

# BAYESIAN ASSESSMENTS USING MODELS WHICH ALLOW FOR INTERCHANGE ON THE BREEDING GROUNDS OF SOUTHERN HEMISPHERE HUMPBACK WHALE BREEDING SUB STOCKS C1 AND C3.

SUSAN J. JOHNSTON AND DOUG S. BUTTERWORTH<sup>1</sup>

Contact e-mail: *Susan.Holloway@uct.ac.za*

## ABSTRACT

Bayesian stock assessment results for breeding sub-stocks C1 and C3 using models which allow for interchange on the breeding grounds as well as mixing on the feeding grounds are illustrated for four models – the sabbatical, tourist and migrant models and the resident model (for which interchange is set to zero.) Results are also presented for a range of sensitivity tests. The availability of photo-id data allows the estimation of interchange rates. The estimates of these interchange rates are generally low with posterior median estimates all below 6% p.a., and estimated trajectories are fairly similar for all models considered. With single exceptions, current (2006) posterior median population sizes relative to pre-exploitation levels are all estimated to exceed 80% for C1 and 90% for C3.

KEYWORDS: HUMPBACK WHALES, BAYESIAN ASSESSMENT, INTERCHANGTE

## INTRODUCTION

This document reports Bayesian stock assessment results for breeding stock C, which is considered to consist of two sub-stocks:

- C1: east coast of South Africa and Mozambique
- C3: where C3 refers to C2+3 (strictly C2 refers to whales wintering around the Comoros Islands, and C3 refers to whales wintering in the coastal waters of Madagascar).

There are several sources of trend data available for sub-stock C1, whereas no direct measurements of trend from the breeding area for sub-stock C3 are available. Although historic catches from the breeding grounds are available for each sub-stock's breeding area, the historic catches from the feeding grounds (south of 40°S) are for both sub-stocks combined. The modelling approach reported here allows for mixing of the C1 and C3 sub-stocks on both the feeding grounds and breeding grounds.

In Butterworth and Johnston (2009), four alternate models were put forward, with three of these allowing for different possible mechanisms of interchange between the C1 and C3 breeding substocks. Here we present results for the resident (no interchange) and sabbatical, tourist and migrant models (which allow interchange). Detailed descriptions of these models are given later in the text.

## DATA

The data used for these analyses are deliberately identical with those adopted for the assessment reported in IWC (2008) except for one further years data for the C1 photo-ID database.

### Historic Catch data

There are two sources of historic catch data that relate to breeding sub-stocks C1 and C3.

- i) Catches north of 40°S
  - C1 those from "SCape", "Natal", and "Mozamb" from Allison's database (Allison pers. commn)
  - C3 those from "W Indian Ocean" from Allison's database.

These catches also include the Russian catches, which are reported north of 40°S for 10°E-60°E. These catches have been split equally between C1 and C3.

---

<sup>1</sup> MARAM (Marine Resource Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch, 7701, South Africa

ii) Catches south of 40°S

This series refers to catches recorded for 10°E-60°E and thus includes both C1 and C3 whales. Table 1a and Figure 1 show these three historic catch series.

### Absolute abundance data

The absolute abundance data considered in these analyses are presented in Table 1b. For breeding stock C1, an estimate of 5965 (CV = 0.17) for the 2003 season has been provided by Findlay *et al.* (in press). For breeding stock C3, upper and lower abundance estimates are suggested in Cerchio *et al.* (2008a); these were obtained using the MARK program applied to capture-recapture data from both photo-ID and genotypic data. These estimates are 6737 (CV=0.31) and 7715 (CV=0.24) for the year 2005. These estimates are for sub-stock C3 – primarily for Antongil Bay in the northeast of Madagascar. The lower of these estimates (6737) is used in the initial step of model fitting procedure (backwards method) where given a random value of  $r^{C3}$  a corresponding value of  $K^{C3}$  is needed – and this is done by fitting exactly to a recent population abundance estimates (in this case the 6737 in 2005 for C3). This C3 estimate is however not incorporated in the likelihood function because the capture-recapture data that underlie it are used instead.

