A NOTE ON POSSIBLE CHANGES IN SOME DEMOGRAPHIC PARAMETERS FOR SOUTHERN RIGHT WHALES OFF SOUTH AFRICA

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ABSTRACT

The possibility of changes in demographic parameters for right whales off South Africa is examined through analysis of resightings data for females with calves over the 1979–2006 period. No statistically significant change in either adult survival rate or population growth rate is detected. However the mean calving interval shows a decrease from 3.2 to 3.1 years somewhere between 1985 and 1990.

INTRODUCTION

In Brandão *et al*. (2010) a simple approach was applied to investigate whether resightings of female right whales with calves on annual aerial surveys off South Africa provide any evidence for a change in calving interval over the period from 1979 to 2006 for which data are now available. This paper extends the results reported in Brandão *et al*. (2010) by investigating two further cases; a possible change in the annual survival rate of females, and a possible change in the annual instantaneous growth rate. For completeness, the results previously reported in Brandão *et al*. (2010) are reproduced in this paper.

Updated data, including some corrections to the data from 1979 to 2003 that were considered in previous reports (Best *et al*., 2001, 2005), are shown in Table 1. The methodology applied is that of Cooke *et al*. (1993) and Payne *et al*. (1990), and is set out in the Appendix.

METHODS AND RESULTS

Change in the probability distribution of calving intervals

Two possible parameterisations of a change in calving interval probabilities are considered, as reflected in Equations (9) and (10) of that Appendix.

The results obtained are shown in Tables 2 and 3, which first reflect the small impact of three further years data on estimates of unchanging calving interval probabilities. The estimation of the additional parameters required to estimate a change in the calving interval frequencies is statistically justified in terms of AIC. For either model considered, there is an indication that a decrease in the mean calving interval from 3.2 to 3.1 years occurred somewhere between about 1985 and 1990. This corresponded to an increase in the proportion of calvings at 3-year intervals from about 0.84 to 0.90, with a corresponding decrease from about 0.14 to 0.08 in the proportions of larger intervals. The biological significance of such a change is uncertain.

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Change in the annual instantaneous growth rate

Equation (11) of the Appendix has been used to model a change in annual instantaneous growth rate obtained from Equations (7) and (8) and the results are shown in Table 4. There is no indication that a change in the growth rate has occurred. Any estimated change in population growth rate is not statistically significant from zero at the 5% level (and there is hardly any change in the log-likelihood values) regardless of the year in which a change is assumed.

Change in the annual survival rate of females

A change in the annual survival rate of females is confounded in the available data because a change in survival rate cannot be distinguished from a change in sightability for the model based on the Payne *et al*. (1990) model of Equations (1) to (6) of the Appendix. To be able to investigate the possibility of a change in the annual survival rate after a specified year x within the model based on Payne *et al*. (1990), the observed data on the number of females recorded to calve in both year i and in year j (n_{ij}, see Table 1a) was split into two separate blocks of data; one for the years $j \leq x$ and the other for $j > x$.

The results are shown in Table 5. They show no indication that a change in the annual survival rate of females has occurred. As for a possible change in population growth rate, the estimated change in the survival rate is not statistically significant from zero at the 5% level for any of the years in which a change is assumed.

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Table 1. Observed right whale cow-calf pairs on the south coast of South Africa between 1979 and 2006. Number of calvings recorded in each year as well as the number of females that have been resighted with a calf in later years are shown.

a) The number of females recorded to calve both in year *i* and in year *j* (n_{ij}), where $i < j$.

