Appendix 8

MAXIMUM POSSIBLE HUMPBACK WHALE INCREASE RATES AS A FUNCTION OF BIOLOGICAL PARAMETER VALUES

A. Brandão, D.S. Butterworth and M.R. Brown
MARAM (Marine Resource Assessment and Management Group), Dept. of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa

Abstract
Maximum possible rates of increase of humpback whales are calculated over ranges of values of biological parameters: the post-first-year annual survival rate, the age at first parturition and the annual pregnancy rate. To simplify the analysis, baseline computations set the proportion of births that are female equal to that of males, and it is assumed that equalising first-year and post-first-year survival rates provides upper bounds on possible population growth rates. Sensitivity tests are carried out for these two assumptions. The results show that population growth rates exceeding 10% (yr^{-1}) can be obtained given a two-year calving interval, provided survival rates are high (0.96 at least) and the age at first parturition low (no greater than 8 yrs).

Introduction

The differences (real or apparent) in rates of population growth of Northern and Southern Hemisphere humpback whales have recently been under consideration. In this paper maximum possible humpback whale increase rates are calculated as a function of biological parameter values. The pertinent biological parameters are the annual post-first-year survival rate, the age at first parturition, the annual pregnancy rate, the proportion of births that are female and the juvenile (first year of life) survival rate.

Methods

Leslie matrix theory applied to the mature female component of a population can readily be used to show that after transient effects have died out and the age composition of the population has steadied, the growth of the population (in the absence of reproductive senescence) becomes exponential at a rate given by:

$$e^{t_m\delta} = e^{(t_m-1)\delta}S + pq_f S_j S^{t_m-1} \qquad (1)$$

where:
t_m = age at first parturition (yr);
δ = instantaneous growth rate (yr^{-1}) (i.e. corresponding to the slope parameter of a regression of the logarithm of population size against time);
S = annual survival rate (assumed constant for ages 1 and above);
p = annual pregnancy rate;
q_f = proportion of births that are female;
S_j = juvenile survival rate (for the first year of life).

Using this equation, rates of increase can be calculated as functions of biological parameter values, i.e. Equation (1) can be solved for the parameter δ given values of the other parameters. In the light of feedback received from the Scientific Committee's Intersessional Working Group on this subject, the range of biological parameter values investigated is:

S = (0.91, 0.99);
p = (0.3, 0.5);
t_m = (4, 11).

For the purposes of simplification, the baseline computations performed assume that the proportion of births that are female is equal to 0.5. Furthermore, it is customary to assume that $S_j \leq S$, because if the mother dies during a calf's first year of life, the calf will likely die also. Hence, by setting $S_j = S$ for computations, *maximum* possible population growth rates are provided.

Sensitivity tests are carried out to test the effect that these two specifications have on the calculations of δ. To test the sensitivity of the specification for the juvenile survival rate, rates of population increase are also calculated assuming that juvenile survival rate is 3% less than that of the older animals. Sensitivity to the value of q_f is examined by assuming that the proportion of births that are female is 0.4.

Results and discussion

Tables 1a-c give the results for the maximum possible rate of increase of humpback whale populations as a function of biological parameter values. Results are shown for various values of the age at first parturition and post-first-year survival rate. The different sub-tables give results for values of annual pregnancy rates of 0.3, 0.4 and 0.5 respectively. From these three sub-tables, given a pregnancy rate, the maximum possible rate of increase of humpback whales can be determined for a given age at first parturition and a given post-first-year survival rate. To aid the reader, growth rates in excess of 10% (yr^{-1}) in these tables are shown in bold.

Tables 2a-c show the maximum population rates of increase under the sensitivity tests described above. Table 2a duplicates Table 1b to allow for easy comparison. A decrease in the proportion of females at birth (q_f) from 0.5 to 0.4 leads to decreases in the maximum possible population growth rate of up to 2% (yr^{-1}). By comparison, the effect of the 3% decrease in the juvenile survival rate is negligible.

Much of the discussion concerning differing growth rates reported for Northern and Southern Hemisphere humpback whales has centred on whether estimated rates for the latter as high as 10% are biologically feasible. Table 1c shows that they are (given a two-year calving interval cycle), provided either or both the post-first-year survival rate is sufficiently high and the age at first parturition is sufficiently low.

Appendix 8 [Tables on next page]

Table 1

Maximum growth rates (δ in yr^{-1}) for humpback whales as a function of biological parameter values. Juvenile (first year) survival rate is assumed to be equal to post-first-year survival rate to provide maximum possible values of δ, and the proportion of births that are female is assumed to be 0.5. Results of 10% or greater are shown in bold.

