SC/68C/SH/05

Sub-committees/working group name: SH

Updated extension of a photo-identification based assessment model to southern right whales in South African waters to allow for the possibility of an early abortion of the calf in the model

Anabela Brandão, Andrea Ross-Gillespie, Els Vermeulen, Doug S. Butterworth

Updated extension of a photo-identification based assessment model to southern right whales in South African waters to allow for the possibility of an early abortion of the calf in the model

Anabela Brandão[1], Andrea Ross-Gillespie[1], Els Vermeulen[2], and Doug S. Butterworth[1]

ABSTRACT

This paper updates analyses (Brandão *et al.,* 2020) of an extension of the model developed by Brandão *et al.* (2019) so as to now include sightings data for 2019 and 2020. Brandão *et al.* (2020) had been modified to include the possibility of an early abortion so that a pregnant (receptive) whale in year y can again be pregnant in year y+1 (the "delta-loop"). This was to be able to account for an increase in calving intervals that are dependent on environmental conditions, and in a way that differs from a change in the value of the β (whale rests for another year) or the γ (late abortion) parameters; this was to be able to explain the low number of sightings of females with calves observed over the 2015 to 2017 period. The further data now available show that following a large number of cow-calf pairs sighted in 2018, there were again low numbers of sightings for 2019 and 2020. From initial work, it has become clear that the low sighting probabilities estimated for 2015 to 2017 and for 2019 to 2020 are not eliminated by the incorporation of this "delta-loop" in the model. A weighted penalty function for the sighting probabilities is necessary to obtain recent sighting probability values in the region of earlier ones; this seems necessary for realism in circumstances where there has not been any marked reduction in the survey sighting effort over these recent years. A weight of 5.0 is able to achieve estimates close to the average of previous sighting probabilities for both periods of low sightings. Thus, low numbers of sightings of females with calves for five of the last six years can be explained by changes in reproduction-related demographic parameters without the need to postulate an increase in the adult mortality rate. Changing environmental (particularly feeding) conditions seem the likely cause, and to be associated with a changed distribution.

INTRODUCTION

Brandão *et al.* (2019) updated the results 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). After three preceding years of very low sightings of females with calves, 2018 saw these numbers increase to reach a record level of 426. This pattern of results was best explained by variation with time

---

[1] MARAM (Marine Resource Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7700, South Africa.

[2] Mammal Research Institute Whale Unit, Department of Zoology and Entomology, University of Pretoria, Lynnwood Rd, Hatfield, Pretoria 0002, South Africa.

in the probability that a resting female rests again the following year. Another surprising feature of these results was one extremely high and three extremely low estimates of the probability of sighting a female with calf after 2013. The low estimates do not seem compatible with near unchanged survey conduct for the years concerned, so that a penalty term was added to the assessment to force these to be closer to earlier values.

In Brandão *et al.* (2020), the *β* time varying model of Brandão *et al.* (2019) was modified to include the possibility of an early abortion so that a pregnant (receptive) whale in year *y* can again be pregnant in year *y*+1 (a possibility introduced in Cooke *et al.,* 2015). This was done in order to account for increased calving intervals and eliminate the low probabilities of sightings of females with calves over the 2015 to 2017 period. In this paper, previous results for this extension to the model as reported in Brandão *et al.* (2020) are updated to include sightings data for 2019 and 2020.

NOTATION AND METHODOLOGY

Details of the methodology used and its modification from the previous version – both the population dynamics model and the likelihood maximised to estimate parameter values from the photo-identification data – are given in Appendix 1. The methodology for computing the probabilities for sighting histories are given in Appendix 2. The notation used in providing results is as follows:

α probability that a mature whale that calves ovulates the next year
β probability that a resting mature whale rests for a further year
δ probability that a pregnant whale is pregnant the next year (i.e. following an early abortion)
γ probability that a pregnant whale rests (i.e. following a late abortion) 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, ω 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) parous female growth rate estimated over the whole period of cow-calf sightings.

Note that the basic model allows for a three-year reproductive cycle: receptive to calving to rest. In simple terms the *α* parameter allows for the possibility of a two-year cycle, the *β* a four-year cycle, the *δ* a four-year cycle (due to an early abortion), and the *γ* a five-year-cycle (due to a late abortion). 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" and "pregnant" respectively.

There is a concern that there might be confounding amongst the reproductive cycle parameters ($\propto, \beta, \gamma$ and δ), especially if time dependence is assumed. Between instances of sighting a cow-calf pair there are several combinations of the state that a female whale could be in (resting, had an early or a late abortion or a sighting was missed) and it is questionable how distinguishable these effects are from the sighting histories. It is anticipated that the low sighting probabilities estimated for the 2015 to 2017 period (Brandão *et al.,* 2019) will

allow for the effect of an early abortion (the δ parameter) to be distinguished from that of a β (the whale rests for another year) or a γ (late abortion) effect.

The inclusion of the "delta-loop" (i.e. allowing for the state of a pregnant whale being pregnant again the following year) is applied to the model in Brandão *et al.* (2019). That is, a model in which the α_y and δ_y probabilities are considered to be time invariant, while the β_y probabilities may vary with time. The δ_y probabilities must necessarily be time dependent but are estimated for the period 2014 to 2019 only (the data do not allow for an estimate in 2020) to reflect the period of low sightings and to reduce the number of parameters. For all other years these probabilities are taken to be zero. With the added model complexity, the Hessian (and therefore standard error estimates for parameters) was not always obtainable.

Initial results when incorporating the "delta-loop" modification showed that this did not successfully eliminate the low sightings probabilities ($\hat{P}_y^A$) estimated for 2015-2020. Therefore, a penalty function was used to ensure that the estimates of $\hat{P}_y^A$ for the years after 2014 were in the range of the average over earlier years commencing in 1982. Three weights applied to the contribution of the penalty on $\hat{P}_y^A$ to the likelihood were investigated: a weight of 1.0 (i.e. no weight), 2.5 and 5.0. In the most recent analyses (Brandão *et al.,* 2020), a weight of 2.5 was chosen to obtain the standard deviations of sighting probabilities about the average pre-2015 for the pre- and post-2015 periods to be similar. The previous results showed that a weight of 2.5 was able to achieve estimates close to the average of previous sighting probabilities and therefore was amongst those used for the analyses presented here. The weight of 5.0 was chosen to obtain sighting probabilities close to the average of previous sighting probabilities for the second drop in sightings now observed in the data.

There is not enough information for the 2019 and 2020 random variations for the βs to be estimated. These are always estimated as zero in the random effects model so that the β values for these years follow from the estimated mean for the random effects distribution which is based on all years.

RESULTS

Table 1 gives results for the "delta-loop" modified model with various weights applied to the penalty on the probabilities for observing a female whale with its calf. For comparison, results obtained previously in Brandão *et al.* (2020) (with data up to 2018) for a weight of 2.5 applied to the contribution of the penalty on $\hat{P}_y^A$ to the likelihood are also given (referred here as 2.5pen(2020)). The contributions to the penalised negative log-likelihood function from these models by its various components are given in Table 2.

Figure 1a plots the number of females with calves actually observed annually, while Figure 1b shows the annual number of unaccompanied adults (both in absolute terms and as a proportion of the number of females with calves) and Figure 1c shows the apparent calving intervals since 2007 (note "apparent" in the sense of as observed, without adjustment for females with calves missed in the surveys). Note the appreciable drop over the 2015 to 2017 period below the earlier general trend, with a record number of females with calves observed in 2018 which was then followed again by another appreciable drop over the 2019 and 2020 period.

The estimated probabilities that a calf is catalogued hardly change between the various models (Figure 2).

The probabilities of observing a female whale with its calf on aerial surveys under these models hardly change for the pre-2015 period (Figure 3 – the bottom panel shows a close up of the last few years). The inclusion of the "delta-loop" in the model together with a penalty on $\hat{P}_y^A$ does not eliminate the low estimates of the sighting probabilities from 2015 (when a weight of 1.0 is applied). Applying a weight of 2.5 to the penalty on $\hat{P}_y^A$ brings these estimates closer to the average of previous estimates for the 2015 to 2017 observed drop in sightings, but not for the 2019-2020 period. A higher weight of 5.0 is able to achieve estimates close to the average of previous sighting probabilities for both periods of lower sightings (Figure 3).

The modified model with the high weight results in higher estimates of the probabilities that a resting whale will rest in the following year (β) for the period after 2012 (Figure 4).

Figure 5a shows the expected number of mature female southern right whales that are in the calving, receptive and resting stages for several models. In general, for the post-2015 years the modified models estimate lower numbers of females to be calving (especially for 2016 and 2020) and whales that are in the receptive stage (though with peaks in 2018 and 2020), and higher numbers that are resting (except for 2017, 2018 and 2020 for models with a weight applied to the penalty on $\hat{P}_y^A$ which estimates lower resting numbers) (see Figure 5b).

The modified models, with higher weights applied to the penalty on $\hat{P}_y^A$, lower estimates of the number of parous females (Figure 6) and of the total population (including males and calves and assuming a 50:50 sex ratio) for the post-2015 years (Figure 7).

The modified model estimates the probability of an early abortion (a pregnant whale being pregnant again the following year) to be 0.52 in 2019 and essentially zero otherwise if no weight is applied to the penalty on $\hat{P}_y^A$. If weights are applied, then this probability increases to values in the region of 0.66 to 0.67 in 2015, 0.45 to 0.47 in 2016 and 0.57 to 0.58 in 2019 (depending on the weight) (Table 1 and Figure 8).

The estimated cohort numbers at each stage of the right whale reproductive cycle under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" with a weight of 5.0 applied to the penalty for $\hat{P}_y^A$ have been fairly similar until around 2010, but since then this is no longer the case (Figure 9).

Figure 10 shows a comparison of the observed to the model predicted annual average apparent calving intervals of mature female South African southern right whales. The predicted values are as determined using the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" with a weight of 5.0 applied to the penalty for $\hat{P}_y^A$. The model predictions match the observations well.

DISCUSSION

The results of Brandão *et al.* (2018) suggested that the hypothesis of lengthened calving intervals was to be favoured over mass mortality to account for the low survey numbers over 2015-2017. The possibility of an early abortion (which is dependent on environmental conditions) would account for an increase in the proportion of four-year calving intervals. It is hoped that such occurrences would be distinguishable from the β-associated probabilities (also leading to a four-year cycle caused by a female resting for another year), and also from the γ-associated probabilities (late abortion), by the low sightings of calf-cow pairs.

4

The modification to the time varying model (Brandão *et al.,* 2019) to include the "delta-loop" (Brandão *et al.,* 2020) further complicates the model for which there are already concerns of confounding of parameters and whether it is possible to distinguish the effects of the different reproductive states a female on the instances when it is sighted with its calf. From initial work it has become clear that the low sightings observed for 2015 to 2017 and now 2019 to 2020 were not fully explained by the incorporation of the "delta-loop" in the model. A weighted penalty on the sighting probabilities is necessary to obtain recent values which are in the region those for previous years. A weight of 5.0 is able to achieve estimates close to the average of those earlier sighting probabilities.

