

A photo-identification-based assessment model of southern right whales *Eubalaena australis* surveyed in South African waters, with a focus on recent low counts of mothers with calves

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Photo-identification data for southern right whale cow–calf pairs on the South African calving grounds provide one of the longest abundance time-series for any whale population worldwide. Following a very steady increase from a heavily depleted state, surveys since 2015 reflect many notably low counts. These data are analysed to investigate whether these low counts can be explained by changes in reproduction-related parameters. This necessitates a modification to an earlier reproduction model for these whales, fit to photo-identification data to allow for early abortions; hence, a whale pregnant one year can again be pregnant the next. This can account for an increase in calving intervals in a way that differs from a whale resting for another year or an increase in late-abortion probability. This modification was able to account for the low number of sightings of cow–calf pairs over the 2015 to 2020 period (excepting for 2018), though the estimated probability of sighting a cow–calf pair in 2018 is somewhat low given a nearly unchanged annual survey effort. Hence, low numbers of sightings of females with calves for five of the years from 2015 to 2020 can be explained by changes in reproduction-related parameters rather than an increased natural mortality which is inconsistent with the photo-identification data. Changing environmental (particularly feeding) conditions seems to be the likely cause, possibly associated with a changed distribution of these whales. The estimated number of all whales in the population in 2020 is 6 470 (SE 285), with the number of parous females estimated to have increased 15-fold over the last four decades.

Keywords: calving interval, cow–calf pairs, demographic parameters, population growth rate, sightings histories, three-year reproductive cycle population model

Online supplementary material: The Supplementary Information, available at <https://doi.org/10.2989/1814232X.2023.2172455>, provides results additional to those given in the main text; it also provides the details and equations for the calculations of the probabilities for the sighting histories, which are used to develop the likelihood maximised in the model-fitting process.

Introduction

The South African population of southern right whales *Eubalaena australis* has been extensively studied since 1979 using annual helicopter surveys on the South African calving ground. These surveys have been conducted each year in late September to early October along the southern Cape coast, from Nature's Valley to Muizenberg, at a time when most calves seem to be present along the coast (Best 1990). The surveys are flown with the main purpose to photograph all females with associated calves as well as any individual with a distinct dorsal colour pattern, for subsequent individual identification. Operating procedures have been largely standardised over this 43-year survey series, although technological advances have been incorporated to facilitate data collection (e.g. inclusion of a GPS device and digital photography). For more details on the survey procedures, see Best (1990). The resultant annual counts of cow–calf pairs are shown in Figure 1, and Figure 2 shows the distributions of the apparent calving

intervals over time. This is one of the longest consistently conducted surveys of any whale population worldwide and provides important insight concerning whale dynamics as a population recovers from reduction to a very low level caused by earlier whaling.

In earlier analyses, the associated sighting histories were modelled by applying the approach of Payne et al. (1990), developed further by Cooke et al. (1993), to obtain estimates of calving interval and adult survival rate (Best et al. 2001). Incorporating information on the observed ages of first reproduction of grey-blazed calves, which are known to be female, allowed for the estimation of the age at first parturition and the first-year survival rate, as well as the instantaneous population increase rate (Best et al. 2001). Since 2012, a reproduction model (also termed the 'receptive, calving and resting' model) of Cooke et al. (2003), has been used to estimate the demographic parameters of this population (Brandão et al. 2012, 2013, 2018, 2019).

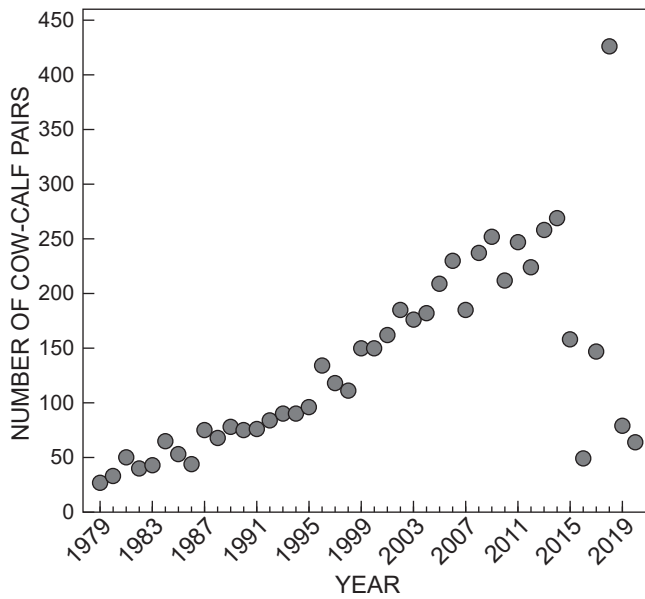


Figure 1: Number of cow–calf pairs sighted during annual southern right whale surveys off South Africa

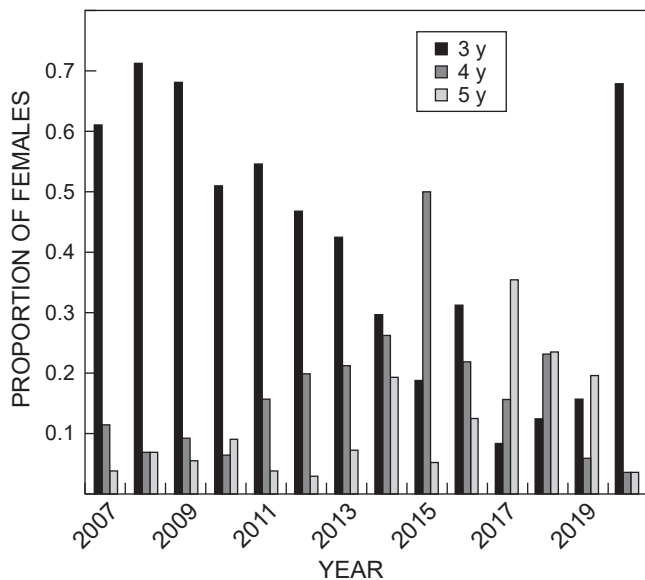


Figure 2: Distribution of apparent calving intervals for the year in which a southern right whale calf was most recently observed off South Africa. Note ‘apparent’ is in the sense of observed, and without adjustment for cow–calf pairs present but missed during the surveys

However, since 2010 a decreasing trend in the ratio of unaccompanied adults to cow–calf pairs has been evident (see Figure 3). Furthermore, despite a standardised survey method, the earlier general trend of a steady increase in the number of cow–calf pairs on the breeding ground has varied dramatically since 2014, with an appreciable drop between 2015 and 2017, a record high number in 2018, and then another appreciable drop to low levels in 2019 and 2020 (Vermeulen et al. 2021) (Figure 1).

