CONCERNING DEMOGRAPHIC LIMITATIONS ON THE POPULATION GROWTH RATE OF WEST AUSTRALIAN (BREEDING STOCK D) HUMPBACK WHALES

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ABSTRACT

The upper bound of 0.126 on the maximum demographically possible annual population growth rate for humpback whales that is currently imposed on age-aggregated assessment models for this species, is based on an analysis that assumes steady age structure. It is conceivable that transient age-structure effects could admit greater population growth rates than suggested by such a bound for short periods. This possibility is addressed by developing an age-structured population model in which possible density dependent changes in pregnancy rate, age at first parturition and natural mortality are modeled explicitly, and allowance is made for the possibility of senescence. The model is applied to the case of the west Australian humpback whale population (breeding stock D), for which breeding ground surveys over the 1982-1994 period provide a point estimate of 0.10 for the annual population growth rate. Results based upon the breeding population surveys estimate of abundance of 10032 in 1999 suggest that 0.12 is the maximum feasible annual rate of increase for this stock over 1982-1994 if it is closed. This result is based on essentially the same parameter choices as led to the earlier r = 0.126 bound, *viz*. that in the limit of low population size the age at first parturition approaches 5 years from above, the annual pregnancy rate 0.5 from below, and the annual natural mortality rate 0.01 from above.

INTRODUCTION

Considerable debate has arisen over the extent to which the population growth rates suggested by time series of survey estimates of abundance for various South Hemisphere humpback whale populations are consistent with the bounds imposed by the species' demographics. More specifically, the current upper bound on the maximum per capita annual growth rate, r, of 0.126 imposed on age aggregated model assessments of these populations has been questioned as perhaps too high (IWC 2006).

The origin of this bound is calculations by Brandão *et al*. (2000) relating population growth rates to biological parameter values. Essentially the higher the pregnancy rate (shorter the calving interval), the greater the annual survival rate and the lower the age at first parturition, then the higher the growth rate that the population can attain. The value of 0.126 selected as a bound corresponds to the following choices regarded as "pushing the limits" for plausible values of biological parameters for humpback whales:

ρ (annual pregnancy rate) = 0.5
S (annual survival rate) = 0.99
a^{mat} (age at first parturition) = 5 yrs

However, the calculations of Brandão *et al*. (2000) are based upon the assumption of a steady age structure. It is conceivable that over short periods of time, transient effects could lead to the attainment of higher population growth rates than indicated by the results of that paper.

The purpose of this paper is to investigate this possibility for the specific case of the west Australian humpback population (breeding stock D). Results from five breeding ground surveys of this population over the period 1982-1994 (IWC 1996) suggest an annual increase rate (the slope parameter from a log-linear regression against year) of 0.10 (95% CI: 0.03-0.18). This paper explicitly models possible density dependent changes in various biological parameters to determine to what extent this estimate is consistent with the feasible behaviour of a closed population of humpback whales.

DATA

The historic catch data used for these analyses are as agreed at a recent Southern Hemisphere humpback whale workshop (IWC 2006). Two series are considered, the “Core” and the “Fringe” series, corresponding to different assumptions for the allocation of catches made in high latitude feeding areas among breeding stocks (Table 1).

METHODS

The age-structured population model used for these computations is described in detail in the Appendix. For simplicity, sexes are not distinguished. The selectivity ogive for past catches is taken throughout to be knife-edge at age $a_r = 5$ (see Table 2).

The model is “fit” to the data by adjusting the (initial) carrying capacity K so that the population’s trajectory hits a target total (1+) population of 10032 in the year 1999 as estimated from surveys of the breeding grounds (Paxton *et al*. 2006).

Initially the maximum possible pregnancy rate for the population (ρ_{max}) is taken to be 0.5, corresponding to a minimum possible calving interval of two years. This applies in the limit of very low population size (so that values observed would be less than this). For an illustrative reference case (see Table 3), pregnancy rate is assumed to be the only (linearly) density dependent demographic parameter, decreasing to $\rho_{min} = 0.1$ when the population is at carrying capacity. Other biological parameters for this reference case are taken to be fixed (density independent): age at first parturition $a^{mat} = 5$ years and an annual natural mortality rate $M = 0.03$.

Sensitivity to changes in these assumptions is then examined, first for single factors, and then for these factors in combination. Initially four factors are considered:

- Density dependence (linear) in the age at first parturition, first with $a_{\max}^{mat} = 10$.
- Lower values for natural mortality.
- Non-linear density dependence for ρ and a^{mat} reflected by the parameter μ (see Appendix equations A14 and A15); note that μ = 1 reflects linear dependence, and $\mu > 1$ means that density dependent effects do not come into play as rapidly when the population grows from a low level, so that high growth rates can be sustained through to larger population sizes.
- Density dependence (linear) is natural mortality (equation A16).

