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Preliminary demographic estimates for southern right whales off Australia using the common model and comparison to the South African population

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Abstract

The Common demographic model is applied to the photo-identification data for southern right whales in Australian waters. Given problems with estimating some model parameters because of the scarcity of data, the Base case Common model for the Australian right whale population considers the parameters S_j, ρ, and τ to be fixed to their values for the Base case Delta-loop model for southern right whales off South Africa (Brandão *et al*., 2023), while the probabilities P_y^C are fixed to the average of their estimated values for the model without time-variation in other parameters. For the time-variant Base case model, the number of parous females in 2018 is estimated to be 850, the total population (including males and calves) 2 821, and the annual population growth rate at 5.6%. Comparing estimates of key demographic parameters for populations in Australia and South Africa indicates that the age at which 50% of the female population has reached the age of first parturition (a_m) is much lower for the Australian population (4.6 years) than for that of South Africa (8.1 to 8.5 years). However, this difference might be due to the limited number of female calf sighting histories available in the Australian data, as these data inform the estimation of the maturity ogive. The annual population growth rates for parous females are very similar, with a slightly larger growth rate estimated by the South African Base case Delta-loop model (6.5%) compared to the 5.6% for the Australian population. The predicted average apparent calving intervals for the two populations are similar, the Australian population being slightly larger (4.6 years) than the South African one (around 4.0 years) and both being larger than previous estimates for the species. Estimating demographic parameters in this comparative common model framework is essential for undertaking a species assessment for the southern right whale and investigating changes to apparent mean calving intervals and growth rates over time.

Keywords: Australian southern right whale, demographic parameters, photo-identification, population growth rate, sighting histories

Introduction

The Common demographic model is applied to the available photo-identification data for southern right whales from south-western Australia. This paper lists some of the limitations of the data presently available and what assumptions have been made when fitting the Common model. The time-variant Base case estimates of some key demographic parameters for the Australian population are compared to those obtained from the South Africa Base case Delta-loop model as well as the South African Common model. Future work is suggested to attempt to overcome some of the limitations of fitting the Common model to the presently available Australian photo-identification data.

Data

The data consist of reconciled photo-identification records from the annual aerial surveys conducted in south-western Australia (1993 to 2011) and from shore-based surveys at the primary calving ground at the Head of Bight (1993 to 2018). There are 395 unique sighting histories of cow-calf pairs (from a total of 981 different females). There are 13 unique female calf sighting histories when first seen as a calf and later seen/not seen with her own calf. Of these, only two records catalogue a female whale first seen as a calf and then never sighted again. Between 1993 and 2018, in only seven of those years is a whale catalogued as first sighted as a female calf.

Notation and Methodology

Details of the methodology used in the Common model and the likelihood maximised to estimate parameter values from the photo-identification data are provided in the Appendix. Figure 1 schematically shows the Common model which accommodates the various states of reproduction of the different SRW populations. The Delta-loop model (Brandão *et al*., 2023) is shown schematically by the text and arrows in black in Figure 1. Reproductive females are divided into (newly) Pregnant, Calving (lactating) (i.e., successful mothers), Unsuccessful mothers (females experiencing late abortions or early calf deaths) and Resting stages. The "normal" reproductive cycle is three years, consisting of one Austral winter season in each of the pregnant, calving and resting phases, with the calving phase disaggregated into successful mothers and unsuccessful mothers (Figure 1). However, there are various alternative paths that are each associated with a probability parameter which is to be estimated from each dataset (where possible). Some or all of these probability parameters may vary with time. These probability parameters correspond to the following events:

- α — a female becomes pregnant again after weaning its calf and skips the usual resting year (resulting in a 2-year calving interval if that pregnancy proceeds to term);
- β — a resting female rests for a further year (resulting in a 4-year calving interval if followed by a normal cycle);
- γ — a pregnant female loses its foetus too late to become pregnant again the same year, and reverts to the resting phase without having given birth (resulting in a 5-year calving interval if followed by a normal cycle);
- δ — a pregnant female loses its foetus early and becomes pregnant again, thus spending two consecutive years in the pregnant phase (resulting in a 4-year calving interval if followed by a normal cycle);
- λ — a pregnant female is an "unsuccessful mother", i.e., experiences a late abortion or an early calf death and rests the following year;

β^* an unsuccessful mother (that rested a year after losing its calf in a late abortion or in an early calf death before the calf could be observed) rests an additional year.

Further notation used in providing results is as follows:

S is the post-first-year annual female survival proportion;

S_j is the first-year female survival proportion;

ρ is the probability that a grey blazed female calf is identified when itself calving;

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, in the initial conditions for the model;

a_m, ω are 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 is the annual (instantaneous) parous female growth rate estimated over the whole period of cow-calf sightings;

$\hat{P}_y^A$ is the probability that a female whale with a calf seen in year y; and

$\hat{P}_y^C$ is the probability that a female calf seen in year y is grey blazed and catalogued.

The parameters α_y, β_y, γ_y, λ_y and β_y^* can be estimated in two ways: either they are assumed to be time-invariant or one or more 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. After some initial model fits to the Australian photo-identification data, for the analyses conducted here, the γ_y probabilities are considered to be time-invariant, while the β_y probabilities are set to be either time-invariant or variant. For the moment, the probabilities δ_y, λ_y and β_y^* are all taken to be zero.

Given that there are very few individual female calf sighting histories when first seen as a calf and later seen/not seen with its own calf, some of the model parameters such as S_j and ρ that are informed by these data are poorly estimated (with estimates hitting their boundaries). Also, estimating the τ parameter results in estimates at the boundary of zero. Another limitation of the available data is that out of twenty-six years of photo-identification data (1993-2018), in only seven of those years is there a record of a whale catalogued as first sighted as a female calf. This was influenced by the research effort to capture photo-identification images of calves with developed callosities in late season, and not using grey blazes to classify females. This means that the probabilities P_y^C will be estimable only for those seven years for which data are available. With these data limitations, the Base case Common model for the Australian photo-identification data of southern right whales considers these parameters to be fixed. The S_j, ρ, and τ are fixed to their values for the Base case Delta-loop model for southern right whales off South African (Brandão *et al*., 2023), while the probabilities P_y^C are fixed to the average of their estimated values for the model without time variation in other parameters. For comparison, a model fit in which all parameters are estimated is also considered.

Initial results when considering β to be time-variant show quite variable estimates for the probabilities of observing females with calves ($\hat{P}_y^A$) for the years 2012 to 2018. However, as the dataset for this period consists of systematic surveys of cow-calf pairs from the Head of Bight only, one would not expect the sighting probabilities to vary too much from year to year. Thus, as a sensitivity has been carried out where a penalty function is applied to these probabilities over the 2012-2018 period in the negative log-likelihood to attempt to constrain the high variability in these estimates ($\hat{P}_y^A$) (Equation A.26). The penalty applied assumes $P_y^A \sim N(P^*, \sigma_{P^*}^2)$, where P^* is the average of the estimated sighting probabilities for the time-invariant model for the same period and $\sigma_{P^*}^2$ is their variance. Various weights are also applied to the penalty for $\hat{P}_y^A$ to attempt to constrain the extent to which these estimated probabilities vary. For example, applying a weight of zero to the penalty is equivalent to applying no penalty.

Hessian-based estimates of standard errors are obtained except for the time-variant models.

Results

Results for the time-invariant and variant Base case are provided in Table 1. For comparison, results when all parameters are estimated are also given. For both time-invariant and variant models, estimating all parameters results in estimates of the first-year female survival rate S_j of 100%, as well as for the probability that female calves are identified when adults (ρ), while 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 in the initial conditions of the model (τ) is estimated to be zero. The contributions to the penalised negative log-likelihood function of these models for these various components are given in Table 2. The annual instantaneous growth rate of the parous female population per annum, r, is estimated to be 5.5% for the time-invariant model and 5.6% for the time-variant model.

The estimated probabilities that a calf is catalogued do not change too much between the time-variant and invariant models (Figure 2). However, these probabilities can be estimated for only seven of twenty-six years because of the lack of calf sighting data. Figure 2 also shows the fixed value assumed for the Base case.

There is a marked difference in the probabilities of observing a female whale with its calf on aerial surveys under the time-variant and invariant models (Figure 3). Under the time varying model, the detectability of mothers with calves are much more variable. These estimates do not change too much between the Base case and when all parameters are estimated.

Allowing for time varying probabilities that a resting whale will rest in the following year (β) results in very variable estimated probabilities from year to year (Figure 4).

Figures 5a-b show the expected number of mature female southern right whales that are in the calving, receptive or resting stages for the time-invariant and variant models for the Base case, as well as for when all parameters are estimated. Again, the time-variant model shows a higher variability in these expected numbers than for the time-invariant model, especially for the post-2010 years.

The time-variant model shows 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-2010 years (Figure 7).

Results for the sensitivity to the time-variant Base case that applies a penalty on $\hat{P}_y^A$ (with various weights) to attempt to constrain the variability of these probabilities for the period with less survey coverage (2012-2018) are shown in Tables 3 and 4. Figure 8 shows the estimated probabilities of observing a cow-calf pair when applying a penalty on $\hat{P}_y^A$. There is a slight decrease in the variability of these probabilities, with higher weights having more impact. However, none are able to lower the very high probability estimate of P_y^A in 2014, which is estimated to be 1.0.

The estimates of the probabilities (β) that a resting female whale will rest in the following year under the time-variant Base case when different weights are to the penalty for $\hat{P}_y^A$ are shown in Figure 9. Figures 10a-b show the expected numbers of mature whales in the three reproductive stages, while the expected total number of parous females is given in Figure 11 and the estimated total number of the whole population is shown in Figure 12. Slightly lower numbers of parous females and the total population are estimated the higher the weight applied to the penalty for $\hat{P}_y^A$.

Table 5 compares some key demographic parameter and abundance estimates obtained for the southern right whale populations wintering in South African and in Australian waters. For the South African population, results for the Base case Delta-loop and the Common models are given (both applied a weight to the contribution of the penalty on $\hat{P}_y^A$ to the likelihood from 2015). Results for the Australian population are those for the time-variant Base case with no restriction applied to $\hat{P}_y^A$ from 2012. The post-first year annual female survival proportions are very similar for both populations. The age at which 50% of the female population has reached the age of first parturition (a_m) is much lower for the Australian population (4.6 years) than for that of South Africa (8.1 to 8.5 years). However, this difference might be due to the limited number of female calf sighting histories available in the Australian data, as these data inform the estimation of the maturity ogive. The annual population growth rates are very similar (around 5.5%), with a slightly larger growth rate estimated by the South African Base case Delta-loop model (6.5%, calculated over the 1979 to 2020 period). The predicted average apparent calving intervals for the two populations are similar, being slightly larger for the Australian population (4.6 years; calculated for the 1996 to 2018 period) than for the South African one (around 4.0 years; calculated for the 1982 to 2020 period).