Thus, the low numbers of females with calves sighted in five of the last six years can be explained by changes to the values of some reproduction-related parameters of the demographic models which allow for longer resting periods and for early abortions. Note the associated trend towards an increase in the average length of apparent calving intervals that commenced in 2011 (Figure 1c). The alternative possibility of higher mortalities seems unlikely for two further reasons: the very high number of sightings of female-calf pairs made in 2018, and the decrease in the annual number of strandings of dead animals on the South African coast since 2009 (from an average of 5.5 pa over the period 1998-2008 to an average of 2.8 pa for 2009-2019; see Vermeulen et al. 2021).

Rather than an increase in the (adult) mortality rate, it seems more probable that changed environmental (particularly feeding) conditions may be the cause of the changes to these reproduction-related parameters. This could well have led also to changes in distribution and/or migration routes, as is suggested by the decreasing trend in the ratio of unaccompanied adults to females with calves that has been evident in the survey results since 2010 (see Figure 1b). This hypothesis is supported by a study of van den Berg et al. (2021) which revealed a recent dramatic northward shift and diversification in foraging strategy of this capital breeder. In line of the decreased reproductive output of the population evident over recent years, this study furthermore concluded that the altered foraging strategy may not be sufficient to adapt to the changing environment. This hypothesis of a decreased foraging success is supported by the observed drastically decreased body condition of adult female southern right whales since the late 1980s (see Thavar et al. 2021 for more detailed information).

REFERENCES

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.

Brandão, A., Vermeulen, E., Ross-Gillespie, A., Findlay, K. and Butterworth, D.S. 2018. Updated application of a photo-identification based assessment model to southern right whales in South African waters, focusing on inferences to be drawn from a series of appreciably lower counts of calving females over 2015 to 2017. IWC document SC/67b/SH22.

Brandão, A., Vermeulen, E. and Butterworth, D.S. 2019. Updated application of a photo-identification-based assessment model to southern right whales in South African waters to include data up to 2018. IWC document SC/68a/SH14.

Brandão, A., Ross-Gillespie, A., Vermeulen, E. and Butterworth, D.S. 2020. Extension of a photo-identification-based assessment model to southern right whales in South African waters, to allow for the possibility of an early abortion of the calf in the model. Unpublished document.

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.

Cooke, J., Rowntree, V. and Sironi, M. 2015. Southwest Atlantic right whales: interim updated population assessment from photo-id collected at Peninsula Valdes, Argentina. IWC document SC/66a/BRG23.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A. and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27:233-249.

Thavar, T., Christiansen, F., Ganswindt, A. and Vermeulen, E. 2021. Body condition of female southern right whales (*Eubalaena australis*) on the South African breeding ground. Report presented to the 68C Scientific Committee meeting of the International Whaling Commission.

van den Berg, G.L., Vermeulen, E., Ganswindt, Valenzuela, L.O., Bérubé, M., Ganswindt, A., Gröcke, D.R., Hall, G., Hulva, P., Neveceralova, P., Palsbøll, P.J. and Carroll, E.L. 2021. Decadal shift in foraging strategy of a highly migratory marine capital breeder. Global Change Biology, 27: 1052-1067. Doi: 10.1111/gcb.15465

Vermeulen, E., Jouve, E., Cliff, G., Dicken, M., Meÿer, M., Saekamela, M., Thompson, G., Wilkinson, C. and Best, P.[B.] 2021. Mortalities of southern right whales (*Eubalaena australis*) and related anthropogenic factors in South African waters, 1999 – 2019. Report presented to the 68C Scientific Committee meeting of the International Whaling Commission.

Table 1. Estimates of various demographic parameters for right whales off South Africa for various modified β time varying model which include the "delta-loop" (see text and Appendices for explanation of symbols). The parameter $r*$ is the implicit growth rate in period immediately before monitoring commenced in 1979 (=-log(τ)). The parameter $\bar{\beta}*$ is the average of the β 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 parameter r is the parous female instantaneous growth rate (in units of yr^{-1}) over the whole period of cow-calf sightings. For comparison, the values previously obtained (Brandão *et al.,* 2020) (with data up to 2018) for a weight of 2.5 are also shown. Text in red gives the corresponding name in the legend of the Figures.

Parameter	Previous 2.5*penalty on $\widehat{P}_y^A$ (2.5pen(2020))	1.0*penalty on $\widehat{P}_y^A$ (1.0pen)	2.5*penalty on $\widehat{P}_y^A$ (2.5pen)	5.0*penalty on $\widehat{P}_y^A$ (5.0pen)
α(time invariant)	0.019	0.019	0.018	0.017
$\bar{\beta}*$	0.231	0.225	0.224	0.244
γ(time invariant)	0.070	0.068	0.068	0.070
δ_{2014}	0.000	0.000	0.139	0.138
δ_{2015}	0.588	0.000	0.655	0.668
δ_{2016}	0.314	0.000	0.469	0.446
δ_{2017}	0.000	0.000	0.034	0.000
δ_{2018}	—	0.000	0.000	0.000
δ_{2019}	—	0.515	0.582	0.574
S	0.987	0.987	0.987	0.986
S_j	0.788	0.835	0.818	0.786
ρ	0.752	0.815	0.794	0.804
a_m	8.562	8.064	8.123	7.707
ω	2.454	2.094	2.155	1.941
$r*$	-0.040	-0.030	-0.033	-0.034
N_{1979}^{calv}	44	40	40	42
N_{1979}^{recp}	53	58	63	66
N_{1979}^{rest}	70	64	66	70
$N_{1979}^{mature*}$	145	143	150	158
N_{2020}^{calv} †	641	141	102	91
N_{2020}^{recp} †	786	1129	1367	1409
N_{2020}^{rest} †	435	895	626	497
$N_{2020}^{mature*}$ †	1 744	1865	1809	1743
N_{2020}^{all} †	5 682	6829	6367	5829
r	0.060	0.063	0.060	0.058

† For 2.5pen(2020) the year is 2018.

Table 2. Contributions to the penalised negative log-likelihood function by its various components of the "delta-loop" modified models. Text in red gives the corresponding name in the legend of the Figures. For comparison the values obtained previously (Brandão *et al.,* 2020) (with data up to 2018) for a weight of 2.5 are also shown.

	Previous 2.5*penalty on $\widehat{P}_y^A$ (2.5pen(2020))	1.0*penalty on $\widehat{P}_y^A$ (1.0pen)	2.5*penalty on $\widehat{P}_y^A$ (2.5pen)	5.0*penalty on $\widehat{P}_y^A$ (5.0pen)
Adult histories	2196	2329	2342	2357
Calf histories	517.7	572.9	584.0	589.4
Beta random effects	29.48	28.02	28.25	31.59
Penalty on $\widehat{P}_y^A$ at the beginning of series (1979 – 1981)	0.074	0.086	0.159	0.152
Penalty on $\widehat{P}_y^A$ at the end of series (2015-2020†)	1.981‡	27.27	11.96‡	5.295‡
Total	2745‡	2958	2966‡	2984‡

‡ Does not include the multiplication of $\widehat{P}_y^A$ penalty by the weight applied to it.
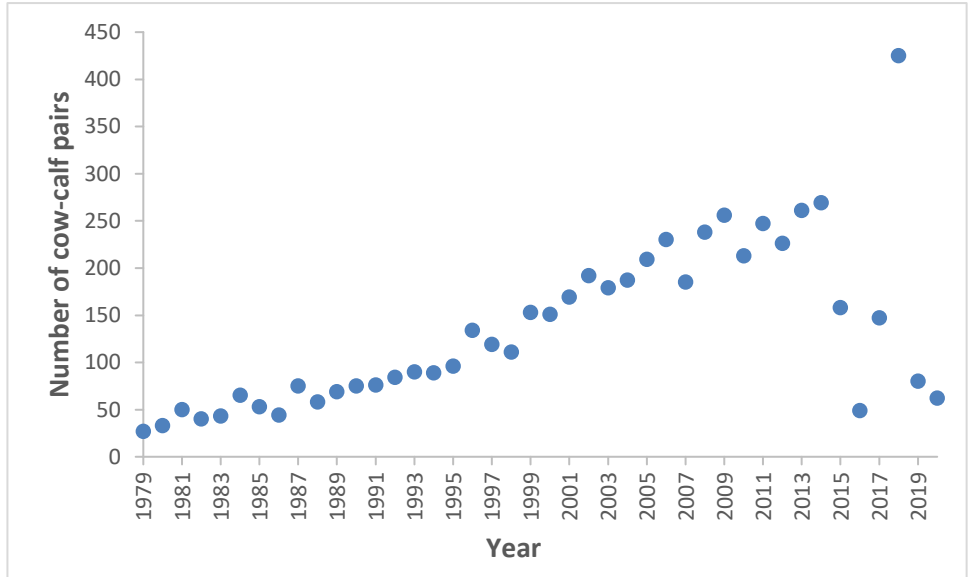
† For 2.5pen(2020) this is 2018.

Figure 1a. Number of adult female-calf pairs sighted during the annual southern right whale surveys off South Africa.
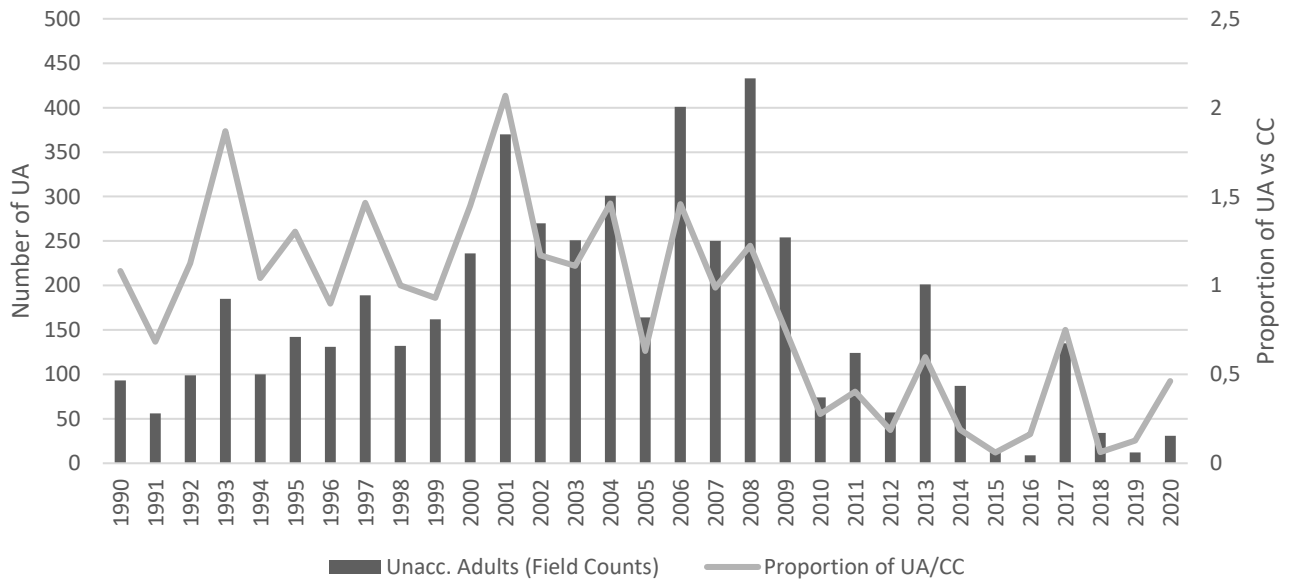

