# UPDATED ESTIMATES OF DEMOGRAPHIC PARAMETERS FOR SOUTHERN RIGHT WHALES OFF SOUTH AFRICA

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## ABSTRACT

*Aerial counts of right whale cow-calf pairs on the south coast of South Africa between 1971 and 2003 indicate an annual instantaneous population increase rate of 0.069 a year (SE 0.003) over this period. Annual photographic surveys since 1979 have resulted in 1,504 resightings of 793 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 3.15 years with a 95 % confidence interval of (3.11, 3.18). The same model produces an estimate for adult female survival rate of 0.990 with a 95% confidence interval of (0.983, 0.997). 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 7.69 years with 95% confidence interval (7.06, 8.32)). First year survival rate was estimated as 0.734 (0.518, 0.95) and the instantaneous population increase rate 0.073 (0.066, 0.079). The current population is estimated as some 3,400 animals, or about 17% 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) analysed the results up to and including the 1998 survey 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, i.e. up to and including 2003. Population growth rates are computed from the estimated biological parameters, and compared with growth rates obtained from the number of expected annual calvings and from direct field counts of cow-calf pairs on the surveys.

## 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

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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 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. 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. In total, 2 298 cow-calf pairs were photographed between 1979 and 2003, with a final catalogue of 793 individual cows. Intervals between calves were established on 1 504 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:

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

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:

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

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, $\delta$ 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. In the catalogue of adult females from 1979 to 2003 there was a total of 97 such “grey-blazed” individuals, and from 1979 to 1992 a total of 113 grey-blazed calves was photographed. A total of 48 matches have been used in this analysis, all for 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, …, 2003, and $t_k$ be the number of such females seen to first reproduce at age *k,* where $k$ = 6, …, 13. Define $\lambda_k$ 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 $\Delta$ 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 $\lambda_k$. 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 calf's first year of life, the calf would die too.

[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.

# RESULTS

## Counts on annual surveys

Fig. 1 shows the counts of right whales with calves seen on fixed-wing surveys from 1971 to 1987, and helicopter surveys from 1979 to 2003. The counts for the helicopter surveys are based on the actual numbers photographed, as obtained after the photographs have been matched and any inadvertent duplicates omitted. For the period of overlap between surveys (1979-1987), correlation between counts on the two surveys is excellent ($r^2$ = 0.914), indicating that survey efficiencies using fixed-wing and helicopter aircraft were similar**.** If the counts are expressed as natural logarithms and plotted against time, then annual instantaneous increase rates (i.e. $\delta$ of Equation (7)) of 0.068 (SE 0.010) are obtained for the fixed-wing surveys from 1971 to 1987, and 0.071 (SE 0.004) for helicopter surveys from 1979 to 2003. These rates of increase are not significantly different ($t$ = 0.30, two-tailed $p$>050), and a common regression line indicates that the population has been increasing at an instantaneous rate of 0.069 (SE 0.003) per year for the last 33 years.

## 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.2 shows the distributions of observed calving intervals from 1979 to 2003 (n = 1,504). The distribution has an obvious mode at 3 years (n = 1,043), and smaller modes at 6 (n = 152) and 9 years (n = 29. The longest observed interval is 23 years, and the arithmetic mean 3.92 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 3.15 years with a (Hessian matrix-based) 95% confidence interval of (3.11, 3.18). Fig. 3 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 good ( $\chi^2$ = 10.09, $p$ = 0.90).

The model also provides estimates of the probability that a calving which occurs in a particular year is recorded (Table 3); from this, the “true” number of calvings occurring in that year can be estimated (Fig. 4). Recording probabilities are generally high (>70%), and seem to have declined over time.

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 1998 of 0.073 per annum, with a 95% confidence interval (0.066, 0.079) (Fig. 5). This is very similar to the rate estimated from counts on the same helicopter surveys from 1979 to 2003 (0.071).

## 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 8.48 years and a standard deviation of 1.86 years (Fig. 6). 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[5]. 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. 6 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 ( $\chi^2 = 3.46$, $p = 0.177$).

From the first parturition ogive fitted by the model (Fig. 7), the age at which 50% of females have their first calf is estimated as 7.69 years with a 95% confidence interval of (7.06, 8.32).

## 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 (0.983, 0.997) 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 0.734, with a 95% confidence interval of (0.518, 0.95).

