

SC/67B/SH/22

Updated application of a  
photo-identification based assessment  
model to southern right whales in South  
African waters, focussing on inferences to  
be drawn from a series of appreciably  
lower counts of calving females over  
2015 to 2017

Anabela Brandao , Els Vermeulen , Andrea  
Ross-Gillespie , Ken Findlay and Doug S.  
Butterworth



INTERNATIONAL  
WHALING COMMISSION

# Updated application of a photo-identification based assessment model to southern right whales in South African waters, focussing on inferences to be drawn from a series of appreciably lower counts of calving females over 2015 to 2017

Anabela Brandão<sup>1</sup>, Els Vermeulen<sup>2</sup>, Andrea Ross-Gillespie<sup>1</sup>, Ken Findlay<sup>3</sup> and Doug S. Butterworth<sup>1</sup>

## ABSTRACT

This paper extends the analyses of Brandão *et al.* (2013) which applied the three-mature-stages (receptive, calving and resting) model of Cooke *et al.* (2003) to photo-identification data available from 1979 to 2012 for southern right whales in South African waters, by taking five further years of data into account. The lower counts of calving females over 2015 to 2017 are indicated to be a reflection of time variability in the probability that a resting whale rests another year, rather than of any mass mortality. The 2017 number of parous females is estimated to be 1 765, the total population (including males and calves) 6 116, and the annual population growth rate 6.5%. This reflects a small decrease to the 6.6% increase rate estimated previously; even in the instance of lesser numbers seen 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 0.852, a slight increase from the previous estimate of 0.850, compared to a subsequent annual rate of 0.988.

## INTRODUCTION

This paper updates the results of Brandão *et al.* (2013) 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.*

---

<sup>1</sup> MARAM (Marine Resource Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa.

<sup>2</sup> Mammal Research Institute Whale Unit, Department of Zoology and Entomology, University of Pretoria, South Africa.

<sup>3</sup> Cape Peninsula University of Technology, Zonnebloem, Cape Town, South Africa

(2011). However it is to be noted that in 2016 and 2017 the stretch of coastline surveyed was extended to Lamberts Bay on the West coast due to the paucity of southern right whale sightings. This paper includes five further years' data than in Brandão *et al.* (2013), and incorporates corrections for missed matches and errors in the previous set.

A point of particular interest is the much lower level of sightings of mothers with calves over the 2015-2017 period, despite no change in survey methodology (see Figure 1). This document focuses on the inferences to be drawn from this – the first occasion that this survey series that has shown other than a fairly steady continuing increase.

## NOTATION AND METHODOLOGY

The notation used in providing results is as follows:

$\alpha$	probability that a mature whale that calves ovulates the next year
$\beta$	probability that a resting mature whale rests for a further year
$\gamma$	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
$\rho$	probability that a grey blazed female calf is identifiable when itself calving
$a_m, \delta$	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: receptive to calve to rest. In simple terms the  $\alpha$  parameter allows for the possibility of a two-year cycle, the  $\beta$  a four-year cycle, and the  $\gamma$  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

The key question to which the recent lower counts give rise is whether these reflect a mass mortality or rather reduction in the area surveyed because of a lower proportion of the adult female population being present. Information on apparent calving intervals plotted in Figure 2 suggests a recent drop in the three- and increase in the four-year interval, seemingly supporting the latter hypothesis. But these proportions are potentially confounded by changing sighting efficiency, so that a full modelling exercise is necessary to take due account of the contribution of these confounding effects. Previously the base case assumption was that the  $\theta$  parameter

(the probability that a resting whale rests for a further year) was time invariant, but with these indications of changes, a run allowing this parameter to change over time takes on added importance,

