# Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identifications of calving females observed off Península Valdés, Argentina, during 1971-2000

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## ABSTRACT

Photo-identification studies of the right whales (*Eubalaena australis*) which congregate in the waters surrounding Pensinsula Valdés, Argentina, between June and December each year have been conducted each year from 1971 to the present, using aerial surveys. Resightings of previously catalogued individuals enable the demography of the population to be analysed. A total of 1,828 distinct individuals have been catalogued up to and including the 2000 season, of which 564 have been observed to calve at least once. A total of 1298 definite calving events have been observed. A total of 405 whales have been catalogued as calves, and hence are of known age, of which 53 have since been observed to have calves themselves. A 3-stage model of the adult female population, incorporating calving, resting and receptive stages, is developed and fitted to the observed calving histories. The modal calving interval is three years, representing one year in each stage. Calving intervals of four years or more years can result from remaining two or more years in the resting stage. Calving intervals of five or more years can result from transitions back from the ready stage to the resting stage. Parameters of the transition matrix between stages are estimated from the data. Results of fitting of alternative models of temporal variation in transition probabilities yields strong evidence for inter-annual variation in the probability of a backward transitions from the receptive stage to the resting stage, but not in the probability of spending an extra year in the resting phase. The result indicates the point in the reproductive cycle at which environmental influences may have most effect. Updated estimates of other demographic parameters include: mean calving interval 3.42 yr (S.E. 0.11 yr); mean age at potential first calving 9.1 yr (S.E. 0.4 yr); adult female annual mortality rate 0.020 (S.E. 0.004); annual percentage rate of population increase 6.8% (S.E. 0.5%); reproductive female population size in 2000: 697 animals (S.E. 48).

## INTRODUCTION

Southern right whales *Eubalaena australis* return regularly to the area around Península Valdés in Argentina in winter and spring (June through December) , although there has been some variation over time in their distribution within this general area (Rowntree *et al*, 2001). Photo-identifications of individual whales based on natural markings have been obtained from aerial surveys each year since 1971.

Analyses of the data to estimate populations sizes and demographic parameters were conducted by Payne *et al* (1990) using data from 1971 through 1986, and by Cooke *et* al (2001) using data from 1971 through 1990. The analyses of this paper use the 30-year data series from 1971-2000. The length of the time series, longer than for most studies of cetaceans, offers an opportunity not only to estimate demographic parameters but also to examine their variation over time with a view to understanding which aspects of the demography are most susceptible to change under the influence of environmental or other factors.

Because the amount of survey effort varied from year to year, the numbers identified in each year do not necessarily reflect the numbers of whales present. The observed calving history of a female is only a subset of the true calving history, because the female is not necessarily observed in each year that it calves, or, if it is observed, the calf is not necessarily seen. The observed calving intervals contain many

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long apparent intervals that result from missed calving events. A probabilistic model is thus required to infer the true distribution of calving intervals from the observed histories.

Unstructured mark release models are not suitable for these data because of the periodic nature of the calving process: the majority of females calve at intervals of 3 years. In this paper, the calving interval model used by Payne et al (1990) and Cooke et al (2001) is reformulated using matrices of transition probabilities between reproductive stages, as described by Caswell (1989). The new formulation provides a more convenient framework for incorporating possible temporal variability in parameters into the model.

## METHODS

### Field methods

The methods used to record natural markings and to identify resightings of individual whales, and the characteristics of the study season and area, are described by Payne (1986) and Payne *et al* (1983). As the length of the data series and size of the catalogue increases, unaided matching of new photographs against the catalogue becomes increasingly time consuming. The computer-based method of Hiby and Lovell (2001) has therefore been used. For each photograph sequence, a computer algorithm searches the catalogue and offers a set of candidate matches which are then examined manually to identify actual matches.

### Data

For the reasons discussed by Payne *et al* (1990), only the sightings of females accompanied by calves are used to estimate population parameters, apart from the use of known-age animals (those first identified as calves) to determine the age at first calving. Known adult females are seen in the area in years where they are not seen to calve, but at a substantially lower rate (Rowntree *et al*, 2001) . Furthermore, failure to observe a calf does not imply that one is not present, because multiple sightings of a female in a given year often contain a mixture of observations with a calf present and a calf not present. Only positive identifications of females with calves are used for this analysis. Positive identifications are defined as cases where an identified whale is seen at least once in clear association with a calf, or at least twice in probable association with a calf.

Two types of individual annual sighting history are included in the analysis: (i) histories beginning with the first observed calving of a previously unidentified whale, plus subsequent observed calvings of that whale, if any; (ii) histories beginning with the identification of a whale as calf, followed by the history of observed calvings of that whale, if any.

### Models

In order to draw inferences about demographic parameters from these data, two closely related models are required: (i) a probabilistic model of the reproductive careers of individual whales and of the observation process; (ii) on aggregate model of the population which relates the individual reproductive careers to population-level parameters such as the population size, rate of population change change, survival and reproductive rates. The population parameters are estimated by fitting the models to the data set of individual sighting histories.

### Model of the reproductive cycle of the adult female population

The female reproductive population is represented as a 4-stage model as shown in Fig 1. The three living stages are:

*Receptive:* the whale is ready to conceive this year
*Calving*: the whale gives birth to a calf this year

*Resting*: one or more rest years following a calving

A fourth, ‘dead’ class represents mortality.

