0.98
10	-0.06	0.03	0.38	10	0.99	0.98	1.11

* Used for previous calculations.

Table 13

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the age at recruitment t_r. 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	t_r(yr) 3	5*	7	MSYR (%)	t_r(yr) 3	5*	7
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.89	-0.90	-0.90	0	0.49	0.49	0.48
1	0.14	0.05	-0.04	1	0.39	0.40	0.41
2	0.95	0.80	0.64	2	*0.27*	*0.29*	0.31
3	*1.54*	*1.38*	*1.18*	3	*0.19*	*0.21*	*0.24*
4	*1.90*	*1.82*	*1.60*	4	*0.15*	*0.17*	*0.19*
5	*1.91*	*2.16*	*1.97*	5	*0.14*	*0.15*	*0.16*
6	-0.00	*2.31*	*2.30*	6	*0.26*	*0.13*	*0.15*
8	0.00	-0.02	-0.22	8	1.03	0.93	0.56
10	0.00	0.03	-0.86	10	1.02	0.98	1.02

* Used for previous calculations.

Table 14

Sensitivity tests for the case $\mu_C = 2$ (for 1846-1900) and $\mu_A = 2$ (for 1600+) to variations in the value of the MSY level (MSYL). 'Slope' and 'N^{tot}' are as for Table 3.

MSYR (%)	MSYL 0.5	0.6*	0.7	MSYR (%)	MSYL 0.5	0.6*	0.7
(a) Slope				**(b) 1900 pop'n/1846 pop'n**			
0	-0.90	-0.90	-0.90	0	0.49	0.49	0.49
1	0.14	0.05	-0.05	1	0.37	0.40	0.42
2	0.84	0.80	0.70	2	*0.25*	*0.29*	0.31
3	*1.34*	*1.38*	*1.35*	3	*0.18*	*0.21*	*0.24*
4	*1.69*	*1.82*	*1.90*	4	*0.14*	*0.17*	*0.19*
5	*1.94*	*2.16*	*2.36*	5	*0.13*	*0.15*	*0.17*
6	*2.07*	*2.31*	0.07	6	*0.12*	*0.13*	0.40
8	*1.09*	-0.02	-0.18	8	*0.11*	0.93	0.98
10	-0.00	0.03	-0.24	10	0.97	0.98	0.77

* Used for previous calculations.

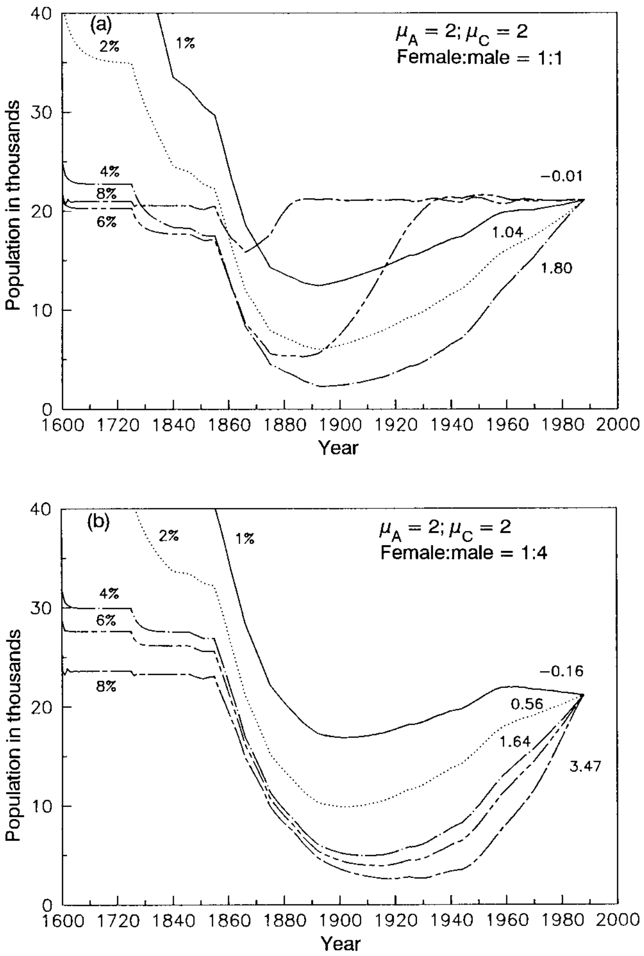


Fig. 7. Illustrations of the consequences of changing the female:male ratio from 2:1 as previously assumed for commercial catches for which this information is not available, for the case μ_C = 2.0 and μ_A = 2.0. Trajectories are shown for various MSYR values for female:male ratios of (a) 1:1 and (b) 4:1.