Table 1 gives results for these two model variants: the first has time invariant  $\beta$  and  $\gamma$  parameters, and the second allows  $\beta$  to be time dependent. A variant where  $\gamma$  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 estimated probabilities that a calf is catalogued do not change too much between the time variant and time invariant models (Figure 3 – top panel). However there is a marked difference in the probabilities of observing a female whale with its calf on aerial surveys under these two models (Figure 3 – bottom panel). Under the time varying model the detectability of mothers with calves decreases from 2015, after a large peak in 2014 corresponding to a peak in the presence of cow-calf pairs of southern right whales in South African waters in 2014, followed by a drop off since 2015. Allowing for time varying probabilities that a resting whale will rest in the following year ( $\beta$ ) results in very high estimated probabilities for the period 2012 to 2015 before dropping to similar values obtained for previous years (Figure 4). For the time invariant model, the estimate of this probability increases from 0.141 estimated previously to 0.201 (Table 1 and Figure 4). These results show that the time invariant model is no longer able to reflect the observed data of the cow-calf pairs in Southern Africa waters in the last few years properly. The very marked changes in the  $\beta$ s over time, reflecting the drop in the observation of cow-calf pairs in the 2015-2017 period, show that the time varying  $\beta$  model is to be preferred as the base case model and further discussion will centre on this model.

Figure 5 shows the expected number of mature female southern right whales that are in the calving, receptive or resting stages for the base case model. A large number of females is expected in the resting stage in the later years, but this drops to similar levels as previously in 2017. The number of receptive females increases from 2015, while the number of calving females drops in 2014 and then gradually increases again.

The estimate of the first year female survival rate  $S_j$  of 0.852 is very similar to that reported in Brandão *et al.* (2013) (0.850). The estimate for annual post-first-year female survival  $S$  of 0.988 (Table 1) has not changed. The base case annual instantaneous growth rate of the mature female population  $r$  is estimated at 6.5% (s.e. 0.3%), very similar to the previous estimate of 6.6%. This mature female population increase rate  $r$  is estimated 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 1979–2017. The probability that female grey blazed calves are no longer identifiable when reaching adulthood is estimated at 13% ( $1-\rho$  where  $\rho = 0.874$ ). This estimate is statistically compatible with the independent estimate of 0.90 deduced from comparative proportions of grey blazed whales amongst calves and amongst adults.

For the time-invariant model the current (2017) estimate of the number of parous females is 1 765 (Table 1 and Figure 6), and of the total population (including males and calves and assuming a 50:50 sex ratio) is 6 116 (Table 1 and Figure 7). 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 the 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.

## DISCUSSION

The  $\beta$  time varying model shows marked changes over the years in the expected number of resting females and the probability that a resting female will also rest for the next year. This result combined with the result that the annual instantaneous growth rate of the mature female population remains very similar to that estimated previously (6.5% rather than 6.6% previously) and that the adult and the first year survival rates have hardly changed if at all suggests that the hypothesis of lengthened calving intervals is to be favoured over mass mortality to account for the low survey numbers over 2015-2017.

In general, calving intervals of 4 and 5 years are interpreted as resulting from calving failures. More specifically, 4 year calving intervals are believed to result from a failure to initiate gestation (i.e. the female spends an extra year resting) or foetal loss early in gestation after which the female switches to resting until the next mating season (Knowlton et al. 1994). Five year calving intervals are generally believed to be the result of foetal loss late in gestation or the loss of a newborn calf which frequently remains unobserved (i.e. a 3-year calving interval plus a 2-year interval) (Knowlton et al. 1994). Although so far no effects are visible in the data, an increase in calving intervals was projected to eventually lead to decreased population growth rates in other breeding grounds (e.g. Maron et al. 2015).

The reproductive success of southern right whales is dependent on their body condition and therefore foraging success (Leaper et al. 2006). Direct links between a decreased calving success and decreased krill densities at feeding grounds due to climate anomalies have been found for the breeding areas of Argentina (Leaper et al. 2006) and Brazil (Seyboth et al. 2016). Considering the South African southern right whales are believed to feed across three major feeding grounds in summer, the increased calving intervals of recent years would require poor feeding conditions in all of these feeding grounds since before 2014.

## ACKNOWLEDGEMENTS

Funding support from the International Whaling Commission is gratefully acknowledged.

