

# **A review of some implications of environmental variability for the management of baleen whale populations**

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## **ABSTRACT**

The effects of environmental variability on whale population dynamics can be substantial, and simulation studies have shown that the fitting of deterministic population models to data from whale populations in the presence of such variability can yield misleading inferences with the potential for significant management consequences, including overestimation of sustainable offtakes. A theoretical framework that extends the standard Pella-Tomlinson for baleen whale population dynamics model to include environmental variability, predicts that population growth rates will become more variable as populations increase towards their carrying capacity, and that even when the relationship between mean growth rates and population size is nearly linear or only gently curved, individual population trajectories are likely to exhibit abrupt changes and reversals in trends after periods of apparently steady growth. A simple and widely applicable means to incorporating environmental variability into the individual parameters of life-history-based population models is illustrated. Life history models fitted to longitudinal data on individuals tracked over time, such as from photo-id studies, offer the best prospect of detecting and estimating variability in parameters, but variations in some parameters, such as calving intervals, are easier to detect than variations in others, such as survival rates.

## **1. Introduction**

Variability is the norm rather than the exception in marine ecosystems, and whales are not immune from the effects of environmental variability, including but not limited to variability in food availability. However, as slow-breeding long-lived mammals, the demographic effects of environmental variability may manifest themselves in whale populations in a somewhat different manner compared to some other organisms. This purpose of this paper is to summarise in an accessible form recent theoretical work some implications of environmental variability for the modelling and management of baleen whale populations.

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## 1. Theoretical background and aggregated population models

### 1.1. Theory

Whale demographics can be examined at a variety of levels of detail. At the coarsest level, the population is modeled in bulk using a density-dependent production model. All individuals are lumped together and the combined effects of demographic parameters (reproduction, survival, age at maturation) are subsumed into a *per capita* population growth rate or net recruitment rate,  $r$ , which is positive in a growing population and negative in a declining population.

The classical model of whale population dynamics is based on the deterministic density-dependent growth curve. The population growth rate  $r$  is assumed to have a maximum at low population sizes, where the maximum value is variously referred to as  $r_0$  or  $r_{\max}$ . The population has a fixed maximum level, the carrying capacity  $K$ , such that the growth rate  $r$  tends to zero as the population level approaches  $K$ . The net recruitment rate as a function of population size decreases from  $r_0$  to 0 as the population increases from low levels to  $K$  using a formula such as the Pella-Tomlinson model:

$$r_t = r_0 \left(1 - (N_t/K)^z\right) \quad (1)$$

where  $N_t$  is the population size in year  $t$  and  $z$  is an exponent that reflects the curvature of the relationship between  $r$  and  $N$ , with  $z = 1$  corresponding to a linear relationship, and higher values of  $z$  corresponding to a more curved relationship. Conventionally for baleen whales it has been assumed that  $z = 2.39$  to give a maximum net annual increment (MSY level) at  $N = 0.6K$ . The predicted trajectory of a population increasing from low levels is shown in Fig.1. A quantity of central management importance is  $r_{\text{MSY}}$ , the net recruitment rate when the population is at its MSY level. The Revised Management Procedure (RMP) has been tuned to ensure that catches remain sustainable even when  $r_{\text{MSY}}$  is as low as 0.01 (1%) (Kirkwood 1992), but subsequently there have been initiatives to increase the assumed minimum plausible level of  $r_{\text{MSY}}$  towards 4% in order to retune the RMP to allow higher catches (IWC 2007).

The growth rate of a population depends not only on density-dependent effects but also on external influences, including fluctuations in food availability, such that the increase in a population towards its carrying capacity is not necessarily smooth. If  $K$  itself is variable, then a population may appear to increase smoothly until it suddenly finds itself well above the current carrying capacity, and can then plunge dramatically (examples are superimposed on Fig. 1), as appears to have happened with eastern North Pacific gray whales during 1999-2002 (Rugh *et al.* 2005).

