

Application of a photo-identification based assessment model to southern right whales in South African waters, now including data up to 2012

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ABSTRACT

This paper extends the analyses of Brandão *et al.* (2012) which applied the three-mature-stages (receptive, calving and resting) model of Cooke *et al.* (2003) to photo-identification data available from 1979 to 2010 for southern right whales in South African waters, by taking two further years of data into account. The 2012 number of parous females is estimated to be 1 321, the total population (including males and calves) 5 062, and the annual population growth rate 6.6%. This reflects a small reduction to the 6.8% increase rate estimated previously; this is a result of slightly lesser numbers in recent years than estimated previously. Information from resightings of grey blazed calves as adults with calves allows estimation of first year survival rate of 0.850, compared to a subsequent annual rate of 0.988. This information also suggests that 7% (s.e. 6%) of grey blazed calves are not recognised as such when adults; this estimate is much less than that of 27% obtained previously by Brandão *et al.* (2012), and is more compatible with the relative proportions of grey blazed animals amongst calves and amongst calving adults which suggest a value of 10% (s.e. 8%).

INTRODUCTION

This paper updates the results of Brandão *et al.* (2012) of a photo-id based assessment of southern right whales in South African waters using the three-mature-stages (ovulating - also termed "receptive", calving, and resting) model of Cooke *et al.* (2003). The application of the approach is near-identical to that of Cooke *et al.* (2003), except that here the starting population is not assumed to reflect a steady age-structure corresponding to the Leslie matrix model describing the population dynamics. The photo-id data for grey blazed calves, which are known to be female and are identifiable when giving birth themselves, are used to link the dynamics of the mature females with the output of their reproduction by allowing for estimation of parameters for first-year mortality and the maturity ogive. The data used to fit the models has been described in detail in Brandão *et al.* (2011). This paper includes two further years' data than did that of Brandão *et al.* (2012) and incorporates corrections for missed matches and errors in the previous set.

NOTATION AND METHODOLOGY

The notation used in providing results is as follows:

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α	probability that a mature whale that calves ovulates the next year
β	probability that a resting mature whale rests for a further year
γ	probability that an ovulating mature whale rests (or aborts) rather than calves the next year
S	post-first-year annual female survival rate
S_j	first year female survival rate
ρ	probability that a grey blazed female calf is identifiable when itself calving
a_m, δ	parameters of the logistic function of age for the probability that a female whale of that age becomes parous (i.e. has reached the age at first parturition) that year
r^*	mature female growth rate in the period immediately before observations commenced in 1979
r	annual (instantaneous) mature female growth rate.

Note that the basic model allows for a three-year reproductive cycle, keyed to the events ovulating, calving and resting, the first two of which occur more or less contemporaneously in mid-winter.. In the South African situation where observations are made in spring, the adult classifications of “ovulating” and “calving” would effectively translate to whales which were “pregnant” or “lactating” respectively. In simple terms the α parameter allows for the possibility of a two-year cycle, the β a four-year cycle, and the γ a five-year-cycle.

Details of the methodology used – both the population dynamics model and the likelihood maximised to estimate parameter values from the photo-identification data – are given in the Appendix.

RESULTS

Table 1 gives results for the three model variants run: the first (base case) has time invariant β and γ parameters, and the second allows β to be time dependent. A variant where γ was allowed to vary with time was run in a previous analysis, but the results showed hardly any variation and therefore no results are shown for that case. The base case run estimates ρ , the probability that a grey blazed calf maintains its identifiability until it reaches maturity, to be 0.92 (s.e. 0.07) compared to the previous analyses of Brandão *et al.* (2012) which resulted in an estimate of 0.73. The updated estimate compares well to an independent estimate available of 0.90 (s.e. 0.08) (see Appendix). There is a decrease in the first year female survival rate S_j estimate from 0.914 in Brandão *et al.* (2012) to 0.850. Note that the mature female population increase rate r is estimated externally to the main assessment model by fitting a log-linear regression to the annual total number of mature females (i.e. pregnant+lactating+ resting) estimated by the model over the period 1979–2012.

Plots for a number of the model outputs are shown in Figs 1-7.

For the time-invariant model the current (2012) estimate of the number of parous females is 1 321, and of the total population (including calves and assuming a 50:50 sex ratio) is 5 062. The number of parous females is calculated by excluding whales ovulating for the first time from the number of mature females, and is cited following earlier practice in the Scientific Committee of referring to the numbers of females having reached the age at first parturition in right whales as the “mature” component of the population.