The thicker arrows in Fig. 1. represent high probability transitions, while the thin arrows represent lower probability transitions. The “standard” 3-year reproductive cycle is Calving→ Resting→ Receptive→ Calving. The symbols $\alpha$, $\beta$, $\gamma$, and $\mu$ represent the probabilities of the following deviations from the standard cycle: :

$\alpha$: a calving whale becomes receptive the following year without the usual rest year
$\beta$: a resting whale takes an additional rest year
$\gamma$: a whale that is receptive this year returns to the resting phase next year without producing a surviving calf (for example following abortion or ante- or perinatal mortality).
$\mu$: the whale dies.

In principle, the mortality probability ($\mu$) could be stage-specific. However, since the average mortality rate was found to be low (~0.02), there is currently little prospect of detecting inter-stage differences from this data set, nor would such differences be demographically important in the context of such a low average rate. Thus a single mortality parameter is assumed for this analysis.

A receptive whale could fail to conceive and remain receptive for another year. However, since receptive and resting whales are not observationally distinguished, there is no way of distinguishing between an additional receptive year and an additional rest year from these data. It is an arbitrary matter of definition as to whether an additional year is labelled as a rest year or a receptive year: both result in a lengthening of the calving interval by one year. Therefore, the probability of both events is subsumed into the parameter $\beta$ for the purpose of this analysis.

The event of a receptive whale returning to the resting phase without producing a calf is potentially distinguishable from the above two events, because it lengthens the calving interval by two years. Hence its probability is included in the model as a separate parameter, $\gamma$.

The probability of a 1-year calving is assumed to be zero or negligible. A 1-year calving interval is *a priori* unlikely given Best’s (1994) estimate of 357-396 days for the gestation period of southern right whales based on observations of foetuses in animals taken in pelagic whaling operations. Furthermore, only one 1-year interval was observed in the data used for this study, out of 558 observed intervals.

Following Caswell (1989), it is convenient to represent the transition probabilities as matrices:

$$Q_t = \left( \begin{array}{ccc|c} 0 & (1-\alpha_t)(1-\mu_t) & \alpha_t(1-\mu_t) & \mu_t \\ 0 & \beta_t(1-\mu) & (1-\beta_t)(1-\mu_t) & \mu_t \\ (1-\gamma_t)(1-\mu_t) & \gamma_t(1-\mu) & 0 & \mu_t \\ \hline 0 & 0 & 0 & 1 \end{array} \right) \qquad (1)$$

The rows and columns correspond to the Calving (0), Resting (1), Receptive (2) and Dead (3) states. The subscript $t$ denotes time (year) and implies that all parameters are potentially time-varying. The entry $Q_t(i,j)$ denotes the probability that a whale in stage $i$ in year $t$-1 progresses to stage $j$ in year $t$. The final row is, trivially, 0 0 0 1, because a dead whale remains dead with probability one. The index $t$ runs from zero, the first year of the data series, to $T_{\max}$, the final year.

The transition matrix has two distinct uses: on an individual level it represents the probability distribution of inter-stage transitions for the individual. On a population level, it represents the expected proportions of the population in each stage that progress to the next stage. It is necessary to include the dead class explicitly for modelling the probability of individual sighting histories. It could be discarded when modelling the aggregate population, but is retained here to avoid the need to define two different versions of the transition matrices.

**Modelling recruitment to the adult female population**

The above transition matrix does not include the generation of new recruits to the adult female population. For this purpose, the above transition matrix is embedded into a full Leslie matrix, including rows and columns for juvenile animals. Because the transition from juveniles to adults is age-dependent, the age structure of the juvenile population is represented, along with the age-specific maturation rate.

*Juvenile survival and sex ratio*

Because observations of post-calf juveniles are not used in the analysis, it is not necessary to model the age-specific survival in detail. The survival rate from calf to maturity is lumped together into the single parameter $S$, which is arbitrarily assigned to age class zero. The female sex ratio is assumed to be 0.5, but this assumption has no effect on the analysis: because the sex of calves is not in general observed, the only identifiable parameter is the proportion of calves that become an adult female, which is the product of the survival rate and the sex ratio.

*Age-specific maturation*

An individual female is considered to become sexually mature when it first enters the Receptive stage, which is at least one year before its first calving event. From this time onward, its reproductive career is determined by the transition matrices $Q_t$ specified in (1).

For representing the maturation process, three age ranges are defined:
(i) pre-mature age classes, where no animals are yet sexually mature;
(ii) maturing age classes, in which at least some (and possibly all) animals are sexually mature;
(iii) post-maturing age classes, in which all animals are definitely sexually mature.

The youngest known-age animal observed to calve in this data set was six years, and thus conceived at age five. The three age ranges were taken as: (i) 1-4; (ii) 5-14; (ii) 15+. The upper age limit is chosen high enough so as not to constrain the results, i.e. higher than the age at which the model estimates that maturation is essentially complete.

The parameter $\phi_{at}$ ($a$ = 5, ... ) denotes the probability that a female that was immature at age $a$-1 in year $t$-1, becomes sexually mature at age $a$ in year $t$. For ages 5 through 14, the log-odds ratio $\zeta_{at} = \log(\phi_{at}/(1-\phi_{at})) = \kappa + \lambda a$ is assumed to increase linearly with age. This yields a logistic maturation ogive. The intercept ($\kappa$)and slope ($\lambda$) parameters are estimated as part of the model fitting process. The parameters are estimated from the observations of known-age animals. In view of the small sample size of known-age animals, possible time dependence in the maturation parameters is not considered in this analysis.