## 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.
- 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., Ross-Gillespie, A. and Best, P.B. 2013. Application of a photo-identification-based assessment model to southern right whales in South African waters, now including data up to 2012. IWC document SC/65/BRG17.
- 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.
- Knowlton, A.R., Kraus, S.D., and Kenney, R.D. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Canadian Journal of Zoology* 72:1297–1305
- Leaper, R., Cooke, J., Trathan, P., Reid, K., and Rowntree, V. 2006. Global climate change drives southern right whales (*Eubalaena australis*) population dynamics. *Biology Letters* 2: 289-92.
- Maron, C.F., Rowntree, V.J., Sironi, M., Uhart, M., Payne, R.S., Adler, F.R., Seger, J. 2015. Estimating population consequences of increased calf mortality in the southern right whales off Argentina. IWC document SC/66a/BRG/1.
- Seyboth, E., Groch, K.R., Dalla Rosa, L., Reid, K., Flores, P.A., and Secchi, E.R. 2016. Southern right whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Scientific reports*, 6, 28205.
- Tormosov, D.D., Mikhaliyev, 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  $\beta$  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 parameter  $\bar{\beta}^*$  is the average of the  $\beta$  probabilities. 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. For comparison, estimates obtained in the previous analysis of the time invariant model are also given.

Parameter	Model		
	Time invariant (previously)	Time invariant	Time varying $\beta$
$\alpha$	0.022 (0.003)	0.023 (0.003)	0.019 (0.002)
$\beta$ (time invariant)	0.141 (0.008)	0.201 (0.010)	—
$\bar{\beta}^*$	—	—	0.207 (0.079)
$\gamma$ (time invariant)	0.064 (0.008)	0.086 (0.010)	0.069 (0.007)
$S$	0.988 (0.001)	0.988 (0.001)	0.988 (0.001)
$S_j$	0.850 (0.043)	0.943 (0.044)	0.852 (0.042)
$\rho$	0.923 (0.070)	0.800 (0.056)	0.874 (0.063)
$a_m$	6.402 (0.405)	6.536 (0.624)	8.393 (1.197)
$\delta$	1.047 (0.267)	1.111 (0.396)	2.209 (0.756)
$r^*$	0.016 (0.104)	0.028 (0.105)	-0.032 (0.076)
$N_{1979}^{calv}$	41 (7.9)	38 (7.2)	42 (8.2)
$N_{1979}^{recp}$	48 (9.0)	46 (8.7)	48 (8.9)
$N_{1979}^{rest}$	76 (20.2)	76 (21.8)	61 (17.8)
$N_{1979}^{mature*}$	150 (32.6)	145 (33.2)	129 (31.6)
$N_{2017}^{calv}$	437 (15.3)	623 (21.4)	477 (102)
$N_{2017}^{recp}$	504 (18.0)	739 (25.8)	910 (178)
$N_{2017}^{rest}$	489 (16.9)	760 (25.5)	509 (152)
$N_{2017}^{mature*}$	1 321 (44.9)	1 956 (64.1)	1 765 (71.8)
$N_{2017}^{all}$	5 062 (215)	7 656 (329)	6 116 (446)
$r$	0.066	0.069 (0.003)	0.065 (0.003)