Best (2012) suggests that a valid alternative to a neonatal 50:50 sex ratio based on combined data of right whales is 54:46 (female:male). This alternative sex ratio assumption has been incorporated in a sensitivity run of the base case model variant (Table 1). The parameter estimates most affected by an alternative sex ratio assumption are the first year female survival rate S_j estimate which is lower at

0.784 compared to 0.850, and a corresponding higher value of the estimate for ρ , the probability that a grey blazed calf maintains its markings until becoming an adult, of 1.0 compared to 0.923. The equivalent estimate of the current (2012) number of parous females is 1 311, and of the total population (including calves and assuming a 54:46 female:male sex ratio) is 4 678.

DISCUSSION

The estimates of most parameters hardly differ across the three model variants considered. The estimate of α at 2.2% (Table 1) is similar to that of Cooke *et al.* (2003) for the right whales off Argentina. The base case β estimate of 14.1% is slightly greater than the 9.5% for the Argentine population, whereas γ at 6.4% is much less than the 14% for the Argentine whales. In a reversal of the Argentine case, it is possible to estimate time dependence in the β parameter, for which there are weak indications of some increase in recent years, whereas the γ parameter shows no such variation.

The estimate for annual post-first-year female survival S of 0.988 (Table 1) is slightly less than the corresponding estimate of 0.990 from the simpler model of Brandão *et al.* (2011). There is a corresponding increase in the first year female survival rate S_j estimate from 0.74 in Brandão *et al.* (2012) to 0.850. The detectability of mothers with calves has decreased slightly over the monitoring period (Fig. 2). An interesting new feature is the higher proportion of resting females over recent years under the time-dependent β model (Fig. 5).

The base case annual instantaneous growth rate of the parous female population is 6.6% (Table 1), which is slightly lower than the 6.8% of Brandão *et al.* (2012). This reflects a slight reduction in estimated numbers for recent years compared to the previous analysis (Fig. 6). Estimates of the initial age structure in 1979 do not suggest that this growth rate applied to the years immediately preceding 1979, but instead that the population was increasing more slowly over that period at about 1.6% per year (r^* in Table 1), though this rate is not precisely estimated. In qualitative terms this is what might be expected from the impact of (illegal) Soviet catches, which are estimated to have totalled some 306 whales between 0 and 32°E over the period from 1961/62 to 1966/67 (Tormosov *et al.*, 1998), or an average of 51 a year from a total “mature” population (i.e. doubling the number of parous females) estimated to have been about 300 in 1979.

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REFERENCES

- Best, P.B. 2012. Sex ratios in southern right whale calves. Appendix 4 of Annex F of the Report of the Scientific Committee, Panama City, 2012.
- Butterworth, D.S., Brandão, A., Müller, A. and Best, P.B. 2011. Preliminary results for a photo-identification-based assessment of southern right whales in South African waters. IWC document SC/S11/RW29.
- Brandão, A, Best, P.B. and Butterworth, D.S. 2011. Monitoring the recovery of the southern right whale in South African waters. IWC document SC/S11/RW18.
- Brandão, A., Butterworth, D.S., Müller, A. and Best, P.B. 2012. Application of a photo-identification-based assessment model to southern right whales in South African waters. IWC document SC/64/BRG24rev.
- Cooke, J., Rowntree, V. and Payne, R. 2003. Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identifications of calving females observed off Peninsula Valdes, Argentina, during 1971-2000. IWC document SC/55/O23.
- Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* 27:233-249.
- Tormosov, D.D., Mikhailiev, 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 data and conservation implications. *Biological Conservation* 86: 185-197

Table 1. Estimates of various demographic parameters for right whales off South Africa for the time invariant model as well as when the probability β varies with time (see text and Appendix for explanation of symbols). The parameter r^* is the implicit growth rate in period immediately before monitoring commenced in 1979($=-\log(\tau)$). The N^{mature^*} numbers refer to the number of parous females, while the N^{all} numbers refer to the whole population (including males and calves, under the assumption of a 50:50 sex ratio at birth). The quantities in brackets are Hessian-based estimates of standard errors.