Discussion and future work

The common model has now been applied to the western Australian southern right whale population and outputs have been compared for the Australian and South African populations. Demographic parameters are comparable for the annual rate of increase for parous females (5.6% Australia and 6.5% South Africa), which for both is lower than the maximum biological rate of increase for the species of 6-7% (IWC 2013). The apparent age of first parturition is lower for the Australian compared to other populations (Brandão et al. 2023; Cooke et al. 2003), but is likely biased by the small sample size of calf sightings histories. The apparent mean calving intervals of 4.6 years and 4 years for Australia and South Africa populations, respectively, is higher than previously reported for the species (Brandão et al. 2023, Cooke et al. 2003). The common model output for the mean apparent calving interval is comparable to findings presented in Charlton et al. (2022) using raw data (n=4.2). Biologically southern right whales typically calve on a three-year cycle including a calving, resting and receptive (pregnant) year. Fluctuations and drivers of change to mean apparent calving intervals and growth rates need to be investigated further to inform species recovery assessments and management.

The available calf sighting histories are very limited in the Australian photo-identification data, which leads to the problematic estimation for some of the Common model parameters that are informed by these data. The calf sighting histories are low for the Australian dataset because the method relies on photo identifying calves in their year of birth and late in the season when their callosity patterns are developed. The common model was applied to the dataset for years 1993 to 2018 based on available and comparable data from the two primary long term research programs in Australia. Including reconciled data from 1975-2023 (while considering variation in effort) would increase the sample size. Alternatively, using grey blazed patterns as an indicator of female calves could increase the number of calf sighting histories (this is the method used for the South African dataset). As an initial attempt in this paper, some of these parameters have been fixed by assuming the same values as those obtained by the Base case Delta-loop model when applied to the South African data. Another limitation of the data is the shorter survey coverage from 2012 as the south-western Australian photo-identification data have not yet been reconciled after 2011. The following future work is suggested, which could lead to improvement in fitting the Common model to the Australian photo-identification data:

1) The reconciliation of photo-identification data from south-western Australia and the Head of Bight from 2012 to the present.

2) In the Australian photo-identification data, calves that are never seen again with their own calf can be sexed as female only if the photographs show their genitals. It is suggested that the fact that all grey-blazed calves are known to be female should be used to sex calves in the Australian photo-identification data as is done in South Africa.

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Table 1: Estimates of various demographic parameters for southern right whales off Australia under the Common model for the **time-variant Base case** and when **all parameters are estimated. No restriction is applied to** $\boldsymbol{\widehat{P}_y^A}$ (i.e. a weight of zero is applied to the penalty for $\widehat{P}_y^A$ denoted below as 0.0pen). Time-invariant results are also shown for comparison. 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 yr^{-1}) over the whole period of cow-calf sightings. The quantities in parenthesis are Hessian-based estimates of standard errors. Entries in italics denote fixed values.

Parameter	**Model**			
	Estimate all		**Base case**	
	Time-invariant (0.0pen)	**Time-variant (0.0pen)**	**Time-invariant (0.0pen)**	**Time-variant (0.0pen)**
$\boldsymbol{\alpha}$ **(time-invariant)**	0.036 (0.006)	0.029	0.036 (0.006)	0.029
$\boldsymbol{\overline{\beta}}$ **or** $\boldsymbol{\beta}$ **(time-invariant)**	0.471 (0.021)	0.458	0.479 (0.021)	0.505
$\boldsymbol{\gamma}$ **(time-invariant)**	0.000 (0.000)	0.000	0.000 (0.000)	0.000
$\boldsymbol{\beta^*}$	*0.000*	*0.000*	*0.000*	*0.000*
$\boldsymbol{S}$	0.971 (0.004)	0.969	0.972 (0.003)	0.970
$\boldsymbol{S_j}$	1.000 (0.000)	1.000	*0.874*	*0.874*
$\boldsymbol{\rho}$	1.000 (0.000)	1.000	*0.804*	*0.804*
$\boldsymbol{\tau}$	0.000 (0.001)	0.000	*1.005*	*1.005*
$\boldsymbol{P_y^C}$	See Figure 2	See Figure 2	*0.046*	*0.046*
$\boldsymbol{a_m}$	4.527 (0.187)	4.610	4.353 (0.313)	4.630
$\boldsymbol{\omega}$	0.274 (0.114)	0.180	0.465 (0.338)	0.224
$\boldsymbol{N_{1993}^{calv}}$	87 (21)	108	87 (15)	91
$\boldsymbol{N_{1993}^{recp}}$	53 (15)	67	61 (17)	61
$\boldsymbol{N_{1993}^{rest}}$	261 (34)	179	102 (47)	74
$\boldsymbol{N_{1993}^{mature*}}$	401 (21)	353	216 (39)	191
$\boldsymbol{N_{2018}^{calv}}$	317 (22)	344	281 (19)	295
$\boldsymbol{N_{2018}^{recp}}$	348 (25)	381	304 (21)	254
$\boldsymbol{N_{2018}^{rest}}$	493 (34)	365	448 (30)	349
$\boldsymbol{N_{2018}^{mature*}}$	1 061 (71)	956	953 (62)	850
$\boldsymbol{N_{2018}^{all}}$	3 899 (264)	3 526	3 313 (217)	2 821
$\boldsymbol{r}$	0.047 (0.004)	0.049	0.055 (0.005)	0.056

Table 2: Contributions to the penalised negative log-likelihood function from its various components for the Common model for the **time-variant Base case** and when **all parameters are estimated. No restriction is applied to $\hat{P}_y^A$** (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$ denoted below as 0.0pen). Time-invariant results are also shown for comparison. β is the probability that a resting whale rests in the following year.

	Model			
	Estimate all		**Base case**	
	Time-invariant (0.0pen)	**Time-variant (0.0pen)**	**Time-invariant (0.0pen)**	**Time-variant (0.0pen)**
Adult histories	313.3	234.8	322.5	240.9
Calf histories	85.52	84.95	137.58	130.74
β random effects	—	9.233	—	14.95
Penalty on $\hat{P}_y^A$ at the beginning of series (1979 – 1981)	2.983	2.752	0.971	1.239
Penalty on $\hat{P}_y^A$ at the end of series (2015-2020)	0.000	0.000	0.000	0.000
Total	402	332	461	388

Table 3: Estimates of various demographic parameters for southern right whales off Australia under the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ now fixed on input) when **four different weights** are applied to the penalty for $\hat{P}_y^A$ (denoted below as, for example, 1.0pen when a weight of 1.0 is applied). 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 yr^{-1}) over the whole period of cow-calf sightings.

	Model			
Parameter	**Base case (0.0pen)**	**Base case (1.0pen)**	**Base case (2.5pen)**	**Base case (10.0pen)**
$\boldsymbol{\alpha}$ **(time-invariant)**	0.029	0.030	0.030	0.030
$\bar{\boldsymbol{\beta}}$	0.505	0.503	0.502	0.500
γ **(time-invariant)**	0.000	0.000	0.000	0.000
$\boldsymbol{\beta}^*$	*0.000*	*0.000*	*0.000*	*0.000*
$\boldsymbol{S}$	0.970	0.971	0.971	0.972
$\boldsymbol{S_j}$	*0.874*	*0.874*	*0.874*	*0.874*
$\boldsymbol{\rho}$	*0.804*	*0.804*	*0.804*	*0.804*
$\boldsymbol{\tau}$	*1.005*	*1.005*	*1.005*	*1.005*
P_y^C	*0.046*	*0.046*	*0.046*	*0.046*
$\boldsymbol{a_m}$	4.630	4.714	4.746	4.777
$\boldsymbol{\omega}$	0.224	0.237	0.242	0.244
$\boldsymbol{N_{1993}^{calv}}$	91	90	90	89
$\boldsymbol{N_{1993}^{recp}}$	61	60	59	58
$\boldsymbol{N_{1993}^{rest}}$	74	77	78	78
$\boldsymbol{N_{1993}^{mature*}}$	191	193	193	191
$\boldsymbol{N_{2018}^{calv}}$	295	304	311	320
$\boldsymbol{N_{2018}^{recp}}$	254	231	218	206
$\boldsymbol{N_{2018}^{rest}}$	349	376	387	406
$\boldsymbol{N_{2018}^{mature*}}$	850	868	875	893
$\boldsymbol{N_{2018}^{all}}$	2 821	2 885	2 911	2 977
$\boldsymbol{r}$	0.056	0.056	0.057	0.058

Table 4: Contributions to the penalised negative log-likelihood function from its various components for the Common model for **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$ (denoted below as, for example, 1.0pen when a weight of 1.0 is applied). β is the probability that a resting whale rests in the following year.

	Model			
	Base case (0.0pen)	**Base case (1.0pen)**	**Base case (2.5pen)**	**Base case (10.0pen)**
Adult histories	240.9	243.0	245.0	248.3
Calf histories	130.74	130.91	130.97	131.39
$\boldsymbol{\beta}$ **random effects**	14.95	15.49	16.08	16.99
Penalty on $\hat{P}_y^A$ at the beginning of series (1979 – 1981)	1.239	1.289	1.317	1.333
Penalty on $\hat{P}_y^A$ at the end of series (2015-2020)	0.000	32.62	31.00	30.04
Total	388	423	424‡	428‡

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

Table 5: Comparison of estimates of some key demographic parameters for southern right whales off Australia (under the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ now fixed on input)) and off South Africa (for the Common model and the Base case Delta-loop model). The weights applied to the penalty for $\hat{P}_y^A$ are denoted below as, for example, 1.0pen when a weight of 1.0 is applied. 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). In the case of Australia, the first and last year modelled are 1993 and 2018 respectively, while for South Africa these are 1979 and 2020. The parameter r is the parous female instantaneous growth rate (in units of yr^{-1}) over the whole period of cow-calf sightings.

