Monitoring the recovery of the southern right whale in South African waters

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ABSTRACT

Annual photographic surveys of right whale cow-calf pairs on the south coast of South Africa since 1979 have resulted in 2 270 resightings of 1 070 individual cows with calves. Observed calving intervals ranged from 2 to 23 years, with a principal mode at 3 years and secondary modes at 6 and 9 years, but these made no allowance for missed calvings. Using the model of Payne et al. (1990), a maximum calving interval of 5 years produces the most appropriate fit to the data, giving a mean calving interval of 3.16 years with a 95 % confidence interval of (3.14, 3.19). The same model produces an estimate for adult female survival rate of 0.990 with a 95% confidence interval of (0.985, 0.994). The Payne et al. (1990) model is extended to incorporate information on the observed ages of first reproduction of grey-blazed calves, which are known to be female. This allows the estimation of first parturition (median 7.67 years with 95% confidence interval (7.19, 8.16)). First year survival rate was estimated as 0.737 (0.568, 0.906) and the instantaneous population increase rate as 0.068 (0.064, 0.072). The current (2008) population is estimated as some 4 600 animals, or about 23% of initial population size: the latter parameter needs re-consideration.

INTRODUCTION

The population of right whales *Eubalaena australis* that over-winters on the southern coast of South Africa has been estimated to be increasing at an instantaneous rate of about 7% a year since monitoring started with annual aerial surveys in 1969 (Best, 1990a; Best *et al*., 2001). From 1979 and 1998 these surveys have included a photo-identification component, and Best *et al*. (2001) and then Best *et al*. (2005) have analysed the results of these surveys to provide estimates of mean calving interval, adult female survival rate, mean age at first parturition, and first-year survival rate. In this paper these parameters are re-calculated including a further 5 years of survey data from the latest analyses, i.e. up to and including 2008. Population growth rates are computed from the estimated biological parameters, and compared with growth rates obtained from the number of expected annual calvings.

MATERIAL AND METHODS

Between 1969 and 1987, fixed-wing surveys were flown off the south coast of South Africa from Woody Cape, Algoa Bay, to Muizenberg, False Bay, in late September/early October each year, and counts of all right whales seen were made. The techniques used and results obtained have already been published (Best, 1990a). From 1979, annual photographic surveys of the right whale population on the southern coast of South Africa have been carried out by helicopter. Details of the survey techniques have already been published (Best, 1990b), but in the context of this paper the important point is that the surveys were carried out in as standard a manner as possible. To this

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end they were flown at the same time of year each year (earliest flight 6 October, latest flight 25 October), using the same strategy on each flight. The same stretch of coastline, Nature's Valley to Muizenberg, was searched once each year, usually from east to west so that the pilot and photographer were on the coastward side of the aircraft. Where possible, flights were confined to days of good visibility and when surface winds were less than 15 knots. Searching was undertaken at a height of 1,000 ft (305 m); any whale encountered was inspected for the presence of a calf, and if one was detected, the aircraft would descend to 300 ft (95 m) for photography. Unless supplies were running low, usually 11-12 exposures were taken of each cow-calf pair. Animals without calves were normally not photographed.

For all animals except calves, the photographs from each year's survey were compared with the existing catalogue of known individuals. Until 2004, each animal was compared in turn with the entire catalogue, and potential matches noted. The original photographs of any potential matches were then compared with those of the survey animal. If a match was established, the animal was incorporated in the catalogue as a "synonym". If no match was found, photographs of the survey animal were then compared again with the entire catalogue before it was accepted as a new individual. Beginning in 2004, images have been compared using the Hiby-Lovell automated programme (Hiby and Lovell, 2001), where digitised extracts of the callosity patterns are automatically adjusted for tilt and inclination and then compared with other extracts in the library, and the resultant matches listed in order of similarity (from 1.00 to 0). Images of the unknown whale and those in the list are then compared on screen, starting with the most similar and proceeding (if no match is found) until a similarity index of 0.50. In total, 3 346 cow-calf pairs were photographed between 1979 and 2008, with a final catalogue of 1 070 individual cows. Intervals between calves were established on 2 270 occasions.

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:

$$q_j = \sum_{i=1}^{j} h_i q_{j-i} , \qquad (1)$$

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:

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

This model also provides estimates for p_j given by:

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

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.

Age at first parturition

Photographs of any previously unphotographed adults taken on a survey were compared with those of calves taken four or more years earlier. This analysis was confined to matching calves and adults that carried grey blazes (see Best, 1990b), as these animals are known to be female (Schaeff *et al*., 1999). Restriction of the analysis to known females allows the estimation of the juvenile survival rate in addition to the age at first parturition. From 1979 to 2002 a total of 158 grey-blazed calves was photographed, of which 79 matches have been used in this analysis, all with cows photographed from 1987 onwards (see Table 4). The analysis that follows makes the tacit assumption that all calves with visible grey blazes retain them. This seems plausible because while the blazes tend to darken with age, their shapes remain unchanged over time (Payne *et al*., 1983; Best 1990b).