*Leslie matrix for the population*

The full Leslie matrix, $L$, is for the population is shown schematically below. Ellipses denote intervening age classes that are not listed explicitly. The bottom right four rows and columns are the adult transition matrix $Q$, as specified in equation (1) (shown as blobs here because of space constraints). Entries left blank are to be read as zero. The value 1 near the bottom left represents the litter size of calving whales, assumed to be exactly 1. The zero age class (calves) including both males and females, since these are not usually distinguishable. All other classes include females only. Males are subsumed into the Dead class from age 1 onwards, since they play no further role in the analysis.

$$
L_t = \left(\begin{array}{cccc|cccc|ccc|c}
0 & \frac{1}{2}S & & & & & & & & & & 1-\frac{1}{2}S \\
 & 0 & \cdots & & & & & & & & & \\
 & & & 1 & & & & & & & & \\
 & & & 0 & 1-\phi_5 & & & & & & \phi_5 & \\
\hline
 & & & & 0 & 1-\phi_6 & & & & & \phi_6 & \\
 & & & & & 0 & \cdots & & & & \cdots & \\
 & & & & & & & 1-\phi_{14} & & & \phi_{14} & \\
 & & & & & & & 0 & & & 1 & \\
\hline
1 & & & & & & & & 0 & \bullet & \bullet & \mu \\
 & & & & & & & & 0 & \bullet & \bullet & \mu \\
 & & & & & & & & \bullet & \bullet & 0 & \mu \\
\hline
 & & & & & & & & & & & 1
\end{array}\right)
$$

If the expected numbers in each age/stage in the population in year $t$ are given by the row vector $z_t$, then the expected numbers in the following year are given by:

$$z_{t+1} = z_t L_t$$

The initial age/stage structure of the population is in general unknown. In the population of this study, the population was initially quite small and thus its assumed initial age structure is not particularly critical. The population in the first year of the study is assumed to have the stable age and stage distribution that corresponds to the Leslie matrix remaining constant at $L_0$. The stable age distribution is given by the unique positive (except possibly for the dead component) eigenvector of $L_0$, denoted $\lambda_0$. If $\lambda_0$ is scaled so that its elements corresponding to the mature population stages sum to unity, then the expected population vector in year $t$ is given by:

$$z_t = N_0 \; \lambda_0 \prod_{i=1}^{t} L_t$$

where $N_0$ is the mature female population size at the beginning of the study (taken as $t = 0$; actually 1971). The repeated product is evaluated from left to right in order or increasing years. $N_0$ is one of the unknown parameters to be estimated when fitting the model.

*Individual transition matrix for adult and juvenile females*

The individual transition probability matrix used for modelling the sighting histories of identified individuals is almost identical to the Leslie matrix for the population. The only difference is the absence of the 1-entry near the bottom left, which is reset to zero because identifying marks are assumed not to be inherited.

$$Q_t^* = \left(\begin{array}{cccc|cccc|ccc|c}
0 & \frac{1}{2}S\rho & & & & & & & & & & \\
 & 0 & \ldots & & & & & & & & & \\
 & & & 1 & & & & & & & & \\
 & & & 0 & 1-\phi_5 & & & & & & \phi_5 & \\
\hline
 & & & & 0 & 1-\phi_6 & & & & & \phi_6 & \\
 & & & & & & \ldots & & & & \ldots & \\
 & & & & & & 0 & 1-\phi_{14} & & & \phi_{14} & \\
 & & & & & & & 0 & & & 1 & \\
\hline
 & & & & & & & & 0 & \bullet & \bullet & \mu \\
 & & & & & & & & 0 & \bullet & \bullet & \mu \\
 & & & & & & & & \bullet & \bullet & 0 & \mu \\
\hline
 & & & & & & & & & & & 1
\end{array}\right)$$

If we define the reproduction matrix, $R$, as the matrix consisting of all zeroes except for a 1 in the fourth last row of the leftmost column, then:

$$L_t = Q_t^* + R$$

*Probability of individual sighting histories*

In general, if there are $n$ stages in the model and $m$ possible values of observations for each individual at each time point (year), then the (year-specific) observation probability matrix, $P_t$, is an $m$ x $n$ matrix such that $P_t(i, j)$ is the probability that observation value $i$ will be obtained for a whale in stage $j$ in year $t$.

The observation vector in year $t$ for the whale whose catalogue label is $k$ is a vector of the form (1 0 0 ...) (0 1 0 0 ...) etc. where all entries are zero except the entry for the type of observation actually made. In this analysis, only three types of observation are considered:

(i) the whale is seen as a calf (1 0 0)
(ii) the whale is seen as having a calf (0 1 0)
(iii) the whale is not seen at all or not as a calf and not with a calf (0 0 1)

We assume that the probability is zero or negligible that a whale is erroneously observed to be/have a calf when it is/does not. Evidence for this assumption is discussed below. However, there may be a substantial probability that a whale is not observed to have a calf (or not be seen at all) when it does have one.

The observation probability matrix in year $t$ is given by:

$$P_t = \begin{pmatrix} c_t & 0 & \ldots & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \ldots & 0 & g_t & 0 & 0 & 0 \\ 1-c_t & 1 & \ldots & 1 & 1-g_t & 1 & 1 & 1 \end{pmatrix}$$

where $g_t$ denotes the probability that a calving whale in year $t$ will be observed as such and $c_t$ is the probability that a calf born in year $t$ is identified and included in the catalogue. Since observations of calves and calving females only are included in this analysis, the probability of a null observation (0 0 1) is 1 for all stages other than Calves and Calving. The probabilities $c_t$ and $g_t$ are parameters to be estimated in the model-fitting process.