Parameter	Model		
	Time invariant	Time varying β	Time invariant (54:46 female:male sex ratio)
α	0.022 (0.003)	0.022 (0.003)	0.022 (0.003)
β (time invariant)	0.141 (0.008)	—	0.141 (0.008)
$\bar{\beta}^*$	—	0.125 (0.040)	—
γ (time invariant)	0.064 (0.008)	0.067 (0.008)	0.064 (0.008)
S	0.988 (0.001)	0.988 (0.001)	0.988 (0.001)
S_j	0.850 (0.043)	0.843 (0.043)	0.784 (0.031)
ρ	0.923 (0.070)	0.930 (0.071)	1.000 (0.007)
a_m	6.402 (0.405)	6.446 (0.447)	6.398 (0.402)
δ	1.047 (0.267)	1.085 (0.295)	1.045 (0.265)
r^*	0.016 (0.104)	0.002 (0.098)	0.015 (0.103)
N_{1979}^{calv}	41 (7.9)	42 (8.1)	41 (7.8)
N_{1979}^{recp}	48 (9.0)	48 (8.9)	48 (8.8)
N_{1979}^{rest}	76 (20.2)	71 (19.1)	76 (20.1)
$N_{1979}^{mature^*}$	150 (32.6)	143 (32.1)	150 (32.3)
N_{2012}^{calv}	437 (15.3)	502 (32.4)	433 (14.5)
N_{2012}^{recp}	504 (18.0)	475 (35.6)	500 (16.7)
N_{2012}^{rest}	489 (16.9)	442 (30.8)	485 (16.1)
$N_{2012}^{mature^*}$	1 321 (44.9)	1 314 (46.3)	1 311 (43.0)
N_{2012}^{all}	5 062 (215)	5 030 (220)	4 678 (174)
r	0.066	0.066	0.065

Note: No standard errors are given for the estimates of r , as at present these are estimated externally rather than internal to the model, and therefore would not incorporate the components of uncertainty associated with the model fit.

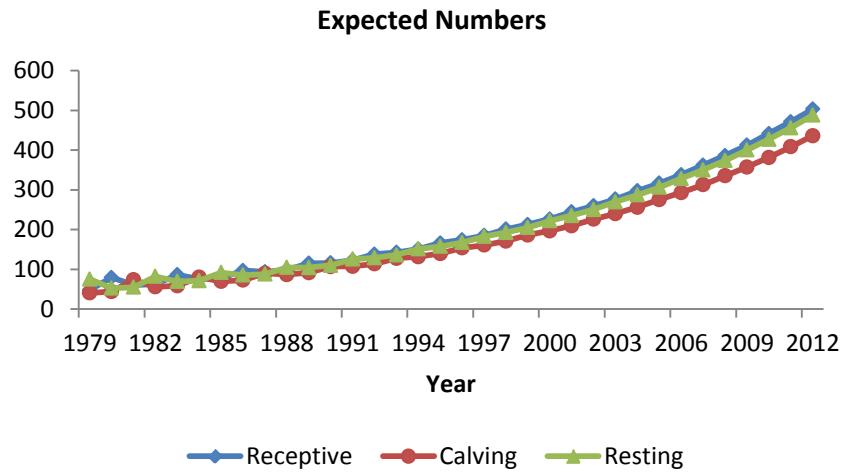


Figure 1. Expected numbers of parous female southern right whales that are in the calving, ovulating or resting stages under the time invariant base case model.

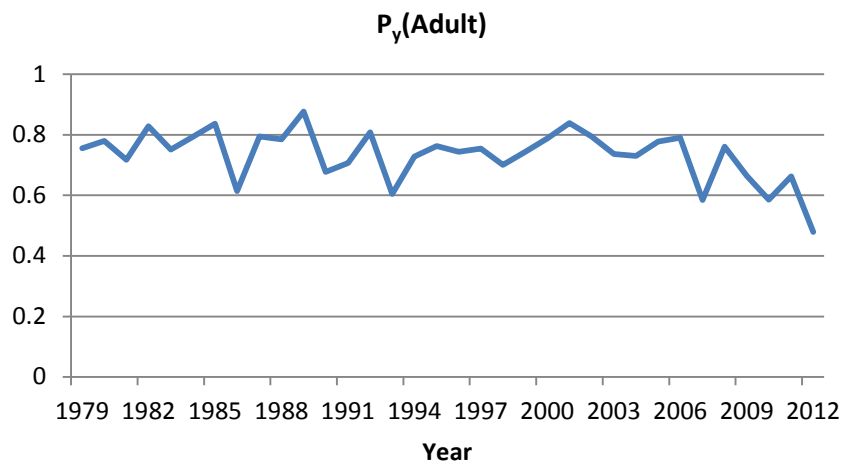


Figure 2. Estimated probabilities of observing a female whale with its calf on aerial surveys under the time invariant base case model. Estimates from the previous analysis of Brandão *et al.* (2012) are indistinguishable from the present ones.