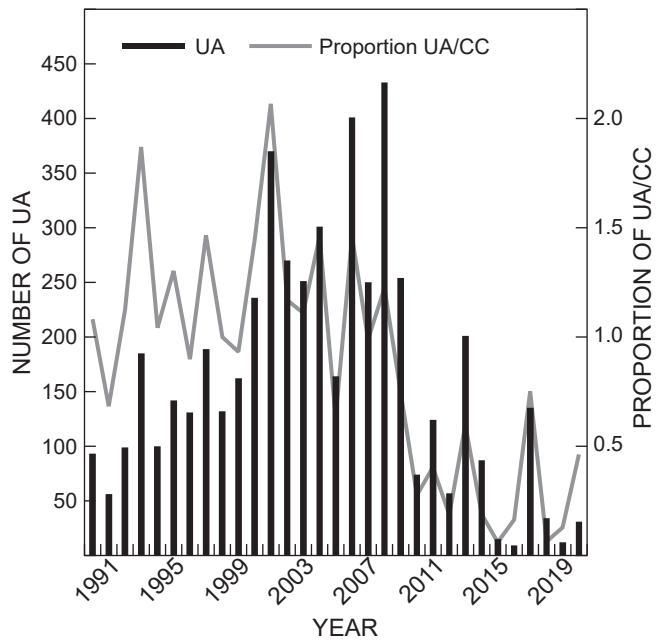


Figure 3: Number of unaccompanied adult southern right whales (UA), as well as UA expressed relative to the number of cow–calf pairs (CC), in the surveys

Brandão et al. (2018) reported on the first analyses that included survey data displaying the drop in cow–calf pairs in the period 2015–2017. Brandão et al. (2019) then provided an updated analysis to include the 2018 data, which reflected a record high number of cow–calf pairs. Results showed a marked decrease from 2015 in the estimated probabilities of observing a female with its calf. These analyses also noted marked changes over the years in the expected number of resting females and the probability that a resting female would rest an additional year. However, the estimated annual instantaneous growth rate of the mature female population, as well as the adult and the first-year survival rates, remained very similar to those estimated previously. These results, reported in Brandão et al. (2018, 2019), suggested that the hypothesis of lengthened calving intervals was to be favoured over mass mortality to account for such low survey numbers during 2015–2017. Brandão et al. (2018) also concluded that the previous assumption of a time-invariant probability that a mature female whale that is in the resting cycle will rest for a further year (the β parameter – see the following section) could no longer be reconciled with the observations of the numbers of cow–calf pairs in South African waters over the last few years.

In this article, the model of Brandão et al. (2019) is extended to include the possibility of an early abortion, so that a pregnant (receptive) female in year y can again be pregnant in year $y+1$ (a possibility that was previously introduced by Cooke et al. [2015]). This extension was implemented to account for increased calving intervals and to eliminate the otherwise low estimates of the probabilities of sighting a cow–calf pair between 2015 and 2017 and in 2019 and 2020. The results of what will hereafter be termed this ‘new model’ are reported and discussed below.

This work also examines whether the available data could alternatively be explained by a recent increase in the whales' natural mortality rate, rather than an increased number of early abortions.

Materials and methods

Photo-identification data obtained from helicopter aerial photographic surveys from 1979 to 2020 were available for analyses. Details of the survey techniques and the photo-identification protocol have been published in Best (1990). Of importance to the following analyses (particularly in their estimation of sighting probabilities) is that these surveys have been carried out in as standard a manner as possible over time. They have used the same methods on each flight, along the same stretch of coastline (Nature's Valley to Muizenberg), and over the same part of the year (during which the vast majority of calves have been born: Best [1990, 1994]). Furthermore, based on additional research, patterns of coastal habitat use and the timing of calving seem to have remained unchanged over time (Vermeulen et al. 2021). During the surveys, photographic effort is focused on cow-calf pairs and on any individual with a distinct dorsal colour pattern (grey-blazing), which is retained from birth. Single whales without a distinct dorsal colour pattern (either males, or females without an associated calf) in the survey area are not photographed. Using the survey and photo-identification method described in Best et al. (2001), a total of 1 838 individual cow-calf pairs have been catalogued from the 1979–2020 surveys. Additionally, 360 individual grey-blazed females have been catalogued, whose sighting histories are used to link the dynamics of the mature females to the output of their reproduction by allowing for estimation of the parameters for first-year mortality and of the maturity ogive.

Details of the methods used—both the population dynamics model and the likelihood maximised to estimate parameter values from the photo-identification data, as well as the adjustment to allow for the possibility of a recent increase in natural mortality—are given in the Appendix. The method for computing the probabilities for sighting histories is given in the Supplementary Information. Figure 4 diagrammatically shows the possible ways in which a mature female can move from one reproductive state to another. The only information that the model uses is that of observed sighting histories of cow-calf pairs. The notation used in providing the results is as follows:

α_y = probability that a mature female whale that calves in year y becomes receptive the next year;

β_y = probability that a resting mature female whale in year y rests for a further year;

δ_y = probability that a pregnant whale in year y is pregnant the next year (i.e. following an early abortion);

γ_y = probability that a pregnant whale in year y rests rather than calves the next year (i.e. following a late abortion, or if the calf dies soon after birth before the cow-calf pair can be sighted);

S = post-first-year annual female survival proportion, alternatively expressed as an annual natural mortality rate M , where $S = e^{-M}$;

S_{2014+} = post-first-year annual female survival proportion

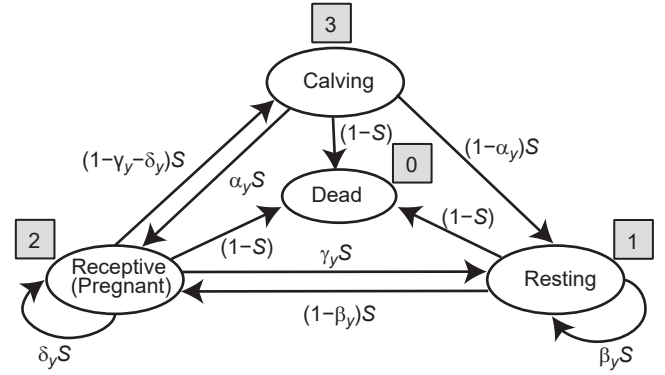


Figure 4: Flow diagram showing the possible ways in which a mature female southern right whale can move from one reproductive stage to another. See text for explanation of symbols

applicable to the years 2014 and onwards when

considering a model with a decrease in this survival rate for this period;

S_j = the first-year female survival proportion;

ρ = probability that a grey-blazed female calf is identified when giving birth later;

P_y^A = probability that a cow-calf pair is seen in year y ;

$a_{m,\omega}$ = 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; and

r = annual (instantaneous) parous female growth rate estimated over the whole period of cow-calf sightings.