# DISCUSSION

The addition of another five years' survey data has made little difference to the estimates of demographic parameters for southern right whales off South Africa obtained previously (Best *et al.*, 2001). At an assumed maximum calving interval of 5 years, and using Equations (9) to (11), adult survival is now estimated as 0.990 (cf 0.986), juvenile survival 0.734 (cf 0.913), age at first parturition 7.69 (cf 7.88) yr, and mean calving interval 3.15 (cf 3.12) yr. Only the juvenile survival rate might appear to have changed substantially, but the wide confidence limits around both estimates indicate that the difference is not statistically significant. The precision for all the other parameter estimates has improved compared to the earlier analysis (i.e. the CVs for mean calving interval from 0.008 to 0.006, adult survival from 0.006 to 0.004, age at first parturition from 0.065 to 0.042 and population increase rate from 0.085 to 0.046)

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

[5] Percentile bootstrap confidence intervals (Efron 1981, 1982) for parameter estimates were also computed for a number of the quantities estimated; the results were near identical to those obtained from the Hessian matrix approach.

Perhaps most important, the estimated rate of population increase, 0.073, is unchanged, 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 "balance equation" for 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

$\rho$ = 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. 8 compares this distribution and that obtained from the estimate of annual instantaneous growth rate parameter $\delta$ 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 0.072.

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. Assuming that all mature females are on a 3-year calving cycle, the best estimate of current abundance would be the sum of the expected calvings of the three most recent cohorts of mature females, or 719. 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 numbers about 3,400 individuals.

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 "over 75%" (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 population stands at about 17% of its original abundance. Given that the initial estimate may be too high, this may well under-estimate the degree 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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## REFERENCES

Best, P.B. 1990a. Trends in the inshore right whale population off South Africa, 1969-1987. *Mar. Mammal Sci.* 6 (2): 93–108.

Best, P.B. 1990b. Natural markings and their use in determining calving intervals in right whales off South Africa. *S. Afr. J. Zool.* 25 (2): 114–123.

Best, P.B., Brandao, A., and Butterworth, D.S. 2001. Demographic parameters of southern right whales off South Africa. *J. Cet. Res. Mgmt* (Special Issue 2): 161-169.

Butterworth, D.S., and Best, P.B. 1990. Implications of the recovery rate of the South African right whale population for baleen whale population dynamics. *Rep. int. Whal. Commn* 40: 433-447.

Cooke, J.G., Payne, R. and Rowntree, V. 1993. Updated estimates of demographic parameters for the right whales (*Eubalaena australis*) observed off Peninsula Valdes, Argentina. Document SC/45/O24 submitted to the Scientific Committee of the International Whaling Commission, Kyoto, Japan, 23 April-3 May.

Efron, B. 1981. Nonparametric standard errors and confidence intervals (with discussion). of *Canadian Journal Statistics* 9: 139–172.

Efron, B. 1982. The jacknife, the bootstrap and other resampling plans. National Science Foundation -–Conference Board of the Mathematical Sciences, Monograph 38. Society for Industrial and Applied Mathematics. Philadelphia, Pennsylvania.

International Whaling Commission (IWC). 2001. Report of the workshop on the comprehensive assessment of right whales: a worldwide comparison. *J. Cet. Res. Mgmt* (Special Issue 2):1-60

Payne, R., Brazier, O., Dorsey, E., Perkins, J., Rowntree, V. and Titus, A. 1983. External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. pp. 371–445. In: R. Payne (Ed.) *Communication and Behaviour of Whales* AAAS Selected Symposia Series 76. Westview Press, Boulder, Colorado. 643pp.

Payne, R., Rowntree, V., Perkins, J.S., Cooke, J.G. and Lankester, K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. *Rep. int. Whal. Commn* (Special Issue 12): 271-278.

Richards, R., and Du Pasquier, T. 1989. Bay whaling off southern Africa, c. 1785-1805. *S. Afr. J. mar. Sci.* 8: 231-250.

Schaeff, C.M., Best, P.B., Rowntree, V.J., Payne, R., Jarvis, C., Portway, V.A., and Rivarola, M. 1999. Dorsal skin color patterns among southern right whales (*Eubalaena australis*): genetic basis and evolutionary significance. *J. Heredity.* 90 (4): 464-471.