### Trend information

Two sources of direct information on trend for sub-stock C1 are used. These are reported in Table 2, and comprise:

- i) Cape Vidal sightings per unit effort data for the 1988-2002 period (Findlay and Best 2006). These are obtained from shore-based surveys of northwards-migrating humpback whales at Cape Vidal, South Africa each year between 1988 and 1991, and in 2002.
- ii) Aircraft sightings per unit effort 1954-1975 from the Durban whaling ground (reported in Best 2003).

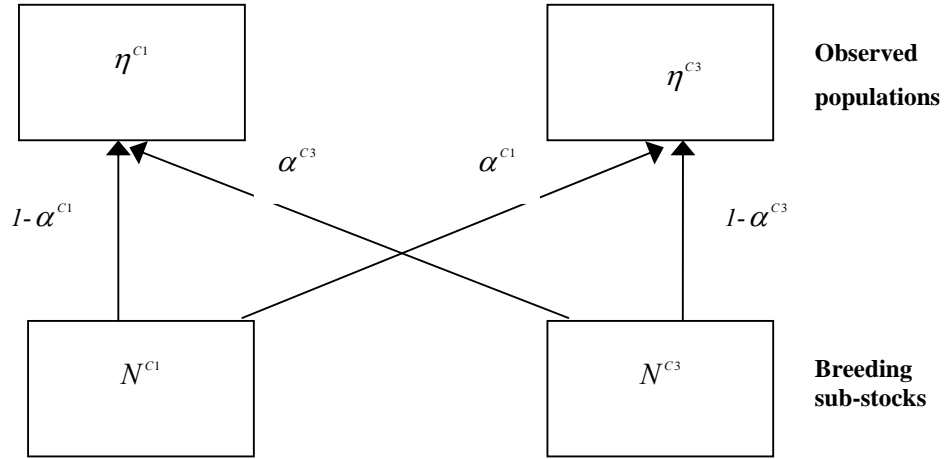
### Capture-recapture data

The capture-recapture data used here are reported in Cerchio *et al.* (2008a and b) except for the addition of C1 data for 2007 provided by Findlay (pers. commn). These consist of photo-ID mark-recapture data from Antongil Bay (C3) (Cerchio *et al.* 2008a), as well as photo-ID mark-recapture data for C1 (Cerchio *et al.* 2008b). The data span the period 2000-2007 for C1 and 2000-2006 for C3 and are reproduced in Tables 3a-c. The years 2000 and 2004 for C1 and the year 2002 for C3 are however excluded in the assessment due to poor temporal coverage of capture effort.

## METHODS

### Sabbatical interchange modelling approach

The sabbatical interchange model considered is shown schematically below (see also Butterworth and Johnston (2009)). There are two breeding substocks C1 and C3 of sizes  $N^{C1}$  and  $N^{C3}$  respectively. However each year there is a probability  $\alpha^{C1}$  that an animal from sub-stock C1 travels to the C3 region instead of C1, and similarly a probability  $\alpha^{C3}$  that one from sub-stock C3 travels to the C1 region instead of C3. Note that the model thus assumes that an animal “visits” only one of these two regions in any one year. The observed numbers in regions C1 and C3 each year are then given by  $\eta^{C1}$  and  $\eta^{C3}$  respectively, and these are the variables to which observations apply (both capture-recapture and survey data).



The following equations then apply:

Breeding sub-stock population dynamics

$$N_{y+1}^{B,C1} = N_y^{B,C1} + r^{C1} N_y^{B,C1} \left( 1 - \left( \frac{N_y^{B,C1}}{K^{C1}} \right)^\mu \right) - C_y^{C1} \quad (1)$$

$$N_{y+1}^{B,C3} = N_y^{B,C3} + r^{C3} N_y^{B,C3} \left( 1 - \left( \frac{N_y^{B,C3}}{K^{C3}} \right)^\mu \right) - C_y^{C3} \quad (2)$$

where

$N_y^{B,C1}$  is the number of whales in the breeding population C1 at the start of year  $y$ ,

$N_y^{B,C3}$  is the number of whales in the breeding population C3 at the start of year  $y$ ,

$r^{C1}$  is the intrinsic growth rate (the maximum per capita the population can achieve, when its size is very low) for breeding population C1,

$r^{C3}$  is the intrinsic growth rate for breeding population C3,

$K^{C1}$  is the carrying capacity of breeding population C1,

$K^{C3}$  is the carrying capacity of breeding population C3,

$\mu$  is the “degree of compensation” parameter; this is set at 2.39, which fixes the MSY level to  $MSYL = 0.6K$ , as conventionally assumed by the IWC Scientific Committee,

$C_y^{C1}$  is the total catch (in terms of animals) in year  $y$  from breeding population C1, and

$C_y^{C3}$  is the total catch (in terms of animals) in year  $y$  from breeding population C3.