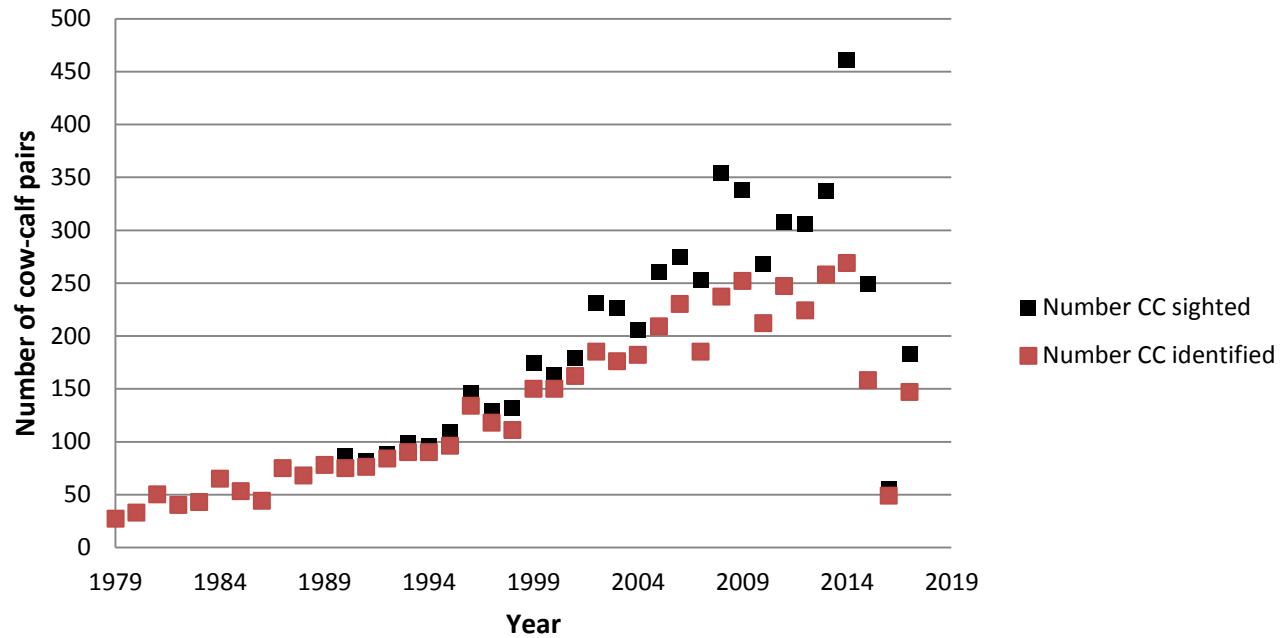


Figure 1. Number of cow-calf pairs sighted and identified during the annual aerial surveys since 1979.