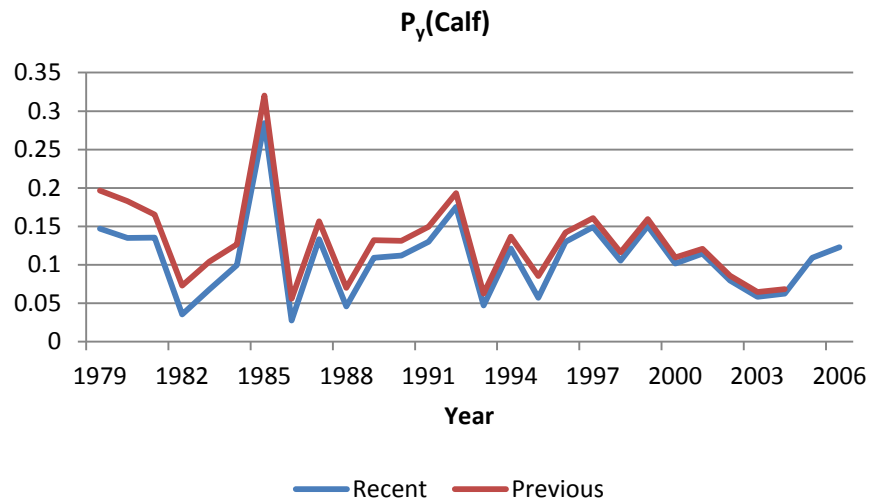


Figure 3. Estimated probabilities that a calf is catalogued (note that only grey blazed calves may be catalogued) under the time invariant base case model coupled to the assumption that calves have a 50:50 sex ratio. For comparison, the estimates from the previous analysis are also shown.

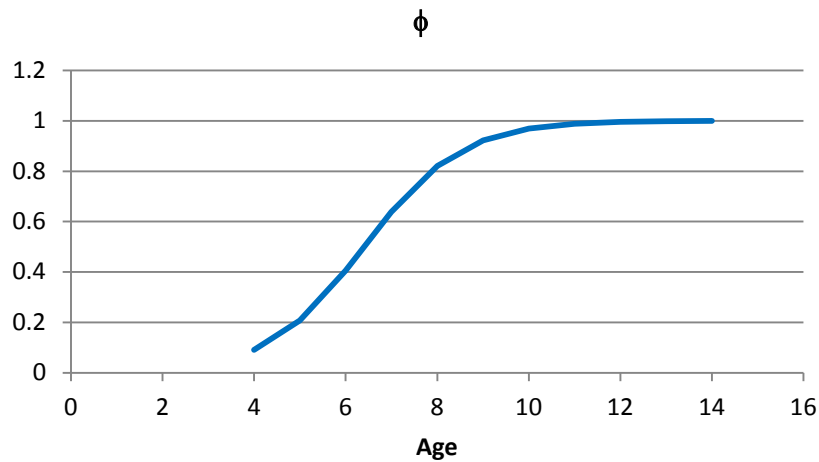


Figure 4. Estimated probabilities of an immature whale of age a ovulating the following year under the time invariant base case model. In implementation the model permits this transition only from age 4 and above. Estimates from the previous analysis are indistinguishable from the present ones.

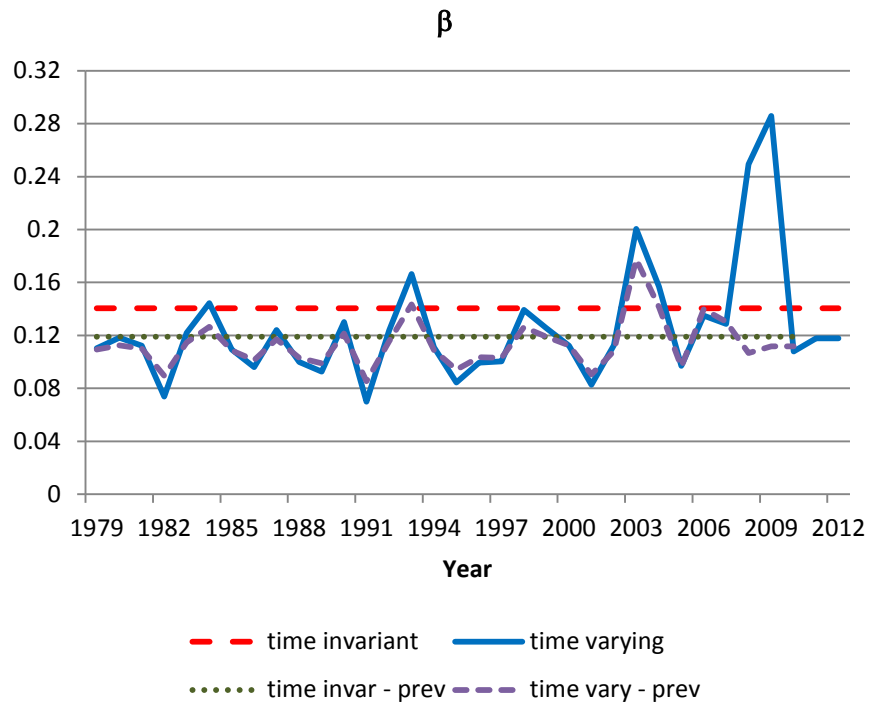


Figure 5. Time varying estimates of the probabilities that a resting whale will rest in the following year. For comparison, the estimates from the previous analysis are also shown.