Not all combinations of parameter values are feasible. The condition of a steady population at carrying capacity *K* leads to restrictions on the value of natural mortality for the first year (M_o). Clearly M_o cannot be negative. The computations reported below insist further that always $M_o \geq M_1$ where M_1 is the natural mortality of age 1 humpbacks (which is identical to that of all older humpbacks for scenarios without age dependence in *M*) (see Appendix equations A11 and A12 with associated text).

The possibility of senescence is introduced by allowing *M* to increase at larger ages (equation A13). Potentially senescence could introduce temporary high growth rates if the population for a time includes an over-representation of younger animals as it recovers from heavy depletion.

Other factors investigated are alternative target population levels and a change in carrying capacity. The alternative levels are:

- 31750 for 2003 from JARPA surveys (Matsuoka *et al*. 2006); and
- 17959 for 1997 from the IDCR surveys (Branch 2006).

An increase in *K* over the period 1930 to 1960 is considered as a manifestation of possible competitive release (as regards utilisation of krill) arising from the major reduction of blue and fin whales over that period as a result of harvesting.

RESULTS AND DISCUSSION

Table 3 lists the specifications of the reference case and other models implemented for breeding stock D, together with shortened names for each for ease of reference.

Results are shown in Table 4 as annual rates of population growth for each model for three periods: the first five (1968-1972) and first ten (1968-1977) years after catching ceased, and the 1982-1994 period over which breeding area surveys suggest an annual rate of increase of 0.10.

Immediately evident from Table 4 is that there is very little difference between results for the Core and the Fringe catch allocation hypotheses. Hence the discussion that follows focuses on results for the Fringe case only.

For virtually all the models considered, the rate of population increase over the first ten years since catches ceased is greater than that over the first five years (the exceptions are for the higher JARPA and IDCR survey based target population sizes). The primary reason for this is likely the time lag associated with the impacts of a changed age at first parturition coming into play. In most cases increase rates over 1982-1994 are less than those over the first ten years since catches ceased. In cases where this is not so, the differences are marginal. Further discussion focuses on the 1982-1994 rates only.

The reference case reflects an annual population increase rate of 0.072 over 1982-1994. Density dependence in the age at first parturition (a^{mat} ranging from 5 to 10 years) and in the natural mortality M (ranging from 0.02 to 0.03 yr^{-1}) each separately increase this by about 0.01, as does non-linearity in the density dependence (μ changed from 1, corresponding to linear dependence, to 3). The fact that lowering M from 0.03 to 0.02 in the absence of density dependence leads to a *drop* in the increase rate may seem surprising; it arises from the fact that balancing births and deaths at carrying capacity given a lower M value requires an increase in M_o, which in turn reduces the rate at which the population can grow when reduced in abundance.

All of these changes together (model 3a) see the annual increase rate raised to 0.10 (which co-incidentally happens to be the point estimate from the observations). If the extent to which M can change with density is maximized subject to the constraint that $M_o > M$ (model 3b), the rate increases to 0.11. Finally if more extreme (but still plausible) ranges/values are used (a^{mat} : 5 to 12; μ = 5; M : 0.01 to 0.032 – model 3c), a rate of 0.12 can be realized. Figure 1 illustrates the population trajectories for a number of these cases.

If senescence is introduced (models 4ai and 4aii), the increase rate for the reference case is increased by about 0.02 (see Figure 2). However, senescence in combination with more extreme ranges for the other parameters (model 4d) can achieve only little extra increase in the growth rate, essentially because the $M_o > M_1$ constraint comes into play.

Constraining the maximum pregnancy rate to 0.5 has an influential effect. Were annual compared to biennial calvings sufficiently frequent to increase the average maximum pregnancy rate from 0.5 to 0.6 (model 5a), the population annual increase rate could approach 14%.

In most instances with higher target levels for recent abundance (from JARPA or IDCR surveys – models 6), the population shows a relatively low rate of increase over 1982 to 1994, essentially because it is estimated to be close to carrying capacity by the start of that period. However the fact that the populations are never reduced to a very low level under some such scenarios (see Figure 3) raises questions about their plausibility. This inconsistency can, however, be resolved if an increase in carrying capacity can be postulated (models 7). An increase of K of 50% sees annual increase rates back near 0.10 (Figure 3).

In summary

Unless the possibilities (in the limit of low population size) of an age at first parturition less than 5 years, or an average pregnancy rate above 0.5 can be entertained, it seems that 0.12 is about the maximum biologically feasible annual increase rate for a closed population of breeding stock D humpback whales over the 1982-1994 period.

ACKNOWLEDGEMENTS

Financial support for this work by the South African National Research Foundation is gratefully acknowledged.

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Table 1. Catch series for stock D humpback whales for the Core and Fringe catch allocation hypotheses (IWC 2006).