	Model		
Parameter	**Australian Common Base case (0.0pen)**	**South African Common (5.0pen)**	**South African Delta-loop (1.0pen)**
$\boldsymbol{S}$	0.970	0.986	0.987
$\boldsymbol{S_j}$	*0.874*	0.690	0.874
$\boldsymbol{a_m}$	4.630	8.535	8.120
$\boldsymbol{\omega}$	0.224	2.621	2.099
$\boldsymbol{N^{mature*}_{1993/1979}}$	191	168	139
$\boldsymbol{N^{all}_{1993/1979}}$	928	692	593
$\boldsymbol{N^{mature*}_{2018/2020}}$	850	1 637	2 092
$\boldsymbol{N^{all}_{2018/2020}}$	2 821	5 630	6 470
$\boldsymbol{r}$	0.056	0.054	0.065
Average apparent calving interval (observed)	4.57 (4.50)	3.98 (4.10)	4.00 (4.10)

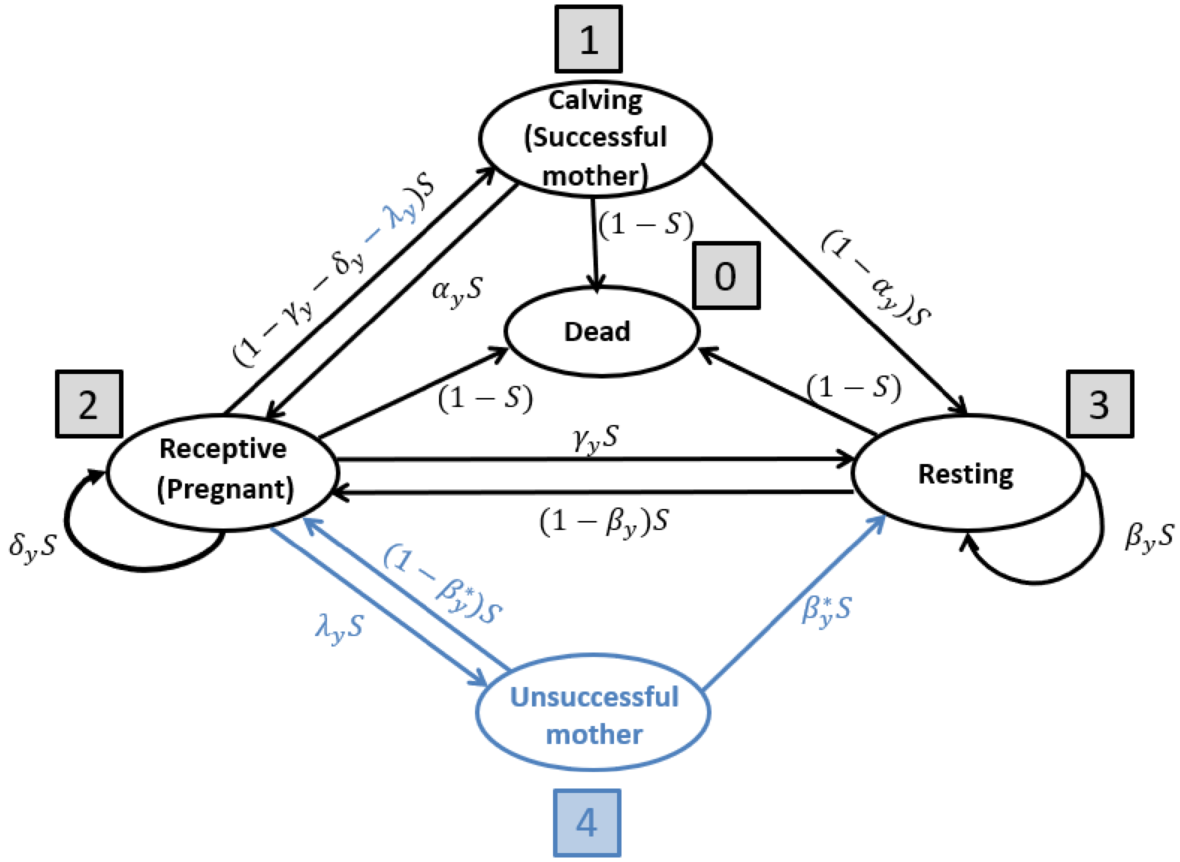


Figure 1. Schematic outline of the Common model with its various southern right whale reproductive states. Text and arrows in black correspond to the Delta-loop model (Brandão *et al.*, 2023), and blue text and arrows to the additional component explicitly modelling the number of females experiencing late abortions or early calf deaths. This component has been added under the guidance of J. Cooke (*pers. comm.*) in accordance with the model previously applied to the SW Atlantic data.

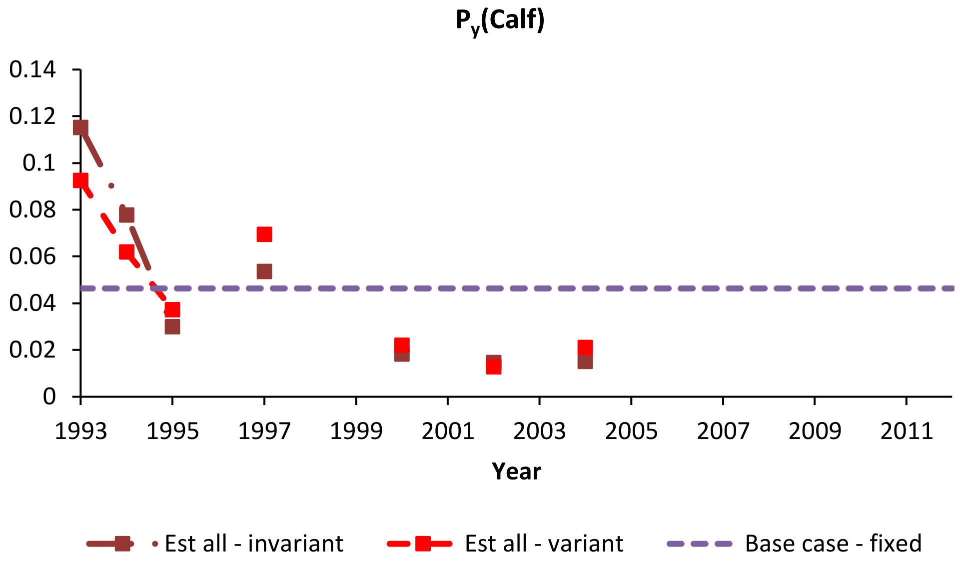


Figure 2. Estimated probabilities that a southern right whale calf is catalogued on aerial surveys under the Common model when **all parameters are estimated** (for both time-invariant and variant cases) and for the **Base case** (for which certain parameters are fixed to the average of their estimated time-invariant values). **No restriction is applied to** $\boldsymbol{\hat{P}_y^A}$ (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$).

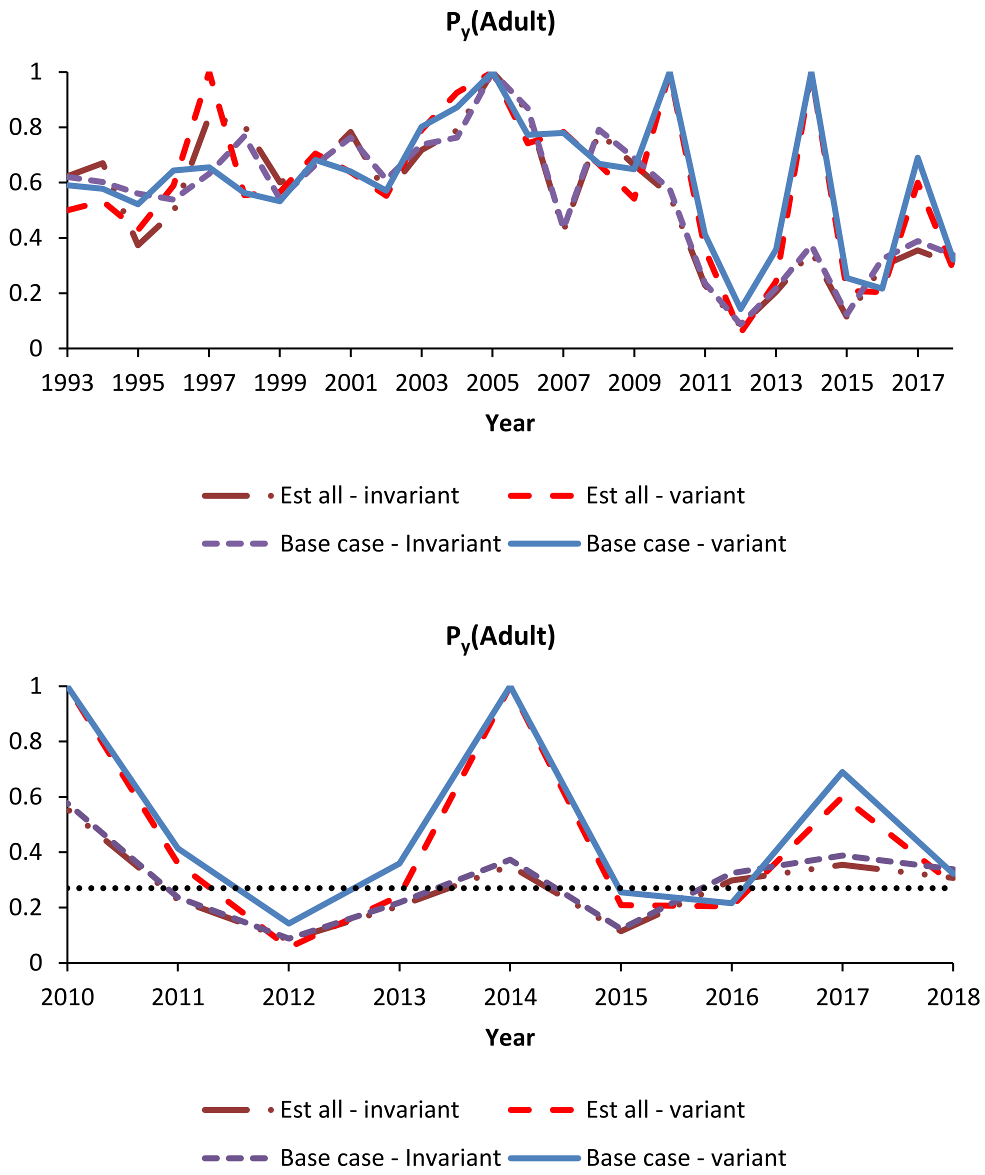


Figure 3. Estimated probabilities of observing a southern right whale cow-calf pair on annual surveys under the Common model (for both **time-invariant and variant cases)** when **all parameters are estimated** and for the **Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed). **No restriction is applied to $\hat{\boldsymbol{P}}_{\boldsymbol{y}}^{\boldsymbol{A}}$** (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$). The dotted horizontal line (at 0.27) is approximately the average of the post-2011 time-invariant estimated probabilities.