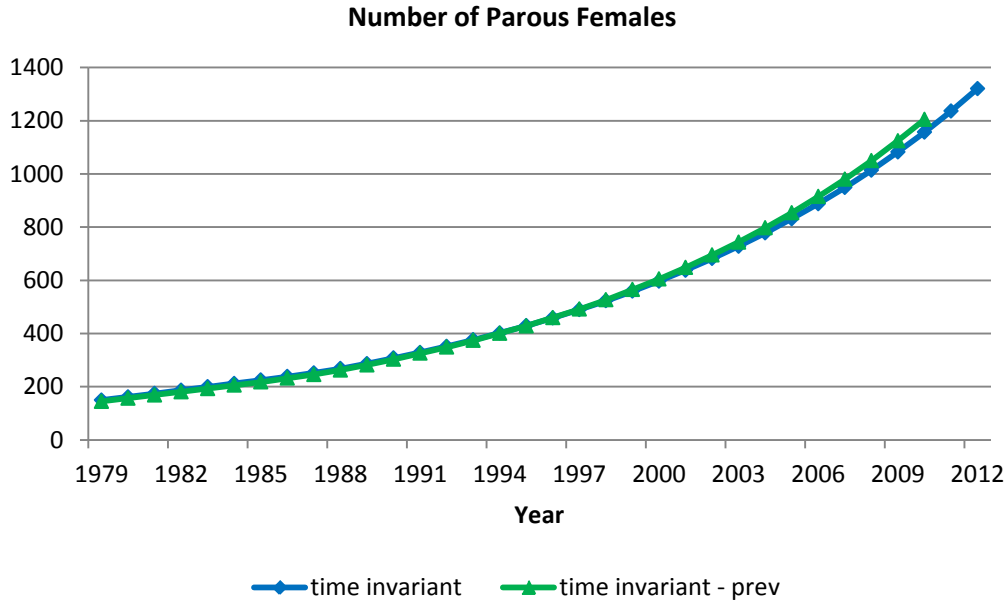


Figure 6. Estimated total number of parous females for the base case time invariant model. The number of parous females for the other two model variants are indistinguishable from the base case model and are therefore not included here. For comparison, the estimates from the previous analysis are also shown.

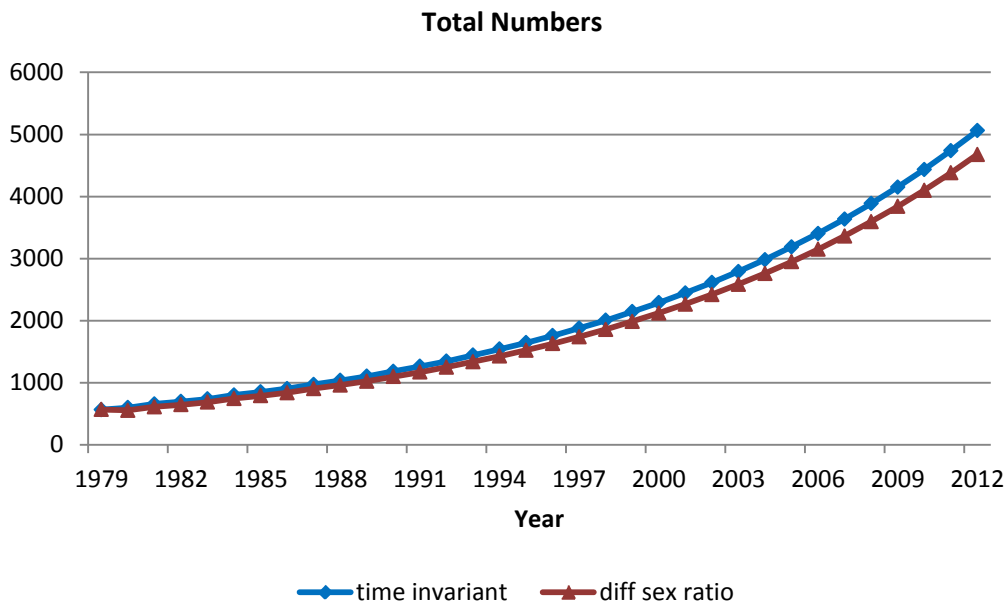


Figure 7. Estimated total number of the whole population (including males and calves, under the assumption of a 50:50 sex ratio at birth) for the base case time invariant model and the variant of the base case which makes the assumption of a 54:46 female: male sex ratio.