At base, the model used here allows for a three-year reproductive cycle: receptive to calving to resting (Figure 4). The probabilities α , β , γ and δ reflect deviations from this three-year cycle. In simple terms, α allows for the possibility of a two-year cycle, β a four-year cycle (because of an extra year of resting), δ a four-year cycle (due to an early abortion), and γ a five-year cycle (due to a late abortion). There are no records of a one-year calving interval in the South African right whale sighting histories. In addition, given a gestation period estimate ranging from 357 to 396 days for the species (Best 1994), the probability of a one-year cycle is therefore assumed to be zero. Note that in the South African situation where survey observations are made in spring, the adult classifications of 'calving' and 'receptive' would effectively pertain to whales that are 'lactating' or 'pregnant', respectively.

The model assumes that all cow-calf pairs in the population in a particular year are available to be sighted, with P_y^A being the estimable probability that the pair are seen in the survey area. It is not possible (without further data or assumptions) to distinguish between cow-calf pairs that were present in the survey area but missed by the observer and those pairs that were not in the survey area.

Earlier versions of this model made no distinction between a receptive female that remains in that state for another year and a resting female that rests again the following year, as both instances would be observed in the resighting histories as a four-year calving interval. As such, both these occurrences were previously modelled

as a resting female resting for another year; that is, the δ parameter would be set to zero and the β estimates would account for both instances of a four-year cycle. Variants of this model were initially investigated by Brandão et al. (2013), where either all the parameters α , β and γ were set to be time-invariant, or either β or γ was allowed to vary with time. As model fits showed hardly any changes in the estimates of the time-varying γ_y parameter, subsequent analyses up to and including Brandão et al. (2019) interpreted the resighting histories for these right whales using the ‘ β time-varying model’—this was a model in which the α_y and γ_y probabilities were considered time-invariant, whereas the β_y probabilities might vary with time.

However, the earlier steadily increasing trend of the number of observed cow–calf pairs has changed recently, with an appreciable drop over the 2015 to 2017 period, and then a record high number of cow–calf pairs observed in 2018, followed again by another appreciable drop over the 2019 and 2020 period (Vermeulen et al. 2021) (Figure 1). These findings, combined with increased apparent calving intervals since 2009 (note ‘apparent’ in the sense of observed, and without adjustment for cow–calf pairs missed in the surveys) (Vermeulen et al. 2021) (Figure 2), led to the modification introduced here (of the model of Brandão et al. [2019]) to include (from 2014) the possibility of an early abortion. Thus, a pregnant (receptive) whale in year y can again be pregnant in year $y+1$ (i.e. to therefore include the δ parameter or so called ‘delta-loop’). An alternative hypothesis to explain this drop in the number of cow–calf pairs observed—that natural mortality has increased—is also considered, specifically an increase in the natural mortality by a fixed amount from 2014, so that annual survival reduces to a lower estimable value of S_{2014+} from that year.

A concern that arises is that there might be confounding among the reproductive cycle parameters (α , β , γ and δ), especially if time-dependence in some of these is allowed. Between years of observing a given cow with her current calf, there are several combinations of the state in which a cow could have been (i.e. resting, had an early or a late abortion, or a sighting was missed), and it is questionable how distinguishable these effects might be given the sighting histories data. However, it is possible that the low number of sightings for the periods 2015–2017 and 2019–2020 (Figure 1) might allow for the effect of an early abortion (δ parameter) to be distinguished from the effect of parameters β (the whale rests for another year) or γ (a late abortion) (Brandão et al. 2021).

The inclusion of this delta-loop in the new model presented here is applied to the β time-varying model of Brandão et al. (2019). The δ_y probabilities must necessarily be time-dependent yet are estimated for the period 2014–2019 only (the data do not allow for an estimate in 2020, the last year of sighting data) to account for the period of low sightings and to reduce the number of parameters estimated. For all other years these probabilities are taken to be zero. Standard errors of the parameter estimates are based on the Hessian, the matrix of second-order partial derivatives of the log-likelihood function with respect to its parameters (see the final section of the Appendix).

Initial results when incorporating the delta-loop modification showed that this alone did not successfully

eliminate the low sightings probabilities (\hat{P}_y^A) estimated for the years 2018 and 2019. The low sightings probabilities in these years seem difficult to reconcile with the nearly unchanged survey methods, the patterns of coastal habitat use by right whales, and the timing of calving over these and adjacent years. A penalty function (Eqn A20) had in any case been added to stabilise the estimates of \hat{P}_y^A near the end of the series and to keep their values similar to those over the earlier years commencing from 1982. The Base case model applied a weight of 1.0 (i.e. no additional weight beyond that for the customary shrinkage to the mean) to the contribution of the penalty on \hat{P}_y^A to the likelihood. Sensitivity to this was investigated, which increased the weight on this penalty term to 8.0 in an attempt to increase the anomalously low estimates of \hat{P}_y^A for 2018 to closer to values for earlier years (weights of >8.0 led to this term inappropriately swamping the other terms in the log likelihood).

There is not enough information for the 2019 and 2020 (the last two years of sighting histories) random variations for the β values to be estimated because of the two-year minimum calving interval observed. Therefore, these random variations are always fixed at 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

Results for the new model for the Base case and for the Sensitivity, as well as for the alternative hypothesis of a recent increase in the natural mortality rate M , are provided in Table 1. In what follows, the parameter estimates given are for the Base case, with those for the Sensitivity given in parenthesis; when estimates apply to the alternative of an increase in M , this is stated specifically. The respective estimate of the first-year female survival rate S_j is 0.874 (0.892), with the estimate for annual post-first-year female survival S being 0.987 (0.987, unchanged). The alternative hypothesis of an increase in M from 2014 requires an appreciable reduction in S of some 20%. The annual instantaneous growth rate of the parous female population per annum (r) is estimated to be 6.5% (6.6%). The probability that female grey-blazed calves are not identified when adults ($1-p$), is estimated to be 19.6% (20.4%).

The probability of observing a cow–calf pair (all of these pairs are assumed to always be present) on aerial surveys under the new model hardly changes from the Base case to the Sensitivity for the pre-2018 period (Figure 5a,b). The Sensitivity estimates the 2019 probability of observing a cow–calf pair to be closer to the average of the estimates for earlier years. When a recent increase in M is considered, these annual sighting probabilities are estimated to vary to a much greater extent over recent years.