Let $y$ denote a sighting history, i.e. a sequence $y_{j,t}$ ($j = 1, ..., m$; $t = 0, ..., T_{\max}$) of observation vectors over time, where $y_{j,t} = 1$ if the history contains observation category $j$ is year $t$, 0 otherwise. Let $T(y)$ denote the year of the first positive observation in history $y$. If all identified whales remain recognisable, the expected number of whales with a sighting history $y$ can be expresses as:

$$e(y) \; = N_0\lambda_0\left(\prod_{t=1}^{T(y)}\left((Q_t+R)\left\langle y_{j,t}P_t\right\rangle\right)\right)\left(\prod_{t=T(y)+1}^{T_{\max}}\left(Q_t\left\langle y_{j,t}P_t\right\rangle\right)\right)1'$$

where 1´ is a column vector of 1s. The angle brackets $\langle\ \rangle$ denote the diagonalization operator: $\langle x\rangle$ is the diagonal matrix whose diagonal elements are the elements of the vector $x$.

For the reasons discussed by Payne *et al* (1990), it is assumed that all identified adults remain recognisable, but that not all identified calves remain recognisable. Let $r$ denote the vector of stage-specific probabilities that identifying marks remain recognisable after one year. In this case, $r = (\rho \;\; 1 \;\; 1 \;\; 1 \;\; ...)$ where $\rho$ is the probability that an identified calf remains recognisable. $\rho$ is a nuisance parameter to be estimated in the model fitting process.

In general, the possibility of mark loss can be handled by subdividing the population vector into identified and unidentified components. Let $x_t$ and $z_t$ represent the vectors of unidentified and identified individuals in the population by stage. These vectors are concatenated into a row vector of twice their length. The transition matrix for the concatenated vector is given by:

$$\left(x_{t+1} \quad z_{t+1}\right) \; = \; \left(x_t \quad z_t\right)\left(\begin{array}{c|c}\langle 1-p_t\rangle & \langle p_t\rangle \\ \hline 0 & \mathrm{I}\end{array}\right)\left(\begin{array}{c|c}\mathrm{I} & 0 \\ \hline \langle 1\text{-}r\rangle & \langle r\rangle\end{array}\right)\left(\begin{array}{c|c}Q_t+R & 0 \\ \hline R & Q_t\end{array}\right)$$

where $p_t$ is the vector of sighting probabilities by stage in year $t$. The three matrices on the right represent, respectively, the observation process, the mark loss process, and the transition/reproduction process. Observations cause unidentified whales to become identified, but not *vice versa*. Mark loss and reproduction each generate additional unidentified whales but no new identified whales.

The expected number of unidentified whales, $u_t$, by stage in year $t$ is then given by:

$$u_t \; = \; N_0\left(\lambda_0 \quad 0\right)\prod_{i=1}^{t}\left[\left(\begin{array}{c|c}\langle 1-p_i\rangle & \langle p_i\rangle \\ \hline 0 & \mathrm{I}\end{array}\right)\left(\begin{array}{c|c}\mathrm{I} & 0 \\ \hline \langle 1-r\rangle & \langle r\rangle\end{array}\right)\left(\begin{array}{c|c}Q_i+R & 0 \\ \hline R & Q_i\end{array}\right)\right]\begin{pmatrix}\mathrm{I} \\ 0\end{pmatrix}$$

The expected number of whales with a sighting history $y$ is given by:

$$e(y) \; = u_{T(y)}\left\langle y_{T(y)}P\right\rangle_t\left(\prod_{t=T(y)+1}^{T_{\max}}\left(Q_t\left\langle y_tP_t\right\rangle\right)\right)1' \qquad (2)$$

Following Cormack (1981), the likelihood of the data set is obtained by treating the observed frequencies of each sighting history as Poisson distributed random variables with expectation given by (2), even though this assumption is not strictly consistent with the inclusion of reproduction in the model. The model is fitted by maximum likelihood.

**Modelling temporal variation in transition probabilities**

Because the data have little power to detect temporal variability in transition probabilities that refer to rare events, such as 2-year calving intervals, attention is focussed on the parameters representing potentially more common events. These are $\beta$, the probability that a resting whale waits another year, and $\gamma$, the probability that a receptive whale returns to the resting state after a failed pregnancy.

The model is first fit without any temporal variability in parameters, and then re-fit allowing temporal variability in each of these parameters. One cannot expect that each annual parameter $\beta_t$ and $\gamma_t$ will be individually well estimated, since there are 30 parameters of each. Therefore, they are treated as random effects, with one variance parameter associated with each parameter time-vector. The log-odds ratios of the respective probabilities are treated as normally distributed random effects with standard deviations $\sigma_\beta$ and $\sigma_\gamma$ respectively.

The information criterion used to judge the best fitting model, the Mixed Model Information Criterion (MMIC), is analogous to Akaike's Information Criterion for free parameters. It is given by:

$$-2L + 2\sum d_i$$

where $d_i$ is the effective degrees of freedom associated with the fitted effect $i$. By analogy with linear models, $d_i$ for a random effect is estimated by:

$$d_i = 1 - \text{var}(\hat{x}_i)/\sigma^2(x)$$

where $\sigma^2$ is the collective prior variance for the effects and $\text{var}(\hat{x}_i) \le \sigma^2$ is the posterior variance of the individual effect. In the limit where there is effectively no information in the data set about a given effect, $\text{var}(\hat{x}_i) = \sigma^2$ and $d_i = 0$. In the limit as $\sigma^2 \to \infty$, $d_i \to 1$, corresponding to a free parameter. In the limit as $\sigma^2 \to 0$, which corresponds to no effective parameter being fitted, $d_i \to 0$.

**Diagnostics**

The acceptability of the model fit can be assessed by comparing the observed and expected distributions of calving intervals. This is actually more a test of whether the model was correctly fitted rather than a test of the assumptions. A test for excess heterogeneity is given by comparing the observed and expected distributions of numbers of times seen. If sighting probabilities are heterogeneous in the population, more whales than expected would be seen once or many times, to the detriment of numbers seen an intermediate numbers of times. The presence of unmodelled heterogeneity tends to lead to underestimation of population size.