Tormosov, D.D., Mikhaliev, Y.A., Best, P.B., Zemsky, V.A., Sekiguchi, K. and Brownell, R.L. Jr. 1998. Soviet catches of southern right whales *Eubalaena australis*, 1951–1971. Biological ata and conservation implications. *Biological Conservation* 86: 185–197.

**Table 1.** Observed right whale cow-calf pairs on the south coast of South Africa between 1979 and 2003. 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 |
| **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 |
| **1980** | | 0 | 0 | 22 | 2 | 2 | 15 | 4 | 3 | 17 | 5 | 3 | 15 | 3 | 3 | 15 | 6 | 3 | 10 | 6 | 3 | 12 | 4 | 4 |
| **1981** | | | 0 | 2 | 31 | 0 | 4 | 27 | 2 | 5 | 15 | 8 | 6 | 12 | 5 | 4 | 16 | 6 | 5 | 14 | 3 | 10 | 14 | 4 |
| **1982** | | | | 0 | 1 | 28 | 3 | 2 | 24 | 4 | 3 | 18 | 5 | 4 | 14 | 5 | 4 | 12 | 3 | 7 | 10 | 5 | 7 | 10 |
| **1983** | | | | | 0 | 2 | 21 | 5 | 4 | 23 | 8 | 4 | 17 | 6 | 5 | 17 | 4 | 3 | 15 | 7 | 5 | 17 | 7 | 5 |
| **1984** | | | | | | 0 | 1 | 42 | 5 | 4 | 30 | 8 | 6 | 25 | 7 | 6 | 26 | 10 | 7 | 21 | 7 | 11 | 18 | 7 |
| **1985** | | | | | | | 0 | 2 | 34 | 4 | 3 | 27 | 4 | 5 | 27 | 6 | 6 | 19 | 6 | 9 | 14 | 8 | 10 | 17 |
| **1986** | | | | | | | | 0 | 1 | 31 | 2 | 4 | 22 | 3 | 3 | 19 | 5 | 4 | 13 | 9 | 7 | 17 | 8 | 6 |
| **1987** | | | | | | | | | 0 | 3 | 43 | 5 | 4 | 34 | 4 | 6 | 35 | 8 | 9 | 28 | 5 | 14 | 30 | 7 |
| **1988** | | | | | | | | | | 0 | 1 | 37 | 3 | 4 | 34 | 5 | 7 | 29 | 4 | 9 | 20 | 8 | 10 | 24 |
| **1989** | | | | | | | | | | | 0 | 2 | 47 | 7 | 4 | 39 | 8 | 10 | 31 | 7 | 13 | 34 | 6 | 10 |
| **1990** | | | | | | | | | | | | 0 | 0 | 39 | 1 | 4 | 36 | 4 | 5 | 32 | 3 | 10 | 32 | 6 |
| **1991** | | | | | | | | | | | | | 0 | 2 | 46 | 5 | 6 | 38 | 7 | 9 | 32 | 10 | 7 | 31 |
| **1992** | | | | | | | | | | | | | | 0 | 1 | 51 | 12 | 4 | 40 | 9 | 8 | 37 | 14 | 10 |
| **1993** | | | | | | | | | | | | | | | 0 | 1 | 50 | 6 | 6 | 44 | 7 | 10 | 41 | 9 |
| **1994** | | | | | | | | | | | | | | | | 0 | 1 | 57 | 3 | 5 | 47 | 7 | 11 | 42 |
| **1995** | | | | | | | | | | | | | | | | | 0 | 1 | 57 | 6 | 4 | 49 | 10 | 10 |
| **1996** | | | | | | | | | | | | | | | | | | 0 | 3 | 76 | 7 | 11 | 61 | 10 |
| **1997** | | | | | | | | | | | | | | | | | | | 0 | 2 | 67 | 9 | 7 | 57 |
| **1998** | | | | | | | | | | | | | | | | | | | | 0 | 0 | 69 | 9 | 10 |
| **1999** | | | | | | | | | | | | | | | | | | | | | 0 | 1 | 91 | 8 |
| **2000** | | | | | | | | | | | | | | | | | | | | | | 0 | 2 | 88 |
| **2001** | | | | | | | | | | | | | | | | | | | | | | | 0 | 2 |
| **2002** | | | | | | | | | | | | | | | | | | | | | | | | 1 |