The contributions of the various components to the penalised negative log-likelihood function for the three models are given in Table 2. These indicate that the Base case model is more consistent than the Sensitivity with the observed adult re-sighting histories, and (slightly) with the penalty on the variations in β . When the recent value of M is allowed to increase rather than introduce the possibility of early abortions, the fit to the data deteriorates by some 30

Table 1: Estimates of various demographic parameters for southern right whales off South Africa under the new model for the Base case and Sensitivity (see text and Appendix for an explanation of the symbols), as well as an alternative to the Base case in which an increase in natural mortality (M) is considered. 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, as calculated under the assumption of a 50:50 sex ratio at birth). The parameter r is the parous female instantaneous growth rate (in units of y^{-1}) over the whole period of cow–calf sightings. The quantities in parenthesis are Hessian-based estimates of standard errors

Parameter	Model		
	Base case	Sensitivity	Increase in M
α (time-invariant)	0.019 (0.002)	0.019 (0.002)	0.018 (0.002)
$\bar{\beta}^*$	0.184 (0.009)	0.181 (0.009)	0.223 (0.007)
γ (time-invariant)	0.068 (0.007)	0.070 (0.007)	0.070 (0.007)
S	0.987 (0.001)	0.987 (0.001)	0.988 (0.001)
S_{2014+}	–	–	0.806 (0.018)
S_j	0.874 (0.042)	0.892 (0.042)	0.856 (0.040)
ρ	0.804 (0.057)	0.796 (0.057)	0.820 (0.059)
a_m	8.120 (1.378)	8.352 (1.347)	8.301 (1.306)
ω	2.099 (0.871)	2.219 (0.850)	2.202 (0.830)
N_{1979}^{calv}	41 (9)	41 (8)	41 (9)
N_{1979}^{recp}	48 (10)	48 (9)	48 (10)
N_{1979}^{rest}	67 (18)	66 (18)	67 (18)
$N_{1979}^{\text{mature}^*}$	139 (32)	138 (30)	140 (32)
N_{2020}^{calv}	83 (15)	82 (11)	98 (15)
N_{2020}^{recp}	1 809 (170)	1 872 (111)	353 (81)
N_{2020}^{rest}	329 (156)	288 (89)	213 (74)
$N_{2020}^{\text{mature}^*}$	2 092 (70)	2 111 (70)	622 (73)
N_{2020}^{all}	6 470 (285)	6 085 (250)	2 296 (252)
r	0.065 (0.002)	0.066 (0.002)	0.052 (0.003)

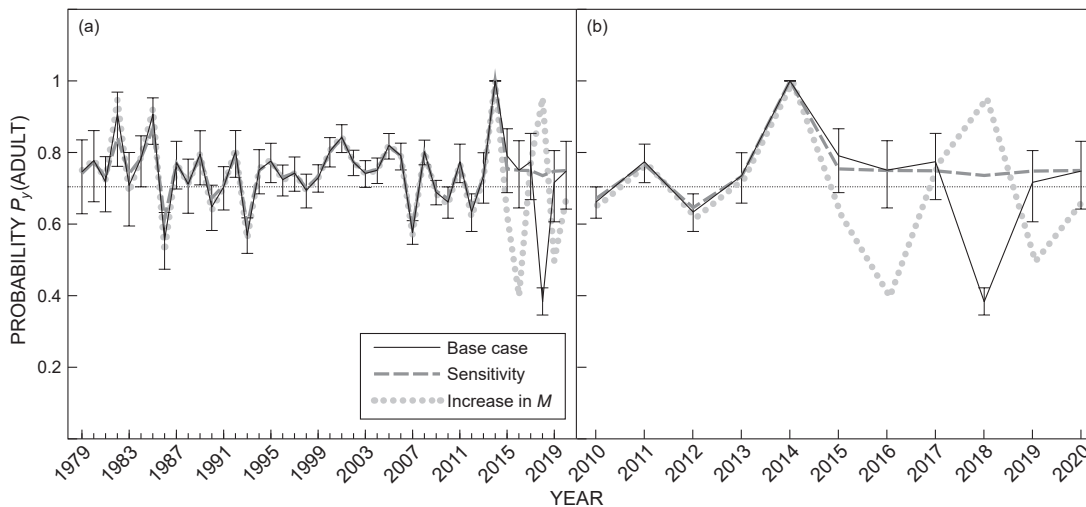


Figure 5: (a) Estimated probabilities of observing a southern right whale cow–calf pair on aerial surveys under the new model for the Base case and Sensitivity, as well as when a recent increase in natural mortality (M) is considered. (b) A magnified version of the probabilities for recent years. The dotted horizontal line at 0.7 is approximately the average of pre-2014 probabilities. The error bars represent the range of one Hessian-based standard error added to and subtracted from the estimate concerned

Table 2: Contributions to the penalised negative log-likelihood function by its various components of the new model of southern right whale reproduction off South Africa. \hat{P}_y^A is the probability that a cow-calf pair is seen in year y . Beta is the probability that a resting whale will rest in the following year

	Model		
	Base case	Sensitivity	Increase in M
Adult histories	2 310	2 321	2 330
Calf histories	569.6	569.6	567.3
Beta random effects	18.30	18.51	27.40
Penalty on \hat{P}_y^A at the beginning of series (1979–1981)	0.075	0.088	0.051
Penalty on \hat{P}_y^A at the end of series (2015–2020)	7.587	0.016*	11.62
Total	2 905	2 909*	2 936

*Does not include the multiplication of \hat{P}_y^A penalty by the weight applied to it

log-likelihood points—a consequence of less compatibility with the assumption of normally distributed values of annual variations of the β parameters and especially less consistency with the adult photo-identification histories.

The new model results in higher estimates of the probabilities that a resting whale will rest in the following year (β) for the period 2009–2013, with another peak in 2015 (Figure 6) (see Supplementary Figure S1 for the corresponding results for the alternative hypothesis of a recent increase in M). Higher probabilities for the period 2012–2015 are estimated to explain the low numbers of cow-calf pairs observed immediately thereafter, before dropping from 2016 to similar values to those for earlier years for the Base case.

The expected numbers of mature females that are in the receptive, calving and resting stages for the Base case and Sensitivity are shown in Figure 7. In general, there is hardly any difference in the numbers of females that are receptive and are calving between these two models, except for 2018 and 2019 for receptive females, for which the Sensitivity leads to higher estimated numbers, with the reverse effect for 2018 for the number of females calving. For the alternative hypothesis of a recent increase in M , these numbers are generally smaller over recent years (Figure 7).

The number of parous females is calculated by excluding whales ovulating for the first time from the number of mature females, and this is reported as the ‘mature’ component of the population.¹ The current (2020) estimate of the number of parous females is 2 092 (2 111) (Table 1; Supplementary Figure S2); this reflects growth from 139 in 1979, by a 15-fold increase over the last four decades. For the total population (i.e. including males and calves, as calculated under the assumption of a 50:50 sex ratio) the current abundance is 6 470 (6 085), with an associated SE of 285 (Table 1; Figure 8). The Sensitivity has lower estimates of the total population for the later years, but similar estimates for the number of parous females (Supplementary Figure S2; Figure 8). For the alternative hypothesis of a recent increase in M , the estimate of current abundance is much lower at 2 296 (Table 1; Figure 8).