## RESULTS

*Summary of observations*

A total of 1,828 distinct individuals were catalogued up to and including 2000, of which 564 whales have been seen to calve at least once with a total of 1,298 calving events. 319 whales have been observed to calve at least twice, providing 734 apparent calving intervals. 405 whales have been identified as calves, of which 53 have themselves been observed to calve.

Fig. 2. shows the number of whales with calves identified each year, divided into those recorded with a calf for the first time, and those observed to calve for the second or subsequent time, plus the estimated number of additional, unrecorded calvings (see analysis below).

*Check on reliability of observations*

The observed distribution of calving and non-calving sighting intervals from 1-5 years for known mature females (those which have been seen to calve at least once) is shown in Table 1. A calving interval is

from one known calving to the next known calving. Other intervals are from one observation to the next observation in a subsequent year, where on one or both occasions no calf was recorded
.

Table 1. Comparison of calving and other sighting intervals

| Interval length (years) | Calving intervals | Other intervals |
|---|---|---|
| 1 | 1 | 119 |
| 2 | 8 | 145 |
| 3 | 222 | 76 |
| 4 | 17 | 50 |
| 5 | 31 | 17 |

The fact that only a single 1-year calving interval was observed , out of 120 1-year intervals, indicates that: (i) 1-year calving intervals are very rare if they occur at all; and (ii) spurious calving records are also rare, because otherwise the substantial number of 1-year non-calving intervals would generate more erroneous 1-year calving intervals. The single 1-year calving interval is thus either a rare event or a rare error. The 8 two-year intervals are probably mainly real: if they were errors, we would expect to see similar numbers of 1- and 2-year intervals. An erroneous calving record can occur in one of two ways: (i) a calf is observed in association with a whale that is not its mother; or (ii) a non-calf, such as a yearling, is still in association with its mother and is falsely recorded as a calf. These results indicate that such errors are rare, if they occur at all. The assumption of the analysis, that calving events may be missed, but that no appreciable numbers of false calving events are recorded, thus appears to be satisfied.

*Model fitting*

The results of model fits involving (a) no variability; (b) variability in $\beta$; and (c) variability in $\gamma$ are shown in Table 2. For model (b), the estimated of $\sigma_\beta$ is very close to zero, so that this fit is virtually identical in all respects to the fit of model (a). The fit of model (c) is substantially better in terms of MMIC. It is also significantly better on an hypothesis test ( $p = 0.003$). Model (c) is therefore used for the results that follow.

Table 2. Comparison of model fits

| Time-varying parameter | AIC | MMIC | $p$ | $\sigma$ |
|---|---|---|---|---|
| None | 1899.89 | 1851.57 | - | 0.0 |
| $\beta$ | 1901.84 | 1851.57 | 0.492 | 0.01 (0.35) |
| $\gamma$ | 1891.46 | 1835.05 | 0.003 | 0.90 (0.31) |

Fig 3. shows the predicted distribution of observed calving intervals as compared with the observed distribution. The fit is acceptable ($\chi^2 = 5.1$, d.f. = 12, $p > 0.5$). The estimated distribution of true calving intervals is also shown. 94% of true intervals are estimated to be 3, 4 or 5 years.

There is a significant discrepancy between the observed an expected distributions of the numbers of times each whale is seen ($\chi^2 = 71.7$, d.f. = 5, $p = 0.000$). The observed distribution has a long tail, with some individuals being seen much more often than expected (Fig. 4.). However, the number of animals seen once only is not more than expected, hence substantial underestimation of the population is unlikely.

The observed an expected distributions of the age of known-age animals at their first observed calving is shown in Fig. 5. The fit is acceptable ($\chi^2 = 3.2$, d.f. = 6, $p > 0.5$). Also shown is the estimated true distribution of ages at first calving. The estimated median age at potential first calving is 9.1 years (S.E.

0.4 yr). The year of potential first calving is defined as the age on entry into the Receptive stage plus one year.

The estimated adult annual mortality rate is low at 0.020 but is well estimated (S.E. 0.004). The annual rate of increase is also well determined (0.068, S.E. 0.005). The adult female population in 2000 is estimated at 697 animals (C.V. 0.068). The point estimate of the survival rate from birth to maturation is implausibly high at 0.985, but in view of the relatively high standard error (0.091) this does not necessarily imply a failure of assumptions.

The estimated population trajectory by stage is shown in Fig. 6. The estimated number of whales calving in each year is compared in Fig. 2. with the observed numbers. Since 1990, survey effort has not kept pace with the expanding population, so that an increasing proportion of calvings are missed.

The estimated values of the mean transition probabilities are shown in Table 4.

Table. 4. Estimated transition probabilities in the adult female population (excluding mortality) (with S.E.s)

| | Calving | Resting | Receptive | Dead |
|---|---|---|---|---|
| Calving | 0 | 0.957<br>(0.008) | 0.023<br>(0.007) | 0.020<br>(0.004) |
| Resting | 0 | 0.095<br>(0.015) | 0.884<br>(0.016) | 0.020<br>(0.004) |
| Receptive | 0.838<br>(0.040) | 0.142<br>(0.041) | 0 | 0.020<br>(0.004) |

The annual deviations in the log-odds ratio for the Receptive→Resting transition are shown in Figure 7. The plotted deviations are scaled by –1, so that years of poor reproductive success appear as negative deviations. The individual year effects are not especially well estimated, but years with notably negative values were 1981 and 1982.