Year *i* ($i < j$)	Year *j* ($i < j$)																										
	80	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	**06**
1979	0	1	17	2	4	14	2	2	10	3	5	8	4	4	6	6	3	4	4	6	4	6	6	6	3	7	5
1980		0	0	22	2	2	15	4	3	17	5	3	15	3	3	16	6	3	10	6	3	12	4	4	11	4	5
1981			0	2	31	0	4	27	2	5	15	8	6	12	5	4	17	6	5	14	3	10	14	4	8	10	4
1982				0	1	28	3	2	24	4	3	18	5	4	14	5	4	12	3	7	10	5	7	10	3	7	9
1983					0	2	21	5	4	23	8	4	17	6	5	18	4	3	15	7	5	17	7	5	12	5	7
1984						0	1	42	5	4	30	8	6	25	7	6	26	10	7	21	7	11	18	7	9	20	8
1985							0	2	34	4	3	28	4	5	28	6	6	19	6	9	14	8	10	17	7	9	17
1986								0	1	31	2	4	22	3	3	19	5	4	13	9	7	17	8	6	12	2	7
1987									0	3	43	5	4	34	4	7	36	8	9	28	5	14	30	7	11	30	10
1988										0	1	38	3	4	35	5	7	30	4	9	21	8	10	24	7	9	22
1989											0	2	47	7	4	39	8	10	31	7	13	34	6	10	23	9	14
1990												0	0	39	1	5	37	4	5	32	3	10	32	6	8	31	9
1991													0	2	47	5	6	39	7	9	32	10	8	31	10	5	29
1992														0	1	51	12	4	39	9	8	37	13	10	27	14	11
1993															0	1	50	6	6	44	7	10	41	9	8	34	15
1994																0	1	58	3	5	48	7	11	43	7	9	37
1995																	0	1	56	6	4	50	9	10	37	10	12
1996																		0	3	77	7	11	63	12	16	54	21
1997																			0	2	67	9	7	57	9	11	49
1998																				0	0	69	9	9	56	11	13
1999																					0	1	91	8	8	75	23
2000																						0	2	91	6	5	80
2001																							0	2	95	10	10
2002																								0	2	104	25
2003																									0	0	106
2004																										0	1
2005																											0

b) Number of calvings recorded in each year *i* (n_i).

Year	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	**06**
n_i	27	33	50	40	43	65	53	44	75	68	78	75	76	84	90	90	96	134	119	111	153	152	169	193	180	186	210	230

Table 2. Estimates of the probability distribution of calving intervals (h_j), mean calving interval (yr) and annual survival rate (S) for right whales off South Africa for a maximum calving interval (j_{max}), of five years, based on the Payne *et al*. (1990) model of Equations (1) to (6) of the Appendix. The change in calving intervals is modelled by Equation (9). Where applicable the estimates for the two time periods are shown. Results in brackets represent 95% confidence intervals based on the Hessian matrix (in the case where a change in the calving intervals has been assumed, these confidence intervals refer to estimates for the first period).

Parameter	**Data up to 2003**	**Data up to 2006**	**Change in 1985**	**Change in 1990**	**Change in 1995**
h_1	0.00	0.00	0.00	0.00	0.00
h_2	0.023 (0.015; 0.031)	0.020 (0.013; 0.026)	0.018 (0.012; 0.024)	0.018 (0.012; 0.025)	0.019 (0.013; 0.026)
h_3	0.853 (0.843; 0.864)	0.853 (0.844; 0.862)	0.826; 0.884 (0.809; 0.842)	0.842; 0.918 (0.831; 0.852)	0.850; 0.925 (0.841; 0.860)
h_4	0.073 (0.065; 0.080)	0.075 (0.068; 0.081)	0.087; 0.058 (0.078; 0.096)	0.079; 0.041 (0.072; 0.086)	0.075; 0.038 (0.069; 0.081)
h_5	0.051 (0.038; 0.064)	0.053 (0.042; 0.064)	0.070; 0.040 (0.057; 0.083)	0.061; 0.023 (0.050; 0.072)	0.056; 0.019 (0.045; 0.067)
S	0.990 (0.983; 0.996)	0.990 (0.985; 0.996)	0.991 (0.986; 0.997)	0.989 (0.983; 0.994)	0.990 (0.985; 0.996)
Mean calving interval	3.149 (3.116; 3.182)	3.158 (3.131; 3.185)	3.205; 3.118 (3.171; 3.240)	3.179; 3.066 (3.151; 3.207)	3.165; 3.054 (3.137; 3.192)
Δ	—	—	0.059 (0.028; 0.089)	0.076 (0.035; 0.118)	0.075 (-0.015; 0.164)
Log-likelihood	7746.8	11207.8	11214.9	11214.0	11209.0