**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** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $n_i$ | 27 | 33 | 50 | 40 | 43 | 65 | 53 | 44 | 75 | 68 | 78 | 75 | 76 | 84 | 90 | 90 | 97 | 134 | 118 | 112 | 153 | 152 | 169 | 194 | 181 |

**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 (4). 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 |
| $h_2$ | 0.06 (0.05; 0.06) | 0.02 (0.015; 0.03) | 0.02 (0.01; 0.03) |
| $h_3$ | 0.87 (0.86; 0.88) | 0.85 (0.84; 0.86) | 0.72 (0.63; 0.80) |
| $h_4$ | 0.07 (0.06; 0.08) | 0.07(0.065; 0.08) | 0.07 (0.07; 0.08) |
| $h_5$ | — | 0.05 (0.04; 0.06) | 0.06 (0.07; 0.08) |
| $h_6$ | — | — | 0.13 (0.05; 0.21) |
| $h_7$ | — | — | — |
| $\tilde{S}$ | 0.991 (0.985; 0.998) | 0.990 (0.983; 0.997) | 0.988 (0.980; 0.995) |
| **Mean calving interval** | 3.01 (3.00; 3.03) | 3.15 (3.11; 3.18) | 3.55 (3.29; 3.80) |
| **Log-likelihood** | 7644 | 7663 | 7666 |
| **Decision** | reject | accept and select | accept |

**Table 3.** The recorded number and expected "true" number of calvings for the years 1979 to 2003, 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 | 0.74 |
| **1983** | 43 | 50 | 0.86 |
| **1984** | 65 | 80 | 0.81 |
| **1985** | 53 | 68 | 0.78 |
| **1986** | 44 | 67 | 0.66 |
| **1987** | 75 | 92 | 0.81 |
| **1988** | 68 | 87 | 0.78 |
| **1989** | 78 | 93 | 0.84 |
| **1990** | 75 | 108 | 0.70 |
| **1991** | 76 | 102 | 0.74 |
| **1992** | 84 | 116 | 0.73 |
| **1993** | 90 | 137 | 0.66 |
| **1994** | 90 | 131 | 0.69 |
| **1995** | 97 | 132 | 0.74 |
| **1996** | 134 | 178 | 0.75 |
| **1997** | 118 | 168 | 0.70 |
| **1998** | 112 | 167 | 0.67 |
| **1999** | 153 | 204 | 0.75 |
| **2000** | 152 | 236 | 0.64 |
| **2001** | 169 | 209 | 0.81 |
| **2002** | 194 | 254 | 0.76 |
| **2003** | 181 | 256 | 0.71 |

**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 1998, 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** | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $m_i$ | 3 | 3 | 5 | 1 | 2 | 4 | 10 | 1 | 5 | 2 | 5 | 6 | 7 | 10 | 3 | 8 | 5 | 10 | 13 | 10 |

**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 |
|---|---|---|---|---|---|---|---|---|
| $t_k$ | 8 | 7 | 10 | 13 | 3 | 3 | 2 | 2 |

**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 |
| $h_2$ | 0.06 (0.050; 0.062) | 0.02 (0.015; 0.032) | 0.02 (0.013; 0.027) |
| $h_3$ | 0.87 (0.862; 0.879) | 0.85 (0.842; 0.863) | 0.72 (0.638; 0.811) |
| $h_4$ | 0.07 (0.065; 0.081) | 0.07 (0.065; 0.080) | 0.07 (0.067; 0.082) |
| $h_5$ | — | 0.05 (0.037; 0.064) | 0.05 (0.046; 0.072) |
| $h_6$ | — | — | 0.12 (0.039; 0.203) |
| $h_7$ | — | — | — |
| $S$ | 0.991 (0.985; 0.998) | 0.990 (0.983; 0.997) | 0.988 (0.981; 0.995) |
| $\delta$ | 0.073 (0.066; 0.079) | 0.073 (0.066; 0.079) | 0.073 (0.066; 0.079) |
| $N_0$ | 49 (43; 55) | 46 (41; 52) | 40 (34; 46) |
| $\tilde{S}$ | 0.739 (0.521; 0.958) | 0.734 (0.518; 0.950) | 0.720 (0.508; 0.932) |
| $a_m$ | 7.62 (6.97; 8.27) | 7.69 (7.06; 8.32) | 7.90 (7.24; 8.56) |
| $\Delta$ | 0.93 (0.55; 1.32) | 0.94 (0.56; 1.32) | 1.01 (0.60; 1.41) |
| **Mean calving interval** | 3.01 (3.00; 3.03) | 3.15 (3.11; 3.18) | 3.52 (3.27; 3.77) |
| **Log-likelihood** | 7679 | 7698 | 7701 |
| **Decision** | reject | accept | accept |