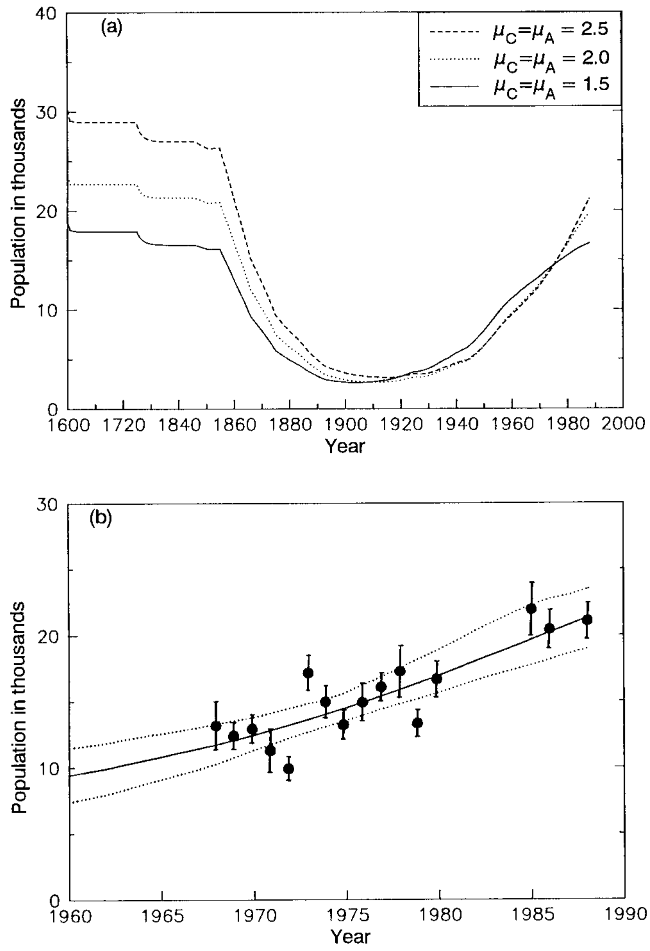


Fig. 8. In (a), population trajectories are shown for the model fitted to the census estimates up to 1987-88 for the cases (μ_C = 1.5; μ_A = 1.5), (μ_C = 2; μ_A = 2) and (μ_C = 2.5; μ_A = 2.5). Only the last of these cases is shown in (b), which reflects only the 1960-1988 period. There the estimated trajectory is shown by the solid line, and the bootstrap 95% CI about this by the dotted lines. Further, the absolute estimates from the censuses (Table 1) are shown by large dots, together with their 95% CIs (assumed to be ±2 SE). σ_2 = 0.012 for all the results shown.

Table 15

Results for fitting the population model to the census estimates as described in the text for various choices for μ_C and μ_A. The HITTER fit is constrained to pass through the 1988 census estimate of 21,113 exactly. The FITTER results are for the choice σ_2 = 0.012 unless otherwise indicated. Quantities in parentheses are CV estimates, evaluated using the bootstrap technique described in the text. 'Slope' and 'N^{tot}' are as for Table 3. $MSYR_{1+}$ is the MSY rate in terms of uniform selectivity harvesting on the 1+ population, rather than the 5+ population to which MSYR refers. N^f_{1988} refers to the number of females past the age at first parturition in that year and K^f is the corresponding number at unexploited equilibrium.