Table 3. Estimates of the probability distribution of calving intervals (h_j), mean calving interval (yr) and annual survival rate (S) for right whales off South Africa for a maximum calving interval (j_{max}), of five years, based on the Payne *et al*. (1990) model of Equations (1) to (6) of the Appendix. The change in calving intervals is modelled by Equation (10). Where applicable the estimates for the two time periods are shown. Results in brackets represent 95% confidence intervals based on the Hessian matrix (in the case where a change in the calving intervals has been assumed, these confidence intervals refer to estimates for the first period).

Parameter	Data up to 2006	Change in 1985	Change in 1990	Change in 1995
h_1	0.00	0.00	0.00	0.00
h_2	0.020 (0.013; 0.026)	0.019 (0.013; 0.026)	0.019 (0.013; 0.026)	0.019 (0.012; 0.025)
h_3	0.853 (0.844; 0.862)	0.828; 0.883 (0.811; 0.845)	0.843; 0.916 (0.832; 0.853)	0.854; 0.907 (0.845; 0.863)
h_4	0.075 (0.068; 0.081)	0.097; 0.048 (0.084; 0.110)	0.083; 0.011 (0.075; 0.091)	0.076; 0.000 (0.069; 0.082)
h_5	0.053 (0.042; 0.064)	0.056; 0.048 (0.039; 0.073)	0.055; 0.054 (0.043; 0.067)	0.052; 0.075 (0.041; 0.063)
S	0.990 (0.985; 0.996)	0.992 (0.987; 0.997)	0.989 (0.983; 0.994)	0.990 (0.984; 0.995)
Mean calving interval	3.158 (3.131; 3.185)	3.188; 3.127 (3.149; 3.226)	3.171; 3.098 (3.142; 3.200)	3.158; 3.128 (3.131; 3.185)
Δ	—	0.055 (0.028; 0.089)	0.073 (0.032; 0.114)	0.053 (-0.047; 0.152)
ξ	—	-0.022 (-0.039; -0.004)	-0.036 (-0.063; -0.008)	-0.049 (-0.118; 0.019)
Log-likelihood	11207.8	11217.8	11217.2	11211.5

Table 4. Estimates of the probability distribution of calving intervals (h_j), mean calving interval (yr) and annual survival rate (S) for right whales off South Africa for a maximum calving interval (j_{max}), of five years, based on the Payne *et al*. (1990) model of Equations (7) to (8) of the Appendix. The change in the annual instantaneous growth rate (γ) is modelled by Equation (11). Results in brackets represent 95% confidence intervals based on the Hessian matrix.

Parameter	**Data up to 2006**	**Change in 1985**	**Change in 1990**	**Change in 1995**
h_1	0.00	0.00	0.00	0.00
h_2	0.020 (0.013; 0.027)	0.020 (0.013; 0.027)	0.020 (0.013; 0.027)	0.020 (0.014; 0.027)
h_3	0.852 (0.844; 0.861)	0.853 (0.844; 0.862)	0.853 (0.844; 0.862)	0.852 (0.844; 0.861)
h_4	0.075 (0.069; 0.081)	0.075 (0.069; 0.082)	0.075 (0.068; 0.081)	0.075 (0.069; 0.081)
h_5	0.051 (0.039; 0.063)	0.052 (0.041; 0.063)	0.0552 (0.042; 0.063)	0.052 (0.041; 0.063)
S	0.991 (0.985; 0.996)	0.990 (0.985; 0.996)	0.990 (0.985; 0.996)	0.991 (0.985; 0.996)
Mean calving interval	3.146 (3.115; 3.177)	3.155 (3.128; 3.182)	3.156 (3.129; 3.183)	3.156 (3.128; 3.183)
δ	0.070 (0.065; 0.075)	0.071 (-0.190; 0.332)	0.071 (0.041; 0.101)	0.072 (0.058; 0.085)
γ	—	-0.001 (-0.265; 0.262)	-0.002 (-0.035; 0.032)	-0.004 (-0.024; 0.015)
Log-likelihood	11193.1	11194.2	11194.2	11194.3