Figure 1b. Number of unaccompanied adults (UA), as well as UA expressed relative to the number of female-calf pairs (CC).
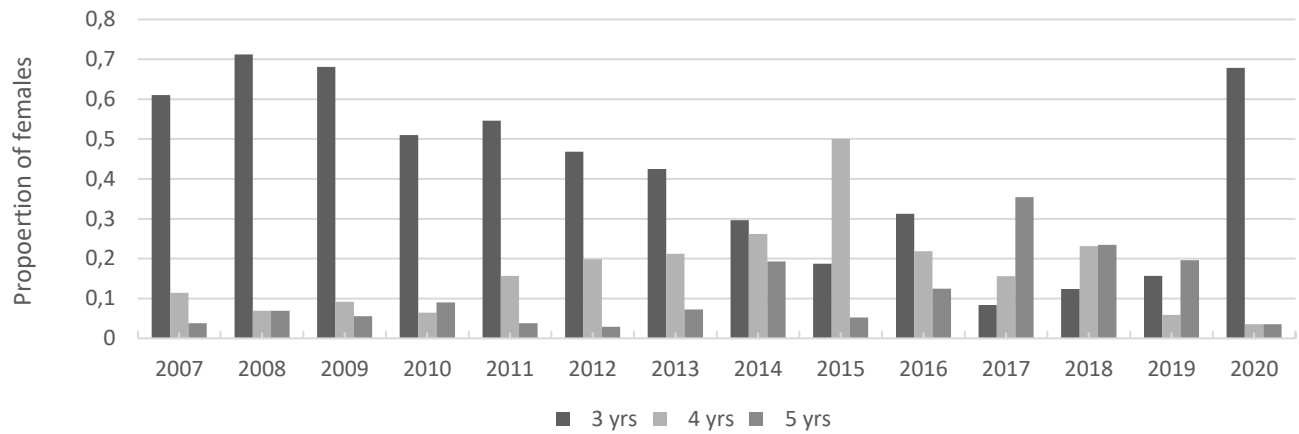
Figure 1c. Distribution of apparent calving intervals for the year in which a calf was most recently observed.
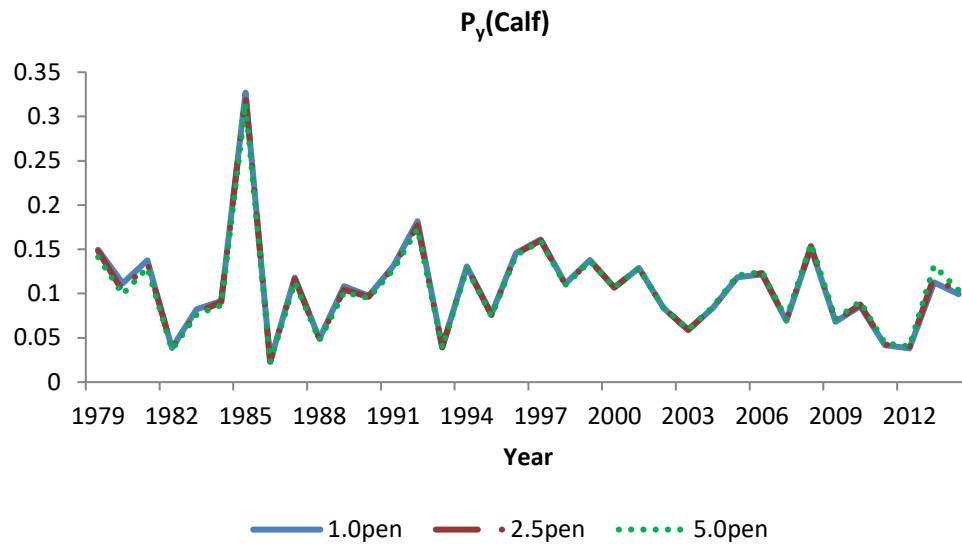

Figure 2. Estimated probabilities that a calf is catalogued on aerial surveys under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$.
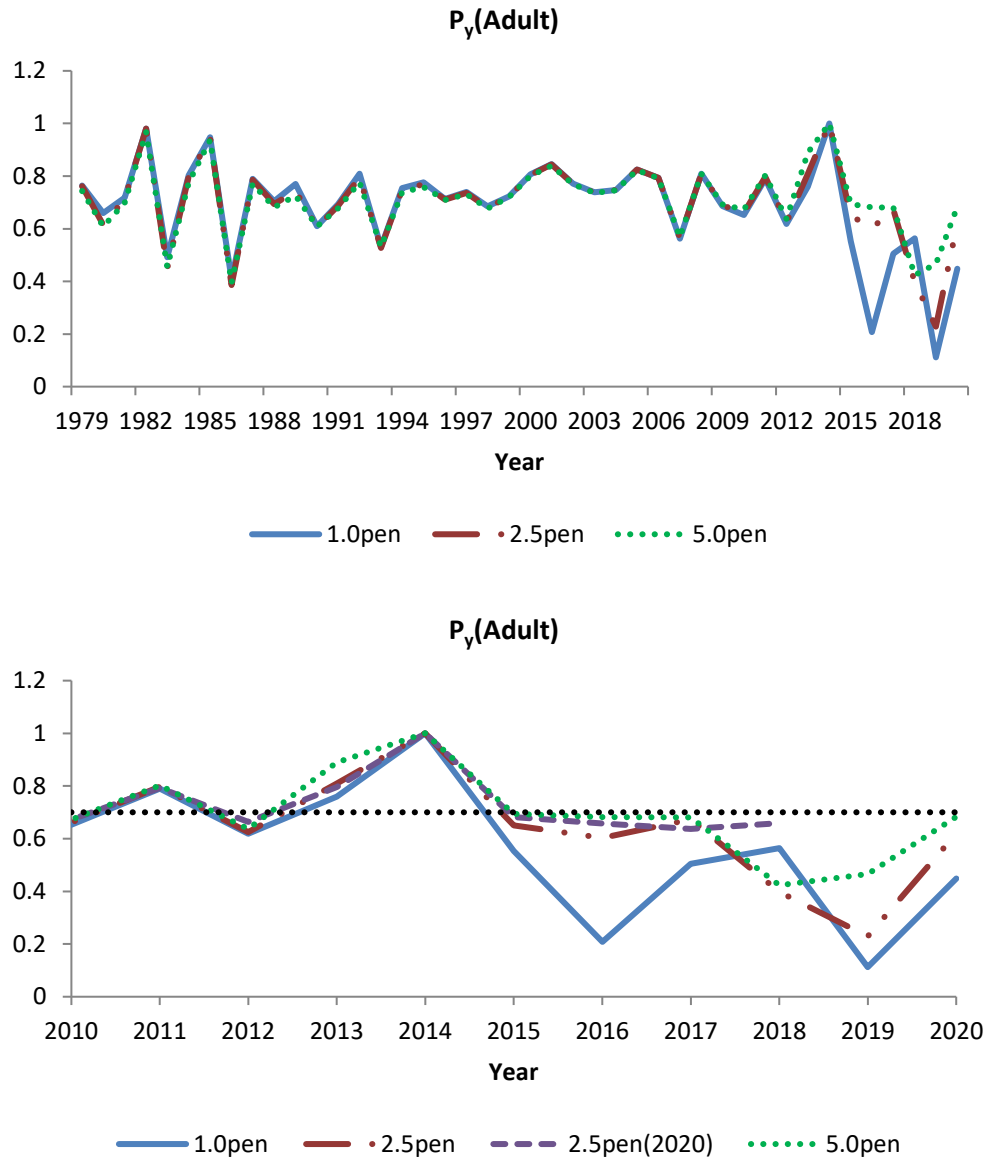
Figure 3. Estimated probabilities of observing a female whale with its calf on aerial surveys under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$ (top). A close up of the probabilities are also shown (bottom). The dotted horizontal line (at 0.7) is approximately the average of pre-2014 probabilities. In the close up, the estimated probabilities obtained previously with data up to 2018 and a weight of 2.5 are also shown (Brandão *et al.*, 2020).
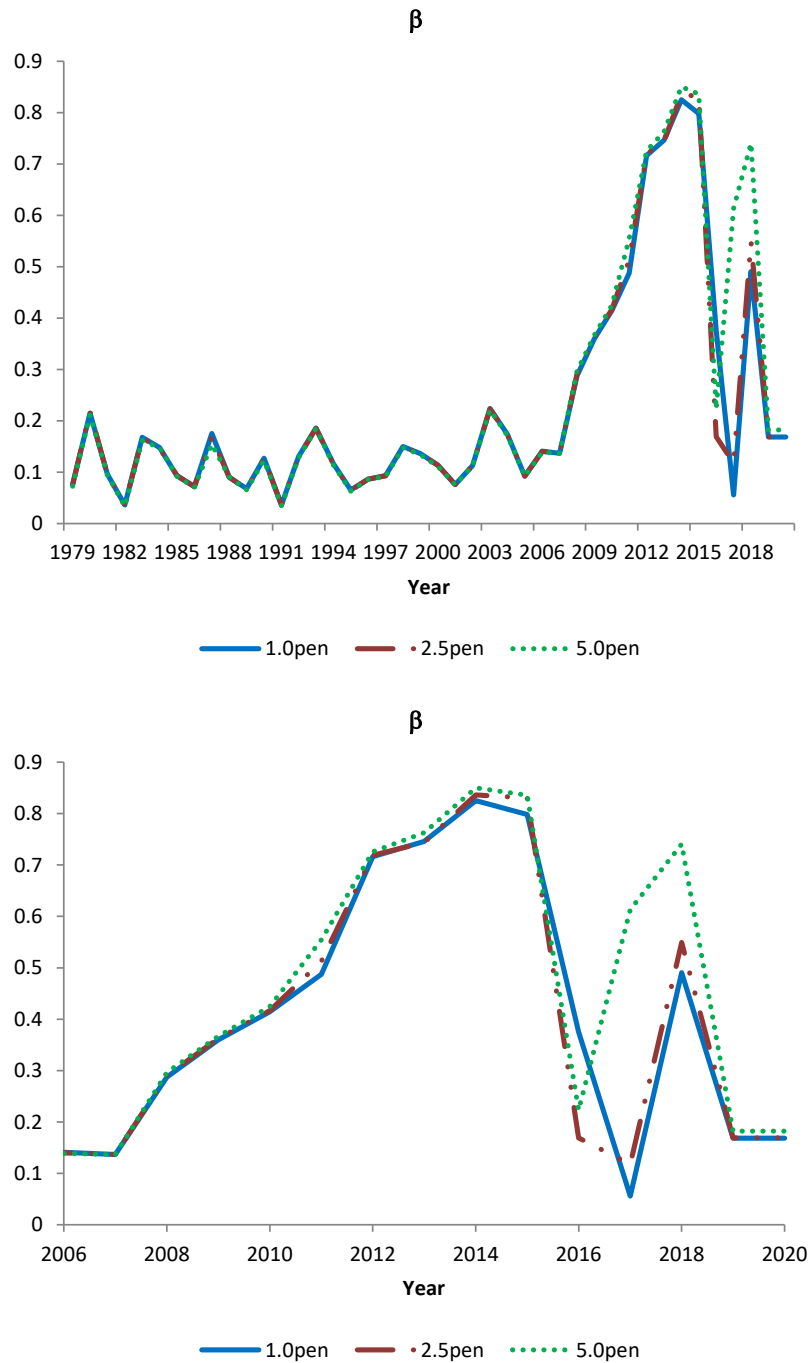
Figure 4. Time varying estimates of the probabilities (β) that a resting whale will rest in the following year under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$ (top), and a close up of these probabilities (bottom).
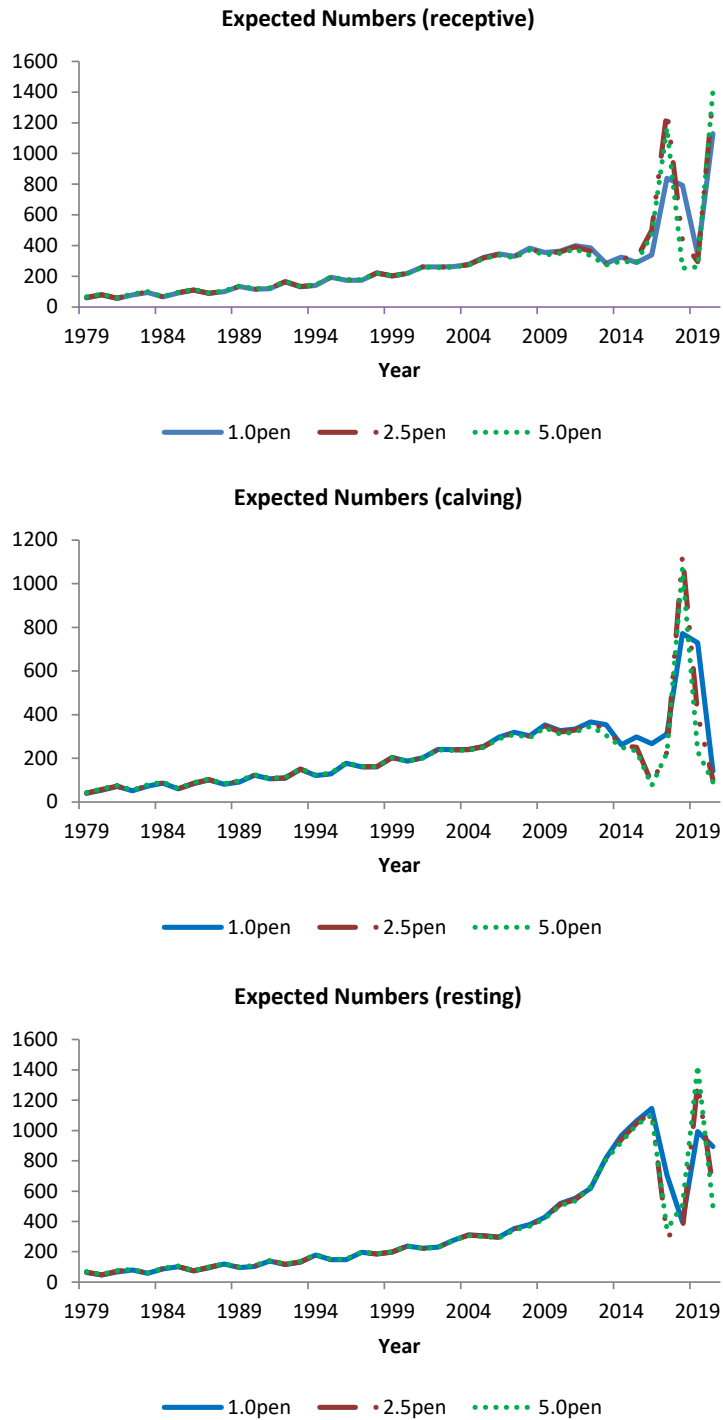
Figure 5a. Expected numbers of mature female southern right whales that are in the receptive (top), calving (middle) and resting (bottom) stages under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$.