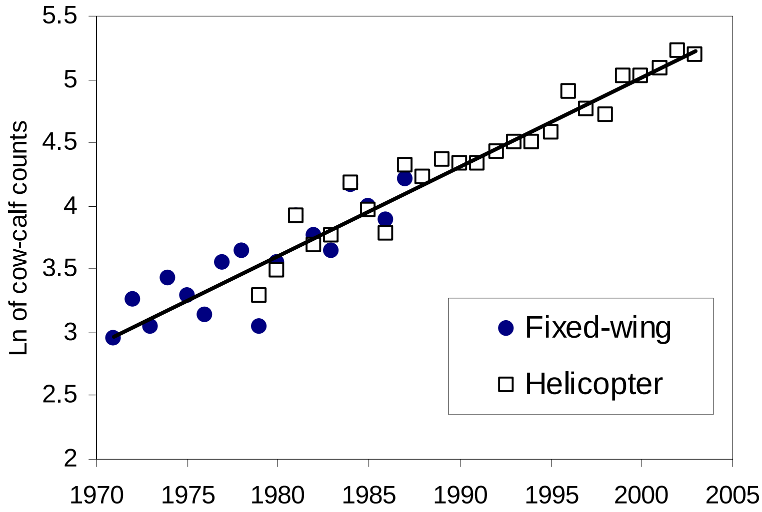


**Figure 1.** Counts of right whales with calves seen on surveys by fixed wing aircraft, 1971 to 1987, and by helicopters 1979 to 2003.