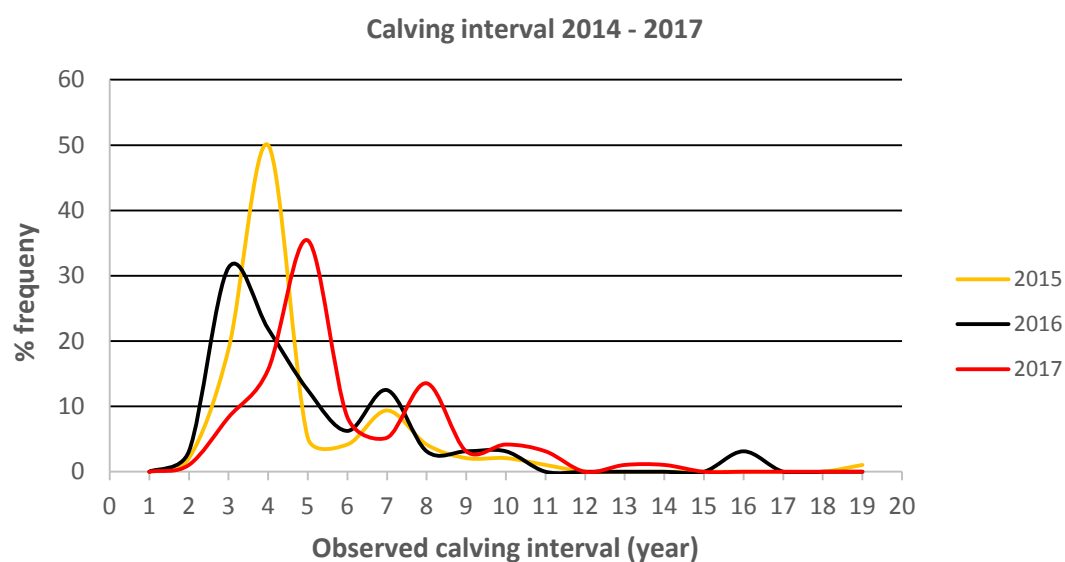
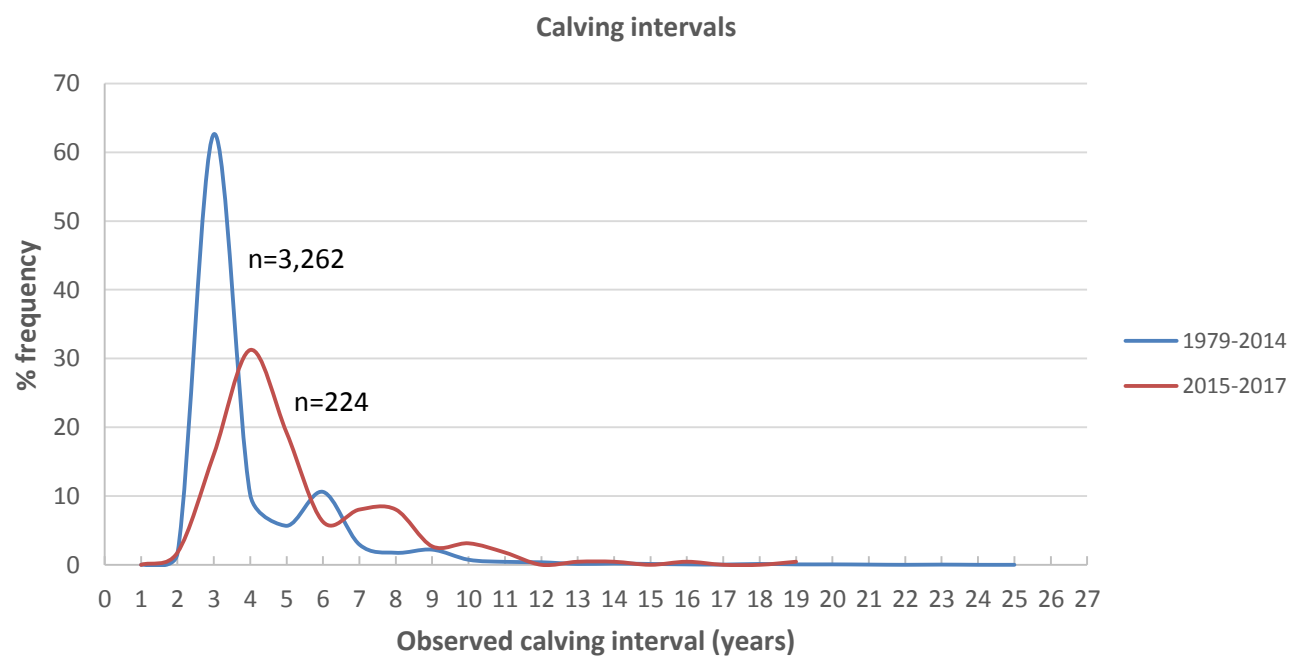
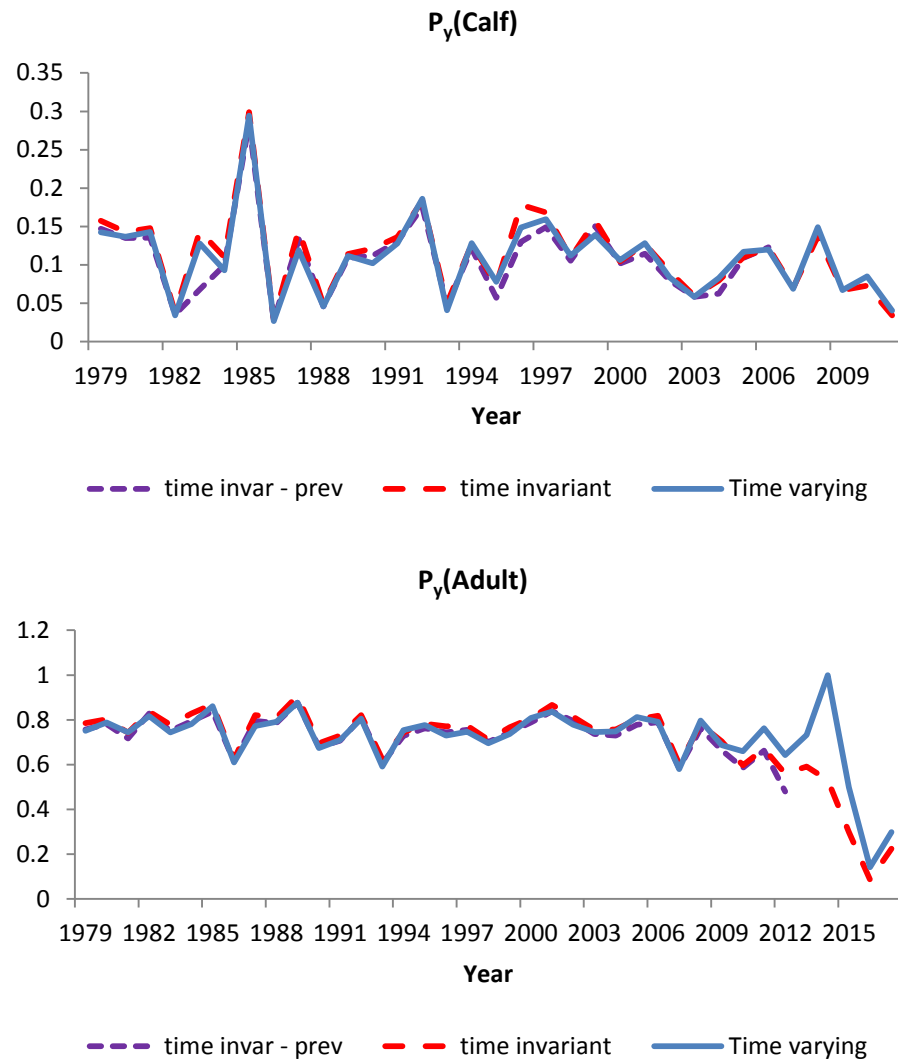
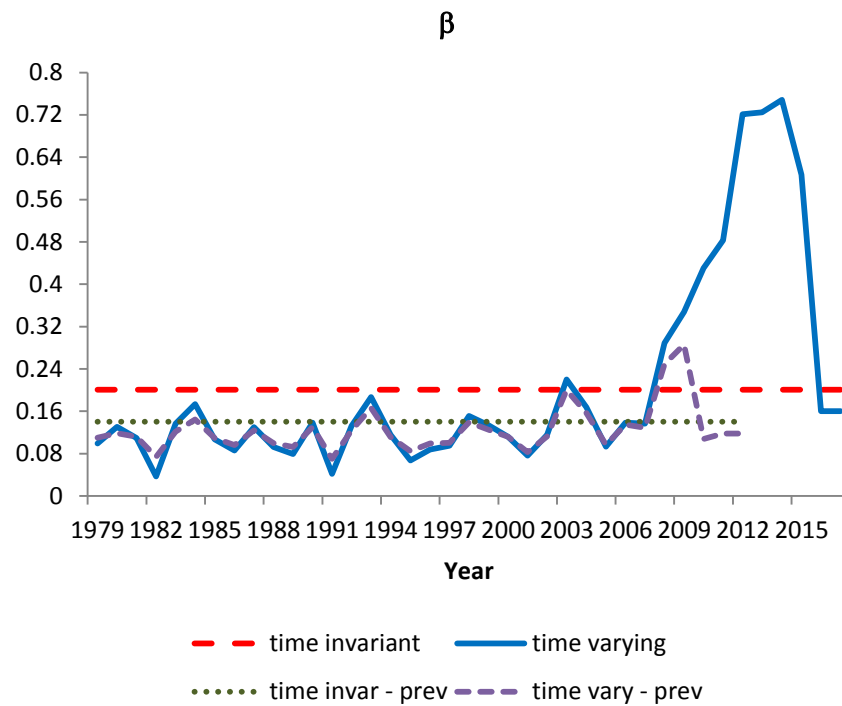