### Feeding stocks

Mixing of the breeding populations in the feeding area (defined by 10°E – 60°E) yields:

$$N_y^F = N_y^{B,C1} + N_y^{B,C3} \quad (3)$$

which is assumed to reflect complete mixing of sub-stocks C1 and C3 in the feeding area.

### Observed populations

$$\eta_y^i = (1 - \alpha^i) N_y^i + \alpha^j N_y^j \quad \begin{Bmatrix} i \\ j \end{Bmatrix} = \begin{Bmatrix} C1 \\ C3 \end{Bmatrix} \text{ or } \begin{Bmatrix} C3 \\ C1 \end{Bmatrix} \quad (4)$$

where

$\eta_y^i$  is the observed population size in year  $y$  in breeding region  $i$ ,

$\alpha^i$  is the probability that animal from breeding population  $i$  moves (for one year) to observation area for breeding population  $j$  instead of that for breeding population  $i$ .

### Catches

$$C_y^{C1} = C_y^{C1,B} + C_y^{C1,F} \quad (5)$$

$$C_y^{C3} = C_y^{C3,B} + C_y^{C3,F} \quad (6)$$

where

$C_y^{C1,B}$  are the catches of animals in year  $y$  from the C1 sub-stock in either breeding area,

$C_y^{C1,F}$  are the catches of animals in year  $y$  from the C1 sub-stock in the feeding area,

$C_y^{C3,B}$  are the catches of animals in year  $y$  from the C3 sub-stock in either breeding area, and

$C_y^{C3,F}$  are the catches of animals in year  $y$  from the C3 sub-stock in the feeding area.

Table 1a provides the reported breeding area catches ( $C_y^{C1,B,reported}$  and  $C_y^{C3,B,reported}$ ), but only the combined catch ( $C_y^F = C_y^{C1,F} + C_y^{C3,F}$ ) for the feeding area. To split this feeding ground catch, it is assumed that the catches each year are proportional to their relative abundances in the feeding area (given that complete mixing is assumed). Thus the breakdown of feeding ground catches is calculated as follows:

$$C_y^{C1,F} = C_y^F \frac{N_y^{C1,B}}{(N_y^{C1,B} + N_y^{C3,B})} \quad \text{and} \quad (7)$$

$$C_y^{C3,F} = C_y^F \frac{N_y^{C3,B}}{(N_y^{C1,B} + N_y^{C3,B})} \quad (8)$$

The reported breeding ground catches are also split proportional to the relative abundance of each breeding sub-stock in each area as follows:

$$C_y^{C1,B} = C_y^{C1,B,reported} \frac{(1-\alpha^1)N_y^{C1,B}}{((1-\alpha^1)N_y^{C1,B} + \alpha^3 N_y^{C3,B})} + C_y^{C3,reported} \frac{\alpha^1 N_y^{C1,B}}{(\alpha^1 N_y^{C1,B} + (1-\alpha^3)N_y^{C3,B})} \quad (9)$$

$$C_y^{C3,B} = C_y^{C1,B,reported} \frac{\alpha^3 N_y^{C3,B}}{((1-\alpha^1)N_y^{C1,B} + \alpha^3 N_y^{C3,B})} + C_y^{C2+3,reported} \frac{(1-\alpha^3)N_y^{C3,B}}{(\alpha^1 N_y^{C1,B} + (1-\alpha^3)N_y^{C3,B})} \quad (10)$$

### Bayesian estimation framework

#### **Priors**

Prior distributions are defined for the following parameters:

- i)  $r^{C1} \sim U[0, 0.106]$  (as there are appreciable trend data to inform on  $r$  for C1)
- ii)  $r^{C3} \sim \text{Post BS A}$  (as there are no trend data to inform on  $r$  for C3)
- iii)  $\ln \tilde{\eta}_{target}^{C1,obs} \sim U[\ln \eta_{target}^{C1,obs} - 4CV, \ln \eta_{target}^{C1,obs} + 4CV]$
- iv)  $\ln \tilde{\eta}_{target}^{C3,obs} \sim U[\ln \eta_{target}^{C3,obs} - 4CV, \ln \eta_{target}^{C3,obs} + 4CV]$
- v)  $\alpha^{C1} \sim U[0, 0.6]$
- vi)  $\alpha^{C3} \sim U[0, 0.6]$

The uninformative  $r^{C1}$  and informative  $r^{C3}$  priors are bounded by zero (negative rates of growth are biologically implausible) and 0.106 (this corresponds to the maximum growth rate for the species agreed by the IWC Scientific Committee (IWC, 2007)). The prior distributions from which target abundance estimates ( $\tilde{\eta}_{target}^{C1,obs}, \tilde{\eta}_{target}^{C3,obs}$ ) are drawn at random are uniform on a natural logarithmic scale.

The lower and upper bounds are set by four times the CV. For these  $N$  targets, the Findlay *et al.* (in press) estimate is used for C1, and the lower Cerchio *et al.* (2008a) estimate is used for C3. The upper bound on the  $\alpha$  priors is to exclude results corresponding to interchange symmetry  $N^{C1} \leftrightarrow N^{C3}$   $\alpha^{C1/C3} \rightarrow 1 - \alpha^{C3/C1}$ .

Using the randomly drawn vector of values of  $\tilde{\eta}_{target}^{C1,obs}, \tilde{\eta}_{target}^{C3,obs}, r^{C1}, r^{C3}, \alpha^{C1}$  and  $\alpha^{C3}$ , a downhill simplex method of minimization is used to calculate  $K^{C1}$  and  $K^{C3}$  such that the model estimates of  $\eta_{target}^{C1}$  and  $\eta_{target}^{C3}$  are identical to the randomly drawn values  $\tilde{\eta}_{target}^{C1,obs}$  and  $\tilde{\eta}_{target}^{C3,obs}$ .

For each simulation, using the  $r^{C1}, r^{C3}, \alpha^{C1}, \alpha^{C3}$  and calculated  $K^{C1}$  and  $K^{C3}$  values, a negative log likelihood is then computed by comparing the model estimates of the (potentially) observed populations (the  $\eta_y^{C1}$  and  $\eta_y^{C3}$ ) to observed data – the recent absolute abundance estimate for C1, aircraft SPUE data for C1, relative abundance trend data from the breeding grounds for C1 (Cape Vidal data), and the capture-recapture photo-ID data for C1 and C3. The components of the negative log likelihood are calculated as follows.

The model treats the SPUE estimates from Cape Vidal (C1) as relative indices of abundance. It is assumed that the observed relative abundance index is log-normally distributed about its expected value:

$$I_{SPUE, Vidal, y}^{C1} = q_{SPUE, Vidal}^{C1} \eta_y^{C1} e^{\epsilon_y} \quad (11)$$

where

$I_{SPUE,Vidal,y}^{C1}$	is the Cape Vidal survey-based relative abundance (SPUE index) for year $y$ for breeding sub-stock C1,
$q_{SPUE,Vidal}^{C1}$	is the catchability coefficient for the Cape Vidal index for breeding sub-stock C1,
$\eta_y^{C1}$	is the model estimate of observed population size at the start of year $y$ for breeding sub-stock C1, and
$\varepsilon_y$	is from $N(0, (\sigma_{SPUE,Vidal}^{C1})^2)$ (see equation 18 below)

The model treats the aircraft SPUE abundance estimates slightly differently as follows, in particular to take proper account of zero sightings in some years. A Poisson distribution is assumed. The expected number of sightings in year  $y$  is:

$$\hat{n}_y^S = q_{SPUE,aircraft} \eta_y^{C1} E_y \quad (12)$$

where

$E_y$  is the aircraft searching effort in year  $y$ .