Appendix

Methodology

The methodology developed by Cooke *et al.* (2003) has been used to analyse photo-identification data for calving female southern right whales (*Eubalaena australis*) that over-winter off the southern coast of South Africa. Their approach as applied to these whales is summarised below. For a more detailed discussion the reader is referred to the reference above.

Population dynamics for juvenile females

As in Cooke *et al.* (2003), juvenile females are modelled to be in a process of maturation, where:

1. from ages 0 to 4 years no whale is mature,
2. from ages 5 to 14 years a proportion of the whales are mature, and
3. whales are assumed to all be mature once they have reached 15 years of age.

The ratio of females to males is assumed to be 50:50. The population dynamic equations for juvenile females are thus:

$$\begin{aligned}
 N_{0,y+1} &= 0.5N_{y+1}^{calv} \\
 N_{1,y+1} &= N_{0,y}e^{-M_j} \\
 N_{2,y+1} &= N_{1,y}e^{-M} \\
 N_{3,y+1} &= N_{2,y}e^{-M} \\
 N_{4,y+1} &= N_{3,y}e^{-M} \\
 N_{5,y+1} &= (1-\phi_4)N_{4,y}e^{-M} \\
 N_{6,y+1} &= (1-\phi_5)N_{5,y}e^{-M} \\
 &\vdots \\
 N_{14,y+1} &= (1-\phi_{13})N_{13,y}e^{-M}
 \end{aligned}$$

where

- $N_{a,y}$ is the number of immature female southern right whales of age a at the start of year y ; $N_{0,y}$ reflects the number of calves at the start of year y and it is assumed that all female whales are mature by the age of 15 years,
- M_j is the natural mortality from birth to the first birthday,
- M is the natural mortality for ages 1+, and
- ϕ_a is the probability that an immature female whale of age a becomes receptive the next year. This is re-parameterized as:

$$\phi_a = \begin{cases} 1/[1 + e^{-(a-a_m)/\delta}] & 4 \leq a \leq 14 \\ 0 & a < 4 \end{cases}$$

where a_m is the age at which 50% of the female population which remain immature become receptive and δ measures the spread of this ogive.

Population dynamics for mature females

The mature female population is modelled to be in one of three stages: receptive, calving or resting. The definition of these stages is as given by Cooke *et al.* (2003) and the equations for the dynamics are:

$$\begin{aligned} N_{y+1}^{recp} &= \left(\sum_{a=4}^{13} N_{a,y} \phi_a + N_{14,y} \right) e^{-M} + (1 - \beta_y) N_y^{rest} e^{-M} + \alpha_y N_y^{calv} e^{-M} \\ N_{y+1}^{rest} &= \beta_y N_y^{rest} e^{-M} + (1 - \alpha_y) N_y^{calv} e^{-M} + \gamma_y N_y^{recp} e^{-M} \\ N_{y+1}^{calv} &= (1 - \gamma_y) N_y^{recp} e^{-M} \end{aligned}$$

where

- N_y^{recp} is the number of receptive southern right whale females at the start of year y ,
- N_y^{rest} is the number of southern right whale females resting in year y ,
- N_y^{calv} is the number of southern right whale females producing a calf at the start of year y ,
- α_y is the probability that a whale calving in year y becomes receptive in year $y+1$,
- β_y is the probability that a whale resting in year y rests again the next year, and
- γ_y is the probability that a whale that is receptive in year y returns to the resting stage the next year without producing a calf.

The population numbers of female whales in each stage of their reproductive cycle can be separated into the portions of previously seen and unseen whales. These are given by:

$$N_{y+1}^{recp,U} = \left(\sum_{a=4}^{13} \phi_a (1 - P_{y-a}^C (1 - \rho)) N_{a,y} + (1 - P_{y-14}^C (1 - \rho)) N_{14,y} \right) e^{-M} + (1 - \beta_y) N_y^{rest,U} e^{-M} + \alpha_y (1 - P_y^A) N_y^{calv,U} e^{-M}$$

$$N_{y+1}^{recp,S} = \left(\sum_{a=4}^{13} \phi_a P_{y-a}^C (1 - \rho) N_{a,y} + P_{y-14}^C (1 - \rho) N_{14,y} \right) e^{-M} + (1 - \beta_y) N_y^{rest,S} e^{-M} + \alpha_y P_y^A N_y^{calv,U} e^{-M} + \alpha_y N_y^{calv,S} e^{-M}$$