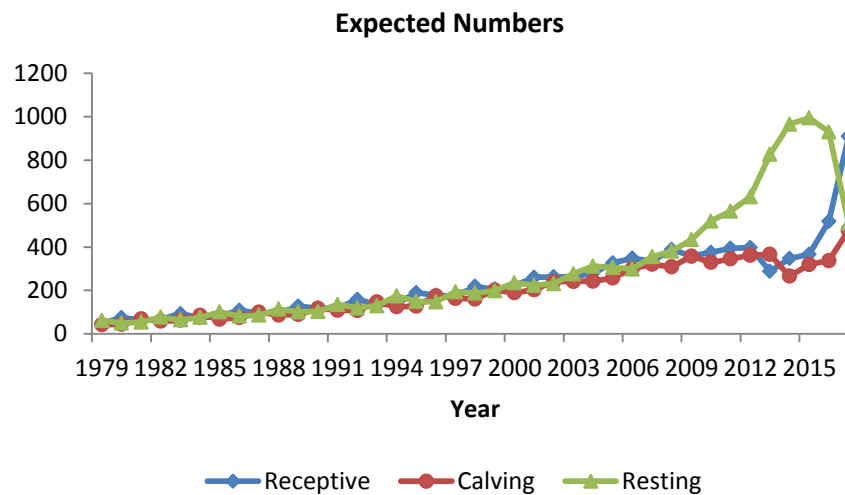
Figure 2: Top; observed calving intervals for the period 1979-2014 and 2015-2017. Bottom; detail of the observed calving interval for each of the years 2015, 2016 and 2017



