Application of a photo-identification based assessment model to southern right whales in South African waters

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ABSTRACT

The three-mature-stages (receptive, calving and resting) model of Cooke *et al.* (2003) is applied to photo-identification data available from 1979 to 2010 for southern right whales in South African waters. The 2010 number of females having reached the age at first parturition is estimated to be 1 205, the total population (including males and calves) 4 725, and the annual population growth rate 6.8%. The probability (average 11%) that a resting mature whale rests for a further year appears to vary annually, whereas the probability (7%) that a receptive whale rest (or aborts) rather than calves the next year appears to be constant. Information from resightings of grey blazed calves as adults with calves allows estimation of first year survival rate of 0.914 (compared to a subsequent annual rate of 0.987, and an age at 50% maturity of 6.4 years. However this suggests also that 27% (s.e. 6%) of grey blazed calves lose their marking before becoming adults. In contrast, the relative proportions of grey blazed animals amongst calves and amongst calving adults suggest rather a value of 10% (s.e. 8%). If the proportion losing markings is in fact 10%, first year survival rates estimate drops to 0.837 and the population growth rate to 6.4% pa.

INTRODUCTION

This paper presents results of a photo-id based assessment of southern right whales in South African waters using the three-mature-stages (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).

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Note that this paper includes two further years of data than an earlier version (Butterworth *et al.,* 2011) tabled at the 2011 intersessional workshop in Buenos Aires, and also corrects some coding errors in those earlier computations.

NOTATION AND METHODOLOGY

The notation used in providing results is as follows:

α probability that a mature whale that calves becomes receptive the next year
β probability that a resting mature whale rests for a further year
γ probability that a receptive 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 mature 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: receptive to calve to rest. 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. In the South African situation where observations are made in spring, the adult classifications of "calving" and "receptive" would effectively pertain to whales which were "lactating" or "pregnant" respectively.

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 four 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 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 markings until becoming an adult, to be 0.73 (s.e. 0.06). This is rather low compared to the independent estimate available of 0.90 (s.e. 0.08) (see Appendix). Therefore two further variants were run: the first incorporates this extra information in the likelihood for the base case model, while the second fixes ρ at this alternative estimate of 0.9. 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. receptives+calvers+resters) estimated by the model over the period 1979–2010.

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

For the time-invariant model the current (2010) estimate of the number of females having reached the age at first parturition is 1 205, and of the total population (including calves and assuming a 50:50 sex ratio) is 4 725.The number having reached the age at first parturition is calculated by excluding whales becoming receptive (i.e. ovulating) for the first time from the number of mature females; the former number is quoted to relate to customary practice in the Scientific Committee for right whales of referring to the numbers of females having reached the age at first parturition as the "mature" component of the population.

Best (2012) suggests that a valid alternative to a 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 survival rate S_j estimate which is lower at 0.843 compared to 0.914, 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 0.795 compared to 0.733. The updated estimate of the current (2010) number of females having reached the age at first parturition is 1 194, and of the total population (including calves and assuming a 54:46 female:male sex ratio) is 4 358.

DISCUSSION

The estimates of most parameters hardly differ across the four model variants considered. The estimate of α at 2.3% (Table 1) is similar to that of Cooke *et al.* (2003) for the right whales off Argentina. The base case β estimate of 11.9% is slightly greater than the 9.5% for the Argentine population, whereas γ at 7.1% is much less than the 14% for the Argentine whales. In a reversal of the Argentinian 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 0.987 (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.* (2011) to 0.914. The detectability of mothers with calves has decreased slightly over the monitoring period (Fig. 2).

The base case annual instantaneous growth rate of the mature female population (see also Fig. 6) is 6.8% (Table 1), which is identical to that of Brandão *et al.* (2011). 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 3% 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 estimated to have been about 300 in 1979.