Year	Core	Fringe	Year	Core	Fringe	Year	Core	Fringe	Year	Core	Fringe
1900	0	0	**1927**	996	996	**1954**	1340	1347	**1981**	0	0
1901	0	0	**1928**	1035	1046	**1955**	1562	2702	**1982**	0	0
1902	0	0	**1929**	0	11	**1956**	1119	1122	**1983**	0	0
1903	0	0	**1930**	20	35	**1957**	2608	3031	**1984**	0	0
1904	0	0	**1931**	52	161	**1958**	2833	5538	**1985**	0	0
1905	0	0	**1932**	79	86	**1959**	808	1010	**1986**	0	0
1906	0	0	**1933**	500	620	**1960**	676.8	1285	**1987**	0	0
1907	0	0	**1934**	1230	1351	**1961**	758	958	**1988**	0	0
1908	0	217	**1935**	940	950	**1962**	1605.2	2328.2	**1989**	0	0
1909	0	118	**1936**	4428	4511	**1963**	308.4	466	**1990**	0	0
1910	0	83	**1937**	3712	4119	**1964**	38.8	96	**1991**	0	0
1911	0	0	**1938**	1090	1776	**1965**	137	178.8	**1992**	0	0
1912	234	234	**1939**	0	0	**1966**	95	177	**1993**	0	0
1913	993	993	**1940**	0	342	**1967**	57	110	**1994**	0	0
1914	1968	1968	**1941**	0	0	**1968**	0	0	**1995**	0	0
1915	1297	1297	**1942**	0	0	**1969**	0	0	**1996**	0	0
1916	388	388	**1943**	0	0	**1970**	0	0	**1997**	0	0
1917	0	0	**1944**	0	0	**1971**	0	0	**1998**	0	0
1918	0	0	**1945**	0	0	**1972**	0	0	**1999**	0	0
1919	0	0	**1946**	0	0	**1973**	0	0	**2000**	0	0
1920	0	0	**1947**	2	3	**1974**	0	0	**2001**	0	0
1921	0	0	**1948**	4	4	**1975**	0	0	**2002**	0	0
1922	155	155	**1949**	754	974	**1976**	0	0	**2003**	0	0
1923	166	166	**1950**	1338	1503	**1977**	0	0	**2004**	0	0
1924	0	0	**1951**	1492	2356	**1978**	0	0	**2005**	0	0
1925	669	669	**1952**	1377	1380	**1979**	0	0	**2006**	0	0
1926	735	735	**1953**	1559	1561	**1980**	0	0			

Table 2. Fixed parameters in the model for the Reference case and variants 2a–4d (see text).

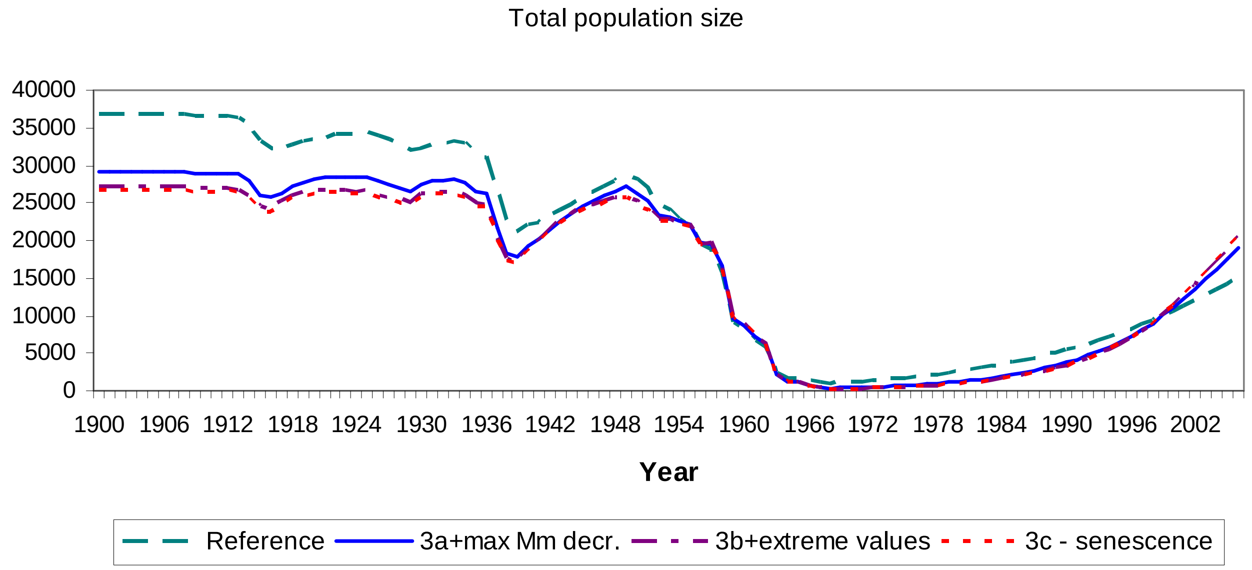
Parameter	Value
a_r	5 yrs
target year (y)	1999
target value (N_y^T)	10 032
ρ_{max}	0.5

Table 3. Description of model variants and how they are referenced in the paper. The model indicated in brackets refers to the model of which the model under consideration is a variant; under description, what has been changed in the model under consideration is shown in bold. See the Appendix for detailed definitions of the symbols.