The associated “catchability” coefficient is calculated as follows:

$$q_{SPUE,aircraft} = \frac{\sum_y \bar{n}_y^S}{\sum_y \eta_y^{C1} E_y} \quad (13)$$

where

$\bar{n}_y^S$  is the observed number of whale sightings in year  $y$ .

### Capture-recapture

Captures:  $n_y^i = p_y^i \eta_y^i$   $i = C1, C3$  (14)

Recaptures:  $m_{y,y'}^{i,j}$  refers to humpbacks captured in region  $i$  in year  $y$  and recaptured in region  $j$  in year  $y'$ , where the expected numbers in terms of the interchange model are:

$$\hat{m}_{y,y'}^{i,j} = p_y^i [(1 - \alpha^i) N_y^i e^{-M(y'-y)} \alpha^i + \alpha^j N_y^j e^{-M(y'-y)} (1 - \alpha^j)] p_{y'}^j \quad (15)$$

$$\hat{m}_{y,y'}^{i,i} = p_y^i [(1 - \alpha^i) N_y^i e^{-M(y'-y)} (1 - \alpha^i) + \alpha^i N_y^i e^{-M(y'-y)} \alpha^i] p_{y'}^i \quad (16)$$

where:

$$\begin{Bmatrix} i \\ j \end{Bmatrix} = \begin{Bmatrix} C1 \\ C3 \end{Bmatrix} \text{ or } \begin{Bmatrix} C3 \\ C1 \end{Bmatrix}; \quad \begin{Bmatrix} i \\ i \end{Bmatrix} = \begin{Bmatrix} C1 \\ C1 \end{Bmatrix} \text{ or } \begin{Bmatrix} C3 \\ C3 \end{Bmatrix}$$

where:  $n_y^i$  is the number of animals captured in breeding region  $i$  in year  $y$ ,  
 $m_{y,y'}^{i,j}$  is the number of animals captured in  $i$  in year  $y$  that were recaptured in  $j$  in year  $y'$ ,

$\hat{m}_{y,y'}^{i,j}$  is the model predicted number of animals in  $i$  captured in year  $y$  that were recaptured in  $j$  in year  $y'$ ,  
 $M$  is the natural mortality rate (set here to equal 0.03), and  
 $p_y^i$  is the probability animal is seen in  $i$  year  $y$ .

The contributions of the various data to the negative of the log-likelihood function are then given by equation (17) below, where the absolute abundance estimate for C1 ( $N_{target}^{C1,obs}$ ) refers to that of Findlay *et al.* (in press):

$$\begin{aligned}
 -\ln L = & [\bar{n}_{SPUE,Vidal}^{C1} \ln \sigma_{SPUE,Vidal}^{C1} + \frac{1}{2\sigma_{CPUE}^{C1\ 2}} \sum_y (\ln I_{SPUE,Vidal,y}^{C1} - \ln q_{SPUE,Vidal}^{C1} - \ln \eta_y^{B,C1})^2] + \\
 & \left[ \sum_y \{q_{SPUE,aircraft} n_y^{C1} E_y - n_y \ln(q_{SPUE,aircraft} n_y^{C1} E_y)\} \right] + \\
 & \left[ \frac{1}{2CV^2} (\ln N_{target}^{C1,obs} - \ln \eta_{target}^{B,C1})^2 \right] + \\
 & \sum_i \sum_j \sum_{y=y_i}^{y_j-1} \sum_{y'=y+1}^{y_j} [-m_{y,y'}^{i,j} \ln \hat{m}_{y,y'}^{i,j} + \hat{m}_{y,y'}^{i,j}] \quad (17)
 \end{aligned}$$

The  $\sigma_{SPUE,Vidal}^{C1}$  parameter is the residual standard deviation which is estimated in the fitting procedure by its maximum likelihood value:

$$\hat{\sigma}_{SPUE,Vidal}^{C1} = \sqrt{1/\bar{n}_{SPUE,Vidal}^{C1} \sum_y (\ln I_{SPUE,Vidal,y}^{C1} - \ln q_{SPUE,Vidal}^{C1} - \ln \eta_y^{C1})^2} \quad \text{for Vidal SPUE data} \quad (18)$$

where

$\bar{n}_{SPUE,Vidal}^{C1}$  is the number of data points in the Cape Vidal SPUE series, and