The slightly higher annual growth rate (r) compared to previous estimates is a reflection of the high first year survival rate estimate S_f = 0.914, which in turn implies that about 26.7% (1-ρ where ρ = 0.733) of female grey blazed calves are no longer identifiable when reaching adulthood. This estimate is only barely statistically compatible with the independent estimate of 0.90 deduced from comparative proportions of grey blazed whales amongst calves and amongst adults. Forcing ρ = 0.90 when fitting the model sees a deterioration in the $-\ln L$ by 1.28 units. Such a change results in only the following notable differences from the results of the base case model run (see also Figs. 6 and 7):

- first year survival drops from 0.914 to 0.837
- the annual increase rate of mature females drops from 6.8 to 6.4%
- the current number of females having reached the age at first parturition drops by about 1%, and the total population numbers by about 8%.

ACKNOWLEDGEMENTS

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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 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 female whales having reached the age at first parturition, 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.

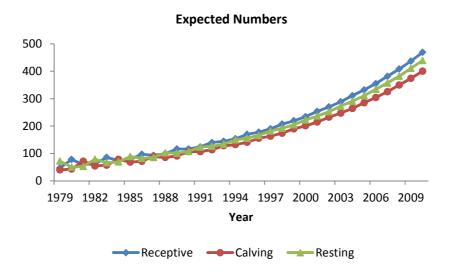| Parameter	Model				
	Time invariant	Time varying β	Time invariant (add ρ penalty)	Time invariant ($\rho = 0.9$)	Time invariant (54:46 female:male sex ratio)
α	0.023 (0.003)	0.0203 (0.003)	0.023 (0.003)	0.023 (0.003)	0.023 (0.003)
β (time invariant)	0.119 (0.008)	—	0.119 (0.008)	0.118 (0.008)	0.119 (0.008)
$\bar{\beta}^*$	—	0.114 (0.029)	—	—	—
γ (time invariant)	0.071 (0.008)	0.071 (0.008)	0.071 (0.008)	0.070 (0.008)	0.071 (0.008)
S	0.987 (0.001)	0.987 (0.001)	0.987 (0.001)	0.987 (0.001)	0.987 (0.001)
S_j	0.914 (0.050)	0.912 (0.050)	0.911 (0.050)	0.837 (0.034)	0.843 (0.046)
ρ	0.733 (0.063)	0.734 (0.064)	0.741 (0.062)	**0.900**	0.795 (0.069)
a_m	6.410 (0.474)	6.423 (0.483)	6.408 (0.473)	6.370 (0.461)	6.407 (0.472)
δ	1.165 (0.357)	1.173 (0.343)	1.165 (0.337)	1.164 (0.335)	1.163 (0.335)
r^*	0.027 (0.105)	0.022 (0.103)	0.027 (0.105)	0.008 (0.105)	0.026 (0.105)
N^{calv}_{1979}	40 (7.9)	40 (7.8)	40 (7.8)	43 (8.4)	40 (7.8)
N^{recp}_{1979}	47 (8.7)	47 (8.7)	47 (8.8)	51 (9.3)	47 (8.7)
N^{rest}_{1979}	73 (19.0)	70 (18.6)	73 (19.0)	78 (20.7)	72 (18.9)
$N^{mature^*}_{1979}$	145 (31.0)	143 (30.9)	146 (31.2)	156 (34.2)	144 (31.0)
N^{calv}_{2010}	401 (14.7)	415 (20.8)	400 (14.6)	389 (13.6)	397 (14.6)
N^{recp}_{2010}	470 (17.4)	452 (25.3)	468 (17.4)	453 (15.7)	465 (17.3)
N^{rest}_{2010}	440 (15.9)	442 (22.1)	439 (15.8)	427 (14.9)	435 (15.8)
$N^{mature^*}_{2010}$	1 205 (42.8)	1 206 (43.3)	1 204 (42.7)	1 174 (40.3)	1 194 (42.6)
N^{all}_{2010}	4 725 (214)	4 729 (216)	4 712 (212)	4 460 (170)	4 358 (197)
r	0.068 (0.0002)	0.068 (0.0001)	0.068 (0.0002)	0.064 (0.0001)	0.068 (0.0002)