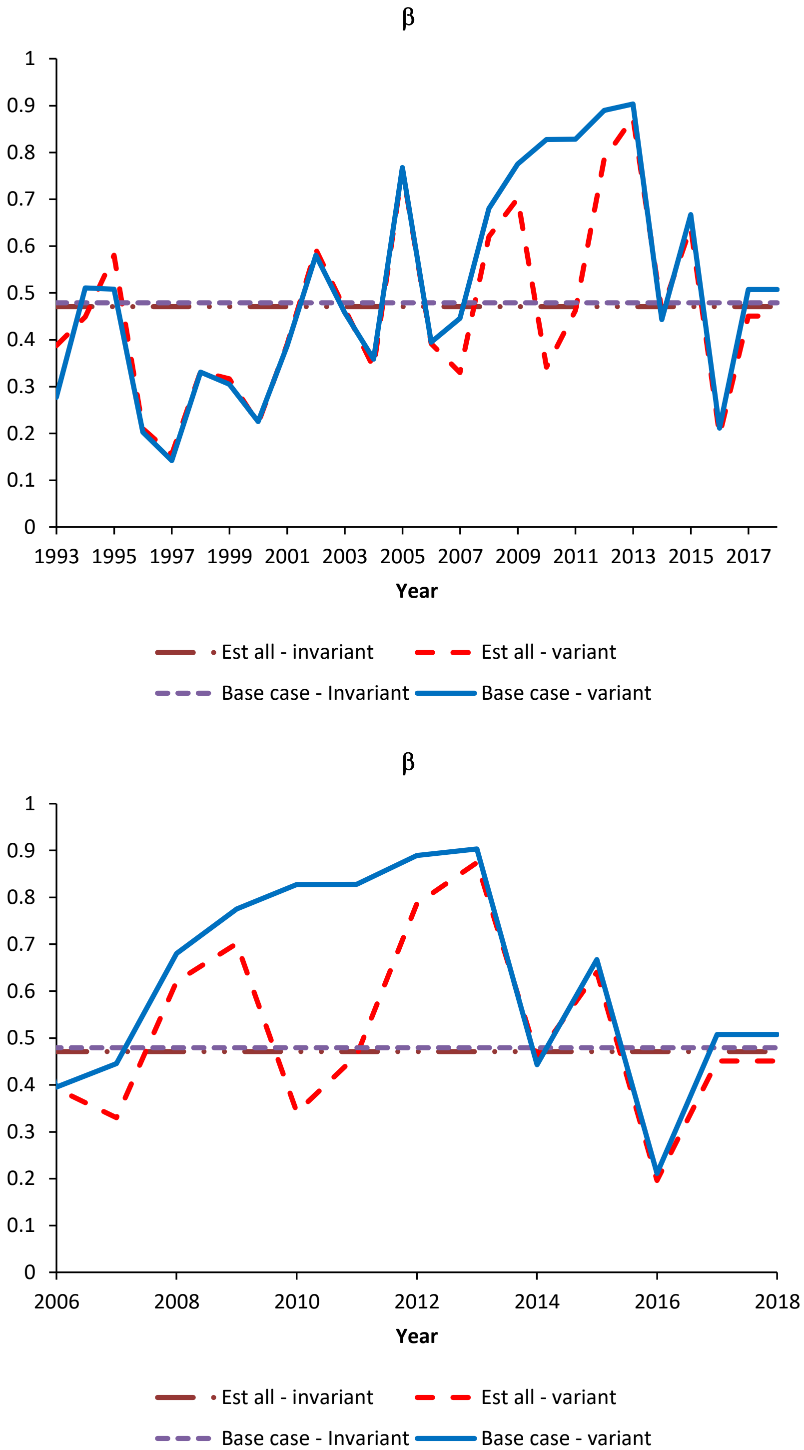


Figure 4. Estimates of the probabilities (β) that a resting southern right whale will rest in the following year under the Common model (for both **time-invariant and variant cases)** when **all parameters are estimated** and for the **Base case** (with $S_j, \rho,\ \tau$ and $\widehat{P}_y^C$ fixed). **No restriction is applied to $\widehat{P}_y^A$** (i.e. a weight of zero is applied to the penalty for $\widehat{P}_y^A$). A magnification for a recent period of these probabilities is also shown (bottom plot).

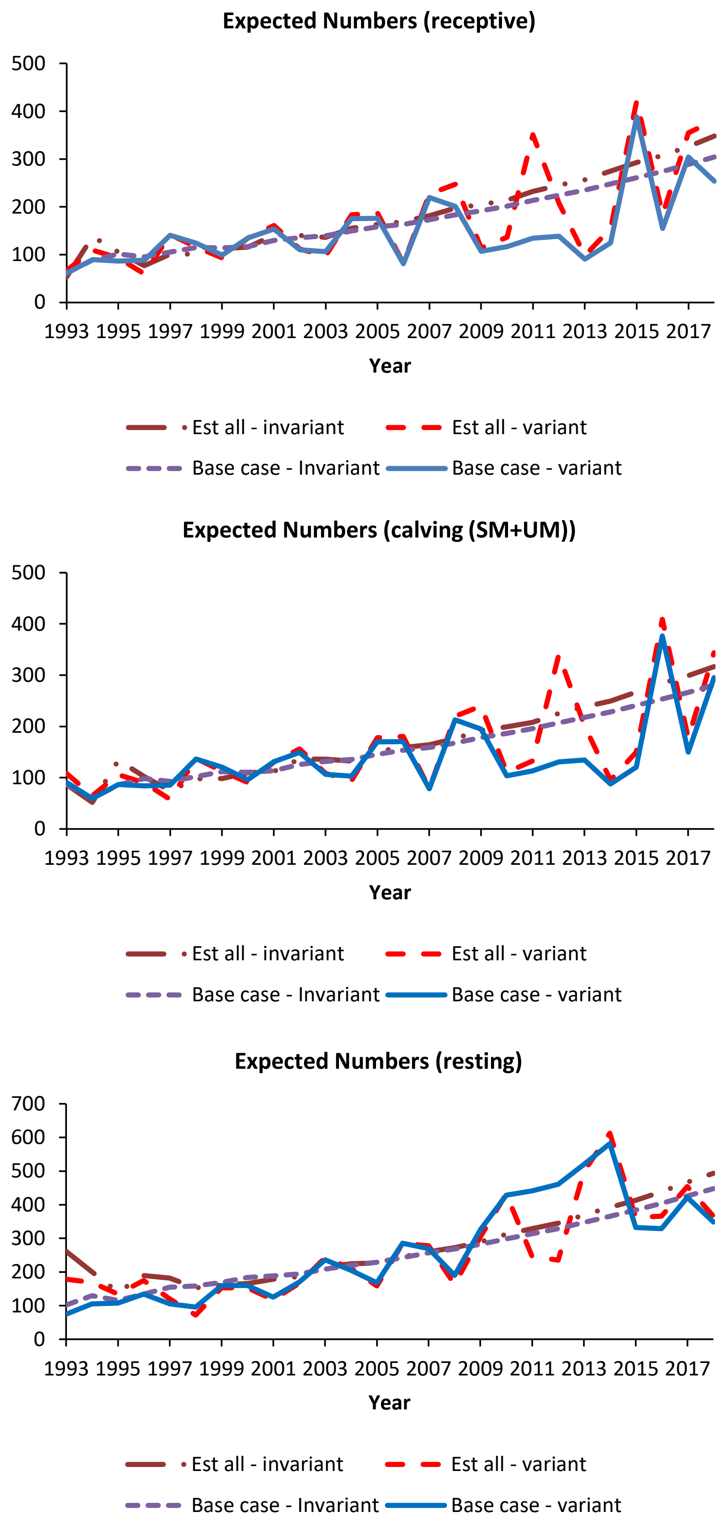


Figure 5a. Expected numbers of mature female southern right whales that are in the receptive (top), calving (middle) and resting (bottom) stages under the Common model (for both **time-invariant and variant cases)** when **all parameters are estimated** and for the **Base case** (with S_j, ρ, τ and $\hat{P}_y^C$ fixed). **No restriction is applied to** $\hat{\boldsymbol{P}}_y^A$ (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$).