A theoretical framework for modeling this behavior is described by Cooke (2007). It is useful to distinguish between  $r_{\max}$ , the biological maximum population growth rate achievable at low (or medium) populations sizes in good environmental conditions, and  $r_0$ , the time-averaged net recruitment rate that would be realized if the population were held at low levels.  $r_{\max}$  is determined mainly by the life history parameters of the species, such as the minimum calving interval and the minimum age at first reproduction. The stochastic equivalent of the Pella-Tomlinson model is of the form:

$$r_t = r_{\max} \left[ 1 - \xi_t \left( 1 - \frac{r_0}{r_{\max}} \left( 1 - (N_t/\bar{K}) \right) \right)^z \right] \quad (2)$$

where  $r_t$  is the growth of the population in year  $t$  as a function of population level,  $N_t$  relative to the mean carrying capacity  $\bar{K}$ , and  $\{\xi_t\}$  are a series of positive-valued annual random variables with mean one. This reduces to the simple Pella-Tomlinson only when both  $r_0 = r_{\max}$  and the variance of  $\xi_t$  is zero. In good environmental conditions in favorable habitats, where  $r_0$  is close to  $r_{\max}$ , and at low to medium population levels, the growth rate is usually close to  $r_{\max}$  and shows little variability from year to year, despite the environmental variability. In poorer environments, or at population levels close to  $K$  in any environment, the population growth rate will be lower and more variable (Fig. 2.).

Demographic variability due to random processes at the individual level (individual births and deaths) becomes more marked in very small populations, because individual factors tend to average out in larger populations. By contrast, environmental variation is predicted to cause more variability in large populations. Fig. 1 shows the expected pattern of recovery from low levels of a population depleted by past exploitation. While the population is below the MSY level, the population usually exhibits fairly smooth exponential growth, which is barely distinguishable from the deterministic case. When the population reaches the MSY level, its subsequent trajectory becomes less predictable. After 50 years the population in the deterministic case would be predicted to be close to the mean  $K$ , but in the stochastic case it can lie anywhere in quite a wide range.

Because the growth rate is bounded above by  $r_{\max}$ , the distribution of growth rates tends to be left-skewed, with a long tail extending into negative values. In this regard whales differ from some other groups of marine organisms, such as teleost fish, where the distribution of recruitment rates is often right skewed (many years of low recruitment interrupted by the occasional very large year class).

In talking about  $K$ , one needs to distinguish between:

- (i) the current  $K_t$  at a given moment in time: the level at which the population would eventually stabilize, if the state of the environment could be frozen at the current state;
- (ii) the long-term average  $\bar{K}$ : the average level around which an unexploited population would eventually fluctuate, after an initial period of recovery from past exploitation has elapsed.

Observations of populations that have increased at a constant, relatively high annual rate over a considerable period, and then shown an abrupt cessation or reversal of population growth, have sometimes been interpreted as the population “hitting  $K$  hard” (Moore *et al.* 2006). The appropriateness of this metaphor depends on how one thinks of  $K$ . The classical model of a fixed glass ceiling above which the population cannot grow can be misleading. Rather than the population hitting a fixed ceiling, it is the ceiling itself which from time to time comes crashing down onto the population.

The relationship between *mean* net recruitment rate and population levels is predicted to be smooth and not sharply curved, while individual population trajectories are liable to show abrupt changes and reversals (Fig. 3). Individual realizations often give the impression of strong density-dependence just below  $K$ , even when this is not true for the average curve.