Expected Numbers

Figure 1. Expected numbers of mature female southern right whales that are in the calving, receptive or resting stages under the time invariant base case model.
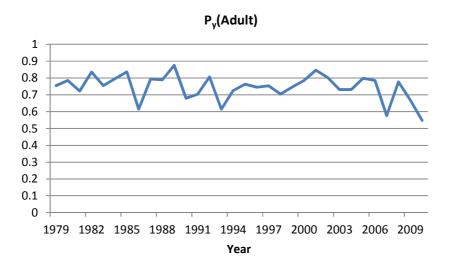
P_y(Adult)

Figure 2. Estimated probabilities of observing a female whale with its calf on aerial surveys under the time invariant base case model.

P_y(Calf)
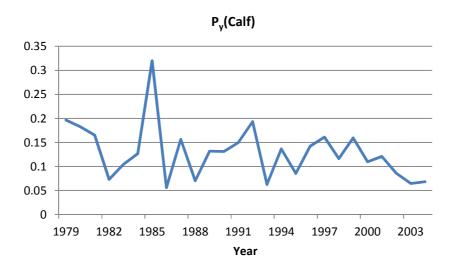
Estimated probabilities that a calf is catalogued.

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.
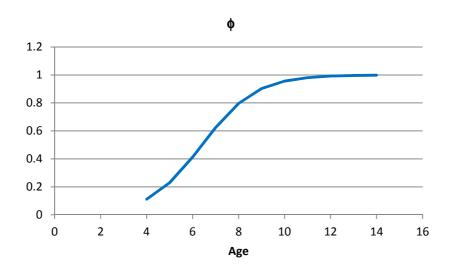
φ

Figure 4. Estimated probabilities of an immature whale of age *a* becoming receptive the following year under the time invariant base case model. In implementation the model permits this transition only from age 4 and above.
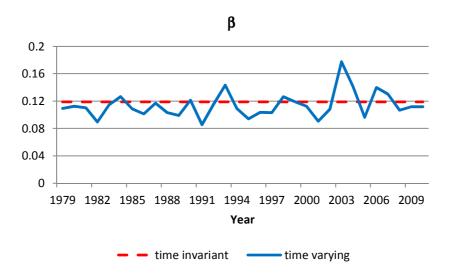
7

β

Figure 5. Time varying estimates of the probabilities that a resting whale will rest in the following year.

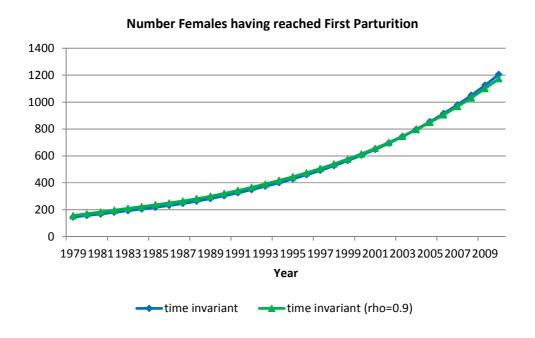### Number Females having reached First Parturition

Figure 6. Estimated total number of females having reached the age at first parturition for the base case time invariant model and the variant of the base case which fixes the ρ parameter at 0.9. The number of females having reached the age at first parturition for the other two model variants are indistinguishable from the base case model and are therefore not included here.
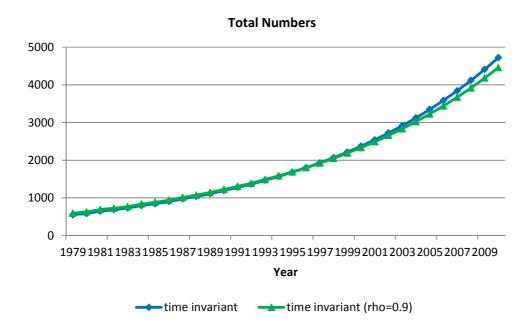
Total Numbers

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 fixes the ρ parameter at 0.9.