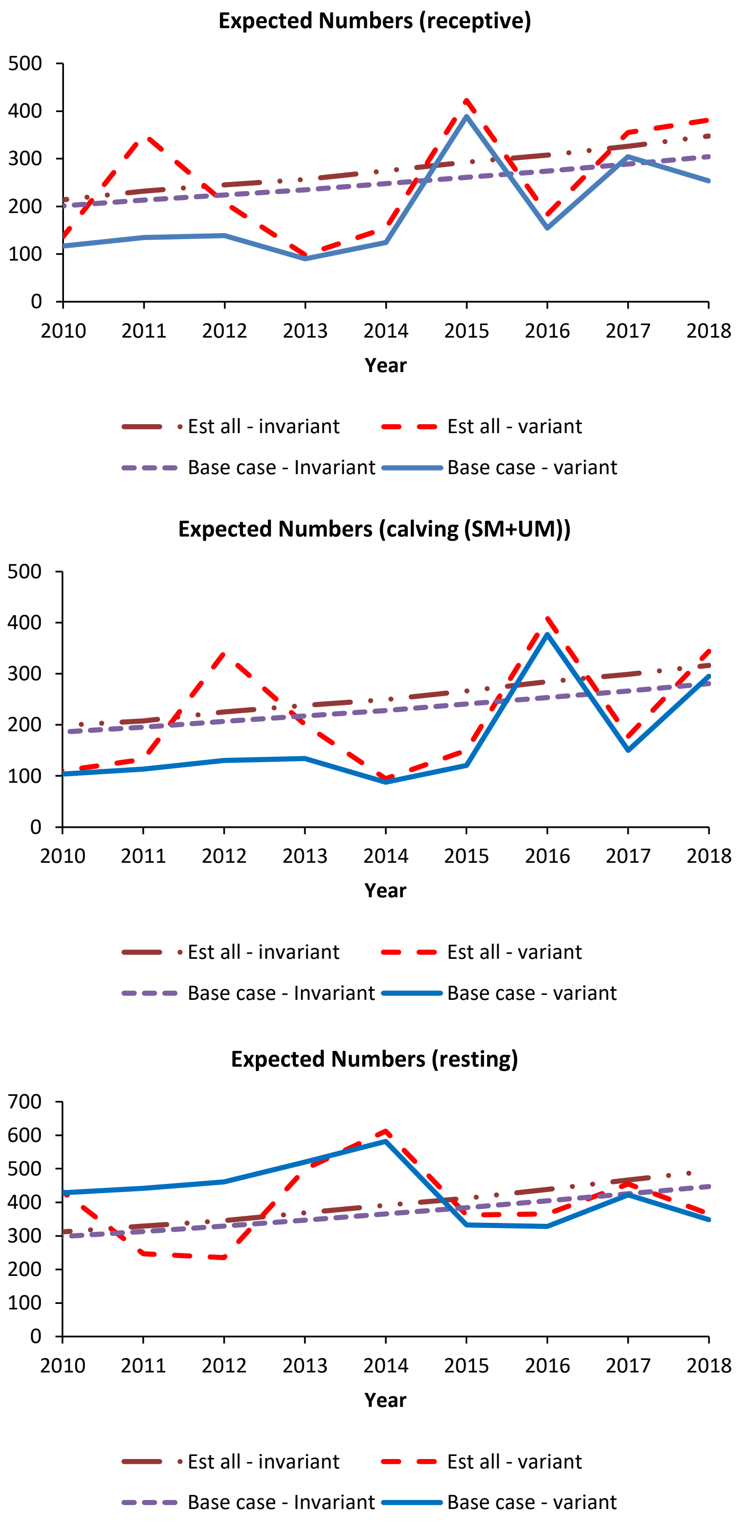
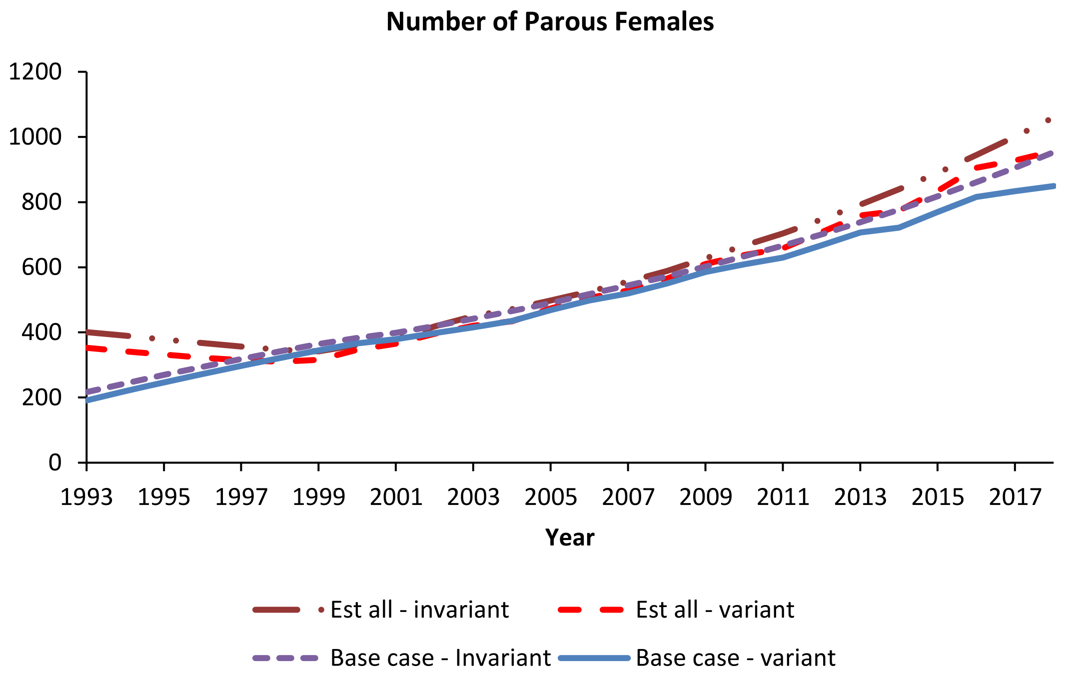


Figure 5b. A magnification of Figure 5a.



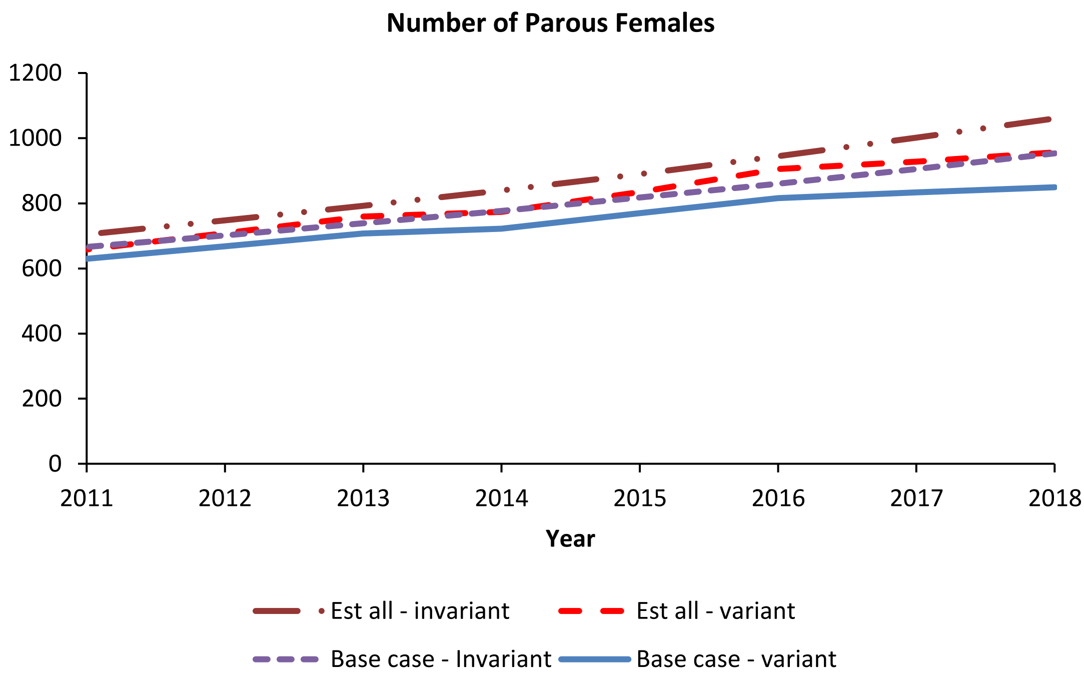


Figure 6. Estimated total number of southern right whale females having reached the age at first parturition for the Common model (for both **time-invariant and variant cases)** when **all parameters are estimated** and for the **Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed). **No restriction is applied to $\hat{\boldsymbol{P}}_y^A$** (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$). A magnified version for recent years are also shown (bottom plot).

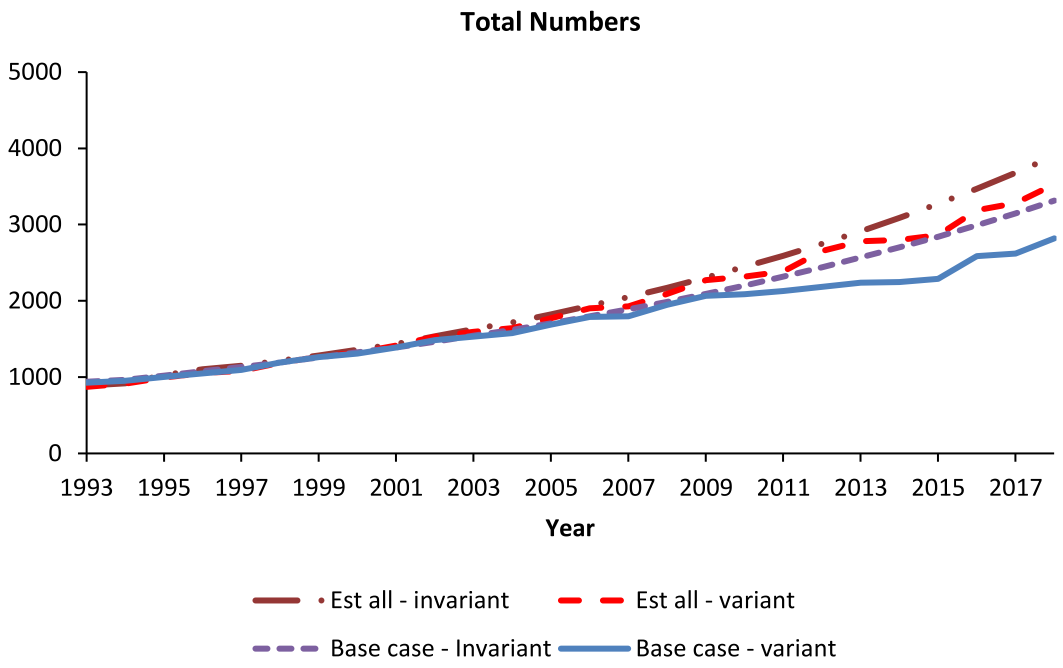


Figure 7. Estimated total number of the whole population of southern right whales off Australia (including males and calves, under the assumption of a 50:50 sex ratio at birth) for the Common model (for both **time-invariant and variant cases)** when **all parameters are estimated** and for the **Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed). **No restriction is applied to** $\boldsymbol{\hat{P}_y^A}$ (i.e. a weight of zero is applied to the penalty for $\hat{P}_y^A$).