## 1.2. Fitting deterministic population models in the face of environmental variability: conclusions from simulation studies

An important question is whether the conventional practice of fitting deterministic population models to whale data can be expected to lead to robust inferences about the dynamics and productivity even in the presence of environmental variability. This question can be addressed by simulation studies, where hypothetical data are generated from simulated scenarios involving environmental variability; these generated data are then fitted using a deterministic model, and key parameters such as  $r_0$  and  $r_{MSY}$  are estimated. The resulting estimates can be compared with the true mean values of these parameters used to generate the data. An extensive series of simulation trials were conducted by Cooke (2007) and reviewed at a Scientific Committee workshop (IWC, 2010). The results of these trials indicate that:

- in the presence of high environmental variability, fitting a deterministic density dependent model to data from a population is liable to seriously overestimate mean growth rates  $r_0$  and  $r_{MSY}$  such that even when the true  $r_{MSY}$  is close to 1%, the median estimate of  $r_{MSY}$  can be close to 4%;
- in the presence of environmental variability, fitting deterministic models to time series of abundance data is liable, with high probability, to substantially overestimate the curvature of the density-dependent relationship, and lead to an erroneous conclusion that the MSY level is close to  $K$ .

When fitting deterministic models using historical catch data, modelers have tended to have difficulty reconciling the past pattern of catches with the recent population sizes and rates of increase (e.g. Butterworth *et al* 2002; Punt *et al* 2006). Recent trends cannot usually be explained as deterministic recoveries from past exploitation, without making additional *ad hoc* assumptions such as increases in  $K$ .

Further simulation studies (Cooke, 2009) have addressed this issue. The conclusions are:

- in the presence of environmental variability, there is a high probability that a deterministic population model that incorporates past catches will exhibit lack of fit (that is: the current rate of increase cannot be explained in terms of a deterministic recovery from past exploitation, given the recorded historical catches);
- attempts to correct the lack of fit by fitting a trend in  $K$  is liable, with high probability, to exacerbate the positive bias already present in estimates of  $r_0$  and  $r_{MSY}$ .

The lessons are that fitting deterministic population models to data from populations subject to moderate or high levels of environmental variability can run a high risk of yielding erroneous conclusions with serious management consequences including the overestimation of sustainable yield rates. Indeed it could be argued that environmental variability should be included as a matter of course in essentially all population models for whales.

Following these findings, the IWC Scientific Committee has embarked on an exercise to estimate typical levels of variability in time series of reproductive and survival rates for baleen whale populations (IWC, 2011).

## **2. Life-history and individually-based models: examples from southern right and Pacific gray whales**

### *2.1. General*

This section addresses how to incorporate environmental variability into more detailed population models. The choice of population model is driven to a large extent by the nature of the data one has collected. In order to fit the data to draw inferences about the population and its dynamics, it is necessary for the population model to incorporate the processes that can explain the data. A further consideration is whether one seeks to use the model to understand some of the processes associated with variability in population growth rates.

The power to detect an environmental variability signal in a crude time series of population abundance tends to be quite low, especially when estimates of abundance are not very precise, as tends to be the case for broad-scale surveys of cetaceans across large ocean areas. Data obtained by tracking the lives of individual whales over time, such as from photo-identification studies, enable detailed demographic processes to be studied and can have considerable power to detect changes in demographic parameters, provided that the time series is long enough (preferably > 10 years).

When individual longitudinal data are available, a number of life history parameters can be estimated, often with remarkably high precision, including:

- adult survival rate
- calf survival rate
- calving intervals
- age at first reproduction (from tracking known-age individuals)

### *2.2. Example: southern right whales*

The incorporation of environmental variability into a life history-based individually-based population model is best illustrated using an example. A good example from the southern hemisphere is the long time series (1971-2010) of photo-id data from the southwest Atlantic right whale population that winters off Península Valdés, Argentina.

The data have been analysed by fitting an individually-based model (Payne *et al.* 1990; Cooke *et al.* 2001, 2003; Leaper *et al.* 2006) that focuses on breeding females. These are both the most important component of the population, and also the most revealing component, because the intervals between successive reproductive events (calvings) provide information on the state of individuals and of the population. The core of the model is shown in Fig. 4. The model of the breeding female population is a state-space model with annual time steps, and with annual partial censusing in winter in the waters of Península Valdés. The three reproductive states are: calving (calf born in current winter); receptive

(ready to become pregnant, to give birth the following year ); and resting (neither). In the data from 1971-2000 there were very few 1- and 2-year calving intervals. The primary calving interval was three years with an admixture of 4-year intervals but in some years, 5-year intervals were more frequent. The 5-year intervals may result from the (cryptic) loss of a calf during pregnancy or shortly after birth, with the next calf being born after only 2 years, because of the skipped lactation.