$$\begin{aligned} N_{y+1}^{rest,U} &= \beta_y N_y^{rest,U} e^{-M} + (1 - \alpha_y) (1 - P_y^A) N_y^{calv,U} e^{-M} + \gamma_y N_y^{recp,U} e^{-M} \\ N_{y+1}^{rest,S} &= \beta_y N_y^{rest,S} e^{-M} + (1 - \alpha_y) P_y^A N_y^{calv,U} e^{-M} + (1 - \alpha_y) N_y^{calv,S} e^{-M} + \gamma_y N_y^{recp,S} e^{-M} \\ N_{y+1}^{calv,U} &= (1 - \gamma_y) N_y^{recp,U} e^{-M} \\ N_{y+1}^{calv,S} &= (1 - \gamma_y) N_y^{recp,S} e^{-M} \end{aligned}$$

where

- P_y^C is the probability that a female calf seen in year y is grey blazed and catalogued,
- P_y^A is the probability that a female whale with a calf is seen in year y , and
- U, S are superscripts which denote whales that have yet to be seen (U), or have already been seen (S).

Initial conditions

The initial numbers at each age a of immature female whales are specified as follows:

$$\begin{aligned}
 N_{0,1979} &= 0.5N_{1979}^{calv} \\
 N_{1,1979} &= \tau N_{0,1979} e^{-M_j} \\
 N_{2,1979} &= \tau N_{1,1979} e^{-M} \\
 &\vdots \\
 N_{5,1979} &= \tau (1 - \phi_4) N_{4,1979} e^{-M} \\
 &\vdots \\
 N_{14,1979} &= \tau (1 - \phi_{13}) N_{13,1979} e^{-M}
 \end{aligned}$$

where τ is the ratio of the number of female whales of age a to the number of female whales of age $a-1$ after allowance for natural mortality. This assumes that the population in 1979 had an age structure reflecting steady growth over the previous 14 years.

Initial numbers for mature females in each of the three reproductive stages (i.e. N_{1979}^{calv} , N_{1979}^{recp} , N_{1979}^{rest}) are estimated by fitting the population model to the data. The portion of the initial population numbers which have previously been seen is zero for all stages of the reproductive cycle, and therefore the unseen portion is the same as the total.

Probability of individual sighting histories

Evaluation of these probabilities (q_h^A for whales first sighted with calves, and q_h^C for catalogued grey blazed calves potentially resighted as adults with calves) is complex so that the details are not recorded here at this stage. The third author will explain how these are calculated on request.

Note that the probabilities of sighting histories for whales first seen as calves take account of the probability (ρ) that such grey blazed calves retain their markings until calving themselves, so that they would not if seen again then be recorded as new animals.

Likelihood function

The observed frequencies of each sighting history n_h^A of female whales first sighted as an adult are assumed to follow Poisson distributions with expected values e_h^A so that the contribution to the log-likelihood function (omitting the constant term) is given by:

$$\ln(e_h^A; \theta) = \sum_{\text{all } h} (n_h^A \ln(e_h^A) - e_h^A),$$

where

- θ is a vector of all estimable parameters attributable to the sighting histories of whales first seen with a calf as an adult,
- h is a possible sighting history,

n_h^A is the observed number of female whales with sighting history h ,
 e_h^A is the expected number of female whales with an individual sighting history h (where the adult female was first seen with a calf in year y), given by:

$$e_h^A = \hat{N}_y^{calv,U} \hat{P}_y^A \hat{q}_h^A,$$

where

$\hat{N}_y^{calv,U}$ is the number of calving whales that have not been observed before the start of year y ,
 \hat{P}_y^A is the estimated probability that a whale is observed with a calf in year y ,
 \hat{q}_h^A is the estimated probability of history h being observed given that the adult whale with its calf was first sighted in year y .

It is not necessary to estimate e_h^A for all possible sighting histories, but for only those histories that are observed (i.e. where $n_h^A > 0$; $n_h^A = 0$ for histories not observed) as well as the total number of sightings expected since:

$$\begin{aligned} \sum_{\text{all } h} (n_h^A \ln(e_h^A) - e_h^A) &= \sum_{\text{obs } h} (n_h^A \ln(e_h^A)) - \sum_{\text{obs } h} e_h^A - \sum_{\text{unobs } h} e_h^A \text{ and} \\ \sum_{\text{unobs } h} e_h^A &= \sum_y \sum_{\text{unobs } h(y)} \hat{N}_y^{calv,U} \hat{P}_y^A \hat{q}_h^A = \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A \sum_{\text{unobs } h(y)} \hat{q}_h^A \\ &= \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A \left(1 - \sum_{\text{obs } h(y)} \hat{q}_h^A \right) = \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A - \sum_{\text{obs } h(y)} e_h^A, \end{aligned}$$

where $h(y)$ is a history for a whale first sighted in year y , and therefore the log-likelihood function can be re-written as:

$$\ln(e_h^A; \theta) = \sum_{h=1}^{n^A} (n_h^A \ln(e_h^A)) - \sum_{y=1979}^{2010} \hat{N}_y^{calv,u} \hat{P}_y^A$$

where

n^A is the total number of observed unique sighting histories.