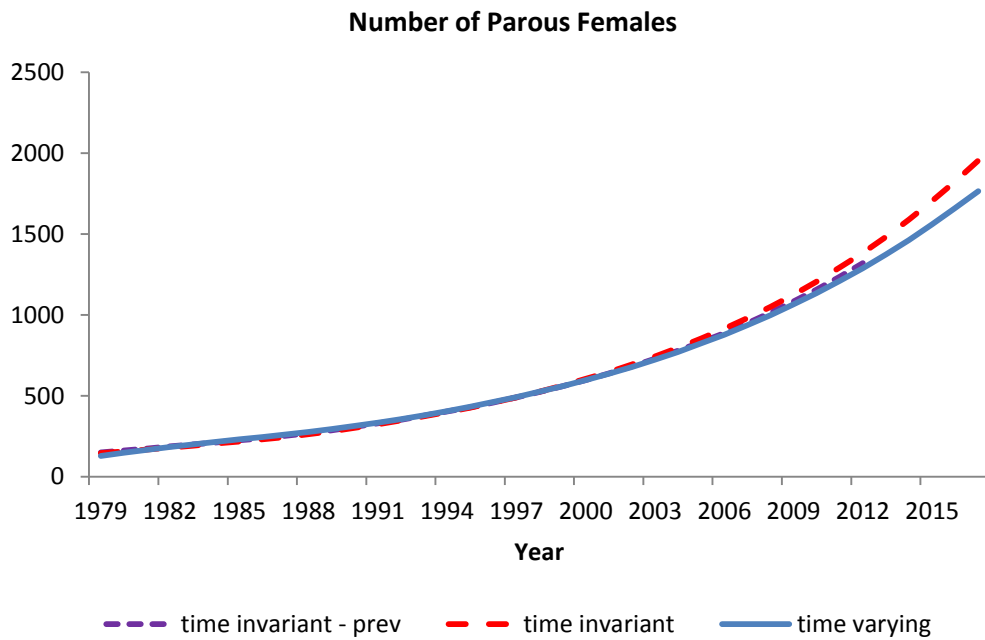
**Figure 3.** Estimated probabilities that a calf is catalogued (top) and of observing a female whale with its calf (bottom) on aerial surveys under the time invariant model and the time varying model. For comparison, the previous estimated probabilities for the time invariant model are also shown.