The observed ages at first parturition are subject to the same types of bias as the observed calving intervals, in that later maturing individuals will be relatively under-represented, and some first calvings will go undetected. Hence a modelling approach has been adopted to estimate the true median age at first parturition.

Let m_i be the number of female calves seen in year i, where i = 1979, é , 2008, and t_k be the number of such females seen to first reproduce at age k, where k = 6, é , 13. Define λ_k to be the proportion of animals of age k which have reached first parturition (either at that age or earlier). This is re-parameterized as:

$$\lambda_k = \begin{cases} 1\Big/\left[1+e^{-(k-a_m)/\Delta}\right] & k \geq 6 \\ 0 & k < 6 \end{cases} \tag{9}$$

where a_m is the age at which 50% of the population reach first parturition and Δ measures the spread of this ogive. Define $\tilde{S}$ as the survival rate for the first year of life (S is assumed to apply for each year thereafter); then for each k the expected value of t_k ($\hat{t}_k$) can be represented in terms of m_i, $\tilde{S}$, S, p_j and λ_k. For example, when k = 6, $\hat{t}_k$ is given by:

$$\hat{t}_6 = \sum_i m_i \tilde{S} S^5 p_{i+6} \lambda_6 \tag{10a}$$

and for k = 7, $\hat{t}_k$ is given by:

$$\hat{t}_7 = \sum_i m_i \tilde{S} S^6 p_{i+7} (\lambda_7 - \lambda_6) + \sum_i m_i \tilde{S} S^6 (1 - p_{i+6}) \lambda_6 h_1 p_{i+7} \tag{10b}$$

and so on for other values of k.

The observed t_k are assumed to follow Poisson distributions with expected value $\hat{t}_k$ so that the likelihood function is given by[3]:

$$L(t_k; a_m, \Delta, S, p_j, h_i, \tilde{S}, \delta, N_0) = \prod_{k=6}^{13} \frac{e^{-\hat{t}_k} (\hat{t}_k)^{t_k}}{t_k!}\,. \tag{11}$$

Incorporating the information available on matched calves and adults as well as the adult resighting information, one can obtain estimates for the calving interval and the age at first parturition concurrently. This was achieved by maximizing the likelihood obtained from the product of the two individual likelihood functions given by Equations (4) and (11). Penalty functions were used to ensure that h_i values were not negative and that the juvenile survival rate ($\tilde{S}$) did not exceed the adult survival rate (S). This last constraint is imposed because it seems likely that if the mother dies during a calfõs first year of life, the calf would die too.

RESULTS

Calving interval

Table 1 gives the observed values for the number of right whale calvings recorded each year and the number of females that were observed to calve in both year i and year j. Fig.1 shows the

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[3] Strictly this product should be extended to values of $k > 13$. However, for the parameter values estimated, the expectation for $k = 14$ is already very small (about 0.2), so that this complication was ignored for simplicity.

distributions of observed calving intervals from 1979 to 2008 (n = 2 270). The distribution has an obvious mode at 3 years (n = 1 554), and smaller modes at 6 (n = 235) and 9 years (n = 43). The longest observed interval is 23 years, and the arithmetic mean 3.91 years.

Table 2 gives the estimated probability distributions of calving intervals from the Payne *et al.* (1990) model, for different choices of the maximum calving interval (j_{max}). The log-likelihood values, together with considerations of parsimony, indicate that the distribution with a maximum calving interval of 5 years produces the most appropriate fit. Although statistically there is a case to include calving intervals of up to seven years, we decided not to pursue the options of six and seven year maxima further. The estimates for such cases indicate an increase in probability for the highest calving intervals after the decreasing trend that follows the peak at a three year interval; such a further rise seems biologically implausible, and more likely an artefact of missed intermediate calvings. Under the assumption of a maximum interval of 5 years, the distribution of calving intervals has a mean of 3.16 years with a (Hessian matrix-based) 95% confidence interval of (3.14, 3.19). Fig. 2 compares the distribution of observed and model predicted (Equation (3) summed over i) frequencies of subsequent calvings in relation to the period (j-i) elapsed since the first sighting of an animal with a calf, on the assumption of a maximum interval of 5 years; the overall fit is significantly different from the assumed Poisson distribution ($\chi^2 = 57.69$, $p < 0.0001$).

The model also provides estimates of the probability that a calving which occurs in a particular year is recorded (Table 3); from this, the ñtrueò number of calvings occurring in that year can be estimated (Fig. 3). Recording probabilities are generally high (>70%), and after an initial slight decline seem to have stabilised between 1990 and 2008.

The true number of calvings annually (provided the reproductive rate remains constant) can be used as an index of the abundance of mature females. The model of Payne *et al.* (1990) for estimating a trend in the number of calvings (Equations (7) and (8)) produces an instantaneous rate of increase from 1982 to 2008 of 0.068 per annum, with a 95% confidence interval (0.064, 0.072) (Fig. 4).