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:

$$N_{0,y+1} = 0.5 N_{y+1}^{calv}$$

$$N_{1,y+1} = N_{0,y} e^{-M_j}$$

$$N_{2,y+1} = N_{1,y} e^{-M}$$

$$N_{3,y+1} = N_{2,y} e^{-M}$$

$$N_{4,y+1} = N_{3,y} e^{-M}$$

$$N_{5,y+1} = \left(1 - \phi_4\right) N_{4,y} e^{-M}$$

$$N_{6,y+1} = \left(1 - \phi_5\right) N_{5,y} e^{-M}$$

$$\vdots$$

$$N_{14,y+1} = \left(1 - \phi_{13}\right) N_{13,y} e^{-M}$$

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:

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

where a_m is the age at which 50% of the immature female population 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:

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

$$N_{y+1}^{rest} = \beta_y N_y^{rest} e^{-M} + \left(1 - \alpha_y \right) N_y^{calv} e^{-M} + \gamma_y N_y^{recp} e^{-M}$$

$$N_{y+1}^{calv} = \left(1 - \gamma_y \right) N_y^{recp} e^{-M}$$

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:

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

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

$$N_{y+1}^{rest,U} = \beta_y N_y^{rest,U} e^{-M} + \left(1 - \alpha_y \right) \left(1 - P_y^A \right) N_y^{calv,U} e^{-M} + \gamma_y N_y^{recp,U} e^{-M}$$

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

$$N_{y+1}^{calv,U} = \left(1 - \gamma_y\right) N_y^{recp,U} e^{-M}$$

$$N_{y+1}^{calv,S} = \left(1 - \gamma_y\right) N_y^{recp,S} e^{-M}$$

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:

$$N_{0,1979} = 0.5 N_{1979}^{calv}$$

$$N_{1,1979} = \tau N_{0,1979} e^{-M_j}$$

$$N_{2,1979} = \tau N_{1,1979} e^{-M}$$

$$\vdots$$

$$N_{5,1979} = \tau \left(1 - \phi_4\right) N_{4,1979} e^{-M}$$

$$\vdots$$

$$N_{14,1979} = \tau \left(1 - \phi_{13}\right) N_{13,1979} e^{-M}$$

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 $\left(\text{i.e. } N_{1979}^{calv}, N_{1979}^{recp}, N_{1979}^{rest}\right)$ 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:

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

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:

$$\sum_{\text{all } h} \left(n_h^A \ln(e_h^A) - e_h^A \right) = \sum_{\text{obs } h} \left(n_h^A \ln(e_h^A) \right) - \sum_{\text{obs } h} e_h^A - \sum_{\text{unobs } h} e_h^A \text{ and}$$

$$\sum_{\text{unobs } h} e_h^A = \sum_y \sum_{\text{unobs } h(y)} \hat{N}_y^{calv,U} \hat{P}_y^A \hat{q}_h^A = \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A \sum_{\text{unobs } h(y)} \hat{q}_h^A$$

$$= \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A \left(1 - \sum_{\text{obs } h(y)} \hat{q}_h^A \right) = \sum_y \hat{N}_y^{calv,U} \hat{P}_y^A - \sum_{\text{obs } h(y)} e_h^A \quad ,$$

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:

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

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 agrey blazed calfare assumed to follow Poisson distributions with expected value e_h^C so that their contribution to the log-likelihood function is given by:

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

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:

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

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

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(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 adults[3]. The ratio of the average proportion of grey blazed adults to the proportion of grey blazed calves ($\rho*$), and its associated standard error ($\sigma_{\rho*}$) 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:

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

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 $\left(q_h^C\right)$ of a sighting history given that the whale was first sighted as a calf.

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[3]Note 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.