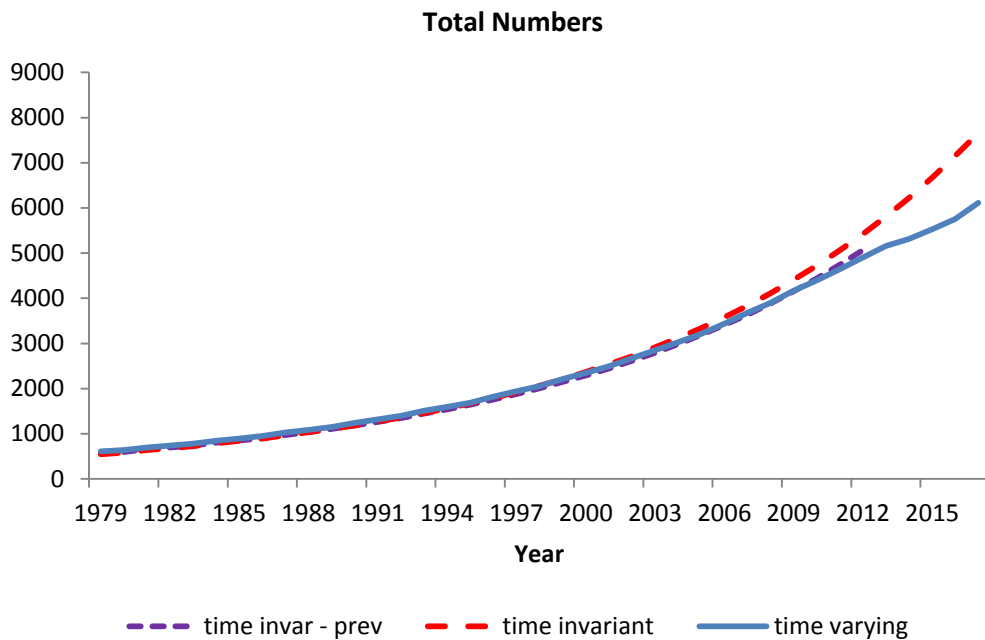
**Figure 4.** Time varying and time invariant estimates of the probabilities that a resting whale will rest in the following year. For comparison, the previous estimated probabilities are also shown.



**Figure 5.** Expected numbers of mature female southern right whales that are in the calving, receptive or resting stages under the time varying model.



**Figure 6.** Estimated total number of females having reached the age at first parturition for the time invariant and the time varying models. For comparison, the previous estimated numbers for the time invariant model 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 time invariant and the time varying models. For comparison, the previous estimated numbers for the time invariant model are also shown.

## 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
- $\phi_a$  is the probability that an immature female whale of age  $a$  becomes receptive the next year. This is re-parameterized as:

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

where  $a_m$  is the age at which 50% of the immature female population become receptive and  $\delta$  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  $y$ ,
- $\alpha_y$  is the probability that a whale calving in year  $y$  becomes receptive in year  $y+1$ ,
- $\beta_y$  is the probability that a whale resting in year  $y$  rests again the next year, and
- $\gamma_y$  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:

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

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  $\tau$  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 ( $\rho$ ) 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

- $\theta$  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:

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

where

- $\hat{N}_y^{\text{calv}, U}$  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:

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

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:

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

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 a 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

$\theta^*$  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

$\sigma_p$  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 ( $\alpha_y$ ), the probabilities of a resting whale remaining in the resting stage ( $\beta_y$ ) and the probabilities

of receptive whale returning to the resting stage ( $\gamma$ ) 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  $\alpha_y$  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  $\sigma_\beta$  (or  $\sigma_\gamma$ ). 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.

### Estimable parameters

The estimable parameters in the model are  $S$ ,  $S_j$ ,  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $a_m$ ,  $\delta$ ,  $P_y^A$ ,  $P_y^C$ ,  $\tau$ ,  $\rho$ ,  $N_{1979}^{calv}$ ,  $N_{1979}^{recp}$ , 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  $\rho$  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.