Model	Name	Description
1	Reference case	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03
2a (ref)	$a^{mat}_{\max}$ = 10	$a^{mat}_{\max}$ **= 10**; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03
2b (ref)	M_m = 0.02	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m = M^{max}_m = **0.02**
2c (ref)	μ = 3	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; $\boldsymbol{\mu}$ **= 3**; M^{min}_m **=** M^{max}_m = 0.03
2d (ref)	M_m: 0.03 → 0.02	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **= 0.02**; M^{max}_m **= 0.03**
3a (ref)	All changes	$a^{mat}_{\max}$ **= 10**; ρ_{min} = 0.1; $\boldsymbol{\mu}$ **= 3**; M^{min}_m **= 0.02**; M^{max}_m **= 0.03**
3b (3a)	3a + max M_m decr.	$a^{mat}_{\max}$ = 10; ρ_{min} = 0.1; μ = 3; M^{min}_m = 0.02; M^{max}_m **= 0.034**
3c (3b)	3b + extreme values	$a^{mat}_{\max}$ **= 12**; ρ_{min} = 0.1; $\boldsymbol{\mu}$ **= 5**; M^{min}_m **= 0.01**; M^{max}_m **= 0.032**
4ai (ref)	Ref – senescence	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03; $\boldsymbol{M_h - M_m}$ **= 0.05**; $\boldsymbol{a_2}$ **= 30;** $\boldsymbol{a_3}$ **= 40**
4aii (ref)	Ref – max senescence	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03; $\boldsymbol{M_h - M_m}$ **= 0.05**; $\boldsymbol{a_2}$ **= 23;** $\boldsymbol{a_3}$ **= 33**
4bi (3a)	3a – senescence	$a^{mat}_{\max}$ = 10; ρ_{min} = 0.1; μ = 3; M^{min}_m = 0.02; M^{max}_m = 0.03; $\boldsymbol{M_h - M_m}$ **= 0.02**; $\boldsymbol{a_2}$ **= 30**; $\boldsymbol{a_3}$ **= 40**
4bii (3a)	3a – max senescence	$a^{mat}_{\max}$ = 10; ρ_{min} = 0.1; μ = 3; M^{min}_m = 0.02; M^{max}_m = 0.03; $M_h - M_m$ = 0.02; $\boldsymbol{a_2}$ **= 29**; $\boldsymbol{a_3}$ **= 39**
4c (3b)	3b – senescence	$a^{mat}_{\max}$ = 10; ρ_{min} = 0.1; μ = 3; M^{min}_m = 0.02; M^{max}_m **= 0.0302**; $\boldsymbol{M_h - M_m}$ **= 0.02**; $\boldsymbol{a_2}$ **= 30;** $\boldsymbol{a_3}$ **= 40**
4d (3c)	3c – senescence	$a^{mat}_{\max}$ **=** 12; ρ_{min} = 0.1; μ = 5; M^{min}_m = 0.01; M^{max}_m **= 0.028**; $\boldsymbol{M_h - M_m}$ **= 0.02**; $\boldsymbol{a_2}$ **= 30**; $\boldsymbol{a_3}$ **= 40**
5a (3c)	3c + preg = 0.6	$a^{mat}_{\max}$ = 12; ρ_{min} = 0.1; μ = 5; M^{min}_m = 0.01**;** M^{max}_m = 0.032; $\boldsymbol{\rho_{max}}$ **= 0.6**
6ai	Ref – 17 959 target	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03; N^T_{1997} **= 17 959**
6aii	Ref – 31 750 target	$a^{mat}_{\max}$ = 5; ρ_{min} = 0.1; μ = 1; M^{min}_m **=** M^{max}_m = 0.03; N^T_{2003} **= 31 750**
6bi	3a – 17 959 target	$a^{mat}_{\max}$ **=** 10; ρ_{min} = 0.1; μ = 3; M^{min}_m **=** 0.02; M^{max}_m **=** 0.03; N^T_{1997} **= 17 959**
6bii	3a – 31 750 target	$a^{mat}_{\max}$ **=** 10; ρ_{min} = 0.1; μ = 3; M^{min}_m **=** 0.02; M^{max}_m **=** 0.03; N^T_{2003} **= 31 750**
7bi	6bi + K^* = 1.5K	$a^{mat}_{\max}$ **=** 10; ρ_{min} = 0.1; μ = 3; M^{min}_m **=** 0.02; M^{max}_m **=** 0.03; N^T_{1997} **= 17 959**; $\boldsymbol{K^*}$ **= 1.5*K***
7bii	6bii + K^* = 1.5K	$a^{mat}_{\max}$ **=** 10; ρ_{min} = 0.1; μ = 3; M^{min}_m **=** 0.02; M^{max}_m **=** 0.03; N^T_{2003} **=** 31 750; $\boldsymbol{K^*}$ **= 1.5*K***

Table 4. Annual rates of increase for the model variants considered. The periods considered are the first five and ten years after catches dropped to zero, and then the 1982–1994 period over which a relative abundance index is available for the breeding grounds which indicates an annual increase rate of 0.101 (95% CI: (0.028; 0.175)).