Expected Numbers (receptive)

Expected Numbers (calving)

Expected Numbers (resting)
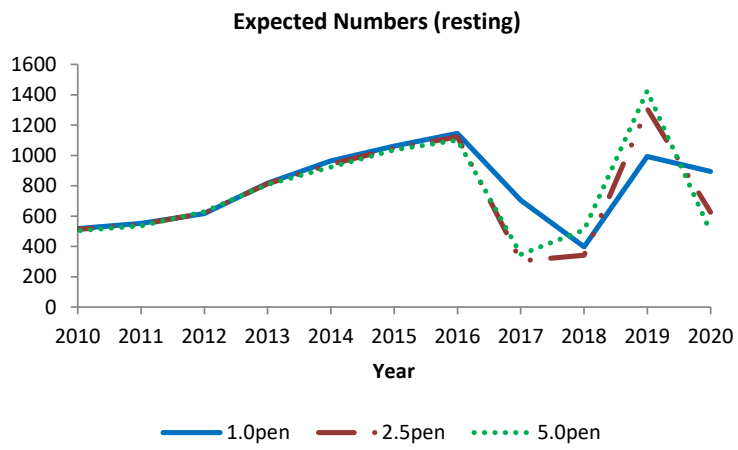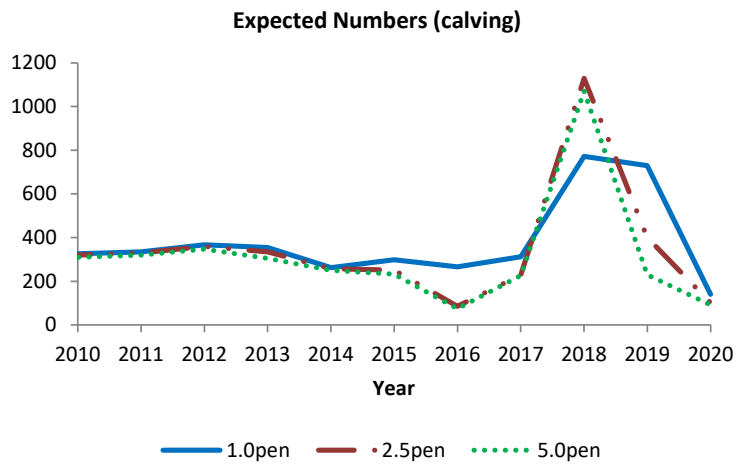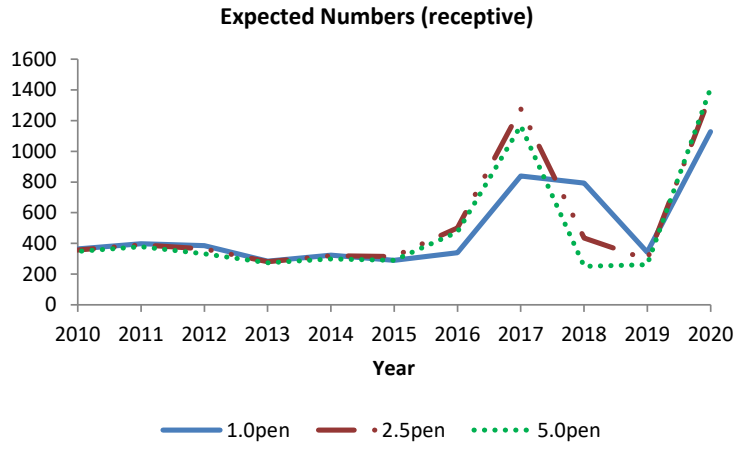
Figure 5b. Close up of Figure 5a.
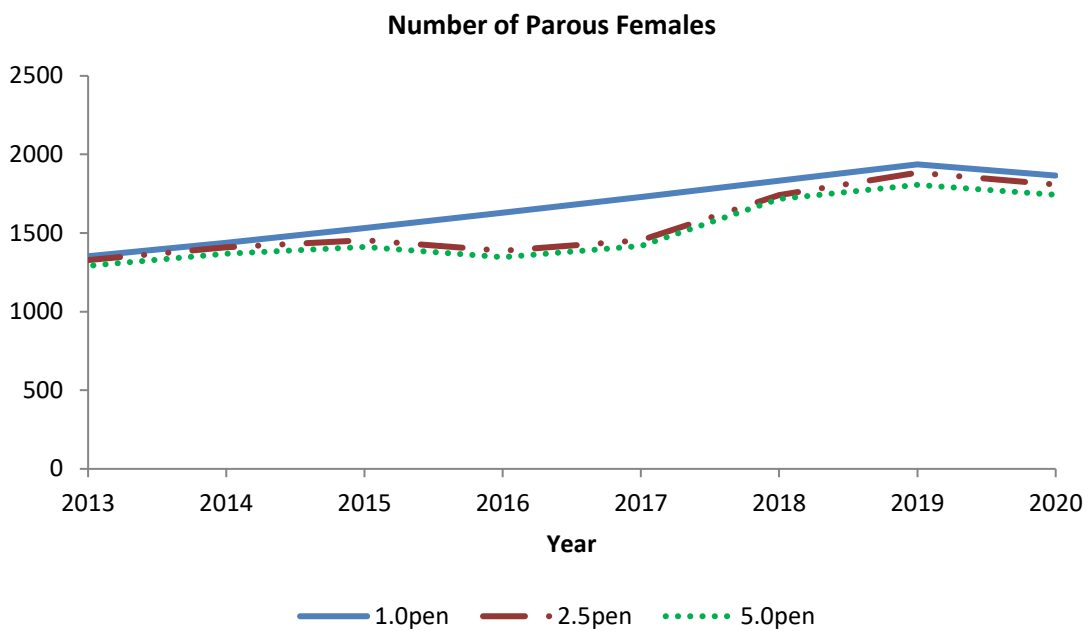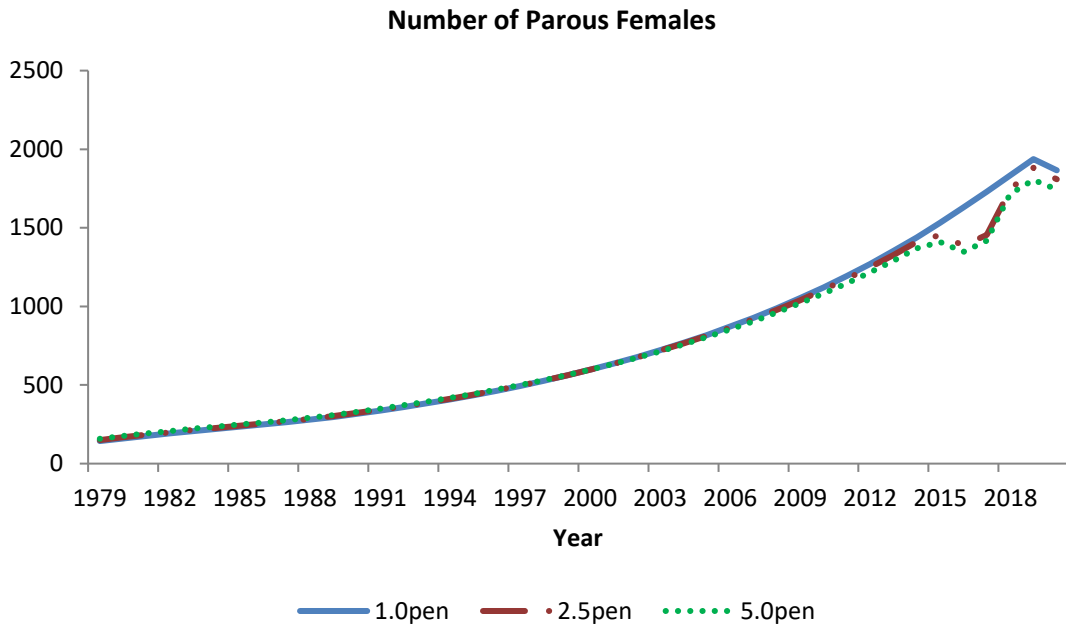
Figure 6. Estimated total number of females having reached the age at first parturition for the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$ (top) and a close up (bottom).
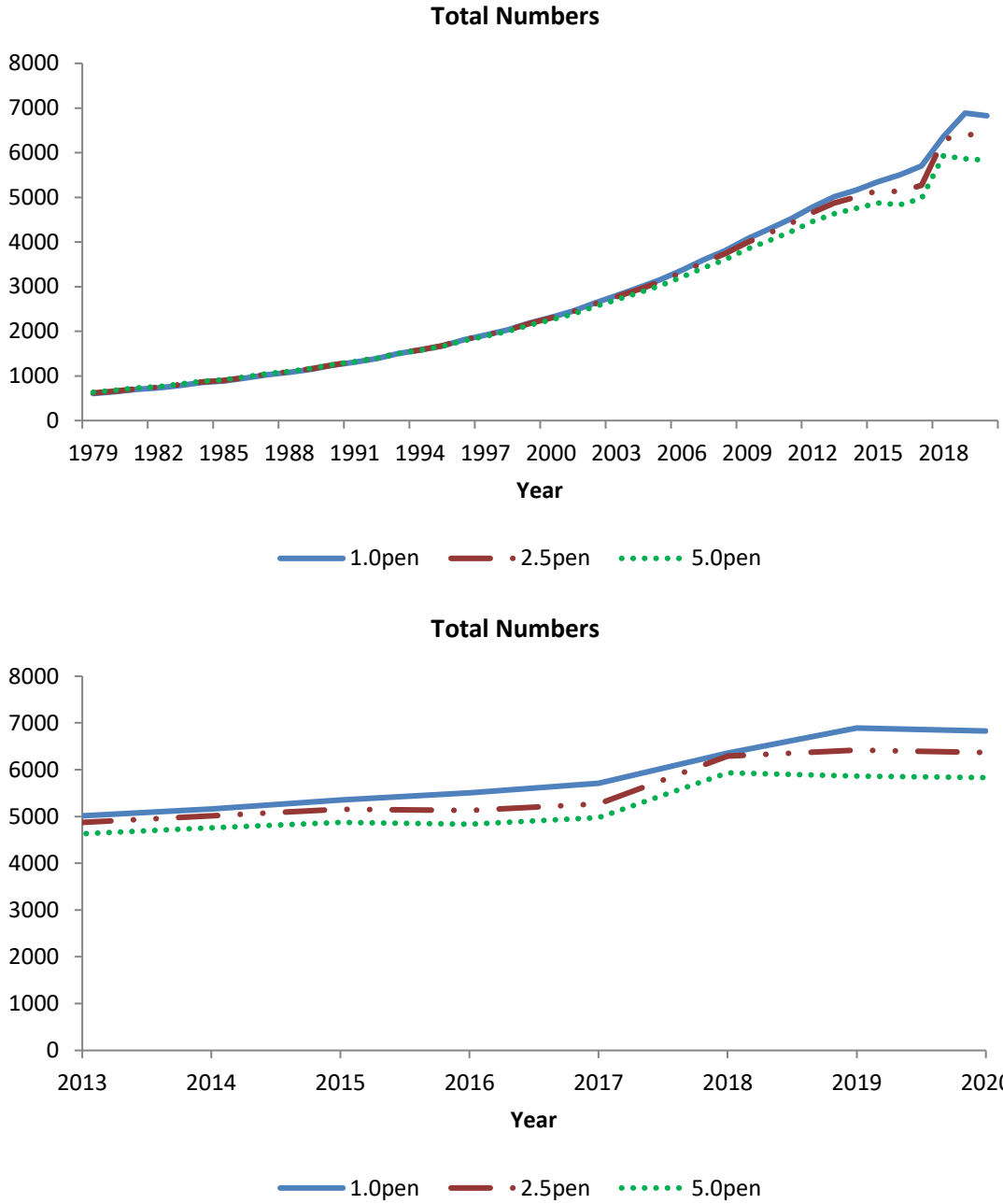
Figure 7. Estimated total number of the whole population (including males and calves, under the assumption of a 50:50 sex ratio at birth) for the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" when various weights are applied to the penalty for $\hat{P}_y^A$ (top), and a close up (bottom).
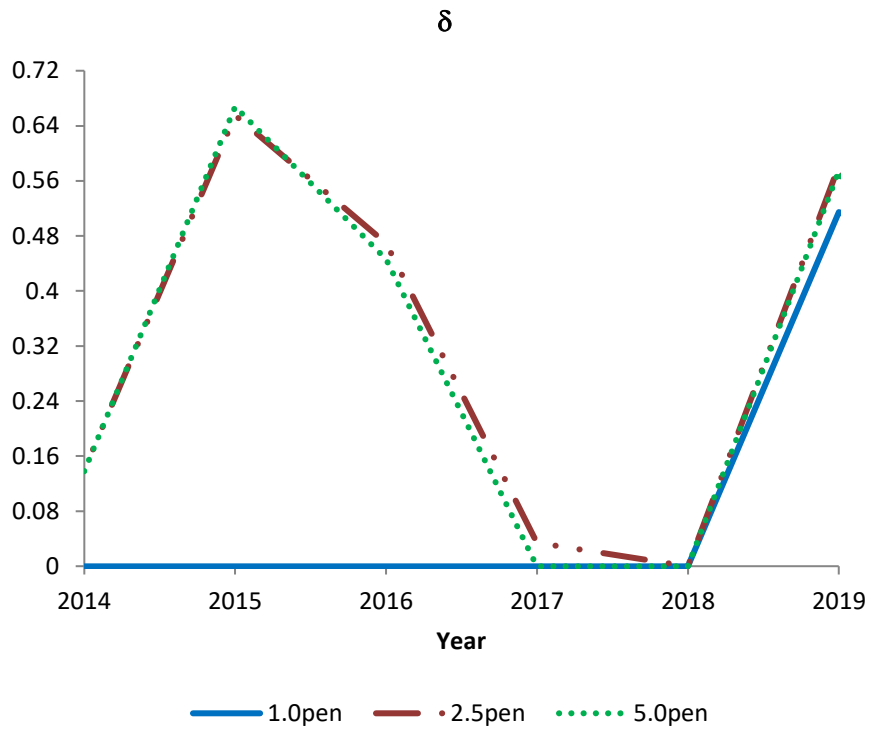
Figure 8. Estimated probabilities (δ) that a receptive whale will remain receptive in the following year.