Similarly, the observed frequencies of each sighting history n_h^C of female whales first sighted and catalogued as grey blazed calf are assumed to follow Poisson distributions with expected value e_h^C so that their contribution to the log-likelihood function is given by:

$$\ln(e_h^C; \theta^*) = \sum_{h=1}^{n^C} (n_h^C \ln(e_h^C)) - \sum_{y=1979}^{2010} \hat{N}_{0,y} \hat{P}_y^C$$

where

θ^* is a vector of all estimable parameters attributable to the sighting histories of whales first sighted and catalogued as a grey blazed calf,
 n^C is the total number of observed unique sighting histories for such whales, and
 e_h^C is the expected number of female whales with an individual sighting history (where they were first seen and catalogued as a grey blazed calf in year y), given by:

$$e_h^C = \hat{N}_{0,y} \hat{P}_y^C \hat{q}_h^C,$$

where

\hat{P}_y^C is the estimated probability that a grey blazed female calf was first catalogued in year y , and

\hat{q}_h^C is the estimated probability of history h being observed given that the calf was catalogued in year y .

The probabilities of observing a whale with a calf (\hat{P}_y^A) in the first three years were not well estimated because of the few sighting histories in the initial period, so that a penalty function was used to ensure that the estimates of \hat{P}_y^A for the first three years were in the range of the average of the subsequent ten years. Thus the following penalty function was added to the total negative log-likelihood function:

$$\frac{1}{2\sigma_P^2} \sum_{y=1979}^{1981} (\hat{P}_y^A - \bar{P})^2,$$

where

\bar{P} is the average of the \hat{P}_y^A estimates for the years 1982 to 1991, and

σ_P is the standard deviation of those \hat{P}_y^A probabilities.

Time variant probabilities

Following the approach by Cooke *et al.* (2003), the probabilities of a calving whale becoming receptive the following year (α_y), the probabilities of a resting whale remaining in the resting stage (β_y) and the probabilities of receptive whale returning to the resting stage (γ_y) are fitted in the model in two ways. In the first they do not change over time, whereas in the second they are allowed to vary over time. Because of the scarcity of observed events in the sighting histories of whales with a calving interval of 2 years, the α_y probabilities are always considered to be time invariant. When the other two probability parameters are considered to be time variant, they are treated as random effects in the model, assuming that they have a normal distribution with mean $\bar{\beta}$ (or $\bar{\gamma}$) and standard deviation σ_β (or σ_γ). The ADMB-RE module for the ADMB package (Fournier *et al.*, 2012) is used for estimation for such time varying parameters when these are introduced.

Incorporating further information on the probability that a grey blazed calf maintains its markings until adult

Annual data on the proportion of adult whales that are grey blazed and the proportion of calves that are grey blazed provides extra information on the probability of calves that are grey blazed keep their markings until becoming adults³. The ratio of the average proportion of grey blazed adults to the proportion of grey blazed calves (ρ^*), and its associated standard error (σ_{ρ^*}) is used in a sensitivity test of the time invariant model in which a penalty is added to the log-likelihood function to take this further information into account, i.e. the following term is added to the total negative log-likelihood function:

³Note that apparent loss of markings might also reflect failure to recognise a marked adult or a higher natural mortality in grey blazed compared to other female calves.

$$\frac{1}{2\sigma_{\rho^*}^2}(\rho - \rho^*)^2,$$

where in this instance $\rho^* = 0.902$ and $\sigma_{\rho^*} = 0.081$.

Estimable parameters

The estimable parameters in the model are S , S_j , α , β , γ , a_m , δ , P_y^A , P_y^C , τ , ρ , N_{1979}^{calv} , N_{1979}^{recp} , and N_{1979}^{rest} . The model parameters that are probabilities are transformed to the logit scale, so that the corresponding log-odds ratios are the estimable parameters in the model. The parameter ρ does not appear in the equations given above, but it appears in the calculation of the probability (q_h^C) of a sighting history given that the whale was first sighted as a calf.