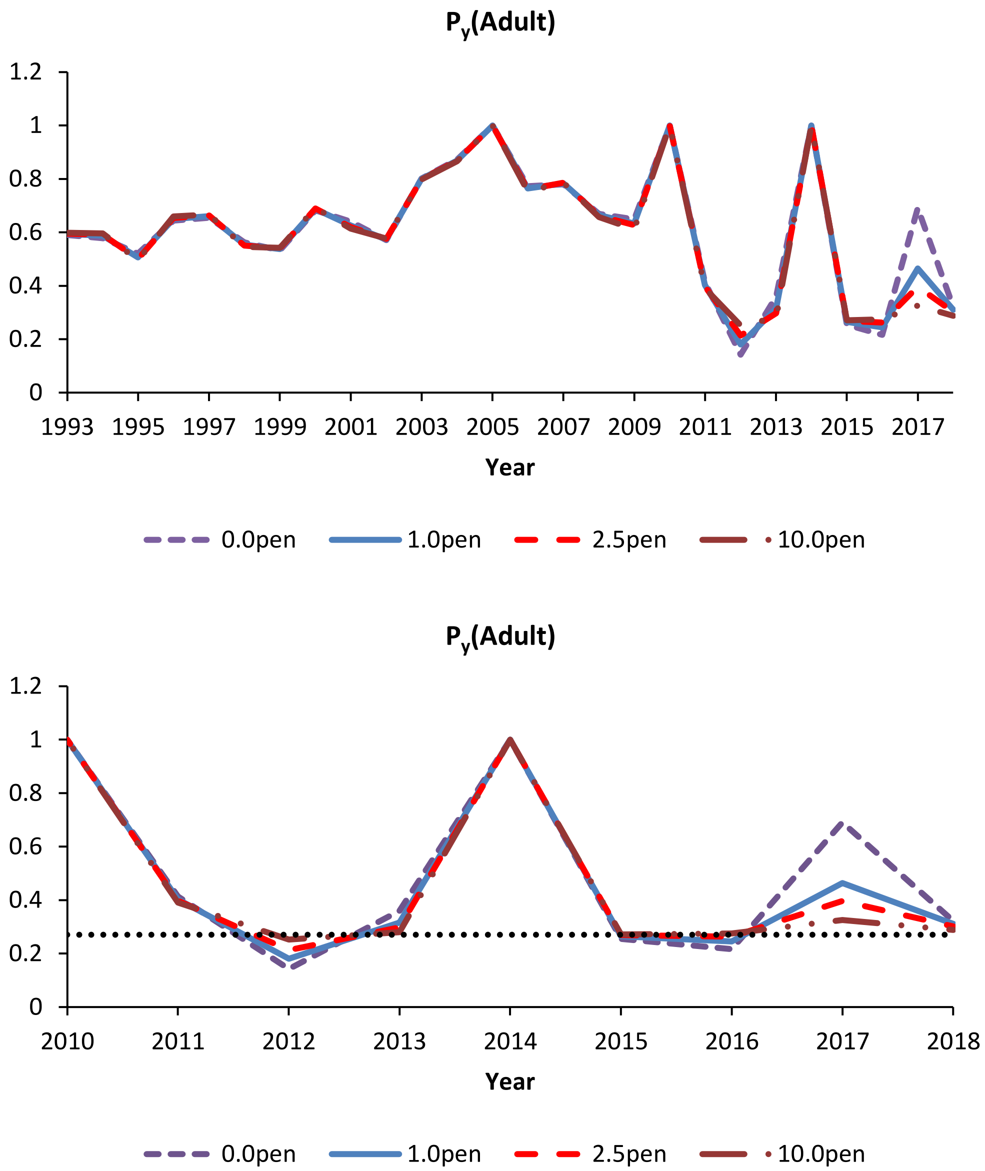


Figure 8. Estimated probabilities of observing a southern right whale cow-calf pair on aerial surveys under the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$(denoted as, for example, 1.0pen when a weight of 1.0 is applied). A magnified version of the probabilities for recent years are also shown (bottom). The dotted horizontal line (at 0.27) is approximately the average of the post-2011 time-invariant estimated probabilities.

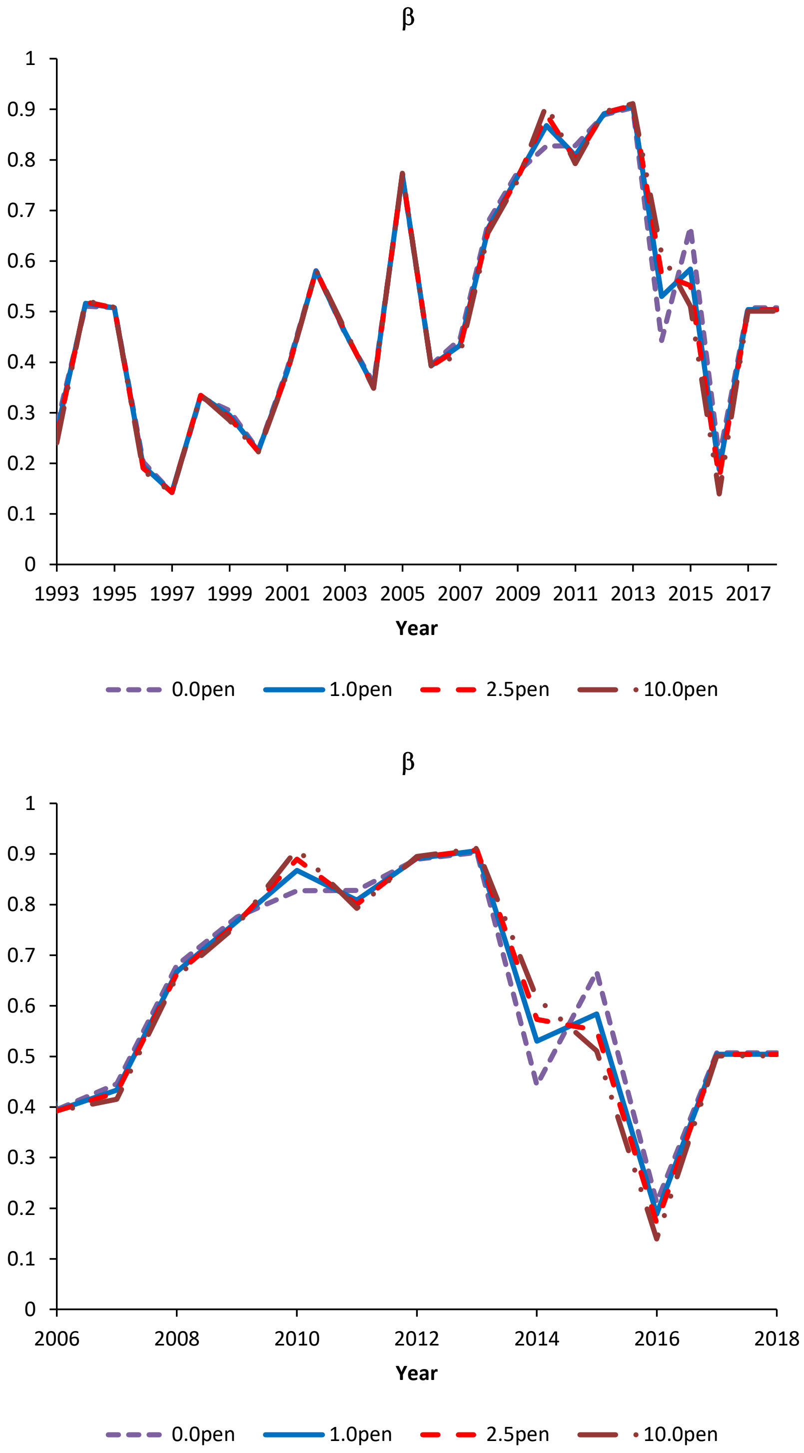


Figure 9. Estimates of the probabilities (β) that a resting southern right whale will rest in the following year under the Common model for the **time-variant Base case** (with $S_j, \rho, \ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$(denoted as, for example, 1.0pen when a weight of 1.0 is applied). A magnification for a recent period of these probabilities is also shown (bottom plot).

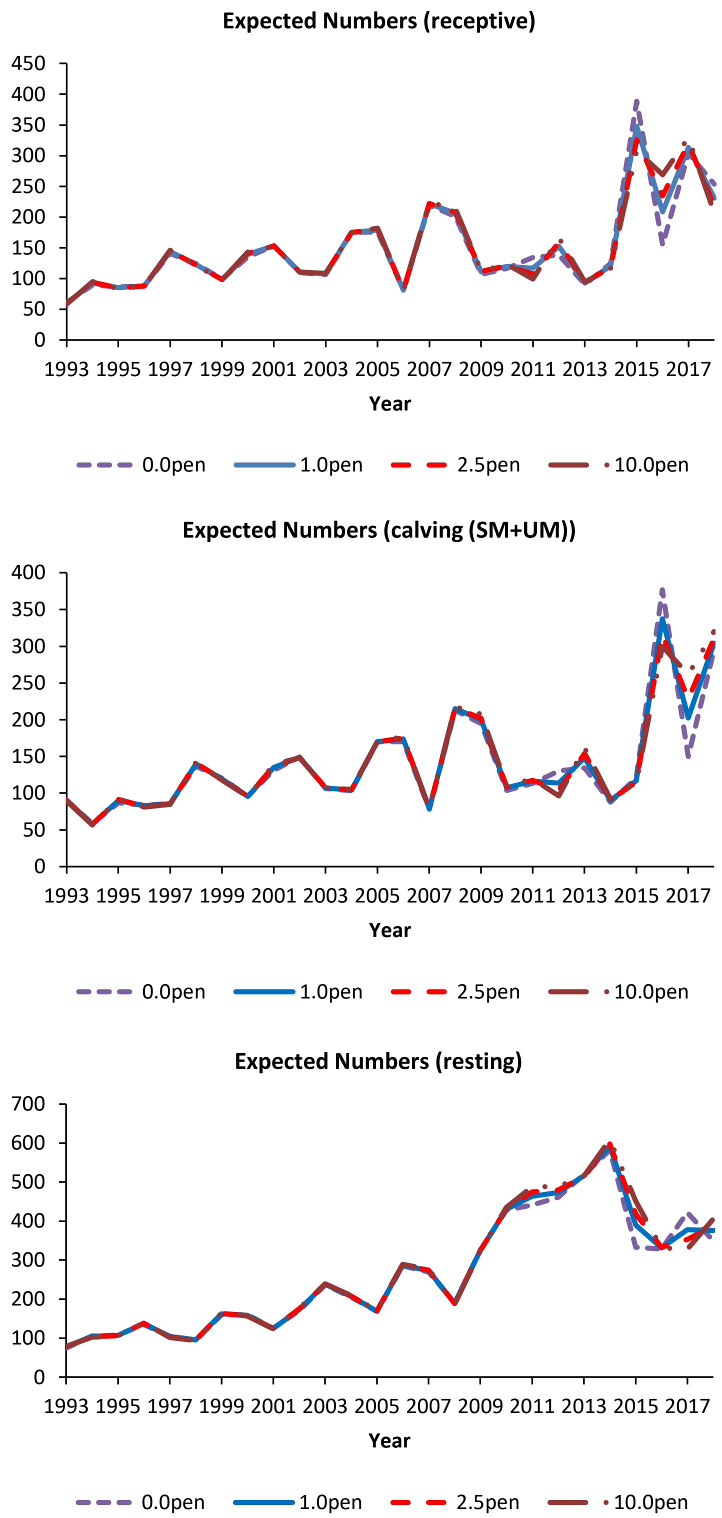


Figure 10a. Expected numbers of mature female southern right whales that are in the receptive (top), calving (middle) and resting (bottom) stages under the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$(denoted as, for example, 1.0pen when a weight of 1.0 is applied).