Expected Numbers
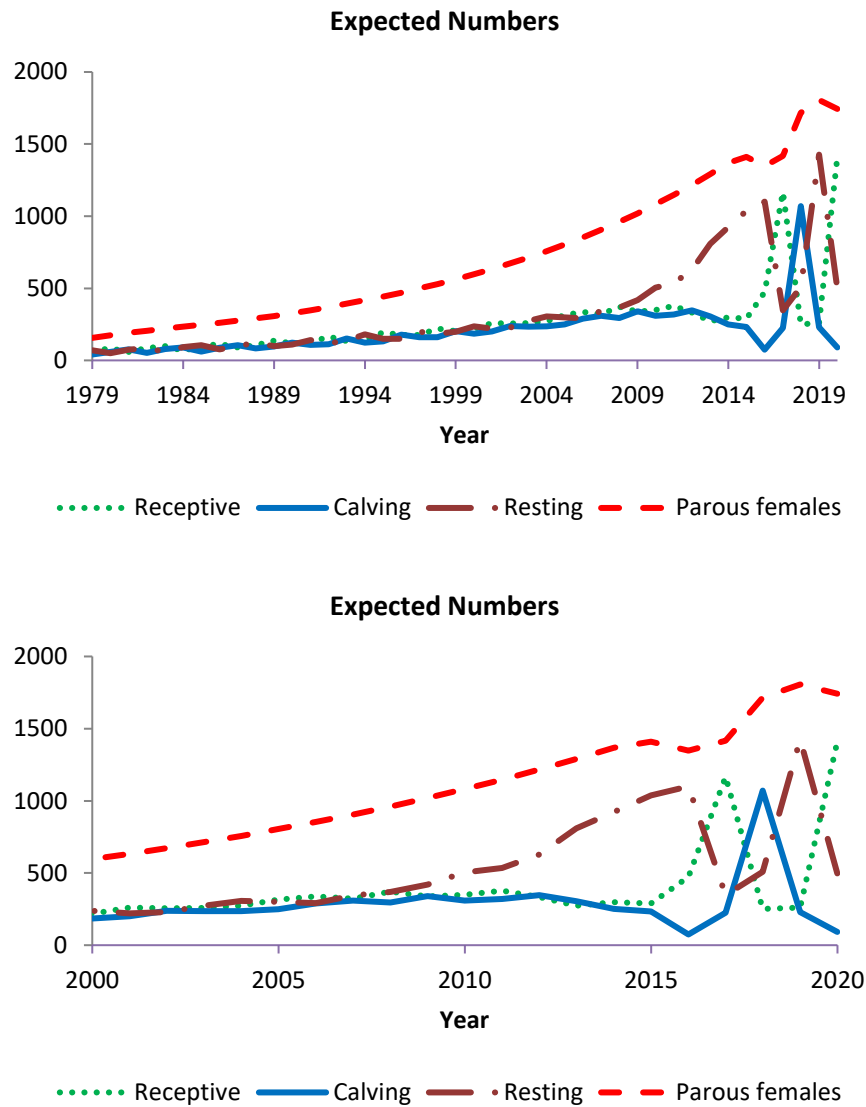
Expected Numbers

Figure 9. Comparison of the expected numbers of mature female southern right whales that are in the receptive, calving and resting stages under the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" with a weight of 5.0 applied to the penalty for $\hat{P}_y^A$. The estimated total numbers of females having reached the age at first parturition are also shown.

18
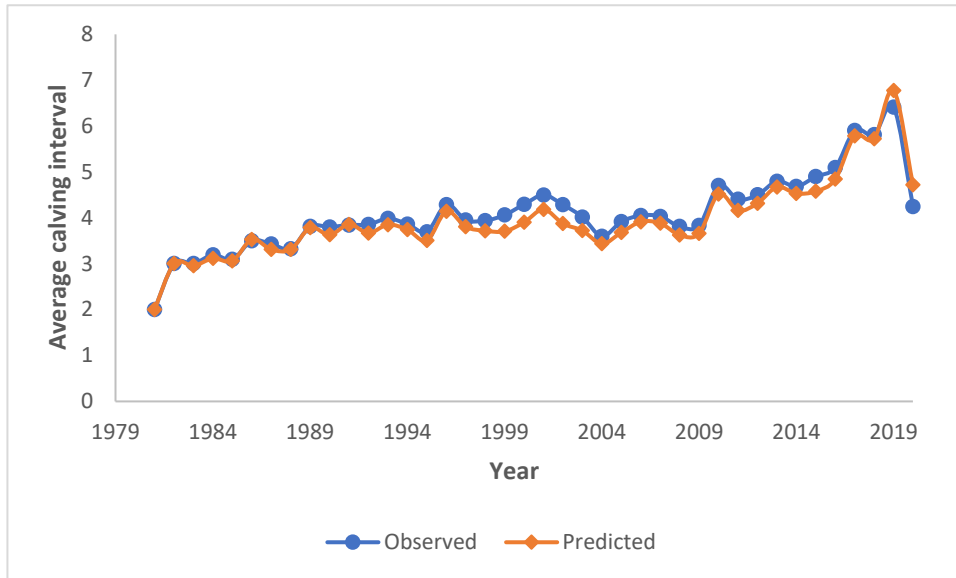
Figure 10. Comparison of the observed and the model predicted annual average apparent calving intervals of mature female southern right whales. Predicted values are as determined using the extended time varying model of Brandão *et al.* (2020) that includes the "delta-loop" with a weight of 5.0 applied to the penalty for $\hat{P}_y^A$.