Because the model is probabilistic, individually-based, the demographic variability arising from individual-level processes is automatically included. While the model itself is simple enough, the fitting of the model to photo-id data is relatively complex, because an animal, once identified, is typically not seen every year subsequently. Mothers are most likely to be seen at the Peninsula when they have a calf, but even then not always, or the mother may be seen but the calf is missed. Thus, apparent calving intervals cannot be taken at face value, because individual calvings may be missed. All these issues are reflected in the likelihood function used to fit the data, contributing to its complexity. The model is fitted by either maximum likelihood or Bayesian methods.

### 3.3 Incorporation of environmental variability

The main parameters to be estimated are the annual transition probabilities between the three reproductive states and the mortality rate (transition to the dead state). Each of these parameters represents a probability. The most convenient way to introduce variation into probabilities is to apply a logit transformation to the transition probabilities:

$$p = e^z / (1 + e^z)$$

where the log-odds ratio  $z$  can take any value from minus infinity to plus infinity. Environmental variation is added by applying an annual random deviate to each  $z$  value:

$$z_t = \bar{z} + \sigma v_t$$

where  $\bar{z}$  is the median value, the  $\{ v_t \}$  are a set of standard random normal deviates, one for each year, and  $\sigma$  is a variance parameter to be estimated.

An advantage of this approach is that all probabilities remain in the range (0,1) regardless of the size of any random deviation. In addition to the mathematical convenience, there are also theoretical grounds for favoring this approach.

The transition probability  $\gamma$  in Fig. 4 (probability of transition from receptive stage back to resting, given survival) showed the greatest variability, being low in environmentally favourable years and high in environmentally poor years. In the first instance, this parameter alone was assumed to vary between years. This model as fitted by Leaper *et al.* (2006) showed that the deviations  $\{ v_t \}$  were significantly correlated with water temperatures around South Georgia, and also with the reproductive success of other krill-feeding predators in the area (seals and penguins). It appears that low krill years around South Georgia, where at least some of the right whales from Peninsula Valdés feed, are associated with warm water influxes, and that other krill predators are similarly affected.

Analysis of recent years of data from the Península Valdés series is underway, but the pattern of calving intervals appears to have changed relative to previous years. Recently, two-year calving intervals have become more common, and this has been associated with a rise in recorded calf mortality in the Pensinsula Valdés area (strandings). Further analysis is required to discern whether calf mortality has increased overall, or whether the shift from a predominantly 3/5-yearly pattern of calving intervals towards a 3/2-yearly pattern is due to more cases of calf loss occurring in the Península Valdés area instead of in unmonitored regions, resulting in a shift from cryptic to visible calf mortality. The outcome of this analysis may have important implications for the issue of whether observed mortality (which typically only represents a small fraction of total mortality) can provide a reliable index of the total mortality rate.

The above approach can be applied to the modeling of random variability in any of the demographically relevant life-history parameters, including survival rates of adults and calves, and the age at first reproduction. This has been implemented, for example, in a model of the gray whale sub-population summering off Sakhalin (Cooke *et al.* 2008). When multiple life-history parameters are allowed to vary, a separate series of annual deviations can be estimated for each life history parameter of interest; alternatively, the parameters can be assumed to vary in unison, sharing a common set of  $\{ \nu_t \}$ .

The power to detect variations in life history parameters depends on the nature of the parameter. Longitudinal individual data yield high power to detect changes in parameters affecting calving intervals, especially when the main calving intervals are co-prime (e.g. 3, 4 and 5 years in the case of right whales; 2 and 3 years in the case of gray whales). The power of these data to detect changes in survival rate is lower, even when the mean survival rate can be estimated fairly precisely. However, variation in survival can be demographically more important than variation in calving intervals, even if it is as near or below the threshold of detectability. Typically, only large fluctuations in survival rate can be readily detected, such as mass die-offs.