Model	**Name**	**Core**			**Fringe**		
		68-72	**68-77**	**82-94**	**68-72**	**68-77**	**82-94**
1	**Reference case**	0.077	0.077	0.070	0.076	0.077	0.072
2a (ref)	$a_{\max}^{mat}$ **= 10**	0.088	0.087	0.075	0.087	0.088	0.080
2b (ref)	M_m **= 0.02**	0.063	0.063	0.057	0.063	0.063	0.059
2c (ref)	μ **= 3**	0.079	0.080	0.080	0.078	0.080	0.080
2d (ref)	M_m**: 0.03 → 0.02**	0.086	0.086	0.078	0.085	0.087	0.081
3a (ref)	**All changes**	0.099	0.101	0.100	0.095	0.100	0.101
3b (3a)	**3a + max** M_m **decr.**	0.107	0.111	0.111	0.101	0.110	0.112
3c (3b)	**3b + extreme values**	0.114	0.120	0.120	0.107	0.118	0.120
4ai (ref)	**Ref – senescence**	0.094	0.095	0.087	0.091	0.094	0.090
4aii (ref)	**Ref – max senescence**	0.099	0.101	0.093	0.095	0.100	0.096
4bi (3a)	**3a – senescence**	0.108	0.112	0.112	0.101	0.111	0.113
4bii (3a)	**3a – max senescence**	0.108	0.113	0.113	0.102	0.111	0.113
4c (3b)	**3b – senescence**	0.108	0.113	0.113	0.102	0.111	0.113
4d (3c)	**3c – senescence**	0.115	0.121	0.122	0.107	0.119	0.122
5a (3c)	**3c + preg = 0.6**	0.121	0.134	0.136	0.109	0.130	0.136
6ai	**Ref – 17959 target**				0.069	0.067	0.046
6aii	**Ref – 31750 target**				0.075	0.074	0.062
6bi	**3a – 17959 target**				0.099	0.101	0.096
6bii	**3a – 31750target**				0.092	0.084	0.012
7bi	**6bi +** K^* **= 1.5**K				0.099	0.101	0.099
7bii	**6bii +** K^* **= 1.5**K				0.100	0.101	0.097