	Age at first parturition (years)							
Survival rate	4	5	6	7	8	9	10	11
(a) Annual pregnancy rate = 0.3								
0.99	0.094	0.087	0.081	0.076	0.071	0.068	0.064	0.061
0.98	0.084	0.077	0.071	0.066	0.061	0.057	0.054	0.051
0.97	0.074	0.066	0.060	0.055	0.051	0.047	0.044	0.041
0.96	0.063	0.056	0.050	0.045	0.041	0.037	0.033	0.03
0.95	0.053	0.046	0.040	0.035	0.030	0.026	0.023	0.02
0.94	0.042	0.035	0.029	0.024	0.020	0.016	0.012	0.009
0.93	0.032	0.024	0.018	0.013	0.009	0.005	0.002	-0.001
0.92	0.021	0.014	0.008	0.002	-0.002	-0.006	-0.009	-0.012
0.91	0.010	0.003	-0.003	-0.008	-0.013	-0.017	-0.020	-0.023
(b) Annual pregnancy rate = 0.4								
0.99	**0.118**	**0.108**	0.099	0.093	0.087	0.082	0.077	0.073
0.98	**0.108**	0.097	0.089	0.082	0.077	0.071	0.067	0.063
0.97	0.097	0.087	0.079	0.072	0.066	0.061	0.057	0.053
0.96	0.087	0.077	0.069	0.062	0.056	0.051	0.046	0.043
0.95	0.076	0.066	0.058	0.051	0.045	0.040	0.036	0.032
0.94	0.066	0.056	0.048	0.041	0.035	0.030	0.025	0.021
0.93	0.055	0.045	0.037	0.030	0.024	0.019	0.015	0.011
0.92	0.044	0.034	0.026	0.019	0.013	0.008	0.004	0.000
0.91	0.033	0.023	0.015	0.008	0.002	-0.003	-0.007	-0.011
(c) Annual pregnancy rate = 0.5								
0.99	**0.138**	**0.126**	**0.115**	**0.107**	**0.100**	0.094	0.088	0.084
0.98	**0.128**	**0.115**	**0.105**	0.097	0.090	0.083	0.078	0.073
0.97	**0.118**	**0.105**	0.095	0.086	0.079	0.073	0.068	0.063
0.96	**0.108**	0.095	0.085	0.076	0.069	0.063	0.057	0.053
0.95	0.097	0.084	0.074	0.066	0.058	0.052	0.047	0.042
0.94	0.087	0.074	0.063	0.055	0.048	0.042	0.036	0.032
0.93	0.076	0.063	0.053	0.044	0.037	0.031	0.026	0.021
0.92	0.065	0.052	0.042	0.033	0.026	0.020	0.015	0.010
0.91	0.054	0.041	0.031	0.023	0.015	0.009	0.004	-0.001

Table 2

Sensitivity tests of effect of changes in the proportion of births that are female (q_f) and juvenile survival rate (S_j) on growth rate (δ in yr^{-1}) of humpback whales, as a function of other biological parameter values for an annual pregnancy rate of 0.4.

	Age at first parturition (years)							
Survival rate	4	5	6	7	8	9	10	11
(a) Annual pregnancy rate = 0.4, q_f = 0.5 and S_j = S (i.e. as for Table 1b)								
0.99	0.118	0.108	0.099	0.093	0.087	0.082	0.077	0.073
0.98	0.108	0.097	0.089	0.082	0.077	0.071	0.067	0.063
0.97	0.097	0.087	0.079	0.072	0.066	0.061	0.057	0.053
0.96	0.087	0.077	0.069	0.062	0.056	0.051	0.046	0.043
0.95	0.076	0.066	0.058	0.051	0.045	0.040	0.036	0.032
0.94	0.066	0.056	0.048	0.041	0.035	0.030	0.025	0.021
0.93	0.055	0.045	0.037	0.030	0.024	0.019	0.015	0.011
0.92	0.044	0.034	0.026	0.019	0.013	0.008	0.004	0.000
0.91	0.033	0.023	0.015	0.008	0.002	-0.003	-0.007	-0.011
(b) Annual pregnancy rate = 0.4, q_f = 0.4 and S_j = S (i.e. lower q_f compared with Table 2a)								
0.99	0.099	0.091	0.085	0.079	0.075	0.071	0.067	0.064
0.98	0.089	0.081	0.075	0.069	0.065	0.060	0.057	0.054
0.97	0.079	0.071	0.064	0.059	0.054	0.050	0.047	0.043
0.96	0.068	0.061	0.054	0.049	0.044	0.040	0.036	0.033
0.95	0.058	0.050	0.044	0.038	0.033	0.029	0.026	0.022
0.94	0.047	0.039	0.033	0.028	0.023	0.019	0.015	0.012
0.93	0.037	0.029	0.022	0.017	0.012	0.008	0.004	0.001
0.92	0.026	0.018	0.012	0.006	0.001	-0.003	-0.006	-0.010
0.91	0.015	0.007	0.001	-0.005	-0.010	-0.014	-0.017	-0.021
(c) Annual pregnancy rate = 0.4, q_f = 0.5 and S_j = S –0.03 (i.e. lower S_j compared with Table 2a)								
0.99	0.115	0.105	0.097	0.091	0.085	0.080	0.076	0.072
0.98	0.105	0.095	0.087	0.081	0.075	0.070	0.066	0.062
0.97	0.095	0.085	0.077	0.070	0.065	0.060	0.055	0.051
0.96	0.084	0.074	0.066	0.060	0.054	0.049	0.045	0.041
0.95	0.074	0.064	0.056	0.049	0.044	0.039	0.034	0.031
0.94	0.063	0.053	0.045	0.039	0.033	0.028	0.024	0.020
0.93	0.052	0.043	0.035	0.028	0.022	0.017	0.013	0.009
0.92	0.042	0.032	0.024	0.017	0.012	0.007	0.002	-0.002
0.91	0.031	0.021	0.013	0.006	0.001	-0.004	-0.009	-0.012