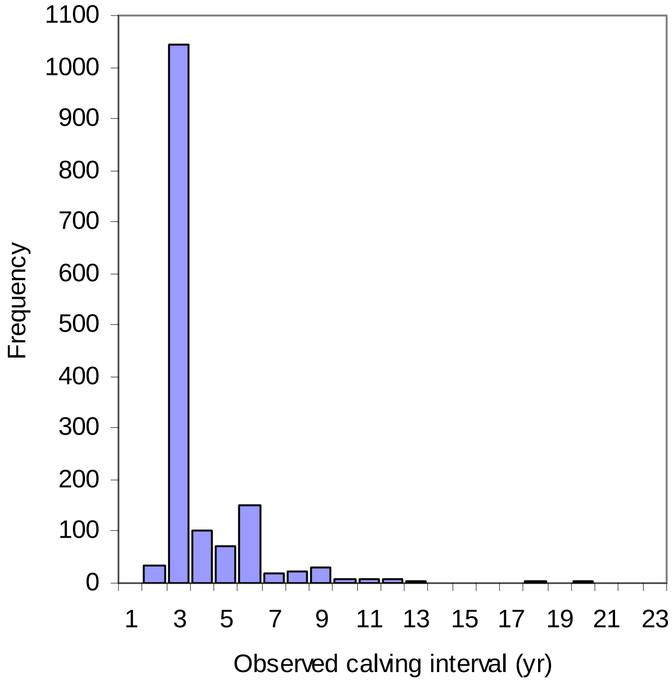


**Figure 2.** The distribution of observed calving intervals in right whales off South Africa, 1979-2003

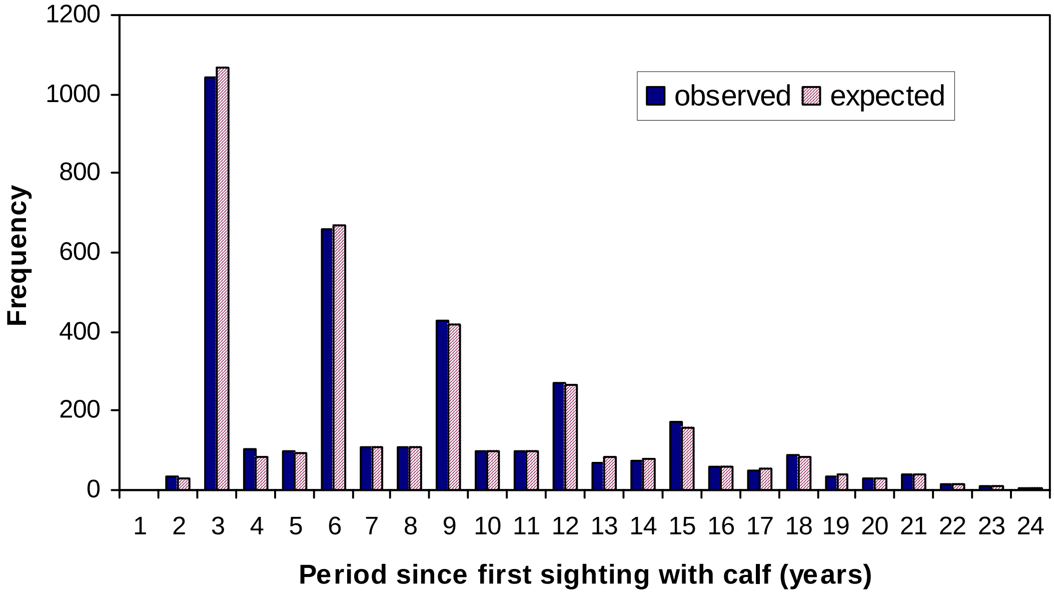


**Figure 3.** The distribution of observed and expected subsequent calvings in relation to the period elapsed since an animal was first sighted with a calf.

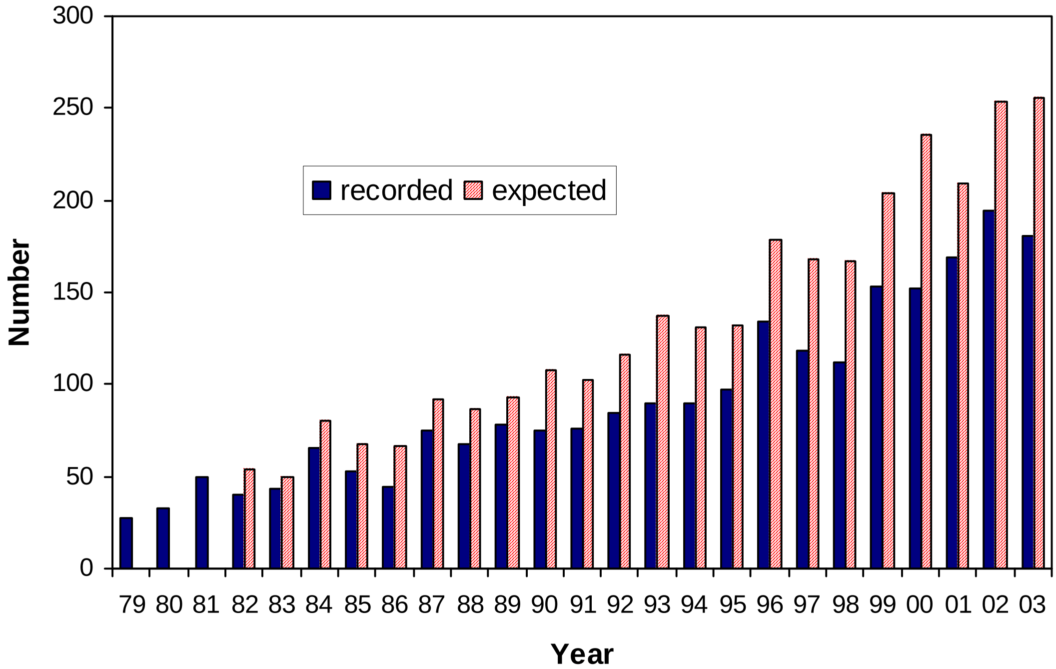


**Figure 4.** The distribution of recorded number and expected "true" number of calvings for the years 1979 to 2003. The available data preclude the model providing expected numbers for the first three years: 1979 to 1981.