Incorporating age at first parturition

Table 4 shows the number of grey-blazed female calves seen in year i and the number of such females seen to calve for the first time at age k. These apparent[4] ages at first parturition range from 6 to 13 years, with a mean of 8.58 years and a standard deviation of 1.88 years (Fig. 5). Table 5 gives the estimated parameters when the model of Payne *et al*. (1990) for calving intervals is updated to include information available on matched female calves and adults to estimate the age at first parturition and improve survival rate estimates. Hessian matrix based confidence intervals are given for the parameter estimates. The log-likelihood values indicate that a maximum calving interval of 5 years should be chosen for the same reasons as given above. The point estimates for the probabilities of different calving intervals do not change from those obtained from the Payne *et al*. (1990) model in isolation (Table 2). Fig. 5 also shows the distribution of apparent age at first parturition predicted by the model of Equations (9) to (11). The overall fit to the observed distribution is good ($\chi^2 = 2.76$, $p = 0.096$).

From the first parturition ogive fitted by the model (Fig. 6), the age at which 50% of females have their first calf is estimated as 7.67 years with a 95% confidence interval of (7.19, 8.16).

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[4] The word ñapparentò is used to signify that the actual first calving of the animal might not have been detected.

Survival rates

The model used for estimating calving intervals can also produce estimates of adult female survival rate. The best estimate for the South African right whale data is 0.990 with a 95% confidence interval of (0.985, 0.994) when the model proposed by Payne *et al*. (1990) is applied. The same estimate and confidence interval is obtained when the combined model of Equations (9) to (11) is used.

There is also the potential for estimating the juvenile mortality rate, given the restriction of the reproduction data used (Table 4) to animals known to be female. This results in a juvenile (to age 1) survival rate estimate of 0.737, with a 95% confidence interval of (0.568, 0.906).

DISCUSSION

The addition of another five yearsô survey data has made little difference to the estimates of demographic parameters for southern right whales off South Africa obtained previously (Best *et al.*, 2005). At an assumed maximum calving interval of 5 years, and using Equations (9) to (11), adult survival is now estimated as 0.990 (cf 0.990), juvenile survival 0.737 (cf 0.713), age at first parturition 7.67 (cf 7.74) yr, and mean calving interval 3.16 (cf 3.16) yr. Only the juvenile survival rate might appear to have changed, but the wide confidence limits around both estimates indicate that the difference is not statistically significant, but its precision has improved (CV from 0.13 to 0.12). The precision for all the other parameter estimates has improved compared to the earlier analysis (i.e. the CVs for mean calving interval from 0.004 to 0.004, adult survival from 0.003 to 0.002, age at first parturition from 0.039 to 0.032 and population increase rate from 0.036 to 0.032).

Perhaps most important, the estimated rate of population increase, 0.068, is hardly changed (cf 0.070), and is virtually identical to that estimated from contemporary field counts on the helicopter surveys. The updated demographic parameter estimates obtained in this paper can also be used to provide independent estimates of the increase rate expected, using the ñbalance equationòfor a growing population with a steady age structure (Butterworth and Best, 1990):

$$(1+r)^{a_m} = (1+r)^{a_m-1}S + q\rho\tilde{S}S^{a_m-1} \qquad (12)$$

where r = the annual rate of population increase
q = proportion of births that are female, and
ρ = calving rate.

Under the assumption that the proportion of births that are female is 0.5 (Tormosov *et al*. 1998), and using the method to compute the calving rate as given in Appendix 1 of Best *et al.*, 2001, the distribution of r has been computed using bootstrap methods (see Appendix 2 of Best *et al*., 2001). Fig. 7 compares this distribution and that obtained from the estimate of annual instantaneous growth rate parameter δ of Equation (7) (i.e. solving for r in the equation $1+r=e^{\delta}$) from annual calvings. Since the distribution from Equation (7) falls entirely within the distribution developed from biological parameter estimates, there is no indication that immigration is needed to account for the annual instantaneous growth rate of 0.070.

These updated data confirm that the southern right whale population visiting the South African coastline in winter continues to increase at around 7% a year, at least up to 2008. Assuming that all mature females are on a 3-year calving cycle, the best estimate of current (2008) abundance would be the sum of the expected calvings of the three most recent cohorts of mature females, or 967. This should be expanded to include immatures of both sexes and mature males, for which a factor of 4.71:1 was developed at the Cape Town workshop (IWC, 2001). From this it can be concluded that the population using the southern coast of South Africa as a winter nursery area numbered about 4 600 individuals in 2008.

Richards and Du Pasquier (1989) have estimated the initial population size of southern African right whales as 20,000. This was based on a cumulative catch estimate of 12,000 animals from 1785 to 1805, assuming ñover 75%ò (or 10,000) were female and doubling the figure to include males. The cumulative catch estimate ignored recruitment over the 20-year period and so is likely to be too high, and it is still an open question whether those right whales historically calving off Namibia and Mocambique belonged to the same population as those calving on the South African coast. If the Richards and Du Pasquier estimate is accepted, and the entire southern African population considered as one unit, then the current (2008) population stands at about 23% of its original abundance. Given that the initial estimate may be too high, this may well under-estimate the extent of population recovery.