Cooke (2011) showed on theoretical grounds that variations in survival and reproductive rates are expected to be positively correlated in whales in the face of environmental variability, as has been observed empirically for many terrestrial mammals. This is in contrast to the negative correlation between reproduction and survival that is observed when reproduction is experimentally suppressed (such as through removal of eggs from birds' nests). This finding has implications for cases where it is possible to observe variability in reproductive rates directly, but where the available data have insufficient power to measure the variability in survival rates. Estimation of variability in net recruitment rates based on observed variability in reproductive rates, with the assumption that survival rates remain constant, will tend to underestimate the true level of variability. Thus, allowing the different life history parameters to vary in unison may represent a better assumption than holding some of them constant.

### **3. Summary of main points**

Both theoretical considerations and evidence from populations studied to date indicate that environmental variability can play a major role in the demography of whale populations. The variability can be linked to oceanographic changes and variability in parameters of species dependent in part on the same resources. The fitting of deterministic population models to whale data can yield substantively misleading conclusions with serious management implications, and should be done only with caution or

not at all. Longitudinal studies in which known individuals are followed for substantial periods of years can provide an invaluable window into the processes underlying the demography of the population, and enable detection and measurement of the effects of environmental variation on at least some of the life history parameters. It is reasonable to assume that all life history parameters are affected by environmental variability, even when the power to detect changes in some of them is low.

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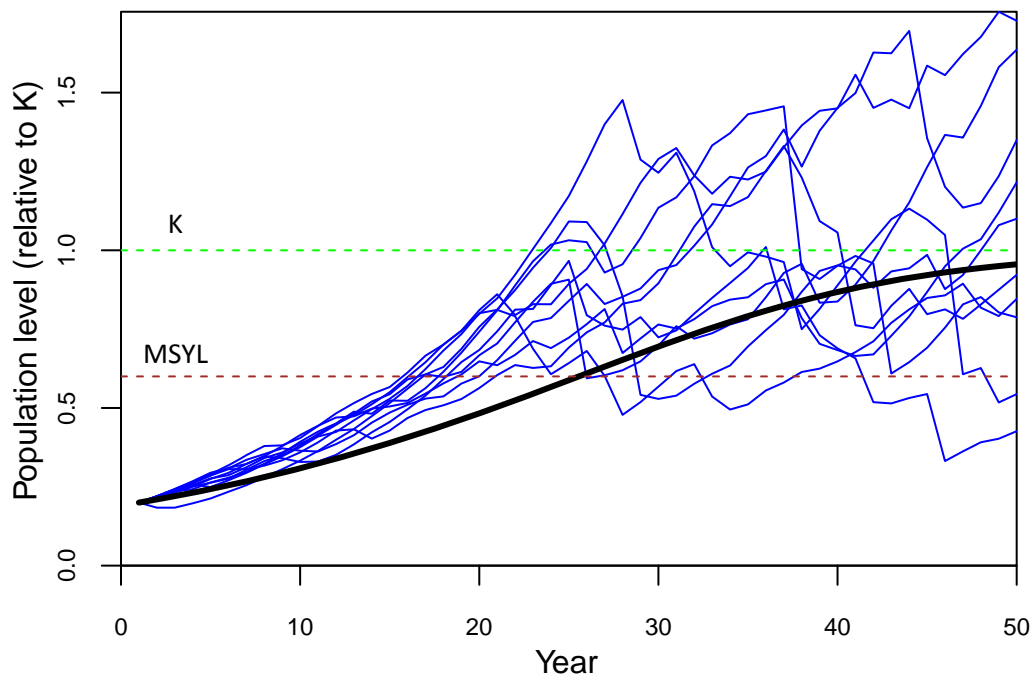


Fig. 1. Trajectory of population recovering to carrying capacity. Solid curve: deterministic trajectory based on equation (1). Thin curves: random examples of stochastic trajectories based on equation (2). Horizontal dotted lines show the levels corresponding to  $K$  and  $MSYL$  respectively.