¹This follows the earlier practice by the International Whaling Commission Scientific Committee of referring to the number of female whales having reached the age at first parturition as the mature component of the population

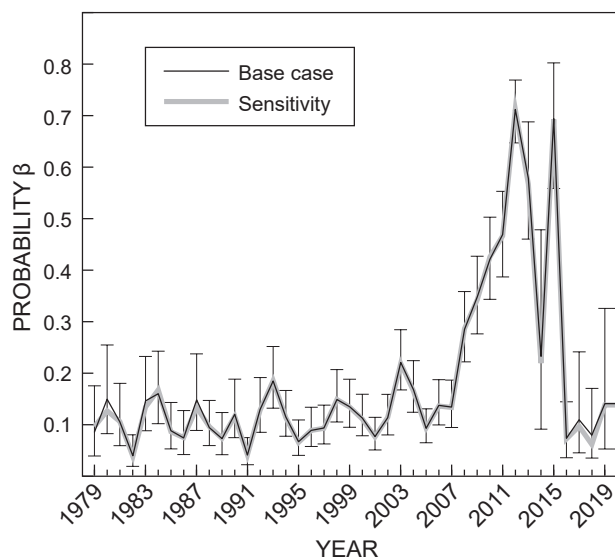


Figure 6: Time-varying estimates of the probabilities (parameter β) that a resting southern right whale will rest in the following year under the new model for the Base case and Sensitivity. The error bars represent the range of one Hessian-based standard error added to and subtracted from the estimate concerned

The new model estimates the probability of an early abortion (a pregnant whale being pregnant again the following year) to be higher for the Sensitivity for the years 2017 to 2019 (Supplementary Table S1; Figure 9).

The estimated cohort numbers at each stage of the right whale reproductive cycle under the new model that includes the delta-loop for the Base case are fairly similar for each stage until about 2010, but not thereafter, as what were originally near-separate cohorts become mixed (Figure 10).

Figure 11 shows a comparison of the observed against the model-predicted annual average apparent calving intervals for mature females. The predicted values are as determined for the Base case. 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

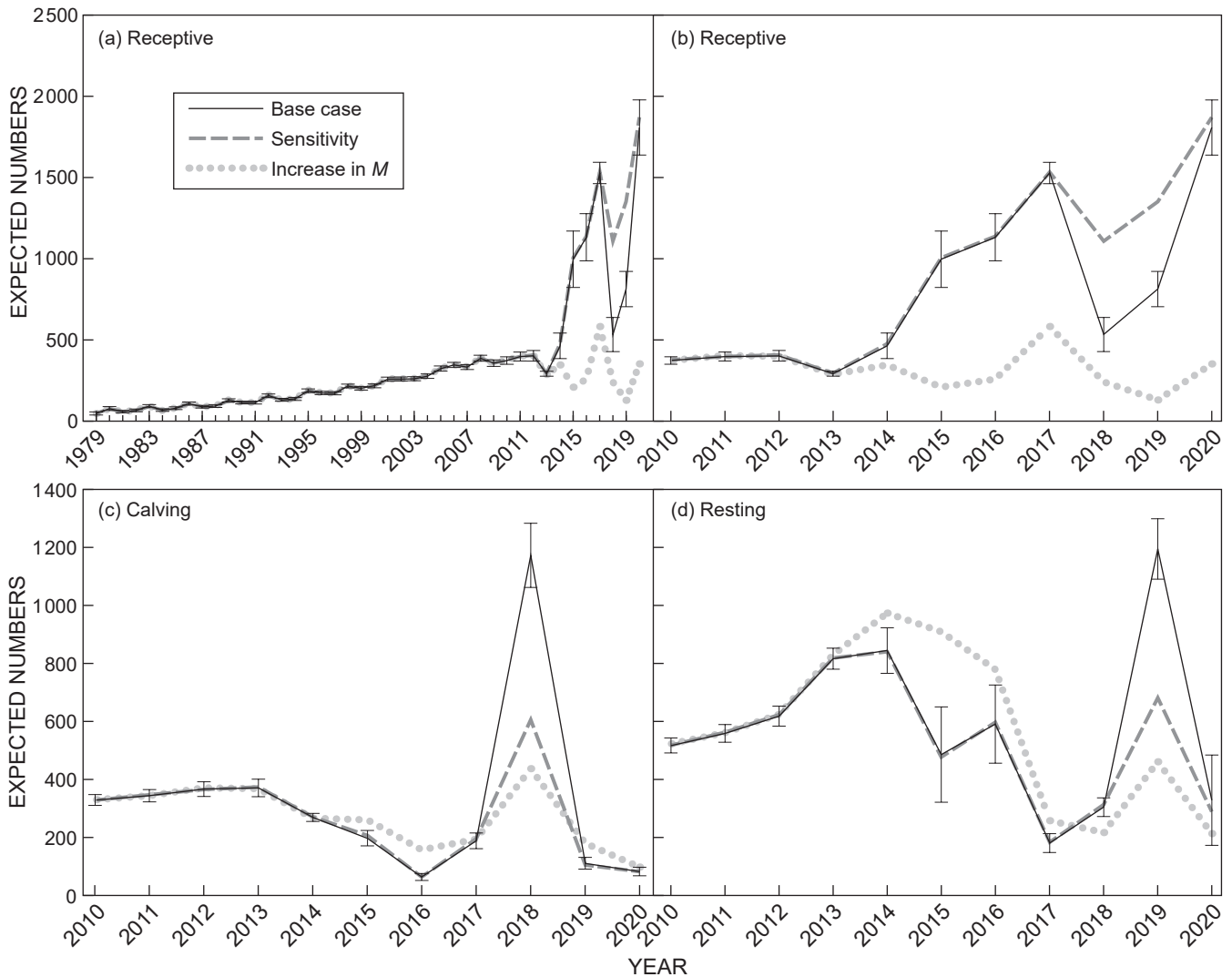


Figure 7: Expected numbers of mature female southern right whales that are (a,b) in a receptive state (where panel 'b' is a magnification of part of panel 'a'), (c) calving, and (d) in the resting stage, under the new model for the Base case and the Sensitivity, as well as when a recent increase in natural mortality (M) is considered. Plot 'a' shows the trends for receptive females for the whole period. The pre-2010 trends for females in the other two stages are similar to those for the receptive females and are therefore not shown. The error bars represent the range of one Hessian-based standard error added to and subtracted from the estimate concerned

favoured over increased mortality to account for the low observation of cow-calf pairs in 2015, 2016 and 2017. These low numbers have continued in 2019 and 2020. The analyses here show that introducing the possibility of an early abortion (the delta-loop) can account for these low observations and an increase in the proportion of four-year calving intervals. The only questionable aspects of this new model, given that survey effort has been virtually constant over time, is the relatively low probability (when compared with earlier years) estimated for observing a cow-calf pair present during the 2018 aerial survey²; this value is, however, no further below the average over time than the largest estimate (for 2014) is higher. In contrast,

²Results presented earlier in Brandão et al. (2019), which indicated such low probabilities to commence in 2015, were subsequently found to be a consequence of a computer code error

the alternative hypothesis of a recent increase in the natural mortality rate M is not supported by the adult photo-identification data in particular (see details of the worse fit for this model, provided in Table 2).