So far there have been no signs of any definite changes in the vital parameters that could signal a density dependent response. Nevertheless, continuity of the survey series and the resultant increasing precision of parameter estimates should allow such density dependent changes to be detected. Such an opportunity is rare indeed for large whale population studies.

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Table 1. Observed right whale cow-calf pairs on the south coast of South Africa between 1979 and 2008. The 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**	**07**	**08**
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	2	6
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	6	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	11	4	4	12
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	4	8
1983					0	2	21	5	4	23	8	4	17	6	5	18	4	3	15	7	5	17	7	5	12	5	7	7	6
1984						0	1	42	5	4	30	8	6	25	7	6	26	10	7	21	7	11	18	7	9	20	8	6	18
1985							0	2	34	4	3	28	4	5	28	6	6	19	6	9	14	8	10	17	7	9	17	9	8
1986								0	1	31	2	4	22	3	3	19	5	4	13	9	7	17	8	6	12	2	7	9	3
1987									0	3	43	5	4	34	4	7	36	8	9	28	5	14	30	7	11	30	10	5	26
1988										0	1	38	3	4	35	5	7	30	4	9	21	8	10	24	7	9	22	9	8
1989											0	2	47	7	4	39	8	10	31	7	13	34	6	10	23	9	14	14	9
1990												0	0	39	1	5	37	4	5	32	3	10	32	6	8	31	9	3	25
1991													0	2	47	5	6	39	7	9	32	10	8	31	10	5	29	10	7
1992														0	1	51	12	4	39	9	8	37	13	10	27	14	11	19	13
1993															0	1	50	6	6	44	7	10	41	9	8	34	15	6	34
1994																0	1	58	3	5	48	7	11	43	7	9	37	8	12
1995																	0	1	56	6	4	50	9	10	37	10	12	26	10
1996																		0	3	77	7	11	63	12	16	54	21	14	46
1997																			0	2	67	13	7	57	13	11	49	11	13
1998																				0	0	69	17	9	56	15	14	36	14
1999																					0	1	91	16	8	76	29	12	54
2000																						0	2	91	15	5	80	15	15
2001																							0	2	95	10	10	58	9
2002																								0	2	104	25	7	84
2003																									0	0	106	15	12
2004																										0	1	79	12
2005																											0	3	124
2006																												0	2
2007																													0

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

Year	n_i	**Year**	n_i
1979	27	**1994**	90
1980	33	**1995**	96
1981	50	**1996**	134
1982	40	**1997**	118
1983	43	**1998**	111
1984	65	**1999**	153
1985	53	**2000**	152
1986	44	**2001**	168
1987	75	**2002**	193
1988	68	**2003**	180
1989	78	**2004**	186
1990	75	**2005**	210
1991	76	**2006**	230
1992	84	**2007**	184
1993	90	**2008**	240

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 different choices of maximum calving interval (j_{max}), based on the Payne *et al*. (1990) model of Equations (1) to (6). Results in brackets represent 95% confidence intervals based on the Hessian matrix.

Parameter	**Assumed maximum calving interval**		
	4	**5**	**6**
h_1	0.00	0.00	0.00
h_2	0.054 (0.049; 0.058)	0.019 (0.013; 0.026)	0.015 (0.010; 0.020)
h_3	0.865 (0.858; 0.872)	0.848 (0.840; 0.856)	0.665 (0.610; 0.720)
h_4	0.081 (0.075; 0.087)	0.081 (0.075; 0.087)	0.084 (0.078; 0.091)
h_5	—	0.052 (0.042; 0.061)	0.061 (0.052; 0.070)
h_6	—	—	0.174 (0.122; 0.226)
$\tilde{S}$	0.991 (0.986; 0.995)	0.990 (0.985; 0.994)	0.987 (0.982; 0.992)
Mean calving interval	3.026 (3.018; 3.035)	3.162 (3.137; 3.186)	3.695 (3.536; 3.854)
Log-likelihood	13635.0	13667.8	13683.1
Decision	reject	accept and select	accept

Table 3. The recorded number and expected ñtrueò number of calvings for the years 1979 to 2008, assuming a maximum calving interval of five years. The estimated probability that a calving in year *j* is recorded is also given. The available data preclude the model providing estimates for the first three years: 1979 to 1981.

Year *i*	**Recorded number**	**Expected number**	**Estimated probability of recording ($\hat{p}_j$)**
1979	27	—	—
1980	33	—	—
1981	50	—	—
1982	40	54	0.745
1983	43	50	0.861
1984	65	80	0.815
1985	53	67	0.785
1986	44	67	0.661
1987	75	92	0.819
1988	68	87	0.782
1989	78	92	0.848
1990	75	107	0.703
1991	76	100	0.759
1992	84	115	0.731
1993	90	136	0.661
1994	90	128	0.703
1995	96	127	0.757
1996	134	174	0.769
1997	118	165	0.716
1998	111	166	0.670
1999	153	202	0.758
2000	152	232	0.654
2001	168	202	0.831
2002	193	245	0.788
2003	180	245	0.735
2004	186	264	0.705
2005	210	290	0.724
2006	230	286	0.805
2007	184	341	0.539
2008	240	340	0.707

Table 4. Observed numbers of grey-blazed right whale calves (known all to be female) on the south coast of South Africa between 1979 and 2002, and the number of such females seen to first reproduce at age *k*.

a) The number of female calves seen in year *i* (m_i).