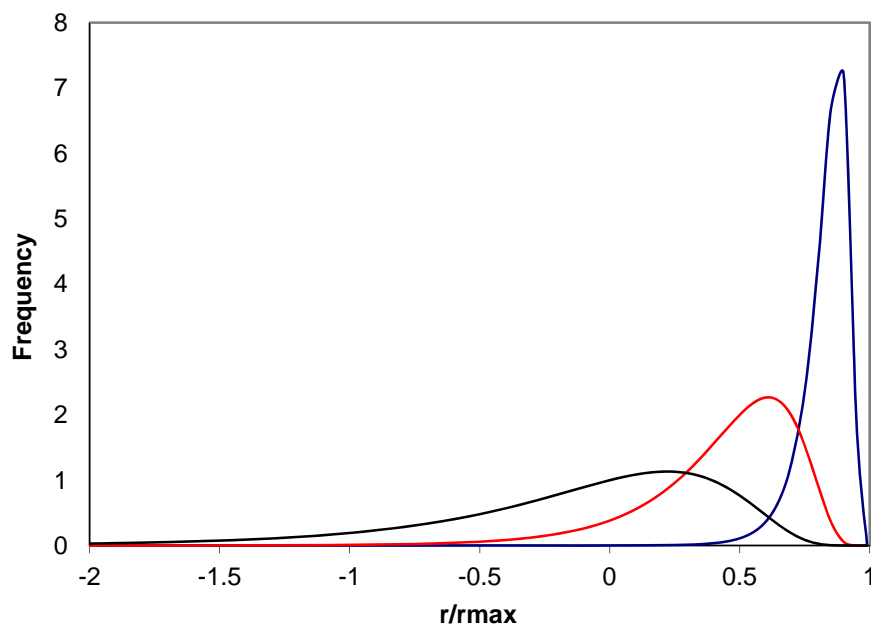


Fig. 2. Distribution of  $r$  (scaled to  $r_{max}$ ) for three values of  $r_0/r_{max}$ .