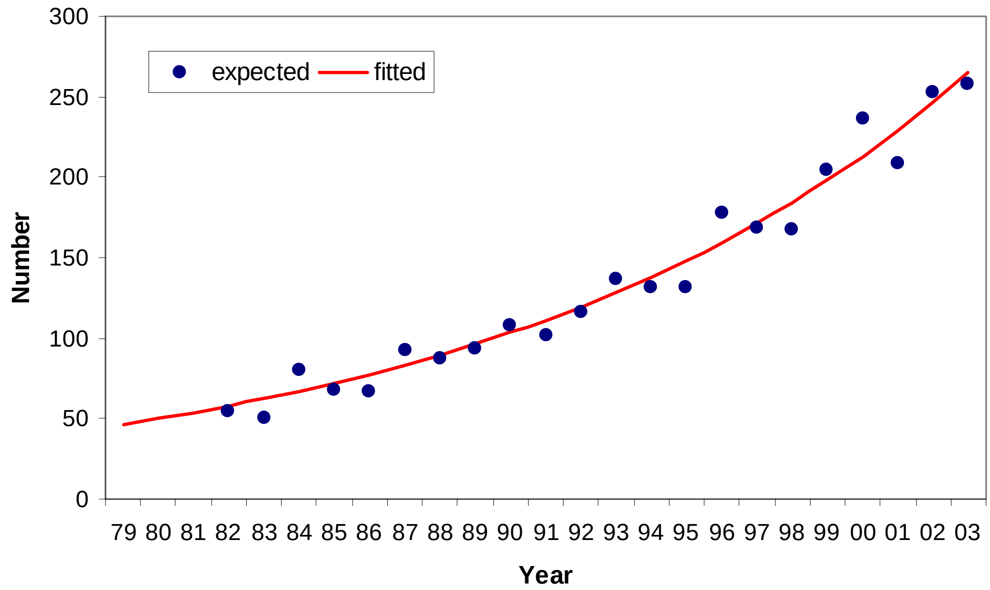


**Figure 5.** Trend in the expected number (from Fig. 4) of total calvings by year off South Africa, 1982 to 2003. The fitted line is estimated using Equations (7) and (8).

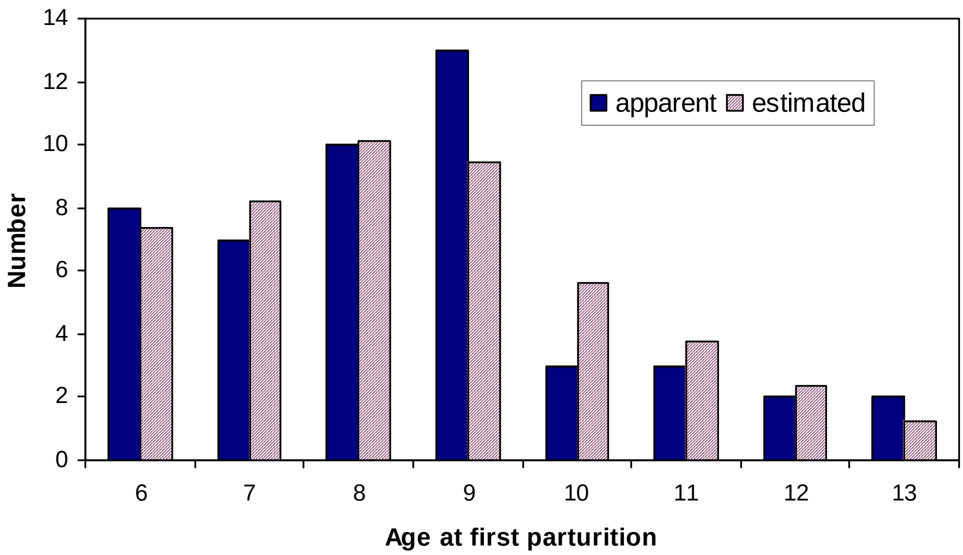


**Figure 6.** The distribution of apparent and corresponding model-estimated (Equations (9) to (11)) ages at first parturition in right whales off South Africa. Note: the word "apparent" is used because missed calvings mean that some observations above reflect subsequent rather than true first parturition.