Year	m_i	**Year**	m_i
1979	3	**1991**	7
1980	3	**1992**	10
1981	5	**1993**	3
1982	1	**1994**	8
1983	2	**1995**	5
1984	4	**1996**	10
1985	10	**1997**	13
1986	1	**1998**	9
1987	6	**1999**	14
1988	2	**2000**	11
1989	5	**2001**	11
1990	6	**2002**	9

b) Number of female calves seen in some year *i* that are later seen to first reproduce in year *j* at age *k* (t_k).

Age(*k*)	6	7	8	9	10	11	12	13
t_k	10	15	17	18	5	6	5	3

Table 5. Estimates of various demographic parameters (see text for definitions) for right whales off South Africa for different choices of maximum calving interval based upon the model of Equations (9) to (11) which incorporates data on observations of apparent first parturition. Results in brackets represent 95% confidence intervals obtained from the Hessian matrix.

Parameter	**Assumed maximum calving interval**		
	4 yr	**5 yr**	**6 yr**
h_1	0.00	0.00	0.00
h_2	0.054 (0.049; 0.058)	0.020 (0.014; 0.026)	0.016 (0.011; 0.021)
h_3	0.865 (0.858; 0.872)	0.848 (0.840; 0.856)	0.676 (0.619; 0.733)
h_4	0.081 (0.075; 0.088)	0.081 (0.075; 0.087)	0.084 (0.078; 0.091)
h_5	—	0.051 (0.041; 0.061)	0.060 (0.051; 0.069)
h_6	—	—	0.164 (0.109; 0.218)
S	0.991 (0.987; 0.995)	0.990 (0.985; 0.994)	0.988 (0.983; 0.992)
δ	0.068 (0.064; 0.072)	0.068 (0.064; 0.072)	0.068 (0.064; 0.072)
N_0	52 (47; 57)	49 (44; 53)	41 (36; 45)
$\tilde{S}$	0.743 (0.574; 0.913)	0.737 (0.568; 0.906)	0.732 (0.563; 0.901)
a_m	7.601 (7.126; 8.077)	7.672 (7.189; 8.155)	8.090 (7. 507; 8.672)
Δ	0.853 (0.574; 1.131)	0.875 (0.585; 1.165)	1.092 (0.749; 1.436)
Mean calving interval	3.026 (3.018; 3.035)	3.160 (3.135; 3.185)	3.663 (3.497; 3.829)
Log-likelihood	13734.5	13766.6	13779.7
Decision	reject	accept	accept

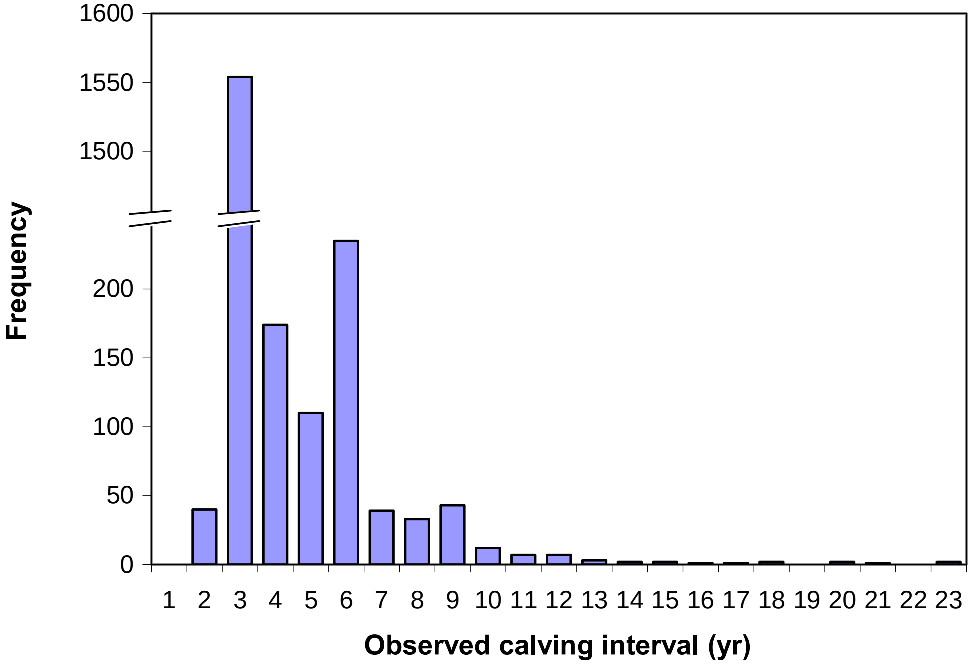

Figure 1. The distribution of observed calving intervals in right whales off South Africa, 1979-2008.