Appendix 1: Photo-Identification model

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. The methodology below has been updated to include the "delta-loop" (i.e. an early abortion occurs so that a pregnant whale can become pregnant again the following year) modification to the model.

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:

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

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

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

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

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

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

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

$$\vdots$$

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

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:

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

where a_m is the age at which 50% of the immature female population become receptive and ω 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:

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

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

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

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,

δ_y is the probability that a whale that is receptive in year *y* becomes receptive in year *y*+1 (i.e. had an early abortion), 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 (i.e. had a late abortion).

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:

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

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

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

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

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

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

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:

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

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

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

$$\vdots$$

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

$$\vdots$$

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

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 given in Appendix 2.

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:

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

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:

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

where

$\widehat{N}_y^{calv,U}$	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:

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

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

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

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:

$$ln(e_h^A; \theta) = \sum_{h=1}^{n^A}\left(n_h^A \ln(e_h^A)\right) - \sum_{y=1979}^{2020} \widehat{N}_y^{calv,u} \hat{P}_y^A$$

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 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:

$$ln(e_h^C; \theta *) = \sum_{h=1}^{n^C} \left(n_h^C \, ln(e_h^C)\right) - \sum_{y=1979}^{2020} \widehat{N}_{0,y} \widehat{P}_y^C$$

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:

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

where

$\widehat{P}_y^C$ 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 ($\widehat{P}_y^A$) 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 $\widehat{P}_y^A$ 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:

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

where

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

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

The modification to the model to include the additional "delta-loop" was not able to eliminate the low sightings probabilities estimated for (in the first instance) the 2015-2017. Therefore, a penalty function was used to ensure that the estimates of $\widehat{P}_y^A$ for the years after 2014 were in the range of the average of the previous years since 1982. Thus, the following penalty function was added to the total negative log-likelihood function:

$$w \left\{ \frac{1}{2\sigma_{P*}^2} \sum_{y=2015}^{2020} \left(\widehat{P}_y^A - \overline{P^*}\right)^2 \right\}$$

where

$\overline{P^*}$ is the average of the $\hat{P}_y^A$ estimates for the years 1982 to 2014,

σ_{P^*} is the standard deviation of those $\hat{P}_y^A$ probabilities, and

w is a weight factor.

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.

The probabilities of a pregnant whale being pregnant again in the following year (δ_y) are fitted as time dependent, but only for the period 2014 to 2019 to reflect the period of low sightings. For all other years these probabilities are taken to be zero.

Estimable parameters

The estimable parameters in the model are S, S_j, α, β, γ, δ, a_m, ω, 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.

Appendix 2: Probability calculations for sighting histories

At any particular point in time, a female adult can be in one of three states: resting (1), receptive (2) or calving (3). When a female with a calf is sighted (i.e. calving state 3), this is recorded as a 1 in the sighting history for that female. For years in which the female is not sighted, however, several possible scenarios could have occurred, including death if the female has not been sighted again to date. This appendix outlines the methodology used to obtain all possible scenarios for a given sighting history, in order to calculate the associated probability. An update to previous versions of this appendix includes the addition of a "delta-loop", allowing a female who is pregnant in year *y* to become pregnant again in year *y+1*. This could occur in a situation where an abortion occurs early enough so that the female does not need to rest a year before conceiving again. This loop has been included to allow for alternative scenarios to the "beta-loop" (where a female resting in year *y* remains resting in year *y+1*).

Figure A2.1 shows the possible directions in which a female can move from one state to another. It should be noted that the following assumptions have been made:

1. A resting female has to first become receptive before calving (i.e. there is no flow from state 1 to state 3).
2. A female that is resting in one year may remain in the resting state the following year

In the equations that follow,

α_y is the probability that a female calving (state 3) in year *y* becomes receptive (state 2) in the following year,

β_y is the probability that a female resting in year *y* remains in the resting state the following year,

γ_y is the probability that a receptive female (state 2) does not produce a calf (i.e. a late abortion) and moves to the resting state instead,

δ_y is the probability that a receptive female is receptive the following year, following an early abortion,

S is the probability that an adult survives from one year to the next,

S_j is the probability that a juvenile survives from one year to the next,

P_y^i is the probability of a sighting history,

p_y is the probability of detecting an adult with a calf (depicted as $\hat{P}_y^A$ elsewhere),

ϕ_a is the probability that an immature whale of age *a* becomes receptive the following year.
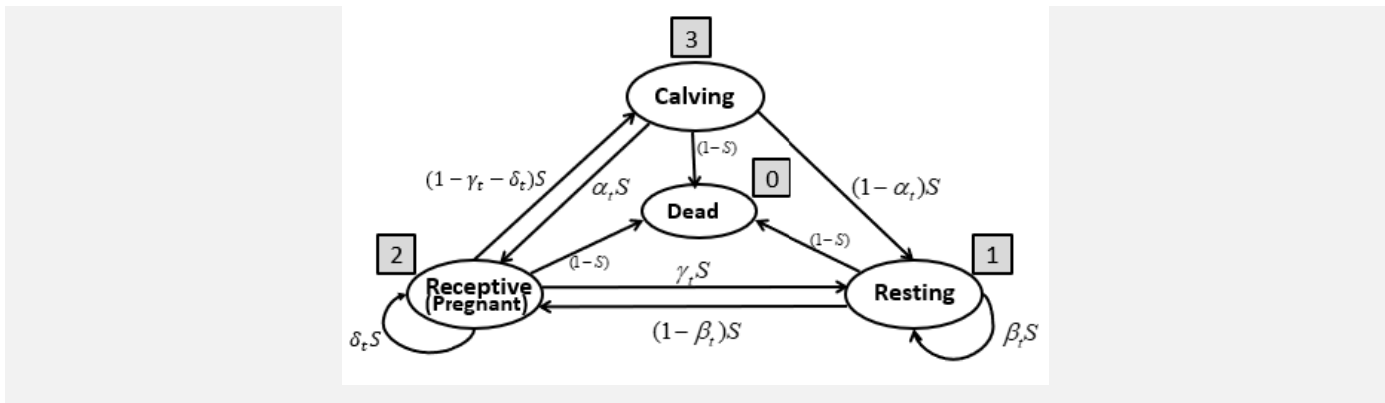
Figure A2.1. Flow diagram showing the possible movements from one state to another.

Sighting histories where the female is first seen as an adult with calf ("mature algorithms")

Given a particular sighting history, the computer program starts with the first sighting, and then proceeds through the rest of the sighting history using various algorithms based on when the next sightings occur. The sighting history is essentially broken into segments, and each unique segment is associated with a unique algorithm that is constructed based on all the possible scenarios that could produce that segment. These scenarios consist of all the possible sequences of states (receptive, calving, resting) that could produce a particular segment, bearing in mind that a '0' in a sighting history could mean that a female was (a) without calf, (b) with calf but not sighted or (c) dead (if there are no further sightings in the sighting history). Probabilities are calculated taking all scenarios into account.

There are three basic kinds of algorithms:
1. "Calving Algorithm (CA)", which is used at the start of the sighting history, as well as after a female has been sighted with a calf. There are four different CAs, which differ depending on when and if the female is sighted again with a calf in the following four years.
2. "Mature Normal Algorithm (MNA)", which is used when the female was not sighted in the previous year, or the following three years.
3. "Mature Upcoming Calf Algorithm (MUCA)", which is used to compute probabilities when the female is sighted with calf in three years' time.

Each algorithm keeps track of the possible states (receptive, calving or resting) that a whale could be in given the segment of the sighting history in question, as well as the associated probabilities. Thus, the program will move from one algorithm to the next depending on the placement of 1's and 0's in the sighting history until the last year is reached. Figure A2 illustrates the manner in which one algorithm flows to the next. Details of each algorithm, the corresponding sighting history segment, the possible states for that segment, along with the associated probabilities, are given in Table A2.1 – Table A2.6.

Sighting histories where the female is first seen as a calf ("immature algorithms")

For females that are first seen as calves, and later as adults with own calves, a fourth state "immature" needs to be taken into account, as it is not known exactly when the female matures. The following assumptions have been made:

1. The youngest possible age for a female to produce a calf is six years. Therefore, the youngest possible age for a female to become receptive is five years.

2. From age 15, all females are considered mature.

The algorithms for a female sighted first as a calf follow similar logic to those for a female first seen as an adult. There are

1. "First Calf Algorithm (FCA)", which is used only at the start of the sighting history when the female is first seen as a calf. There are four different FACs depending on when the female is first resighted with calf.
2. "Immature Normal Algorithm (INA)", which is used when a female has not yet been sighted with own calf, and is not sighted in the next three years.
3. "First Upcoming Calf Algorithm (FUCA)", which is used when the female is spotted for the first time with calf in three years' time.
4. Two additional algorithms for when a whale reaches age 13 to ensure that the whale is mature by age 15.