## DISCUSSION

The results show that such a long time series of data collected using benign methods is valuable not only for obtaining precise estimates of demographic parameters, but also for assessing their temporal variability, which is of especial interest given the recent growing attention to the effects of environmental factors on the viability of whale populations.

The model of this paper provides in principle a better measure of reproductive success than simple estimates of annual calf production would provide, because the model takes into account the variable number of females that are ‘scheduled’ to calve in each year.

The results indicate that the greatest variability is in the parameter that corresponds to late exit from the reproductive cycle (such as failed pregnancies), which lengthen the calving interval from the usual 3 years to 5 years. This result also suggests that it is feeding conditions in the summer of pregnancy which determine the response, rather than the conditions during the resting year. Since the energy cost of late pregnancy and lactation in baleen whales is estimated to be substantially higher than that of early and middle pregnancy (Lockyer, 1987), the best strategy for right whales may be to conceive under almost or all conditions two years after the previous calf, but to “decide” later, on the basis of feeding results in the summer of the pregnancy, whether to continue to full term.

Information on the location of summer feeding grounds of the Península Valdés population can be obtained from photo-identification matches. For example, Rowntree *et al.* (2001) list matches with whales sighted off South Georgia and Shag rocks (4 in summer, 1 in winter). Correlations between the variability in reproductive success and relevant ecological indices on the feeding grounds might throw light on the causes of the variation.

The results presented here cast doubt on the utility of some of the traditional, non-benign methods for estimating reproductive rates from killed whales. For example, they suggest that observed pregnancy rates from carcasses might not be well correlated with the production of live calves, if the females are already pregnant when they exit the current reproductive cycle and return to the resting state.

Although expanding rapidly, South Atlantic right whales appear still to be at a low fraction of pre-whaling abundance (IWC, 2001), and were much lower still in the early 1980’s when the data first indicate that variability in reproductive success was occurring. An implication is that variability in reproductive success can occur in whale populations that are at a low fraction of their carrying capacity. This implies that models which assume that environmental influences on whale reproductive success are mediated only through changes in carrying capacity, may not provide a sufficient representation of whale population dynamics.

## ACKNOWLEDGEMENTS

to be supplied

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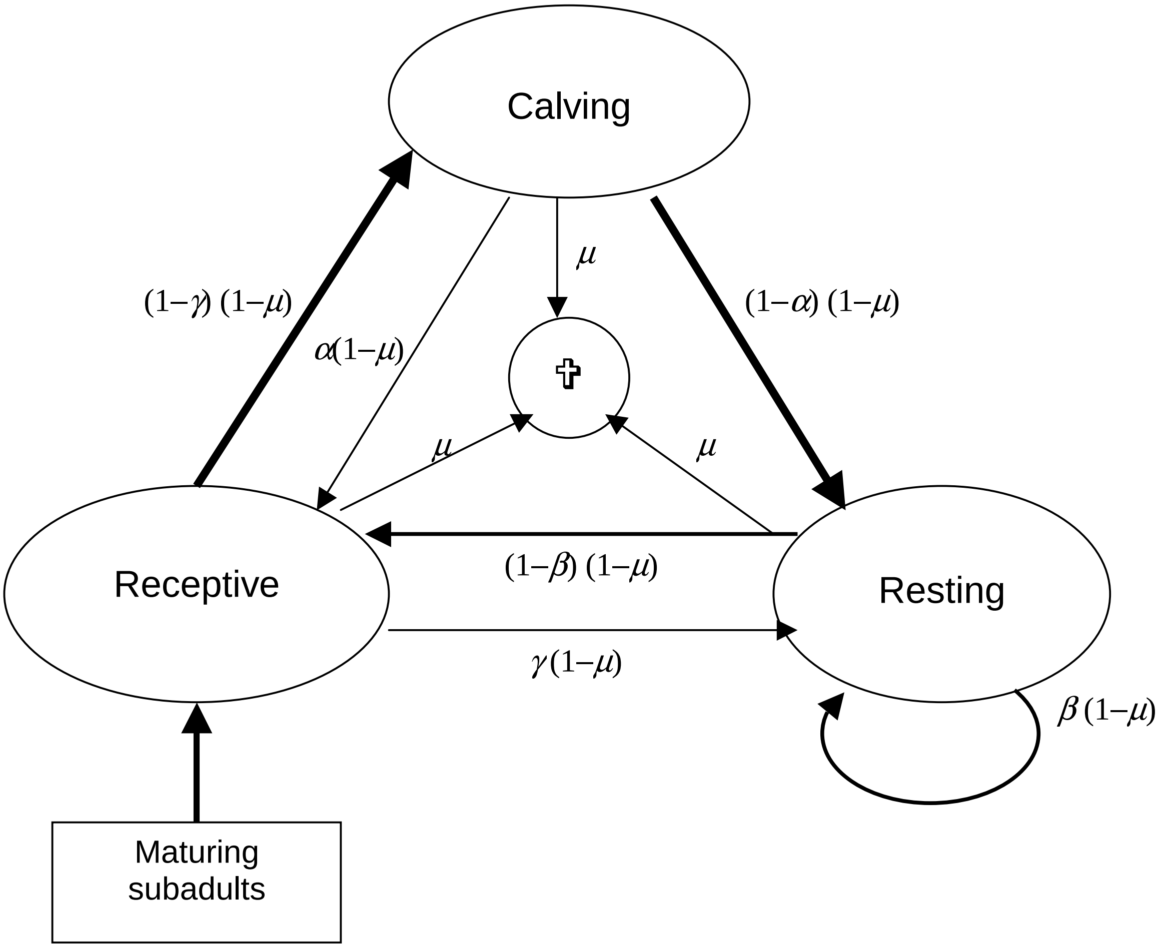

Fig. 1. Model of the female reproductive cycle, with transition probabilities as functions of the parameters.