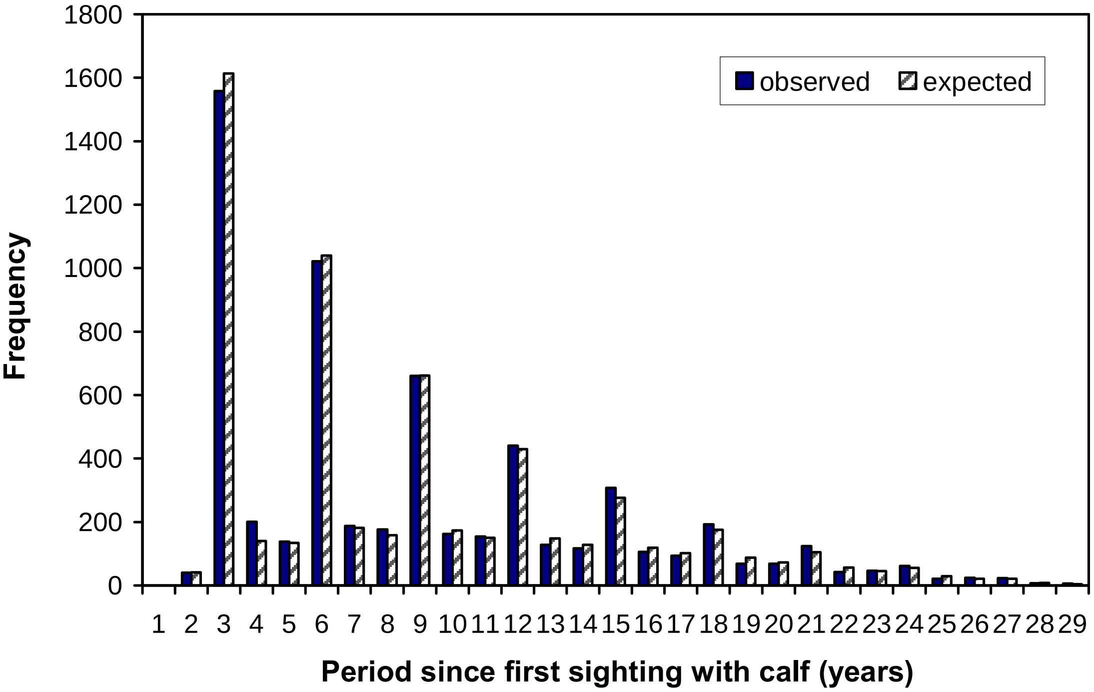

Figure 2. The distribution of observed and expected subsequent calvings in relation to the period elapsed since an animal was first sighted with a calf.

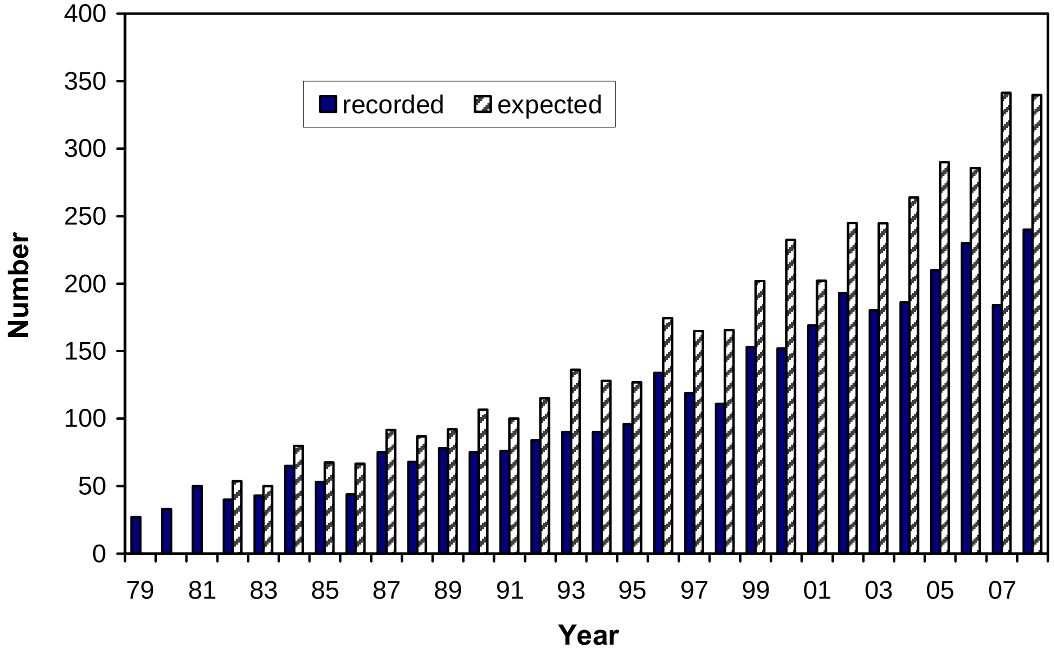

Figure 3. The distribution of recorded number and expected ñtrueò number of calvings for the years 1979 to 2008. The available data preclude the model providing expected numbers for the first three years: 1979 to 1981.