Once a female has been sighted with own calf, the algorithms proceed with the "mature algorithms". The flow diagram is given in Figure A2.3, and the probabilities and possible scenarios associated with each algorithm are given in Table A2.7 – Table A2.13. These tables have been updated to include the new "delta-loop", and red arrows and text have been used to indicate links and probabilities associated with this loop.
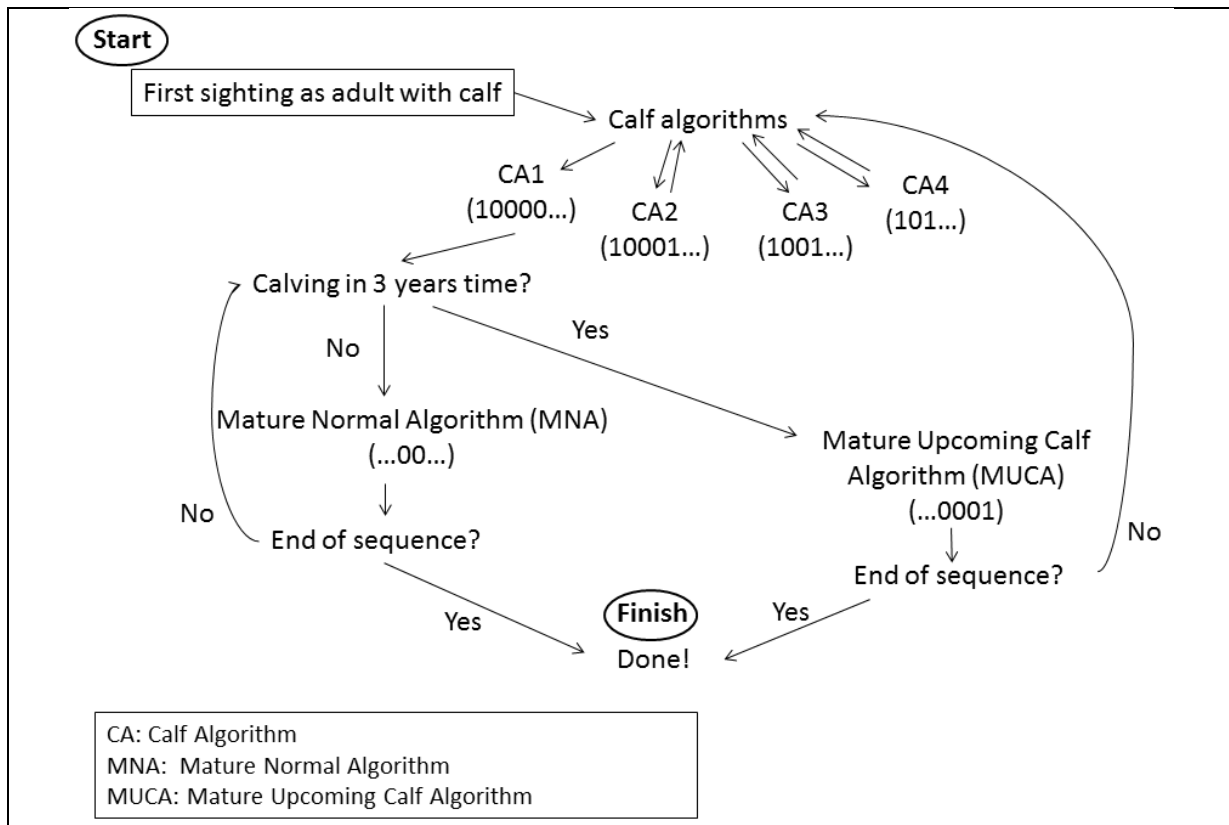
Figure A2.2. Flow chart for whales first seen as an adult with calf. Details for algorithms are given in Table A2.1-A2.6.
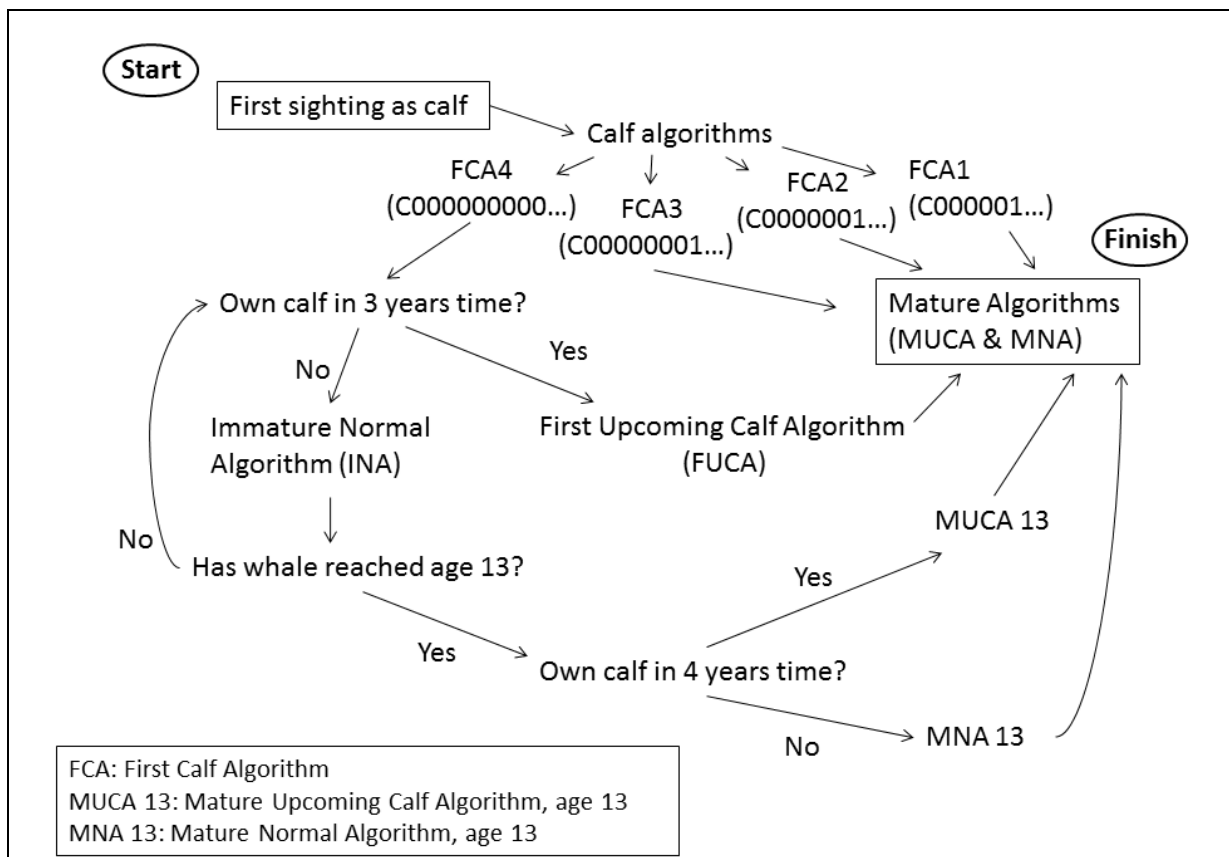

Figure A2.3. Flow chart for whales first seen as a calf, and later seen as adult with calf. Details for the algorithms are given in Table A2.7-A2.10.

29

Table A2.1. Calf Algorithm CA1. For any sequence starting off with 10000..., where '1' is a sighting of the adult female with a calf. Brackets around a (3) indicate a possible calving that occurred but was not sighted. Arrows and text in red indicate links and probabilities associated with the new "delta-loop".

CA1	1	0	0	Probability	
	y	y+1	y+2	y+1	y+2
Calving	3		(3)	$P^3_{k+1} = 0$	$P^3_{y+2} = P^2_{y+1}(1 - \gamma - \delta)S(1 - p_{y+2})$
Receptive		2	2	$P^2_{k+1} = P^1_k(\alpha S)$	$P^2_{k+2} = P^1_{k+1}(1 - \beta)S + P^2_{k+1}(\delta S)$
Resting		1	1	$P^1_{k+1} = P^1_k(1 - \alpha)S$	$P^1_{k+2} = P^2_{k+1}(\gamma S) + P^1_{k+1}(\beta S)$
Dead		0	0	$P^0_{k+1} = P^1_k(1 - S)$	$P^0_{k+2} = P^2_{k+1}(1 - S) + P^1_{k+1}(1 - S)$ if there are no further sightings. $P^0_{k+2} = 0$ otherwise.

Table A2.2. Calf Algorithm CA2. For any sequence starting off with 10001..., where '1' is a sighting of the adult female with a calf. Brackets around a (3) indicate a possible calving that occurred but was not sighted. Note that because the whale was sighted in year *y+4*, the probability if it being dead is zero.

CA2	1	0	0	0	1	Probability			
	y	y+1	y+2	y+3	y+4	y+1	y+2	y+3	y+4
Calving	3		(3)		3	$P^3_{k+1} = 0$	$P^3_{y+2} = P^2_{y+1}(1 - \gamma - \delta)S(1 - p_{y+2})$	$P^3_{k+3} = 0$	$P^3_{y+4} = P^2_{y+3}(1 - \gamma - \delta)S(p_{y+4})$
Receptive		2	2	2		$P^2_{k+1} = P^1_k(\alpha S)$	$P^2_{k+2} = P^2_{k+1}(\delta S)$	$P^2_{k+3} = P^3_{k+2}(\alpha S) + P^2_{k+2}(\delta S) + P^1_{k+2}(1 - \beta)S$	$P^2_{k+4} = 0$
Resting		1	1			$P^1_{k+1} = P^1_k(1 - \alpha)S$	$P^1_{k+2} = P^2_{k+1}(\gamma S) + P^1_{k+1}(\beta S)$	$P^1_{k+3} = 0$	$P^1_{k+4} = 0$
Dead						$P^0_{k+1} = 0$	$P^0_{k+2} = 0$	$P^0_{k+3} = 0$	$P^0_{k+4} = 0$

Table A2.3. Calf Algorithm CA3. For any sequence starting off with 1001..., where '1' is a sighting of the adult female with a calf. Note that because the whale was sighted in year *y+4*, the probability if it being dead is zero

CA3	1	0	0	1	Probability		
	y	y+1	y+2	y+3	y+1	y+2	y+3
Calving	3			3	$P^3_{k+1} = 0$	$P^3_{k+2} = 0$	$P^3_{y+3} = P^2_{y+2}(1 - \gamma - \delta)S(p_{y+3})$
Receptive		2	2		$P^2_{k+1} = P^3_k(\alpha S)$	$P^2_{k+2} = P^1_{k+1}(1 - \beta)S + P^2_{k+1}(\delta S)$	$P^2_{k+3} = 0$
Resting		1			$P^1_{k+1} = P^3_k(1 - \alpha)S$	$P^1_{k+3} = 0$	$P^1_{k+3} = 0$
Dead					$P^0_{k+1} = 0$	$P^0_{k+3} = 0$	$P^0_{k+3} = 0$

Table A2.4. Calving Algorithm CA4. For any sequence starting off with 101..., where '1' is a sighting of the adult female with a calf. Note that because the whale was sighted in year $y+4$, the probability if it being dead is zero

CA4	1	0	1	Probability	
	y	y+1	y+2	y+1	y+2
Calving	3		3	$P^3_{k+1} = 0$	$P^3_{y+2} = P^2_{y+1}(1 - \gamma - \delta)S(p_{y+2})$
Receptive		2		$P^2_{k+1} = P^1_k(\alpha S)$	$P^2_{k+2} = 0$
Resting				$P^1_{k+1} = 0$	$P^1_{k+2} = 0$
Dead				$P^0_{k+1} = 0$	$P^0_{k+2} = 0$

Table A2.5. Mature Normal Algorithm (MNA). No calf in the previous year or the following 3 years. Brackets around a (3) indicate a calving that was not sighted.

MNA	0	0	Probability
	y	y+1	y+1
Calving	(3)	(3)	$P^3_{y+1} = P^2_y(1 - \gamma - \delta)S(1 - p_{y+1})$
Receptive	2	2	$P^2_{y+1} = P^3_y(\alpha S) + P^2_y(\delta S) + P^1_y(1 - \beta)S$
Resting	1	1	$P^1_{y+1} = P^3_y(1 - \alpha)S + P^2_y(\gamma S) + P^1_y(\beta S)$
Dead	0	0	$P^0_{y+1} = P^3_y(1 - S) + P^2_y(1 - S) + P^1_y(1 - S)$ if there are no further sightings. $P^0_{y+1} = 0$ otherwise.

Table A2.6. Mature Upcoming Calf Algorithm (MUCA). Calving in 3 years' time, but none in the previous 3 years. Brackets around a (3) indicate a possible calving that was not sighted. Note that because the whale was sighted in year $y+4$, the probability if it being dead is zero.