Thus, the low numbers of cow-calf pairs 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 (Vermeulen et al. 2021) (Figure 2). The alternative possibility of higher mortalities seems unlikely for two reasons (aside from the associated worse fit to the data): the very high number of sightings of cow-calf pairs in 2018, and the decrease in the annual number of southern right whale strandings on the South African coast since 2009

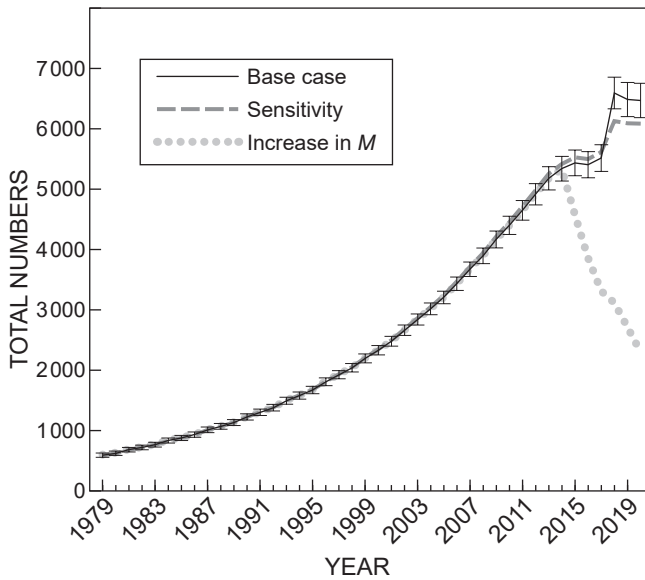


Figure 8: Estimated total number of the whole population of southern right whales off South Africa (including males and calves, as calculated under the assumption of a 50:50 sex ratio at birth) for the new model for the Base case and the Sensitivity, as well as when a recent increase in natural mortality (M) is considered. The error bars represent the range of one Hessian-based standard error added to and subtracted from the estimate concerned

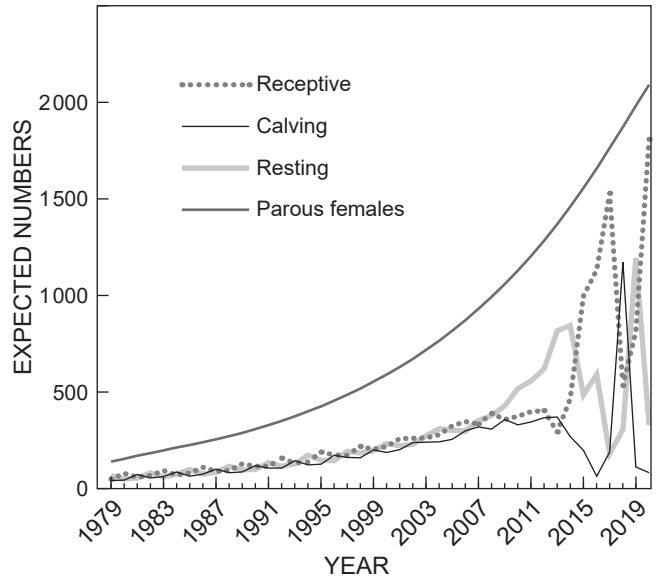


Figure 10: Comparison of the expected numbers of mature female southern right whales that are in the receptive, calving and resting stages, under the new model for the Base case. The estimated total numbers of females having reached the age at first parturition are also shown

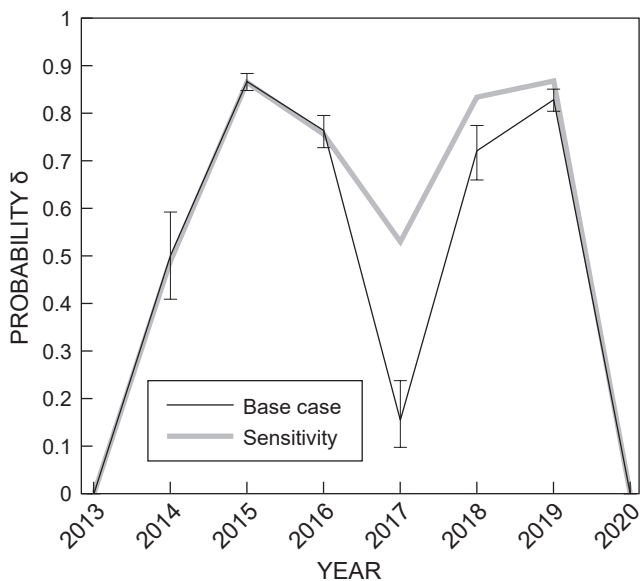


Figure 9: Estimated probabilities (parameter δ) that a receptive southern right whale will remain receptive in the following year under the new model for the Base case and the Sensitivity. For years prior to 2014, these probabilities were taken to be zero. The error bars represent the range of one Hessian-based standard error added to and subtracted from the estimate concerned

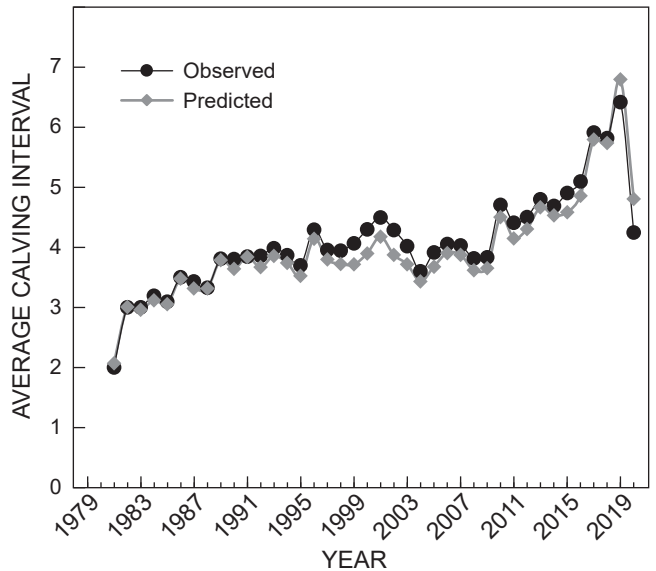


Figure 11: Comparison of the observed and the model-predicted annual average apparent calving intervals of mature female southern right whales off South Africa. Predicted values are as determined using the new model for the Base case

(from an average of 5.5 pa over the period 1998–2008 to an average of 2.8 pa for 2009–2019: Vermeulen et al. 2022). In fact, since southern right whales are capital breeders that rely on their foraging success to

support their reproduction, it seems more probable that altered foraging conditions are the cause of changes to these reproduction-related parameters. This could well be linked to changes in distribution and/or migration routes, as is suggested by the decreasing trend of unaccompanied adults on the South African breeding ground since 2010 (Vermeulen et al. 2021) (Figure 3).