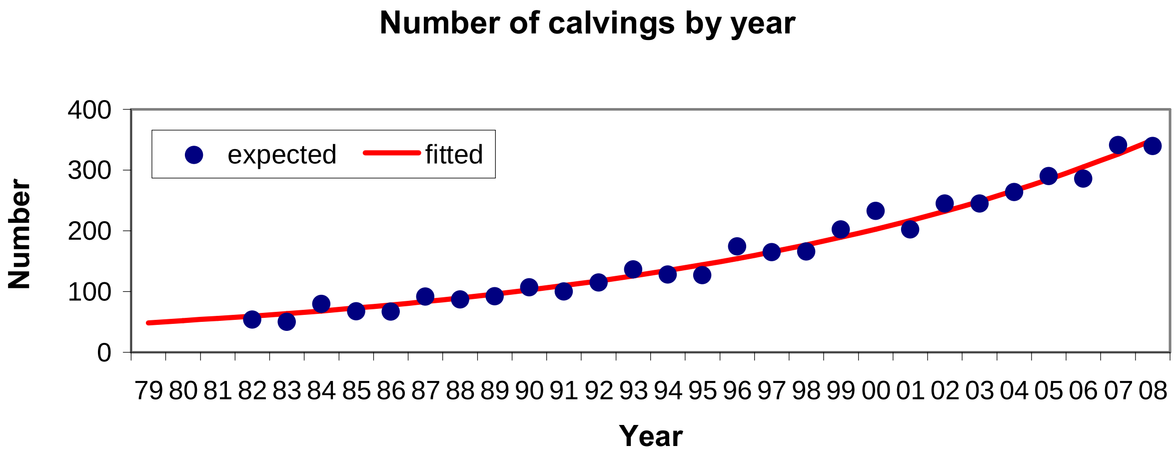

Figure 4. Trend in the expected number (from Fig. 3) of total calvings by year off South Africa, 1982 to 2008. The fitted line is estimated using Equations (7) and (8).

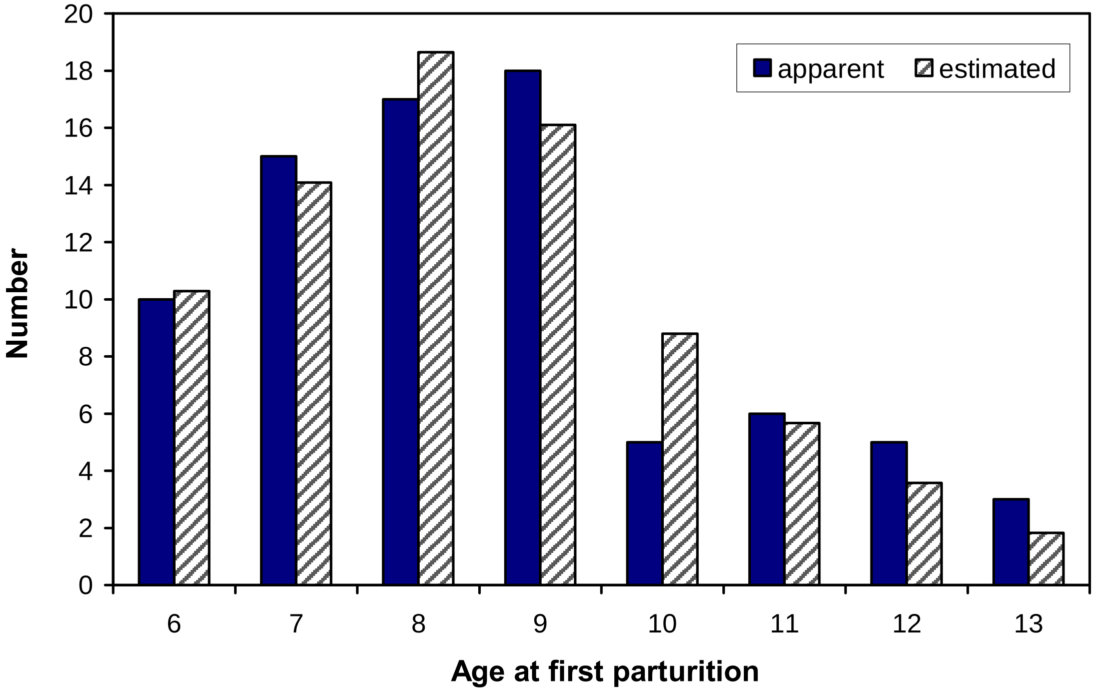

Figure 5. The distribution of apparent and corresponding model-estimated (Equations (9) to (11)) ages at first parturition in right whales off South Africa. Note: the word ñapparentò is used because missed calvings mean that some observations above reflect subsequent rather than true first parturition.