MUCA	0	0	0	1	Probability		
	y	y+1	y+2	y+3	y+1	y+2	y+3
Calving	(3)	(3)		3	$P^3_{y+1} = P^2_y(1 - \gamma - \delta)S(1 - p_{y+1})$	$P^3_{y+2} = 0$	$P^3_{y+3} = P^2_{y+2}(1 - \gamma - \delta)S(p_{y+3})$
Receptive	2	2	2		$P^2_{y+1} = P^3_y \alpha S + P^2_y(\delta S) + P^1_y(1 - \beta)S$	$P^2_{y+2} = P^3_{y+1}(\alpha S) + P^2_{y+1}(\delta S) + P^1_{y+1}(1 - \beta)S$	$P^2_{y+3} = 0$
Resting	1	1			$P^1_{y+1} = P^3_y(1 - \alpha)S + P^2_y(\gamma S) + P^1_y(\beta S)$	$P^1_{y+2} = 0$	$P^1_{y+3} = 0$
Dead					$P^0_{y+1} = 0$	$P^0_{y+2} = 0$	$P^0_{y+3} = 0$

Table A2.7. First Calf Algorithm FCA1. The sequence C000001, where 'C' is the first sighting as a calf, and '1' is the first resighting as an adult with calf. Not that because the whale was sighted in year *y+4*, the probability if it being dead is zero.

FCA1	C	0	0	0	0	0	1	Probability		
	y	y+1	y+2	y+3	y+4	y+5	y+6	y+1	y+5	y+6
Immature	4 —	4 —	4 —	4 —	4			$P^4_{y+1} = S_j\rho$	$P^4_{y+5} = 0$	$P^4_{y+6} = 0$
Calving							3	$P^3_{y+1} = 0$	$P^3_{y+5} = 0$	$P^3_{y+6} = P^2_{y+5}(1-\gamma-\delta)S(p_{y+6})$
Receptive						2		$P^2_{y+1} = 0$	$P^2_{y+5} = P^4_{y+4}(\varphi_4 S)$	$P^2_{y+6} = 0$
Resting								$P^1_{y+1} = 0$	$P^1_{y+5} = 0$	$P^1_{y+6} = 0$

Table A2.8. First Calf Algorithm FCA2. The sequence C0000001, where 'C' is the first sighting as a calf, and '1' is the first resighting as an adult with calf. Not that because the whale was sighted in year *y+4*, the probability if it being dead is zero.

FCA2	C	0	0	0	0	0	0	1	Probability		
	y	y+1	y+2	y+3	y+4	y+5	y+6	y+7	y+5	y+6	y+7
Immature	4 —	4 —	4 —	4 —	4 —	4			$P^4_{y+5} = P^4_{y+4}(1-\varphi_4)S$	$P^4_{y+6} = 0$	$P^4_{y+7} = 0$
Calving								3	$P^3_{y+5} = 0$	$P^3_{y+6} = 0$	$P^3_{y+7} = P^2_{y+6}(1-\gamma-\delta)S(p_{y+7})$
Receptive							2		$P^2_{y+5} = 0$	$P^2_{y+6} = P^4_{y+5}(\varphi_5 S)$	$P^2_{y+7} = 0$
Resting									$P^1_{y+5} = 0$	$P^1_{y+6} = 0$	$P^1_{y+7} = 0$

Table A2.9. First Calf Algorithm FCA3. The sequence C00000001, where 'C' is the first sighting as a calf, and '1' is the first resighting as an adult with calf. Brackets around a (3) indicate a calving that was not sighted.

Probability			
y+5	y+6	y+7	y+8
$P^4_{y+5} = P^4_{y+4}(1-\varphi_4)S$	$P^4_{y+6} = P^4_{y+5}(1-\varphi_5)S$	$P^4_{y+7} = 0$	$P^4_{y+8} = 0$
$P^3_{y+5} = 0$	$P^3_{y+6} = P^2_{y+5}(1-\gamma-\delta)S(1-p_{y+6})$	$P^3_{y+7} = 0$	$P^3_{y+8} = P^2_{y+7}(1-\gamma-\delta)S(p_{y+8})$
$P^2_{y+5} = P^4_{y+4}(\varphi_4 S)$	$P^2_{y+6} = P^4_{y+5}(\varphi_5 S) + P^2_{y+5}(\delta S)$	$P^2_{y+7} = P^4_{y+6}(\varphi_6 S) + P^3_{y+6}(\alpha S) + P^2_{y+6}(\delta S) + P^1_{y+6}(1-\beta)S$	$P^2_{y+8} = 0$
$P^1_{y+5} = 0$	$P^1_{y+6} = P^2_{y+6}(\gamma S)$	$P^1_{y+7} = 0$	$P^1_{y+8} = 0$

Table A2.10. First Calf Algorithm FCA4. The sequence C000000001, where 'C' is the first sighting as a calf, and '1' is the first resighting as an adult with calf. Brackets around a (3) indicate a calving that was not sighted.

Probability		
y+5	y+6	y+7 to y+9
$P^4_{y+5} = P^4_{y+4}(1-\varphi_4)S$	$P^4_{y+6} = P^4_{y+5}(1-\varphi_5)S$	
$P^3_{y+5} = 0$	$P^3_{y+6} = P^2_{y+5}(1-\gamma-\delta)S(1-p_{y+6})$	Proceed with
$P^2_{y+5} = P^4_{y+4}(\varphi_4 S)$	$P^2_{y+6} = P^4_{y+5}(\varphi_5 S) + P^2_{y+5}(\delta S)$	Upcoming Calf Algorithm (FUCA)
$P^1_{y+5} = 0$	$P^1_{y+6} = P^2_{y+6}(\gamma S)$	

Note that if a calf is not seen again as an adult, then the probability of death needs to be taken into account:

$$P^0_{y+1} = (1 - S_j\rho)$$

33

Table A2.11. Immature Normal Algorithm (INA). Not sighted yet with own calf, and no calf in the following 3 years. Brackets around a (3) indicate a possible calving that was not sighted.

INA	0	0	Probability
	y	y+1	y+1
Immature	4 — 4		$P_{y+1}^4 = P_y^4(1 - \varphi_a)S$
Calving	(3)	(3)	$P_{y+1}^3 = P_y^2(1 - \gamma - \delta)S(1 - p_{y+1})$
Receptive	2	2	$P_{y+1}^2 = P_y^4 \varphi_a S + P_y^3(\alpha S) + P_y^2\,(\delta S) + P_y^1(1 - \beta)S$
Resting	1	1	$P_{y+1}^1 = P_y^3(1 - \alpha)S + P_y^2(\gamma S) + P_y^1(\beta S)$

Table A2.12. First Upcoming Calf Algorithm (FUCA). Calving in 3 years' time, but none in the previous 3 years. Brackets around a (3) indicate a possible calving that was not sighted. Note that because the whale was sighted in year *y+4*, the probability if it being dead is zero.

FUCA	0	0	0	1	Probability		
	y	y+1	y+2	y+3	y+1	y+2	y+3
Imm.	4 — 4				$P_{y+1}^4 = P_y^4(1 - \varphi_a)S$	$P_{y+2}^4 = 0$	$P_{y+3}^4 = 0$
Calving	(3)	(3)		3	$P_{y+1}^3 = P_{y+2}^2(1 - \gamma - \delta)S(1 - p_{y+1})$	$P_{y+2}^3 = 0$	$P_{y+3}^3 = P_{y+2}^2(1 - \gamma - \delta)S(p_{y+3})$
Rec.	2	2	2		$P_{y+1}^2 = P_y^4 \varphi_a S + P_y^3(\alpha S) + P_y^2(\delta S) + P_y^1(1 - \beta)S$	$P_{y+2}^2 = P_{y+1}^4 \varphi_a S + P_{y+1}^3(\alpha S) + P_y^2(\delta S) + P_{y+1}^1(1 - \beta)S$	$P_{y+3}^2 = 0$
Resting	1	1			$P_{y+1}^1 = P_y^3(1 - \alpha)S + P_y^2(\gamma S) + P_y^1(\beta S)$	$P_{y+2}^1 = 0$	$P_{y+3}^1 = 0$

Table A2.13. Mature Upcoming Calf Algorithm 13 (MUCA13). Whale aged 13, with sighting with own calf in four years' time. Brackets around a (3) indicate a calving that was not sighted.

FCA3	C	0	0	0	1
	y (13)	y+1 (14)	y+2 (15)	y+3 (16)	y+4 (17)
Immature	4				
Calving	(3)	(3)	(3)		3
Receptive	2	2	2	2	
Resting	1	1	1		

Probability			
y+1	y+2	y+3	y+4
$P_{y+1}^4 = 0$	$P_{y+2}^4 = 0$	$P_{y+3}^4 = 0$	$P_{y+4}^4 = 0$
$P_{y+1}^3 = P_y^2(1-\gamma-\delta)S(1-p_{y+1})$	$P_{y+2}^3 = P_{y+1}^2(1-\gamma-\delta)S(1-p_{y+2})$	$P_{y+3}^3 = 0$	$P_{y+4}^3 = P_{y+3}^2(1-\gamma-\delta)S(p_{y+4})$
$P_{y+1}^2 = P_y^4(\varphi_{13}S) + P_y^3(\alpha S) + P_y^2(\delta S) + P_y^1(1-\beta)S$	$P_{y+2}^2 = P_{y+1}^3(\alpha S) + P_{y+1}^2(\delta S) + P_{y+1}^1(1-\beta)S$	$P_{y+3}^2 = P_{y+2}^3(\alpha S) + P_{y+2}^2(\delta S) + P_{y+2}^1(1-\beta)S$	$P_{y+4}^2 = 0$
$P_{y+1}^1 = P_y^3(1-\alpha)S + P_y^2(\gamma S) + P_y^1(\beta S)$	$P_{y+2}^1 = P_{y+1}^3(1-\alpha)S + P_{y+1}^2(\gamma S) + P_{y+1}^1(\beta S)$	$P_{y+3}^1 = 0$	$P_{y+4}^1 = 0$

Table A2.14. Mature Normal Algorithm 13 (MNA13). Whale aged 13, with no sighting with calf in the following four years. Brackets around a (3) indicate a calving that was not sighted.

MNA13	0	0	0	0	0	Probability		y+3 to y+4
	y (13)	y+1 (14)	y+2 (15)	y+3 (16)	y+4 (17)	y+1	y+2	
Immature	4	4				$P_{y+1}^4 = P_y^4(1-\varphi_{13})S$	$P_{y+2}^4 = 0$	Proceed with
Calving	(3)	(3)	(3)	(3)	(3)	$P_{y+1}^3 = P_y^2(1-\gamma-\delta)S(1-p_y)$	$P_{y+2}^3 = P_{y+1}^2(1-\gamma-\delta)S(1-p_{y+2})$	Mature Normal
Receptive	2	2	2	2	2	$P_{y+1}^2 = P_y^4(\varphi_{13}S) + P_y^3(\alpha S) + P_y^2(\delta S) + P_y^1(1-\beta)S$	$P_{y+2}^2 = P_{y+1}^4(\varphi_{14}S) + P_{y+1}^3(\alpha S) + P_{y+1}^2(\delta S) + P_{y+1}^1(1-\beta)S$	Algorithm (MNA)
Resting	1	1	1	1	1	$P_{y+1}^1 = P_y^3(1-\alpha)S + P_y^2(\gamma S) + P_y^1(\beta S)$	$P_{y+2}^1 = P_{y+1}^3(1-\alpha)S + P_{y+1}^2(\gamma S) + P_{y+1}^1(\beta S)$	