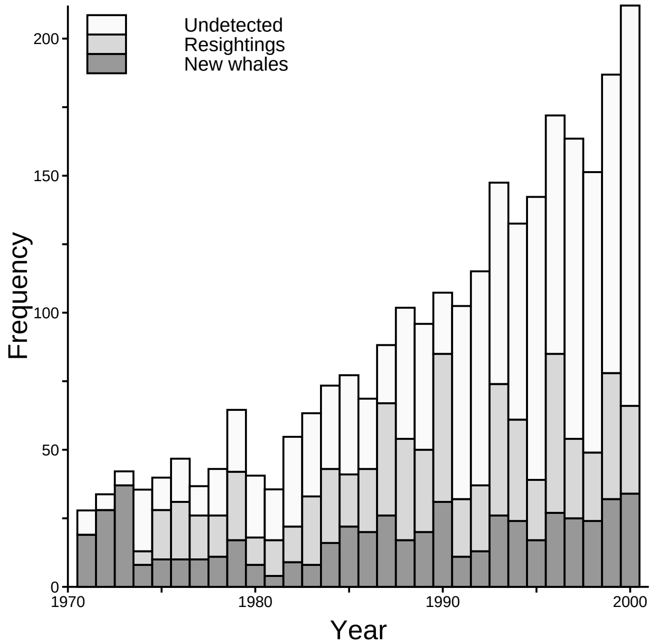

Fig. 2. Number of calvings by year: (i) first observed calvings; (ii) observed repeat calvings; (iii) estimated number of unobserved calvings

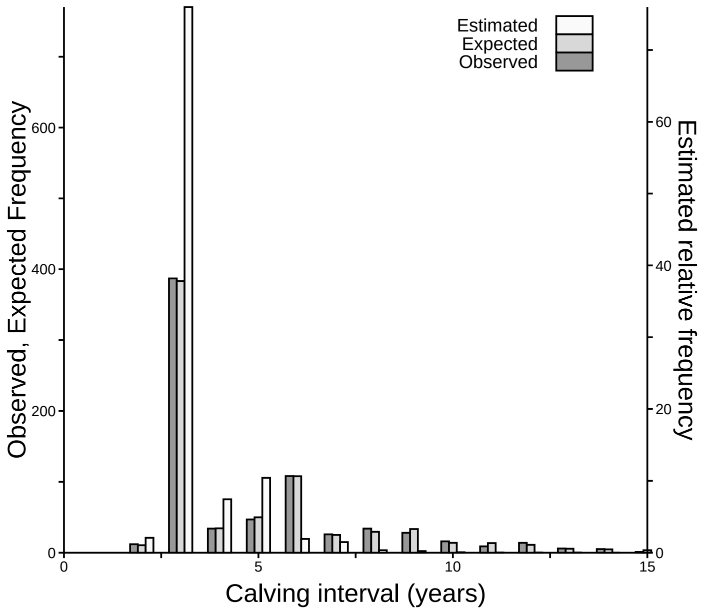

Fig. 3. Distributions of calving intervals: (i) observed distribution of apparent intervals; (ii) expected distribution of apparent intervals. (iii) estimated distribution of true intervals.

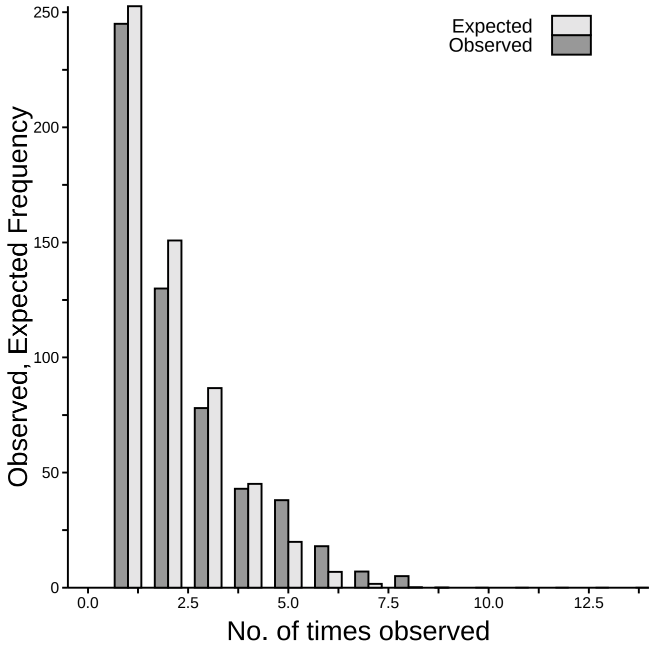

Fig. 4. Observed and expected distribution of the number of times seen.

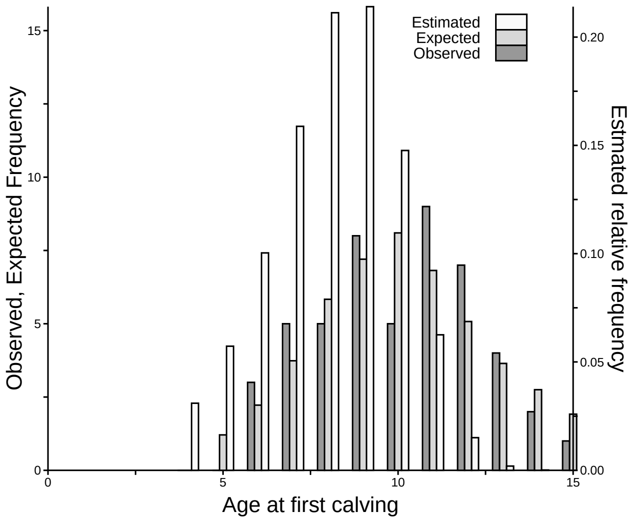

Fig. 5. Age at first calving: (i) ages at first observed calving; (ii) expected distribution of age at first observed calving; (iii) estimated distribution of true age at sexual maturity