$q_{SPUE,Vidal}^{C1}$  is the multiplicative bias, estimated by its maximum likelihood value:

$$\ln \hat{q}_{SPUE,Vidal}^{C1} = 1/\bar{n}_{SPUE,Vidal}^{C1} \sum_y (\ln I_{SPUE,Vidal,y}^{C1} - \ln \eta_y^{C1}) \quad (19)$$

This is a short cut to avoid integrating over priors for the  $q$ 's and  $\sigma^2$ 's, and in fact corresponds to the assumption that these priors are uniform in log-space and proportional to  $\sigma^{-3}$  respectively (Walters and Ludwig 1994).

The negative log likelihood is then converted into a likelihood value ( $L$ ). The integration of the prior distributions of the parameters and the likelihood function then essentially follows the Sampling-Importance-Resampling (SIR) algorithm presented by Rubin (1988) as described in Zerbini (2004). For a vector of parameter values  $\theta_i$ , the likelihood of the data associated with this vector of parameters ( $L$ ) as described above is calculated then modified by an importance function and stored as  $\tilde{L}$ . This process is repeated until an initial sample of  $n_1$   $\theta_i$  s is generated.

To improve calculation efficiency, given that high  $\alpha$  values correspond to very low likelihoods, an importance function was introduced for each  $\alpha$  value. In effect this means replacing the existing uniform priors on the  $\alpha$  values by:

$$\alpha^{C1} \sim \sigma^{C1} N(0,1)$$

$$\alpha^{C3} \sim \sigma^{C3} N(0,1)$$

where  $\alpha^{C1}$  and  $\alpha^{C3}$  are bound by  $[0,0.6]$ , and  $\sigma^{C1}$  and  $\sigma^{C3}$  are set at 0.1, and then modifying the likelihood  $L$  to:

$$\tilde{L}_i = L_i / \left\{ e^{-(\alpha_i^{C1})^2 / 2(\sigma^{C1})^2} e^{-(\alpha_i^{C3})^2 / 2(\sigma^{C3})^2} \right\}$$

This sample is then resampled with replacement  $n_2$  times with probability equal to weight  $w_j$ , where:

$$w_j = \frac{\tilde{L}(\theta_j / data)}{\sum_{j=1}^{n_1} \tilde{L}(\theta_j / data)} \quad (20)$$

The resample is thus a random sample of size  $n_2$  from the joint posterior distribution of the parameters (Rubin 1988).

Values of  $n_1$  (original number of simulations) are 500 000 and the value of  $n_2$  (number of resamples) is 1000. Tests showed that no sample contributed more than 0.5% of the total weight, and that at least 80% of the resamples were unique values.

#### **Nmin constraints**

$N_{\min}$  constraints of 248 and 372 whales are imposed for sub-stocks C1 and C3 respectively. These values are 4 times the number of haplotypes estimated by Rosenbaum *et al.* (2006) and Rosenbaum (pers. commn) for these sub-stocks.

#### **The Resident model**

The resident model is identical to the sabbatical model, except that no interchange between breeding regions C1 and C3 is allowed. This results in both  $\alpha^{C1}$  and  $\alpha^{C3}$  being set equal to zero. Equation (15) is thus not required, and the single recapture that indicates interchange is excluded from the likelihood.

#### **The Tourist model**

The *Tourist* model is an adaptation of the *Resident* model where whales from one breeding sub-stock, in addition to returning to their own breeding area each year, have a probability (denoted by  $\gamma$ ) of also visiting the breeding area for the other sub-stock that same year. Given that same season recaptures are ignored (for reasons of non-independence) in the assessments conducted (and further that no same season recaptures in different breeding grounds have as yet been observed), the *Tourist* model in its simplest form becomes equivalent to the *Sabbatical* model for the analysis method used. This is because spending some time in the other breeding area during the breeding season makes it less likely that a whale will be photographed in its own breeding area, so that the same equations apply as for the *Sabbatical* model. The variant of the *Tourist* model implemented here is therefore a somewhat extreme one which might be termed the “*Photogenic Tourist*” model. It assumes that photographs in each breeding area are taken only at the time all the “tourists” of the year from the other sub-stock are present as well. This is not put forward as a realistic scenario, but rather as a “bounding case” which renders the results of the *Tourist* model as different as possible from those of the *Sabbatical* model.