The hypothesis that altered foraging conditions are the cause of changes to reproduction-related parameters is supported by a study of van den Berg et al. (2021), which revealed a recent dramatic northward shift and diversification in right whale foraging strategy. Given the decreased reproductive output of the population evident over recent years, that study further concluded that the altered foraging strategy may not be sufficient to allow complete adaptation to the changing environment. This hypothesis of a decreased foraging success is supported by observations of substantially worse body conditions of adult females since the late 1980s (see Thavar et al. 2021 for more detailed information). In the southern right whale population calving off the Atlantic coast of South America, direct links have been identified between a decreased calving success and decreased krill densities at feeding grounds caused by climate anomalies (Leaper et al. 2006; Seyboth et al. 2016). Although the population calving off the east coast of South America has recovered to only about 20% of its pre-exploitation levels (IWC 2013), disentangling the possible effects of density dependence is difficult and may also be an influencing factor.

In the light of the substantial recent variability in southern right whale counts (e.g. Vermeulen et al. 2018, 2019) (Figure 1) and the elongation of calving intervals which has been observed across most of the species' wintering grounds (Argentina: Marón et al. 2015; Australia: Charlton 2017; South Africa: Vermeulen et al. 2021) (Figure 2), a new research theme has recently been established under the Southern Ocean Research Partnership of the International Whaling Commission (IWC-SORP) entitled 'The right sentinel for climate change: linking foraging ground variability to population recovery in the southern right whale'. This multi-ocean collaborative project aims to compare southern right whale population demographics across the main Southern Hemisphere wintering grounds. This comparison is to be achieved by applying a common demographic model to the populations in each region: southwest Atlantic (Argentina/Brazil), southeast Atlantic (South Africa), Australia and New Zealand, in order eventually to test hypotheses for the relationships between reproductive success and environmental variables. A crucial aspect of this global research is the collation of long-term photo-identification and sightings datasets to allow for a comprehensive assessment of the global population status of southern right whales under a common statistical and biological model. This common model will be developed from Cooke et al. (2001, 2015), Brandão et al. (2019), and the model presented in this work.

Conclusions

This analysis has shown that the low numbers of sightings of female southern right whales with calves off the South African coast for five of the six years from 2015 to 2020 can plausibly be explained by changes in reproduction-related demographic parameters without the need to postulate an increase in the adult mortality rate. An alternative hypothesis that such an increase occurred recently leads to a much worse fit of the associated model to the data. The estimated number of all whales in the population in 2020 is

6 470 (SE 285), and the parous female component of the population is estimated to have increased 15-fold over the last four decades.

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Appendix: Photo-identification model

The methodology of Cooke et al. (2003) has been used to analyse photo-identification data for calving female southern right whales *Eubalaena australis* that overwinter off the southern coast of South Africa. Their approach as applied to these whales is summarised below (for a more-detailed discussion, refer to the cited work). The methods have also 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.

The application here is near-identical to that of Cooke et al. (2003), except that the starting population is not assumed to reflect a steady age-structure corresponding to the Leslie matrix model describing the population dynamics. The photo-identification data for grey-blazed female calves, which are identifiable when giving birth later, 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.

Modeling population dynamics for juvenile females

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

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 age 15 years.

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

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

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 age 15 years;
 M_j is the natural mortality from birth to the first birthday;
 M is the natural mortality for ages 1+;
 M_{2014+} is the natural mortality for ages 1+ for the years 2014 and onwards in the case of the model when an increase in M is assumed for that period; and
 ϕ_a is the probability that an immature female whale of age a becomes receptive the following year.

This is re-parameterised as follows:

$$\phi_a = \begin{cases} \frac{1}{[1 + e^{-\frac{a-a_m}{\omega}}]} & 4 \leq a \leq 14 \\ 0 & a < 4 \end{cases} \quad (\text{A2})$$

where a_m is the age at which 50% of the female population that remains immature become receptive, and ω measures the spread of this ogive.

Modeling 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 Figure 4 diagrammatically shows the possible ways in which a mature female can move from one reproductive state to another. The equations for the dynamics are:

$$\begin{aligned}
 N_{y+1}^{\text{recp}} &= \left(\sum_{a=4}^{13} N_{a,y} \phi_a + N_{14,y} \right) e^{-M} \\
 &\quad + (1-\beta_y) N_y^{\text{rest}} e^{-M} + \alpha_y N_y^{\text{calv}} e^{-M} + \delta_y N_y^{\text{recp}} e^{-M} \quad (\text{A3})
 \end{aligned}$$

$$N_{y+1}^{\text{rest}} = \beta_y N_y^{\text{rest}} e^{-M} + (1-\alpha_y) N_y^{\text{calv}} e^{-M} + \gamma_y N_y^{\text{recp}} e^{-M} \quad (\text{A4})$$

$$N_{y+1}^{\text{calv}} = (1-\gamma_y - \delta_y) N_y^{\text{recp}} e^{-M} \quad (\text{A5})$$

where

N_y^{recp} is the number of receptive females at the start of year y ;

N_y^{rest} is the number of females resting in year y ;