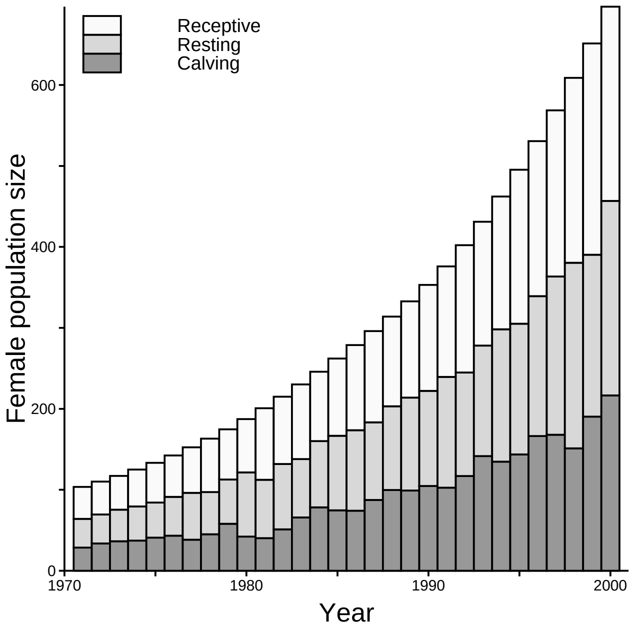

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Fig. 6. Estimated time trajectories of adult female population components.

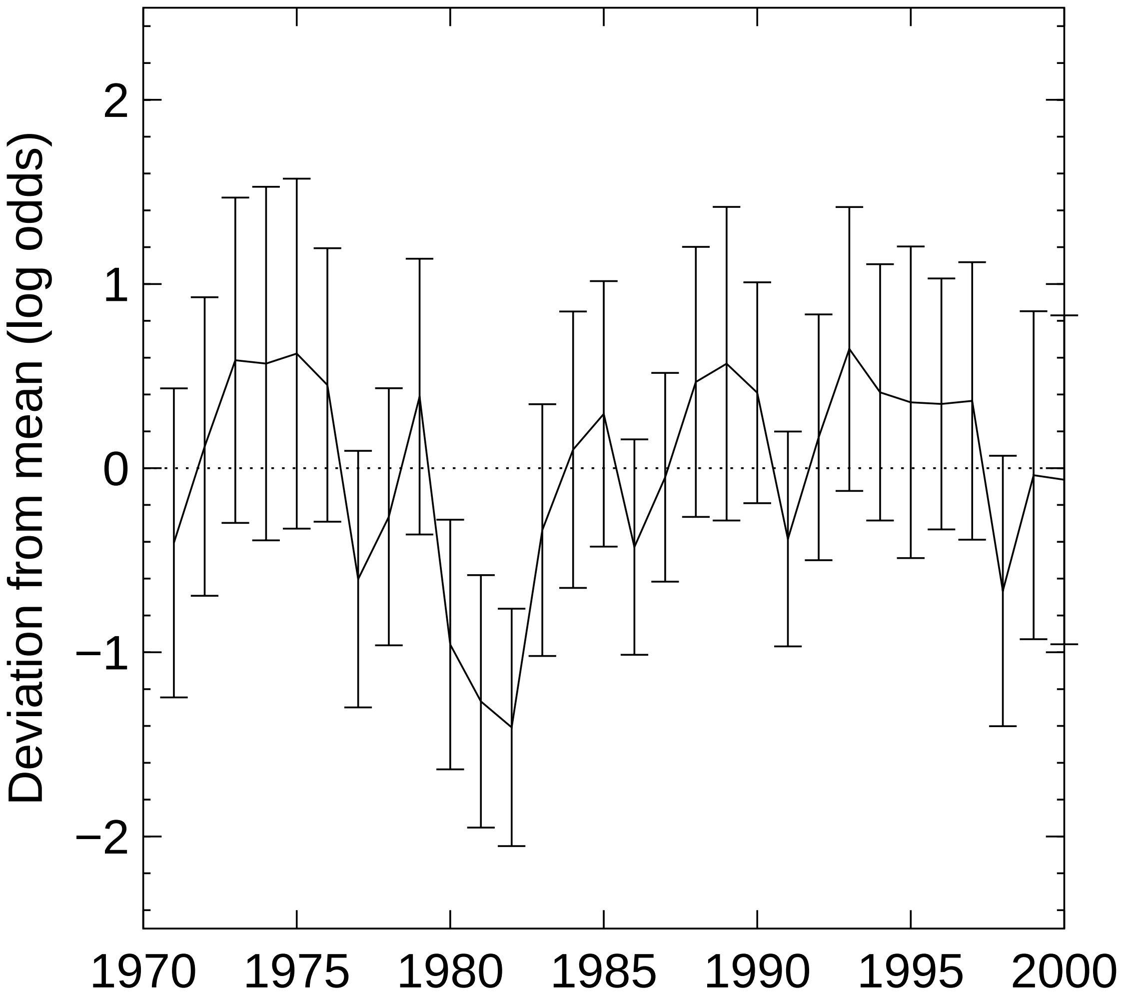

Fig. 7. Annual deviations from mean of minus log-odds ratio for Receptive to Resting transitions. Negative deviations indicate poor calving years and vice versa.