Table 5. Estimates of the probability distribution of calving intervals (h_j), mean calving interval (yr) and annual survival rate (S) for right whales off South Africa for a maximum calving interval (j_{max}), of five years, based on the Payne *et al*. (1990) model of Equations (1) to (6) of the Appendix. The change in the annual survival rate of females is modelled by Equation (12). Where applicable the estimates for the two time periods are shown. Results in brackets represent 95% confidence intervals based on the Hessian matrix (in the case where a change in the survival rate has been assumed, these confidence intervals refer to estimates for the first period).

Parameter	Data up to 2006	Change in 1985	Change in 1990	Change in 1995
h_1	0.00	0.00	0.00	0.00
h_2	0.020 (0.013; 0.026)	0.019 (0.012; 0.025)	0.020 (0.013; 0.027)	0.020 (0.013; 0.027)
h_3	0.853 (0.844; 0.862)	0.851 (0.841; 0.861)	0.845 (0.832; 0.857)	0.840 (0.827; 0.854)
h_4	0.075 (0.068; 0.081)	0.075 (0.067; 0.082)	0.083 (0.074; 0.092)	0.087 (0.077; 0.097)
h_5	0.053 (0.042; 0.064)	0.056 (0.044; 0.068)	0.053 (0.039; 0.066)	0.053 (0.038; 0.067)
S	0.990 (0.985; 0.996)	0.966; 0.995 (0.775; 1.157)	0.978; 0.996 (0.936; 1.020)	0.989; 0.9998 (0.971; 1.007)
Δ_S	—	0.029 (-0.163; 0.220)	0.018 (-0.026; 0.061)	0.011 (-0.019; 0.041)
Mean calving interval	3.158 (3.131; 3.185)	3.158; 3.166 (3.098; 3.218)	3.162; 3.167 (3.129; 3.196)	3.170; 3.173 (3.135; 3.204)
Log-likelihood†	11207.8	9741.8	8252.5	7111.7

† Note that these log-likelihood values are not comparable as the models are fitted to different data sets.

APPENDIX

Calving interval and survival rates

Observed calving intervals are biased representations of the true calving frequency, because *inter alia* cows on longer intervals are under-represented in the sample (having a greater proportion of incomplete calving intervals), and no allowance is made for missed calvings. In reality, a cow calving in a particular year might not be photographed because (a) the calf died before the survey, or was born after the survey, or (b) the cow plus calf were outside the survey area at the time of the survey, or were in the survey area but were overflown. To estimate the true calving interval, the maximum likelihood approach adopted in Payne *et al.* (1990) and developed further by Cooke *et al.* (1993) has been used. Their models are summarised below. For a more detailed discussion of these models the reader is referred to the above references.

The same notation as Payne *et al.* (1990) is adopted:

p_j = the probability that a calving in year j is recorded
h_j = probability that a female calving in year m has her next calf in year $m+j$, given that she has survived to year $m+j$
q_j = the probability that a female calving in year m has a calf in year $m+j$, given that she has survived to year $m+j$
n_i = number of calvings recorded in year i
n_{ij} = number of females recorded to calve both in year i and in year j, where $i < j$
j_{max} = the maximum calving interval, where possible values considered are j_{max} = 4, 5, and 6
s_j = the probability that a female that calved in year m survives to year $m+j$
n = total number of years in which calvings have been recorded.