N_y^{calv} is the number of 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 (implemented only for years 2014 and onwards) becomes receptive in year $y+1$ (i.e. had an early abortion); note that values of δ_y are set to zero for all years for the alternative model that allows for an increase in M from 2014; 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:

$$\begin{aligned}
 N_{y+1}^{\text{recp},u} &= \left(\sum_{a=4}^{13} \phi_a (1-P_{y-a}^C (1-\rho)) N_{a,y} + (1-P_{y-14}^C (1-\rho)) N_{14,y} \right) e^{-M} \\
 &\quad + (1-\beta_y) N_y^{\text{rest},u} e^{-M} + \alpha_y (1-P_y^A) N_y^{\text{calv},u} e^{-M} + \delta_y N_y^{\text{recp},u} e^{-M} \quad (\text{A6})
 \end{aligned}$$

$$\begin{aligned}
 N_{y+1}^{\text{recp},s} &= \left(\sum_{a=4}^{13} \phi_a (P_{y-a}^C (1-\rho)) N_{a,y} + P_{y-14}^C (1-\rho) N_{14,y} \right) e^{-M} + (1-\beta_y) N_y^{\text{rest},s} e^{-M} \\
 &\quad + \alpha_y P_y^A N_y^{\text{calv},u} e^{-M} + \alpha_y N_y^{\text{calv},s} e^{-M} + \delta_y N_y^{\text{recp},s} e^{-M} \quad (\text{A7})
 \end{aligned}$$

$$N_{y+1}^{\text{rest},u} = \beta_y N_y^{\text{rest},u} e^{-M} + (1-\alpha_y) (1-P_y^A) N_y^{\text{calv},u} e^{-M} + \gamma_y N_y^{\text{recp},u} e^{-M} \quad (\text{A8})$$

$$N_{y+1}^{\text{rest},s} = \beta_y N_y^{\text{rest},s} e^{-M} + (1 - \alpha_y) P_y^A N_y^{\text{calv},u} e^{-M} + (1 - \alpha_y) N_y^{\text{calv},s} e^{-M} + \gamma_y N_y^{\text{recp},s} e^{-M} \quad (\text{A9})$$

$$N_{y+1}^{\text{calv},u} = (1 - \gamma_y - \delta_y) N_y^{\text{recp},u} e^{-M} \quad (\text{A10})$$

$$N_{y+1}^{\text{calv},s} = (1 - \gamma_y - \delta_y) N_y^{\text{recp},s} e^{-M} \quad (\text{A11})$$

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 that 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:

$$\begin{aligned} N_{0,1979} &= 0.5 N_{1979}^{\text{calv}} \\ N_{1,1979} &= \tau N_{0,1979} e^{-M_j} \\ N_{2,1979} &= \tau N_{1,1979} e^{-M} \\ &\vdots \\ N_{5,1979} &= \tau (1 - \phi_4) N_{4,1979} e^{-M} \\ &\vdots \\ N_{14,1979} &= \tau (1 - \phi_{13}) N_{13,1979} e^{-M} \end{aligned} \quad (\text{A12})$$

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

Initial numbers for mature females in each of the three reproductive stages (i.e. N_{1979}^{calv} , N_{1979}^{recp} , N_{1979}^{rest}) are estimated by fitting the population model to the data. The portion of the initial population numbers that 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 observing individual sighting histories

Details of the evaluation of the individual sighting 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) are given in the Supplementary Information.

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 (and sufficiently so to be discernible) until calving themselves, as otherwise they would be recorded as new animals in future surveys should they lose their markings.

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:

$$\ln(e_h^A; \theta) = \sum_{\text{all } h} (n_h^A \ln(e_h^A) - e_h^A) \quad (\text{A13})$$

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 ; and

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:

$$e_h^A = \hat{N}_y^{\text{calv},U} \hat{P}_y^A \hat{q}_h^A \quad (\text{A14})$$

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 female whale is observed with a calf in year y ; and

\hat{q}_h^A is the estimated probability of a possible sighting history h being observed given that the adult whale with its calf was first sighted in year y .

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

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

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

$$= \sum_y \hat{N}_y^{\text{calv},U} \hat{P}_y^A \left(1 - \sum_{\text{obs } h(y)} \hat{q}_h^A \right) = \sum_y \hat{N}_y^{\text{calv},U} \hat{P}_y^A - \sum_{\text{obs } h(y)} e_h^A \quad (\text{A15})$$

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

$$\ln(e_h^A; \theta) = \sum_{h=1}^{n^A} (n_h^A \ln(e_h^A)) - \sum_{y=1979}^{2020} \hat{N}_y^{\text{calv},U} \hat{P}_y^A \quad (\text{A16})$$

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:

$$\ln(e_h^C; \theta^*) = \sum_{h=1}^{n^C} (n_h^C \ln(e_h^C)) - \sum_{y=1979}^{2020} \hat{N}_{0,y} \hat{P}_y^C \quad (\text{A17})$$

where

θ^* is a vector of all estimable parameters attributable to the sighting histories of whales first sighted and catalogued as a grey-blazed calf;

n^C is the total number of observed unique sighting histories for such whales; and

e_h^C is the expected number of female whales with an

individual sighting history (where they were first seen and catalogued as a grey-blazed calf in year y), given by:

$$e_h^C = \hat{N}_{0,y} \hat{P}_y^C \hat{q}_h^C \quad (\text{A18})$$

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; hence, 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 10 years. Thus, the following penalty function was added to the total negative log-likelihood function:

$$\frac{1}{2\sigma_P^2} \sum_{y=1979}^{1981} (\hat{P}_y^A - \bar{P})^2 \quad (\text{A19})$$

where

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

σ_P is the calculated standard deviation of those \hat{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 period 2015–2017. 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 of the previous years since 1982. Consequently, the following penalty function was added to the total negative log-likelihood function:

$$w \left\{ \frac{1}{2\sigma_{P^*}^2} \sum_{y=2015}^{2020} (\hat{P}_y^A - \bar{P}^*)^2 \right\} \quad (\text{A20})$$

where

\bar{P}^* is the average of the \hat{P}_y^A estimates for the years 1982 to 2014;

σ_{P^*} is the calculated 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 parameters α_y , β_y and γ_y can be estimated in two ways:

either they are assumed to be time-invariant or else one or more are allowed to vary over time. Because of the scarcity of observed events in the sighting histories of southern right 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 (β_y and γ_y) are considered to be time-variant, they are treated as random effects in the model, assuming that they have a normal distribution with mean β (or $\bar{\gamma}$) and standard deviation σ_β (or σ_γ). The AD Model Builder (ADMB) package (Fournier et al. 2012) is used for model fitting. The ADMB-RE module for the ADMB package is used for the estimation of 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_p , 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 x (i.e. S , S_p , α , β , γ , δ , ρ , P_y^A , P_y^C) are transformed to the logit scale, so that the corresponding log-odds ratios ($x^* = \ln[x/(1-x)]$) are the estimable parameters in the model. The parameter ρ does not appear in the equations given above, but it appears in the calculation of the probability (q_h^C) of a sighting history given that the whale was first sighted as a calf.

The parous female population increase rate r is estimated by fitting a log-linear regression to the annual total number of parous females estimated by the model over the period 1979–2020.

Standard errors reported are estimated from the Hessian, the matrix of second-order partial derivatives of the log-likelihood function with respect to its parameters. These are provided directly for the estimable parameters by the ADMD package used for fitting, which applies the delta method for functions of those parameters. When error bars reflecting ± 1 standard error are shown on plots for probabilities, the reverse logit transformation is applied to those values that are symmetric about the estimate in logit space but may become somewhat skew on reverse transformation.