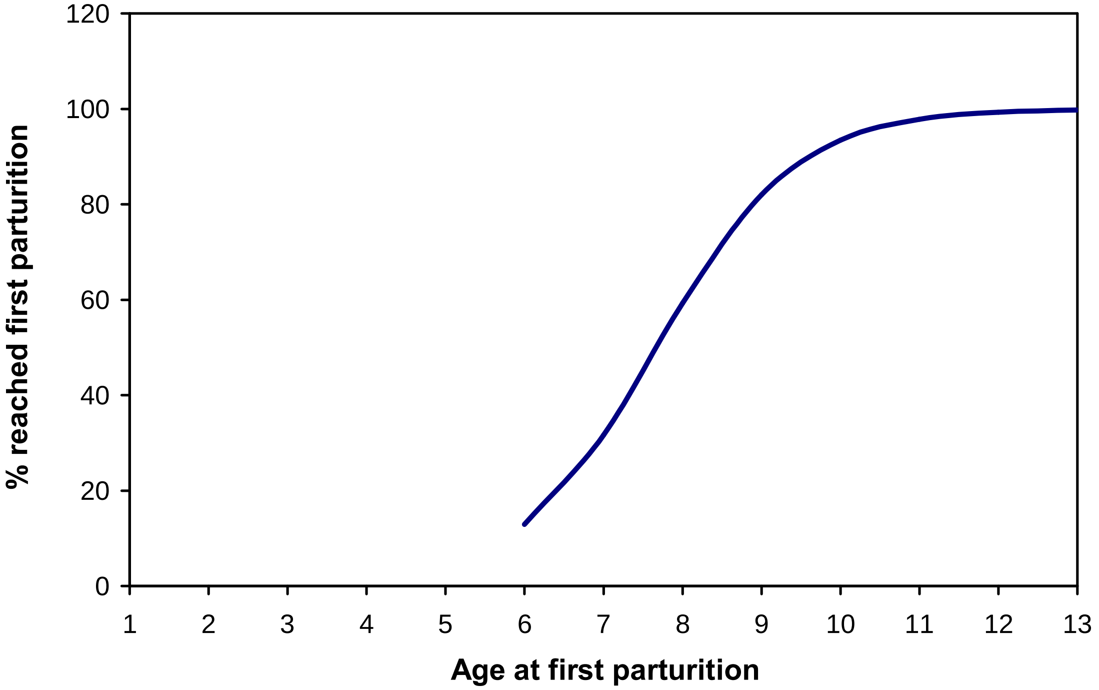

Figure 6. Ogive of estimated proportion of females that at each age that have calved at least once.

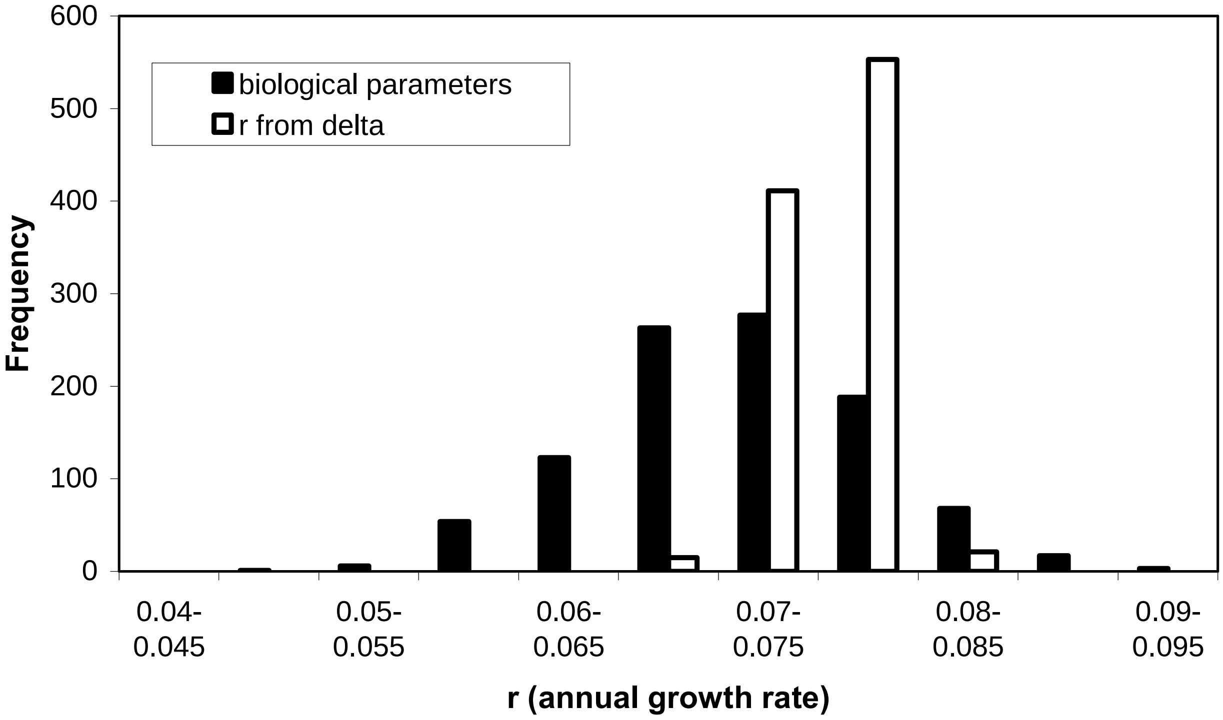

Figure 7. Comparison of distributions of annual growth rate (*r*) computed from biological parameters (Equation (12)) and estimated from annual calvings (Equation (7)).