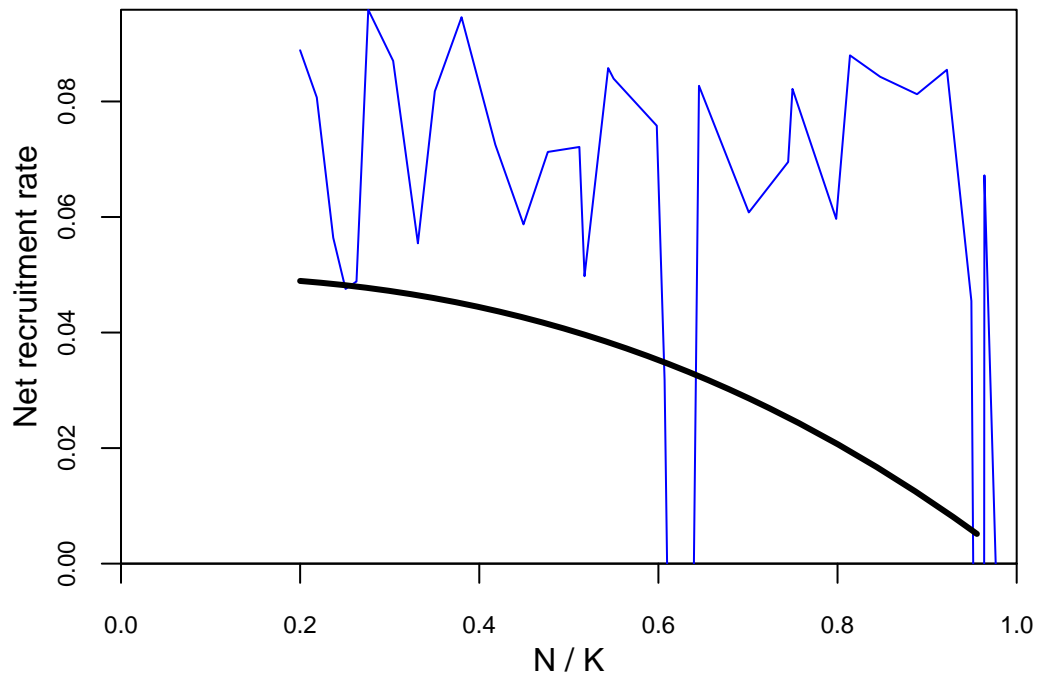


Fig. 3. Net recruitment rate vs. population level. Solid curve: mean net recruitment rate as a function of population size. Thin curve: example of a stochastic realization of the relationship between net recruitment rate and population level.

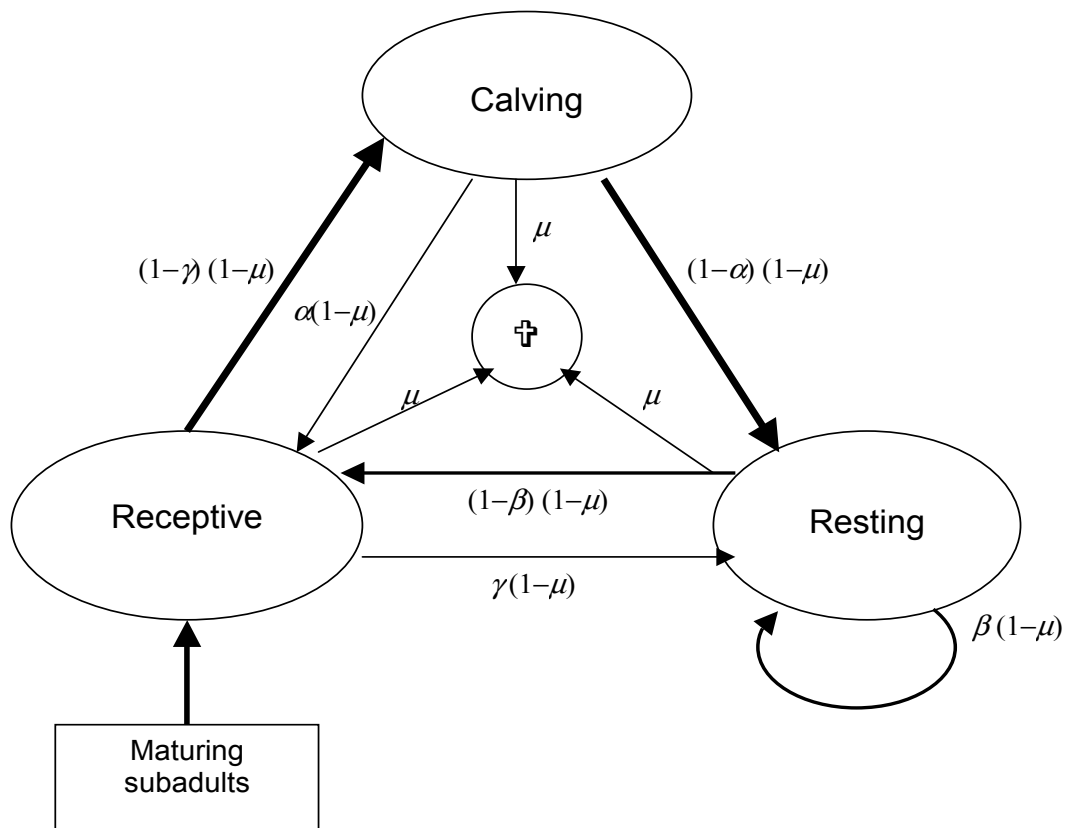


Fig. 4. Structure of southern right whale population model for breeding females. The parameters  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\mu$  determine annual transition probabilities for an individual female, where  $\mu$  is the probability of death. (Source: Cooke *et al.* 2003).