	$\mu_C = 1.5$; $\mu_A = 1.5$	$\mu_C = 2$; $\mu_A = 2$	$\mu_C = 2.5$; $\mu_A = 2.5$		
Quantity	FITTER	FITTER	HITTER	FITTER	FITTER; $\sigma_2 = 0.01$
$N^{tot}_{1600} = K$	18,825	23,584	29,637	29,729 (0.10)	29,726 (0.11)
N^{tot}_{1846}	16,514	21,294	26,681	26,725 (0.05)	26,723 (0.06)
N^{tot}_{1900}	2,655	2,910	3,501	3,517 (0.12)	3,515 (0.13)
N^{tot}_{1968}	12,843	11,884	11,382	10,658 (0.07)	11,496 (0.11)
N^{tot}_{1988}	16,657	19,715	21,113	21,347 (0.06)	21,238 (0.09)
b	1.314	1.317	1.318	1.318	1.310
Slope	1.32	2.58	3.14	3.11 (0.18)	3.12 (0.17)
$N^{tot}_{1900} / N^{tot}_{1846}$	0.16	0.14	0.13	0.13 (0.07)	0.13 (0.08)
N^{tot}_{1988} / K	0.88	0.84	0.71	0.72 (0.16)	0.71 (0.19)
N^f_{1988} / K^f	0.69	0.61	0.49	0.49 (0.16)	0.49 (0.23)
MSYR (%)	5.0	5.6	5.5	5.5 (0.21)	5.5 (0.26)
$MSYR_{1+}$ (%)	3.8	4.2	4.2	4.2 (0.19)	4.2 (0.22)

FITTER model applications

The results of ‘fitting’ the model to the census estimates of Table 1 are shown in Table 15 and Fig. 8a for three different combinations of values for μ_C and μ_A. Essentially all three trajectories pass close to the centroid of the series of absolute estimates in Table 1. However, the fits for the cases (μ_C = 1.5; μ_A = 1.5) and (μ_C = 2; μ_A = 2) are unable to achieve the observed population growth rate estimate of 3.2% over the 1968-1988 period, so that the corresponding population trajectories pass through lower total abundance estimates for 1988 than the 21,113 used above for HITTER evaluations. Clearly some model mis-specification remains for (μ_C = 1.5; μ_A = 1.5) and to a rather lesser extent for (μ_C = 2; μ_A = 2).

All three cases indicate a resource that is at present not far below its unexploited equilibrium level in terms of total numbers (N^{tot}_{1988}/K between 0.70 and 0.88). However, this ratio is somewhat less for the ‘mature’ female component of the population (N^{tot}_{1988}/K^f between 0.48 and 0.69). A resource of relatively high productivity is indicated, with MSYR in terms of the 5+ population in the vicinity of 5%, which corresponds to about 4% for uniform selectivity harvesting on the total (1+) population.

Because of the model mis-specification indicated for two of the cases considered, bootstrap variance estimation was carried out for the (μ_C = 2.5; μ_A = 2.5) scenario only. The results are shown as 95% CIs about estimated trajectories in Fig. 8b and as CVs in Table 15.

These results suggest that the data are able to provide reasonably precise estimates, with CVs for the various quantities listed in Table 15 ranging between about 5 and 20%. A concern, however, is that the results of Buckland and Breiwick (2002) in Table 1 suggest that the scaling factor *b* has been independently estimated with a coefficient of variation (σ_2) only slightly in excess of 1%. This is unrealistically precise (as confirmed by subsequent analyses (Buckland *et al.*, 1993)), so that the ‘fitting’ was repeated for a larger (and possibly more realistic) value: σ_2 = 0.1. The results for this exercise are also shown in Table 15, and suggest that the level of precision originally indicated is not markedly dependent on a small value for σ_2.

To test the reliability of the bootstrap procedure used for variance estimation, 95% CIs for MSYR were computed for this same case (μ_C = 2.5; μ_A = 2.5) by means of both the bootstrap and a likelihood ratio method (Mood *et al.*, 1974). The results are shown in Table 16 and are encouragingly similar, with the bootstrap intervals being slightly larger.

Naturally, these estimates of precision are conditioned on fixed values of μ_C and μ_A, and would increase if uncertainty in these values was also taken into account. A quantitative evaluation of the extent of this increase is beyond the scope of this paper. However, the point estimates of Table 15 for the variety of (μ_C; μ_A) combinations considered suggest that although CV estimates for historic population sizes would increase substantially given such an evaluation, the estimate of MSYR would remain reasonably robustly determined in the vicinity of 5% (in terms of the 5+ population).

The point estimate of $MSYR_{1+}$ (MSY rate in terms of uniform selectivity harvesting on the 1+ population) is 4.2%. In terms of the Pella-Tomlinson model used (see equation 1), this corresponds to a growth rate of some 6% per annum for the stock when at a very low level and protected. This is not incompatible with direct estimates of growth rate of other heavily depleted stocks; Best (1993) provides a list of these estimates which range from 5 to 14% per annum[4].