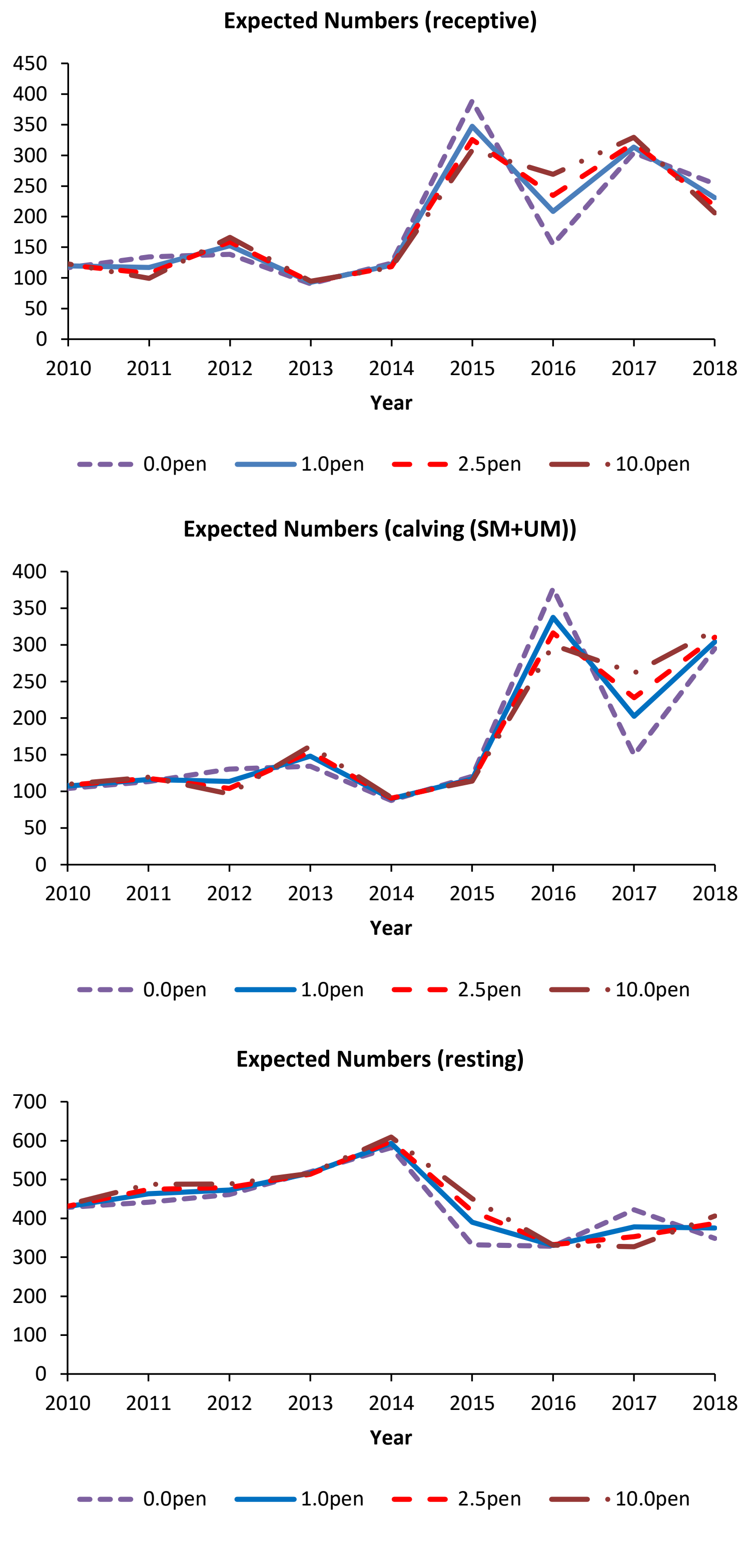


Figure 10b. A magnification of Figure 10a.

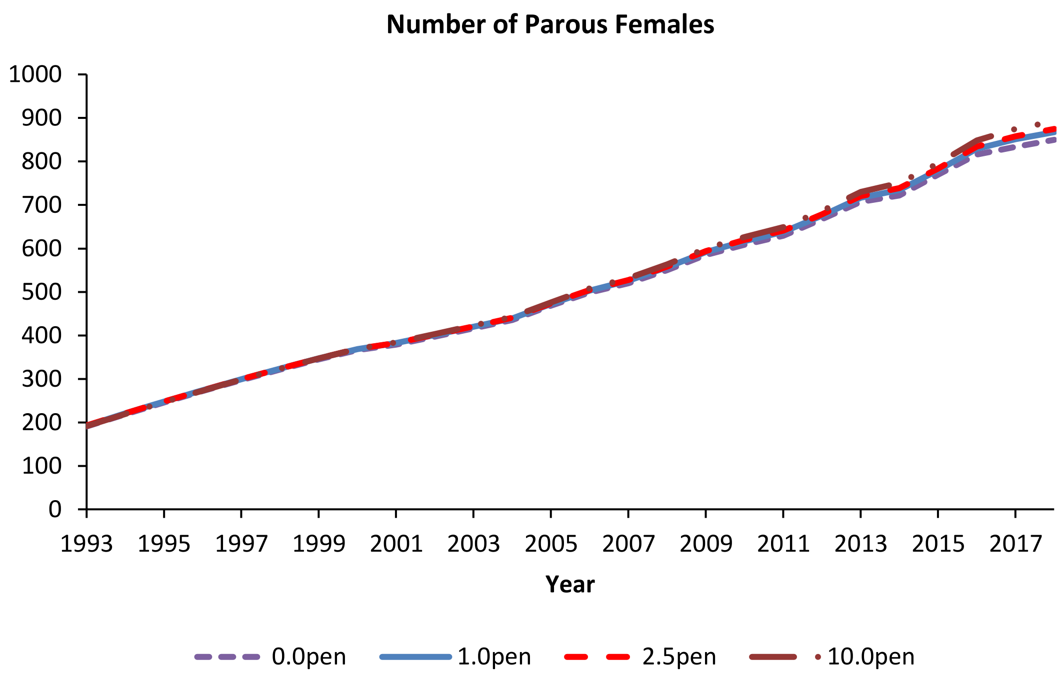


Figure 11. Estimated total number of southern right whale females having reached the age at first parturition for the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$(denoted as, for example, 1.0pen when a weight of 1.0 is applied).

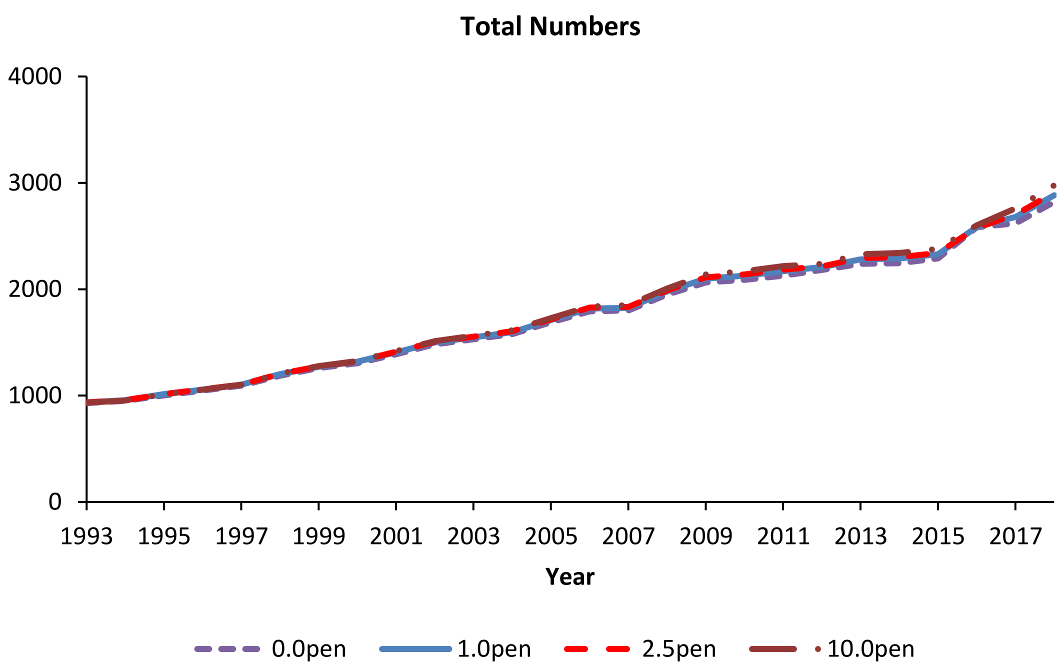


Figure 12. Estimated total number of the whole population of southern right whales off Australia (including males and calves, under the assumption of a 50:50 sex ratio at birth) under the Common model for the **time-variant Base case** (with $S_j, \rho,\ \tau$ and $\hat{P}_y^C$ fixed) when **four different weights** are applied to the penalty for $\hat{P}_y^A$(denoted as, for example, 1.0pen when a weight of 1.0 is applied).

Appendix 1: Photo-Identification Common model

The methodology of the Delta-loop model (i.e., an early abortion occurs so that a pregnant whale can become pregnant again the following year) as applied to the southern right whales off South Africa Brandão *et al*. (2023) has been modified to incorporate the additional component of the Common model specification (blue text and arrows in Figure 1), which explicitly models the number of females experiencing late abortions or early calf deaths . Where appropriate, modifications that are particular to fitting the Common model to the Australian photo-identification, are also made.

Modelling 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 15 years of age.

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

$$\begin{aligned}
N_{0,y+1} &= 0.5N_{y+1}^{calv} \\
N_{1,y+1} &= N_{0,y}e^{-M_j} \\
N_{2,y+1} &= N_{1,y}e^{-M} \\
N_{3,y+1} &= N_{2,y}e^{-M} \\
N_{4,y+1} &= N_{3,y}e^{-M} \\
N_{5,y+1} &= (1-\phi_4)N_{4,y}e^{-M} \\
N_{6,y+1} &= (1-\phi_5)N_{5,y}e^{-M} \\
&\vdots \\
N_{14,y+1} &= (1-\phi_{13})N_{13,y}e^{-M}
\end{aligned} \tag{A1}$$

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 following year.