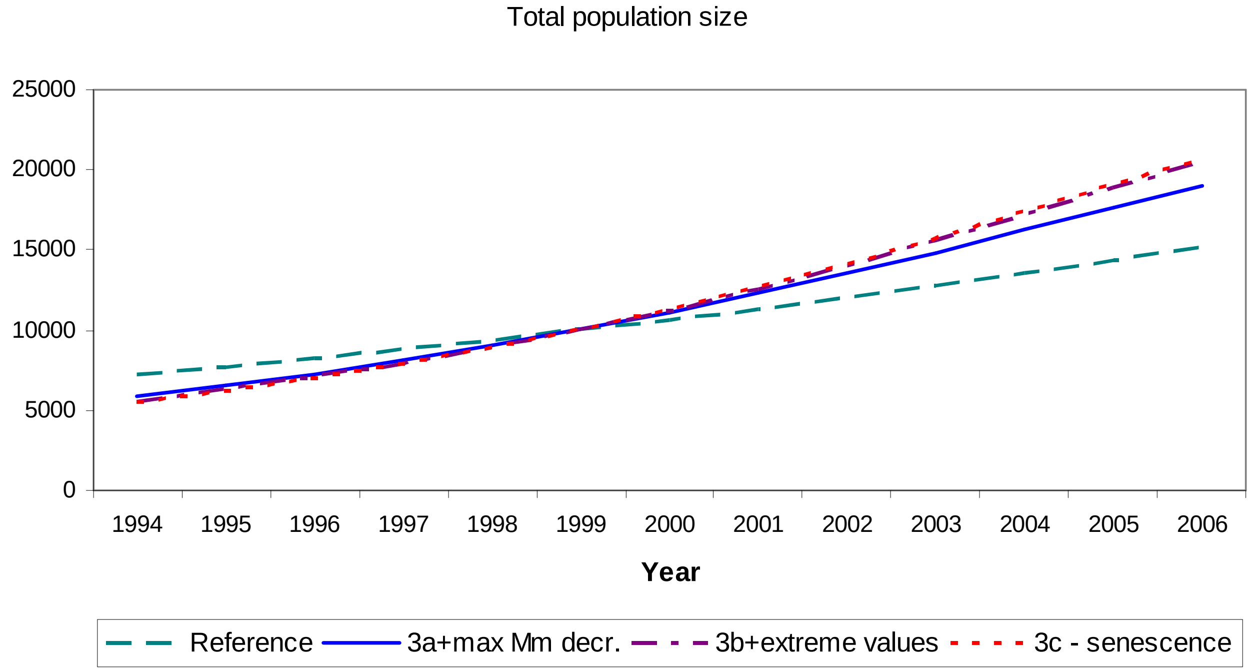
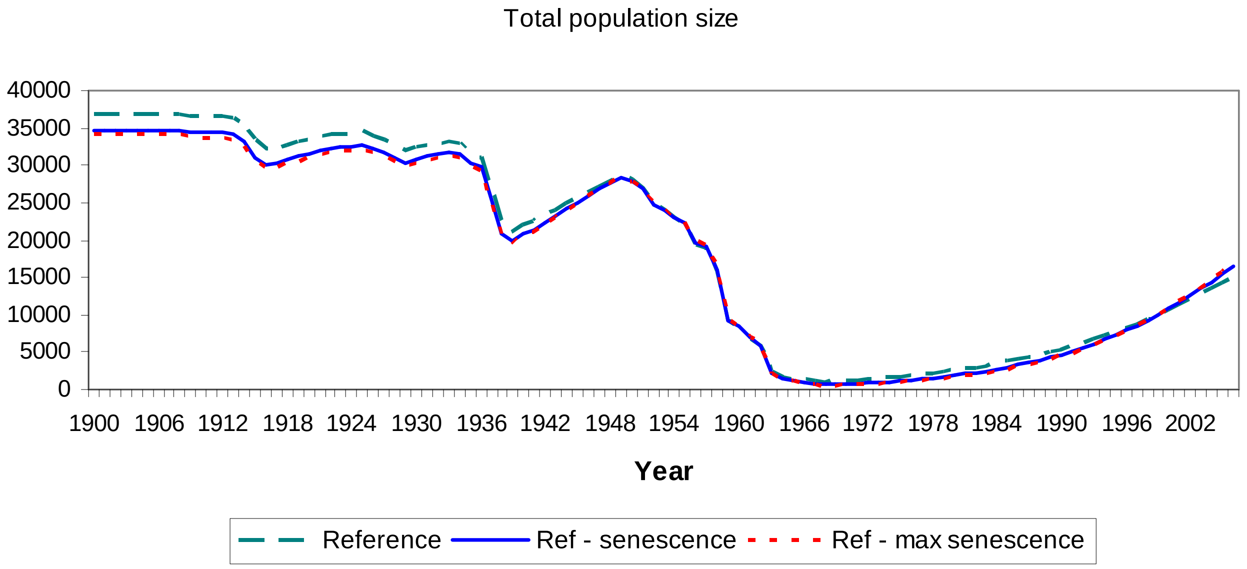


Figure 1. Comparison of population trajectories for stock D humpback whales for the reference case model, and variants of this model in which all the parameters are changed. Trajectories for the whole period (top) and for the 1994–2006 period (bottom) are shown.