Table 16

Estimates of 95% CIs for the estimate of MSYR (in terms of the exploitable component of the population) obtained from the applications of FITTER for μ_C = 2.5 and μ_A = 2.5 whose results are reported in Table 15. Estimates obtained from both the bootstrap and likelihood ratio methods (see text) are shown for the two values of σ_2 considered in Table 15. MSYR values are expressed as percentage.

	MSYR: 95% CI	
	Bootstrap	Likelihood ratio
σ_2 = 0.012	[3.7; 8.1]	[3.7; 7.9]
σ_2 = 0.1	[3.7; 10.3]	[3.7; 8.1]

CONCLUSIONS

It is convenient to summarise the results of the HITTER analyses above for various possible adjustment factors, by reporting the lower limits necessary to achieve an average population increase rate from 1968-1988 of at least 2% per annum. The resultant bounds (where appropriate) are as follows.

(i) Depensation
Cannot alone account for inconsistencies.

(ii) Additional response time-lag
Model used produces unrealistic population oscillations.

(iii) Carrying capacity increase (1846-1988)
$\mu_K \geqslant 2.5$ (and MSYR $\geqslant$ 4%).

(iv) Underestimation of historic commercial catches (1846-1900)
$\mu_C \geqslant 2.5$ (and MSYR $\geqslant$ 5%), or MSYR $\geqslant$ 4% (and $\mu_C \geqslant$ 3.0).

(v) Underestimation of aboriginal catches
$\mu_A \geqslant 3$ (and MSYR $\geqslant$ 4%).

(vi) Combination of μ_C and μ_A
For μ_C = *2.0:*
$\mu_A \geqslant 2.0$ (and MSYR $\geqslant$ 5%)
$\mu_A \geqslant 2.5$ (and MSYR $\geqslant$ 4%).

Note that each one of these cases corresponds to a depletion of less than 23% of the 1846 population over the 1846-1900 period. In all the cases listed which have a μ_C adjustment factor, this depletion level is of 17% or less. These cases therefore all seem reasonably consistent with the commercial extinction of the resource at the turn of the 19th century.

IWC (1993) discussed problems associated with the estimates of historic commercial and aboriginal catches and the extent to which these might have been underestimated. Readers are invited to form their own judgements, based upon these comments, as to whether there is supportive evidence for adjustment factors as large as μ_C of about 2 and/or μ_A of about 2, which would resolve the inconsistencies between simple density-dependent response population models for the gray whale and other information such as the population growth rate deduced from censuses. However, consideration needs to be given to the assumptions of the HITTER analyses that N^{tot}_{1988} = 21,113, and that the female:male ratio of commercial catches in years for which this information is not available is 2:1. Inferences

[4] The choice of 5% for the lower end of this range excludes the estimate for Bering-Chukchi-Beaufort Seas bowhead whales from Best’s list, as the rate he quotes was for a period well after that during which this population was at a very low level.

concerning lower bounds for μ_C or μ_A to resolve inconsistencies are sensitive to these two assumptions. In contrast, such inferences are not particularly sensitive to the values chosen for the population model parameters M, t_m, t_r and MSYL, so that rather less attention need be given to the determination of appropriate values for these parameters.

Relatively 'high' MSYR values (typically 4% or more) are required to obtain recent population growth rates of 2% per year. [Note that an MSYR of 4% for the recruited (5+) component of the population corresponds to one of about 3% for uniform selectivity harvesting on the 1+ population.] Such 'high' values are not altogether surprising, given recent fishing mortalities of about 1% per year coupled with an annual growth rate of about 3%.

'Fitting' the population model to the census estimates gives rise to model mis-specification unless μ_C and/or μ_A are fairly large, because the model cannot otherwise reflect the 'high' observed growth rate. For (μ_C = 2.5; μ_A = 2.5), the estimates of historic population sizes are determined with quite high precision (CVs about 10%), while estimates of recent growth rate and MSYR are also reasonably precise (CVs about 20%). This estimated precision is, of course, conditional on fixed values for μ_C and μ_A, but results suggest that the MSYR estimate of some 5% (or 4% in terms of the 1+ population) is relatively robust to the uncertainty about these levels of underestimation.

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