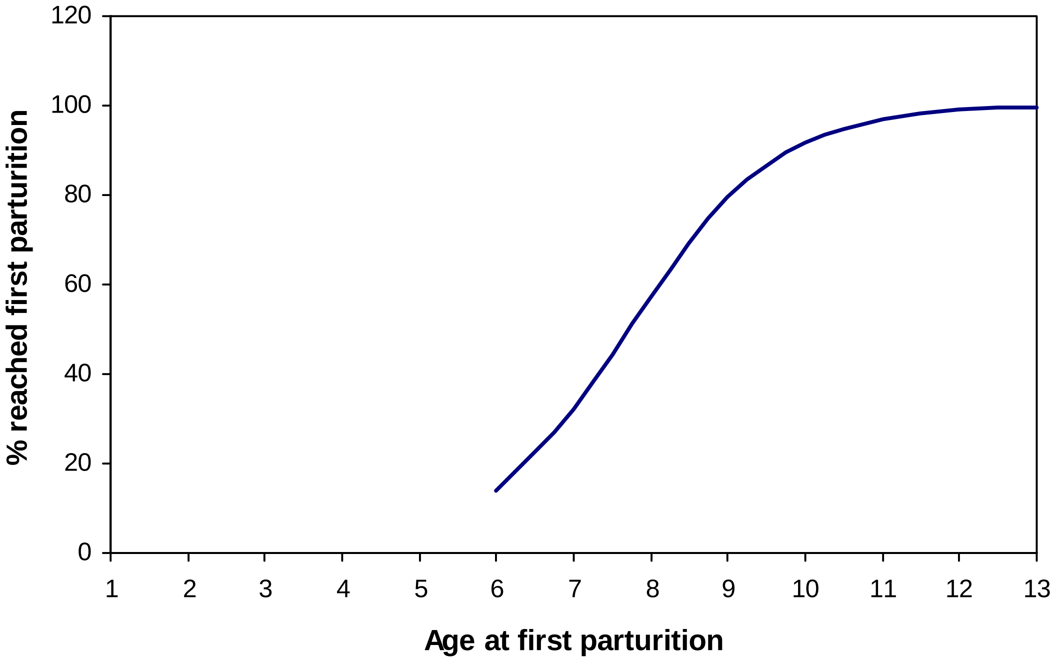


**Figure 7.** Ogive of estimated proportion of females that at each age that have calved at least once.

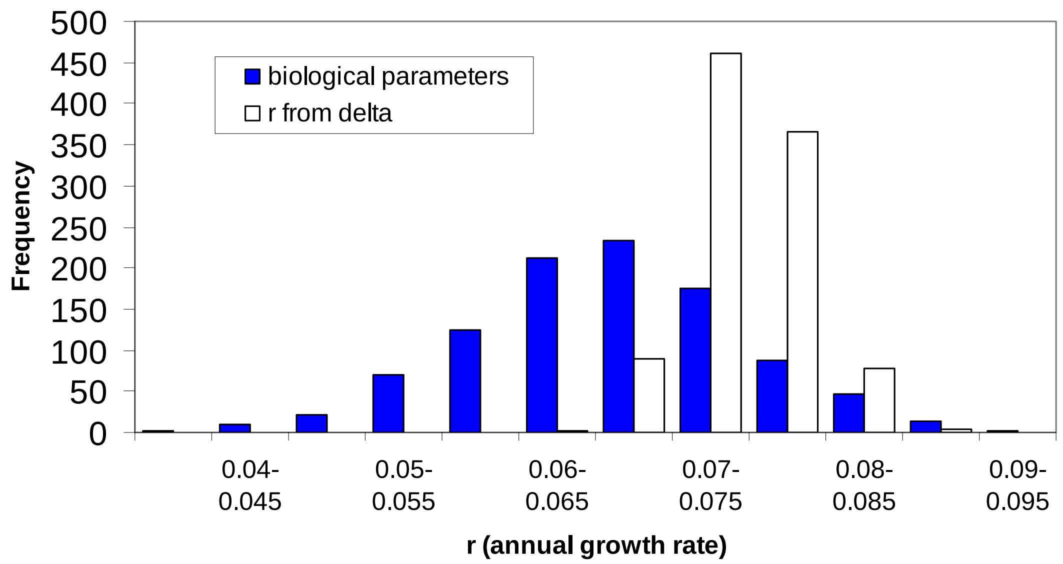


**Figure 8.** Comparison of distributions of annual growth rate (*r*) computed from biological parameters (Equation (12)) and estimated from annual calvings (Equation (7)).