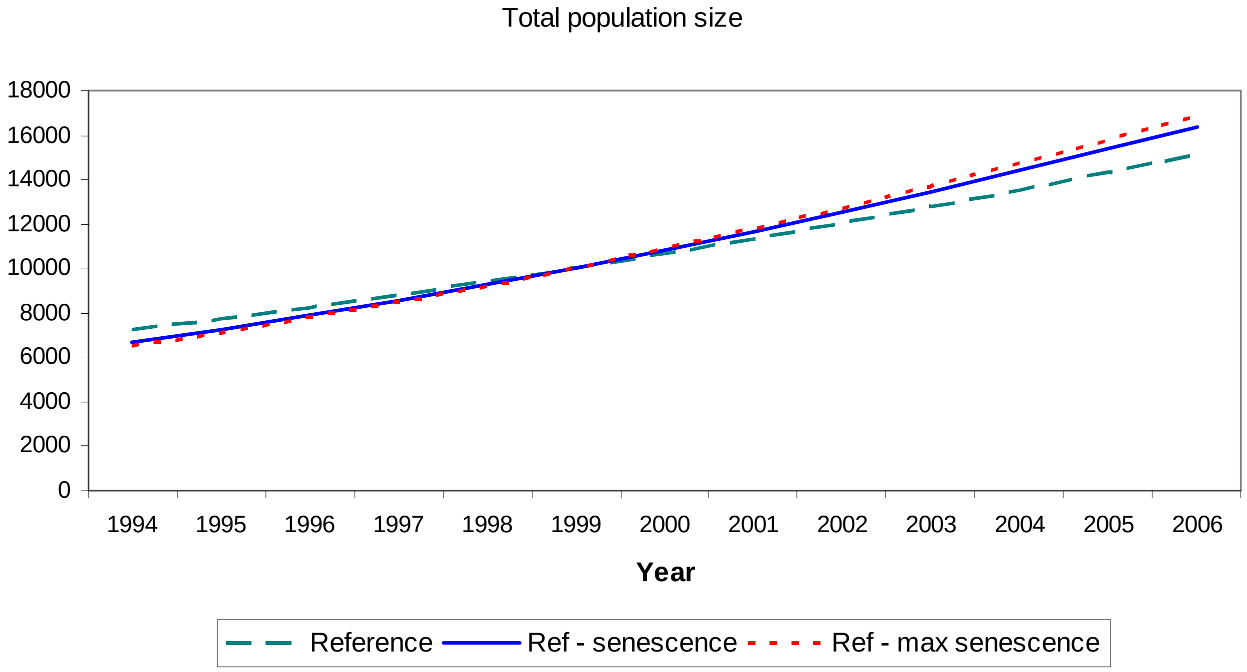


Figure 2. Comparison of population trajectories for stock D humpback whales for the reference case model, and variants of this model which allow for various degrees of senescence. Trajectories for the whole period (top) and for the 1994–2006 period (bottom) are shown.

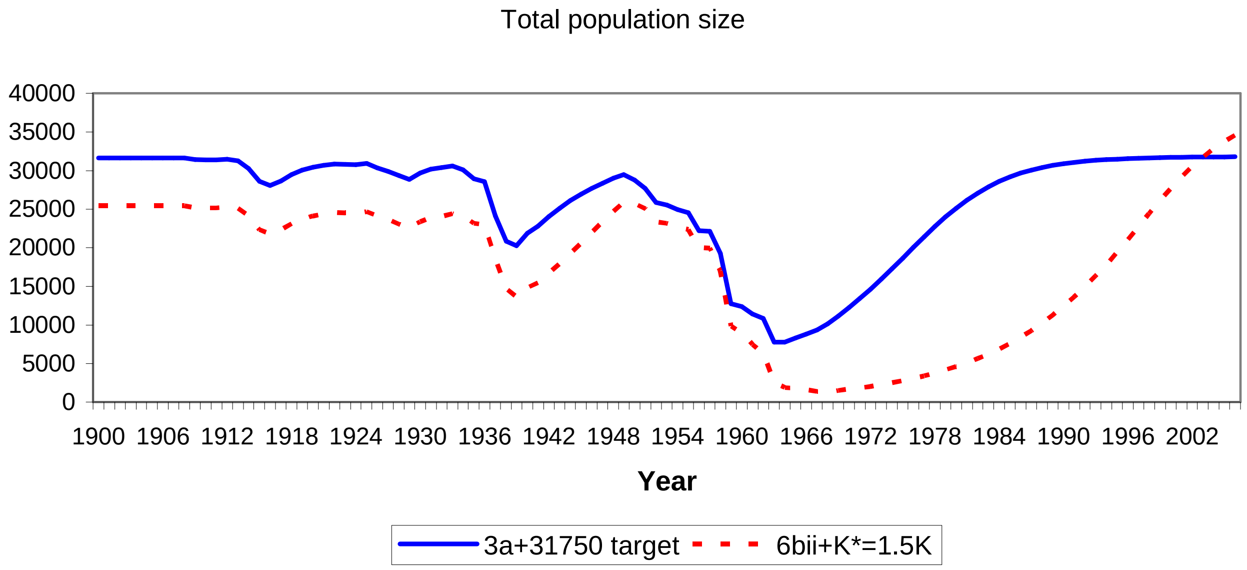


Figure 3. Comparison of population trajectories for stock D humpback whales for the “3a” variant of the reference case model with a target population of 31750 in 2003, and for this model with the inclusion of a 50% increase in carrying capacity from 1930 to 1960.

Appendix

Details of the Age-Structured Population Model

Population dynamics

$$N_{y+1,1} = 0.5\rho\left(N_y^T\right)e^{-M_0}N_y^m \qquad y \geq 0 \tag{A1}$$

$$N_{y+1,a+1} = (N_{y,a} - C_{y,a})e^{-M_a} \qquad 1 \leq a \leq 99 \tag{A2}$$

where:

$N_{y,a}$ is the number of humpback whales of age *a* in year *y*,

$C_{y,a}$ is the number of humpback whales of age *a* caught in year *y*,

M_a is the natural mortality rate at age *a*,

N_y^T is total population in year *y* (defined to be one year old and older humpback whales) given by:

$$N_y^T = \sum_{a=1}^{100} N_{y,a} \ ,$$

N_y^m is the mature population of humpback whales in year *y* given by:

$$N_y^m = \sum_{a=1}^{100} N_{y,a}\gamma_a \ ,$$

where:

γ_a is the fraction of humpback whales of age a that are mature, given by:

$$\gamma_a = \begin{cases} 0 & a < \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right) \\ a^{mat}\left(N_y^T\right) - a & a = \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right), \\ 1 & a > \mathrm{int}\left(a^{mat}\left(N_y^T\right)\right) \end{cases} \tag{A3}$$

where:

$a^{mat}\left(N_y^T\right)$ is the age at first parturition, as a function of the total population size, given by:

$$a^{mat}\left(N_y^T\right) = \left(a_{\max}^{mat} - a_{\min}^{mat}\right)N_y^T \big/ K_y + a_{\min}^{mat} \ , \tag{A4}$$

where:

$a_{\max}^{mat}$ is the maximum age at first parturition,

$a_{\min}^{mat}$ is the minimum age at first parturition, and

K_y is the carrying capacity, which can change over the years as:

$$K_y = \begin{cases} K & 1900 \le y < 1930 \\ \delta + \theta y & 1930 \le a \le 1960 \\ K^* & 1960 < a \le 2006 \end{cases}, \qquad \text{(A5)}$$

where:

δ and θ are the intercept and slope parameters respectively that provide a linear transition in the unexploited population size from K in 1930 to K^* in 1960, and

$\rho(N_y^T)$ is the pregnancy rate, which depends on the total population size, and given by:

$$\rho(N_y^T) = \rho_{max} - (\rho_{max} - \rho_{min}) N_y^T / K_y , \qquad \text{(A6)}$$

where:

ρ_{min} is the minimum pregnancy rate, and

ρ_{max} is the maximum pregnancy rate.

Note that it is assumed that all humpback whales die on reaching the age of 100.

The number of whales of age a caught in year y is given by:

$$C_{y,a} = C_y \frac{N_{y,a}}{\sum_{a'=a_r}^{99} N_{y,a'}} \qquad \text{(A7)}$$

where:

a_r is the age at first capture, and

C_y is the catch in year y.

The initial numbers at each age a are taken to follow an unexploited equilibrium distribution evaluated as follows:

$$N_{0,a} = \lambda N_a^* \quad \text{for a = 1, …, 100,} \qquad \text{(A8)}$$

where:

$$\lambda = \frac{K}{\sum_{a=1}^{100} N_a^*} , \qquad \text{(A9)}$$

$$N_1^* = 1, \quad N_2^* = N_1^* e^{-M_1}, \quad N_3^* = N_2^* e^{-M_2}, \quad etc., \text{ and} \tag{A10}$$

K is the (initial) carrying capacity.

Natural mortality

The natural mortality for the first year of life (M_0) is calculated iteratively to ensure that the number of births (that reach age one) each year balances the number of deaths (of humpback whales of age one and above) per year when the population is unexploited (i.e. when $N_0^T = K$). In this instance the number of births is given by (taking $a_{\max}^{mat}$ here to be integral):

$$0.5\rho_{min} e^{-M_0} \sum_{a=a_{\max}^{mat}}^{100} N_a^*, \tag{A11}$$

and the number of deaths is given by:

$$\sum_{a=1}^{99} N_a^* \left(1 - e^{-M_a}\right) + N_{100}^*. \tag{A12}$$

The natural mortality for the first year of life (M_0) is constrained to be greater than the natural mortality of one year olds (M_1).

To allow for the possibility of senescence, the natural mortality at age is modelled by:

$$M_a = \begin{cases} M_m & 1 \le a < a_2 \\ \alpha + \beta a & a_2 \le a \le a_3 \\ M_h & a_3 < a \le 100 \end{cases}, \tag{A13}$$

where:

M_m is the lowest value for natural mortality,

M_h is the highest value for natural mortality, and

α and β are the intercept and slope parameters respectively that provide a linear transition from M_m at age a_2 to M_h at age a_3.

When the value for M_h is set the same as that for M_m, natural mortality is independent of age.

Alternative forms of density dependence

Alternative formulations are considered to allow for density dependence in the calculation of age at first parturition ($a^{mat}\left(N_y^T\right)$), the pregnancy rate ($\rho\left(N_y^T\right)$) and the natural mortality M_a. Equation (A4) is changed to:

$$a^{mat}\left(N_y^T\right) = \left(a_{\max}^{mat} - a_{\min}^{mat}\right)\left(\frac{N_y^T}{K_y}\right)^{\mu} + a_{\min}^{mat}, \tag{A14}$$

equation (A1.6) is changed to:

$$\rho\left(N_y^T\right) = \rho_{max} - \left(\rho_{max} - \rho_{min}\right)\left({N_y^T}\big/{K_y}\right)^{\mu} \text{, and} \qquad \text{(A15)}$$

the lowest value for natural mortality (M_m) is changed to:

$$M_m = M_m^{\min} + \left(M_m^{\max} - M_m^{\min}\right){N_y^T}\big/{K_y} \, . \qquad \text{(A16)}$$