This is re-parameterized as follows:

$$\phi_a = \begin{cases} \dfrac{1}{\left[1 + e^{-\frac{a-a_m}{\omega}}\right]} & 4 \le a \le 14 \\ 0 & a < 4 \end{cases} \tag{A2}$$

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

Modelling 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 1 shows diagrammatically the possible ways in which a mature female can move from one reproductive state to another. The equations for the dynamics are:

$$N_{y+1}^{recp} = \left(\sum_{a=4}^{13} N_{a,y}\phi_a + N_{14,y}\right)e^{-M} + \left(1-\beta_y\right)N_y^{rest}e^{-M} + \alpha_y N_y^{calv(SM)}e^{-M}$$
$$+\left(1-\beta_y^*\right)N_y^{calv(UM)}e^{-M} + \delta_y N_y^{recp}e^{-M} \tag{A3}$$

$$N_{y+1}^{rest} = \beta_y N_y^{rest}e^{-M} + \left(1-\alpha_y\right)N_y^{calv(SM)}e^{-M} + \left(\beta_y^*\right)N_y^{calv(UM)}e^{-M} + \gamma_y N_y^{recp}e^{-M} \tag{A4}$$

$$N_{y+1}^{calv} = \left(1-\gamma_y-\delta_y\right)N_y^{recp}e^{-M} = N_{y+1}^{calv(SM)} + N_{y+1}^{calv(UM)} \tag{A5}$$

$$N_{y+1}^{calv(SM)} = \left(1-\gamma_y-\delta_y-\lambda_y\right)N_y^{recp}e^{-M} \tag{A6}$$

$$N_{y+1}^{calv(UM)} = \lambda_y N_y^{recp}e^{-M} \tag{A7}$$

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;
$N_y^{calv(SM)}$	is the number of successful mothers that produce a healthy calf at the start of year y;
$N_y^{calv(UM)}$	is the number of unsuccessful mothers that produce a sickly 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);
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);

λ_y is the probability that a whale that is receptive in year y is an unsuccessful mother (i.e. experiences a late abortion or an early calf death) in year $y+1$, and therefore rests that year; and

β_y^* is the probability that a "unsuccessful mother" in year y (and therefore rests that year) rests again the next year.

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:

$$N_{y+1}^{recp,u} = \left(\sum_{a=4}^{13} \phi_a \left(1 - P_{y-a}^C(1-\rho)\right) N_{a,y} + \left(1 - P_{y-14}^C(1-\rho)\right) N_{14,y}\right) e^{-M} + (1-\beta_y) N_y^{rest,u} e^{-M} + \alpha_y (1 - P_y^A) N_y^{calv(SM),u} e^{-M} + (1-\beta_y^*)(1-P_y^A) N_y^{calv(UM),u} e^{-M} + \delta_y N_y^{recp,u} e^{-M} \quad \text{(A8)}$$

$$N_{y+1}^{recp,s} = \left(\sum_{a=4}^{13} \phi_a P_{y-a}^C (1-\rho) N_{a,y} + P_{y-14}^C (1-\rho) N_{14,y}\right) e^{-M} + (1-\beta_y) N_y^{rest,s} e^{-M} + \alpha_y P_y^A N_y^{calv(SM),u} e^{-M} + \alpha_y N_y^{calv(SM),s} e^{-M} + (1-\beta_y^*) P_y^A N_y^{calv(UM),u} e^{-M} + (1-\beta_y^*) N_y^{calv(UM),s} e^{-M} + \delta_y N_y^{recp,s} e^{-M} \quad \text{(A9)}$$

$$N_{y+1}^{rest,u} = \beta_y N_y^{rest,u} e^{-M} + (1-\alpha_y)(1-P_y^A) N_y^{calv(SM),u} e^{-M} + \beta_y^* (1-P_y^A) N_y^{calv(UM),u} e^{-M} + \gamma_y N_y^{recp,u} e^{-M} \quad \text{(A10)}$$

$$N_{y+1}^{rest,s} = \beta_y N_y^{rest,s} e^{-M} + (1-\alpha_y) P_y^A N_y^{calv(SM),u} e^{-M} + (1-\alpha_y) N_y^{calv(SM),s} e^{-M} + \beta_y^* P_y^A N_y^{calv(UM),u} e^{-M} + \beta_y^* N_y^{calv(UM),s} e^{-M} + \gamma_y N_y^{recp,s} e^{-M} \quad \text{(A11)}$$

$$N_{y+1}^{calv,u} = (1-\gamma_y-\delta_y) N_y^{recp,u} e^{-M} = N_{y+1}^{calv(SM),u} + N_{y+1}^{calv(UM),u} \quad \text{(A12)}$$

$$N_{y+1}^{calv,s} = (1-\gamma_y-\delta_y) N_y^{recp,s} e^{-M} = N_{y+1}^{calv(SM),s} + N_{y+1}^{calv(UM),s} \quad \text{(A13)}$$

$$N_{y+1}^{calv(SM),u} = (1-\gamma_y-\delta_y-\lambda_y) N_y^{recp,u} e^{-M} \quad \text{(A14)}$$

$$N_{y+1}^{calv(SM),s} = (1-\gamma_y-\delta_y-\lambda_y) N_y^{recp,s} e^{-M} \quad \text{(A15)}$$

$$N_{y+1}^{calv(UM),u} = (\lambda_y) N_y^{recp,u} e^{-M} \quad \text{(A16)}$$

$$N_{y+1}^{calv(UM),s} = (\lambda_y) N_y^{recp,s} e^{-M} \quad \text{(A17)}$$

where

P_y^C is the probability that a female calf seen in year y is grey blazed and catalogued,

P_y^A is the probability that a female whale with a calf is seen in year y, and

u/s are superscripts which denote whales that have yet to be seen (u) or have already been seen (s).

Initial conditions

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

$$
\begin{aligned}
N_{0,1993} &= 0.5N_{1993}^{calv} \\
N_{1,1993} &= \tau N_{0,1993}e^{-M_j} \\
N_{2,1993} &= \tau N_{1,1993}e^{-M} \\
&\vdots \\
N_{5,1993} &= \tau(1-\phi_4)N_{4,1993}e^{-M} \\
&\vdots \\
N_{14,1993} &= \tau(1-\phi_{13})N_{13,1993}e^{-M}
\end{aligned}
\tag{A18}
$$

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 1993 had an age structure reflecting steady growth over the previous 14 years.

Initial numbers for mature females in each of the three reproductive stages $\left(\text{i.e. } N_{1993}^{calv},\ N_{1993}^{recp},\ N_{1993}^{rest}\right)$ 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 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) for the Delta-loop model are given in the Supplementary Material of Brandão *et al*. (2023). Those for the Common model will follow in a similar way.

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 they would be recorded as new animals in the future 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:

$$ln(\, e_h^A; \theta) = \sum_{\text{all } h} \left(n_h^A \, ln(\, e_h^A) - e_h^A \right) \tag{A19}$$

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:

$$e_h^A = \widehat{N}_y^{calv,U} \hat{P}_y^A \hat{q}_h^A \tag{A20}$$

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

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

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

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

$$\sum_{\text{unobs } h} e_h^A = \sum_{y} \sum_{\text{unobs } h(y)} \widehat{N}_y^{calv,U} \hat{P}_y^A \hat{q}_h^A = \sum_{y} \widehat{N}_y^{calv,U} \hat{P}_y^A \sum_{\text{unobs } h(y)} \hat{q}_h^A \tag{A21}$$

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

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:

$$ln(\, e_h^A; \theta) = \sum_{h=1}^{n^A} \left(n_h^A \, ln(\, e_h^A) \right) - \sum_{y=1993}^{2018} \widehat{N}_y^{calv,u} \hat{P}_y^A \tag{A22}$$

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:

$$ln(\, e_h^C; \theta^*) = \sum_{h=1}^{n^C} \left(n_h^C \, ln(\, e_h^C)\right) - \sum_{y=1993}^{2018} \widehat{N}_{0,y} \hat{P}_y^C \qquad \text{(A23)}$$

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:

$$e_h^C = \widehat{N}_{0,y} \hat{P}_y^C \hat{q}_h^C \qquad \text{(A24)}$$

where

- $\hat{P}_y^C$ is the estimated probability that a grey blazed female calf was first catalogued in year y; and
- $\hat{q}_h^C$ is the estimated probability of history h being observed given that the calf was catalogued in year y.

The probabilities of observing a whale with a calf ($\hat{P}_y^A$) in the first three years were not well estimated because of the few sighting histories in the initial period, so that a penalty function was used to ensure that the estimates of $\hat{P}_y^A$ for the first three years were in the range of the average of the subsequent 10 years. Thus, the following penalty function was added to the total negative log-likelihood function:

$$\frac{1}{2\sigma_P^2} \sum_{y=1993}^{1995} \left(\hat{P}_y^A - \bar{P}\right)^2 \qquad \text{(A25)}$$

where

- $\bar{P}$ is the average of the $\hat{P}_y^A$ estimates for the years 1996 to 2005; and
- σ_P is the calculated standard deviation of those $\hat{P}_y^A$ probabilities.

From 2011, the estimated sightings probabilities are quite variable in the case of the time-variant model fitted to the Australian photo-identification data. However, the survey effort for this period has been fairly similar from year to year. Therefore, a penalty function was used to ensure that the estimates of $\hat{P}_y^A$ for the years after 2011 were in the range of the average of the time-invariant estimates of $\hat{P}_y^A$ for the same period. Thus, the following penalty function was added to the total negative log-likelihood function:

$$w\left\{\frac{1}{2\sigma_{P^*}^2}\sum_{y=2012}^{2018}\left(\hat{P}_y^A - P^*\right)^2\right\} \tag{A26}$$

where

- P^* is the average of the $\hat{P}_y^A$ estimates for the years 2012 to 2018 of the time-invariant model;
- 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 $\alpha_y, \beta_y, \gamma_y, \lambda_y$ and β_y^* can be estimated in two ways: either they are assumed to be time-invariant or one or more 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 four probability parameters ($\beta_y,\ \gamma_y,\ \lambda_y$ and β_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 $\bar{\beta}$ (or $\bar{\gamma}$ or $\bar{\lambda}$ or $\overline{\beta^*}$) and standard deviation σ_β (or σ_γ or σ_λ or σ_{β^*}). The 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.

For the moment, the probabilities of a pregnant whale being pregnant again in the following year (δ_y), the probabilities that a whale that is receptive in year y is an unsuccessful mother (i.e. experiences a late abortion or an early calf death) in year $y+1$, and therefore rests that year (λ_y) as well as the probabilities that a "unsuccessful mother" in year y (and therefore rests that year) rests again the next year (β_y^*) are all taken to be zero.

Estimable parameters

The estimable parameters in the model are S, S_j, α, β, γ, δ, λ, β^*, a_m, ω, P_y^A, P_y^C, τ, ρ, $N_{1993}^{calv(SM)}$, $N_{1993}^{calv(UM)}$, N_{1993}^{recp}, and N_{1993}^{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.

This 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 1993–2018.