The probabilities q_j are related to the probabilities h_j by the following equation:

$$q_j = \sum_{i=1}^{j} h_i q_{j-i} \,, \tag{1}$$

where q_0 = 1 and the h_i satisfy the condition:

$$\sum_{i=1}^{j_{\max}} h_i = 1. \tag{2}$$

The n_{ij} are assumed to follow a Poisson distribution with expected value given by:

$$\mu_{ij} = n_i s_{j-i} q_{j-i} p_j \quad (i < j)\,, \tag{3}$$

so that the likelihood function is then given by:

$$L(n_{ij}; p_j, h_i, S) = \prod_{j=1}^{n} \prod_{i=0}^{j-1} \frac{e^{-\mu_{ij}} \mu_{ij}^{n_{ij}}}{n_{ij}!}\,, \tag{4}$$

where S is the annual survival rate of females (assumed constant), so that $s_j = S^j$.
The mean calving interval is given by:

$$\sum_{j=1}^{j\max} j h_j s_j \Big/ \sum_{j=1}^{j\max} h_j s_j \,. \tag{5}$$

This model also provides estimates for p_j given by:

$$\hat{p}_j = \sum_{i=o}^{j-1} n_{ij} \Big/ \sum_{i=0}^{j-1} n_i q_{j-i} s_{j-i} \tag{6}$$

and these in turn yield estimates of the number of calvings in each year ($\hat{N}_j$, where $\hat{N}_j = n_j \big/ \hat{p}_j$).

The model proposed by Payne *et al.* (1990) to estimate the annual rate of increase expressed as an instantaneous rate is also applied to these data. If N_0 is the number of calvings in the first year of the study, δ is the annual instantaneous growth rate, and the trend in the calving population size is modelled as:

$$N_j = N_0 e^{\delta . j}, \tag{7}$$

then Equation (3) can be rewritten by replacing p_j in terms of N_j as:

$$\mu_{ij} = n_i n_j s_{j-i} q_{j-i} e^{-\delta . j} / N_0 \quad (i < j). \tag{8}$$

and the likelihood function given by Equation (4) can be maximized to give an estimate for the annual instantaneous growth rate. Confidence intervals for the parameter estimates are based on the Hessian matrix.

Change in the probability distribution of calving intervals

Two methods have been used to model a change in the probability distribution of calving intervals after a specified year *x* where *x* = 1985, 1990 or 1995. The change in the probabilities h_j apply to calving intervals of 3, 4 and 5 years as (no change is assumed for calving intervals of one and two years):

a) $h_3 \to h_3 + \Delta;\quad h_4 \to h_4 - \Delta/2;\quad h_5 \to h_5 - \Delta/2.$ (9)

b) $h_3 \to h_3 + \Delta;\quad h_4 \to h_4 - \Delta/2 + \xi;\quad h_5 \to h_5 - \Delta/2 - \xi.$ (10)

Change in the annual instantaneous growth rate

A change in the annual instantaneous growth rate has been modelled by as:

$$e^{\delta} \to e^{\delta} e^{\gamma}, \tag{11}$$

where the change occurs after a specified year *x*, where again *x* = 1985, 1990 or 1995 and calculations are again effected using Equations (7) and (8).

Change in the annual survival rate of females

A change in the annual survival rate of females is confounded given the available data (as a change in the survival rate and a change in sightability cannot be separated). Thus, to be able investigate the possibility of a change in the annual survival rate after a specified year *x*, the observed data on the number of females recorded to calve in both year *i* and in year *j* (n_{ij}, see Table 1a) has to be split into two separate blocks of data; one for the years $j \le x$ and the other for $j > x$. The change in the survival rate of females after a specified year *x*, where *x* = 1985, 1990 or 1995, is modelled as:

$$S \to S + \Delta_S, \tag{12}$$

with Equation (4) again used to compute the likelihood.