#### **The Migrant model**

The only difference between the *Sabbatical* model and the *Migrant* model is that in the latter, when a whale from one sub-stock happens to move to the breeding area for the other sub-stock in a particular year, it “stays” there, losing memory of its origins and behaving in the future exactly as do other members of that other sub-stock. Thus, it has the same probability (now denoted by  $\beta$ ) as those other members of moving back in any particular year to the first-mentioned sub-stock.

The Table below lists the core changes to the *Sabbatical* model in order to parameterize the *Migrant* and *Tourist* models, where the parameter defining the annual exchange (or related) probability is changed from  $\alpha$  for the *Sabbatical* model to  $\beta$  for the *Migrant* model, and to  $\gamma$  for the *Tourist* model.



<i>Sabbatical</i>	<i>Migrant</i>	<i>Tourist</i>
$\alpha$	$\beta$	$\gamma$
	<p>But Equations 1 and 2 change to:</p> $N_{y+1}^{B,C1} = N_y^{B,C1} + r^{C1} N_y^{B,C1} \left( 1 - \left( \frac{N_y^{B,C1}}{K^{C1}} \right)^\mu \right) - C_y^{C1} - \beta^{C1} N_y^{B,C1} + \beta^{C3} N_y^{B,C3}$ <p>and</p> $N_{y+1}^{B,C3} = N_y^{B,C3} + r^{C3} N_y^{B,C3} \left( 1 - \left( \frac{N_y^{B,C3}}{K^{C3}} \right)^\mu \right) - C_y^{C3} - \beta^{C3} N_y^{B,C3} + \beta^{C1} N_y^{B,C1}$	<p>But Equation 15 and 16 change:</p> $1 - \gamma \rightarrow 1$ $\gamma \rightarrow \gamma$

Note that for the *Migrant* model, there is one less estimable parameter, because long-term equilibrium in the absence of exploitation requires migration rates to balance so that  $\beta^{C1} K^{C1} = \beta^{C3} K^{C3}$ . Thus only the  $\beta^{C1}$  parameter is estimated, with this last relationship then determining  $\beta^{C3}$ .

The catches from the breeding grounds are split between the C1 and C3 sub-stocks as for the *Sabbatical* model.

#### Sensitivity tests

The report from the Seattle workshop (IWC 2009) lists a number of sensitivity tests to be explored in the assessment model. These are listed below. The sabbatical model is used as the baseline assessment model in each sensitivity test.

Test 1: Inclusion of IDCR data in the likelihood for trend information.

Test 2: Exclusion of aerial sighting index in the likelihood.

Test 3: Two different forms of density dependence

- a) Density dependence operates on the sum of the abundances of the two stocks, rather than independently for each stock, i.e. equations (1) and (2) are modified as follows:

$$N_{y+1}^{B,C1} = N_y^{B,C1} + r^{C1} N_y^{B,C1} \left( 1 - \left( \frac{N_y^{B,C1} + N_y^{B,C3}}{K^{C1} + K^{C2}} \right)^\mu \right) - C_y^{C1}$$

$$N_{y+1}^{B,C3} = N_y^{B,C3} + r^{C3} N_y^{B,C3} \left( 1 - \left( \frac{N_y^{B,C3} + N_y^{B,C1}}{K^{C3} + K^{C1}} \right)^\mu \right) - C_y^{C3}$$

- b) Density dependence on the number of animals present of the breeding grounds, rather than only on the number of whales in the corresponding breeding substock itself, i.e. equations (1) and (2) are modified as follows:

$$N_{y+1}^{B,C1} = N_y^{B,C1} + r^{C1} N_y^{B,C1} \left( 1 - \left( \frac{\eta_y^{B,C1}}{K^{C1}} \right)^\mu \right) - C_y^{C1}$$

$$N_{y+1}^{B,C3} = N_y^{B,C3} + r^{C3} N_y^{B,C3} \left( 1 - \left( \frac{\eta_y^{B,C3}}{K^{C3}} \right)^\mu \right) - C_y^{C3}$$

Test 4: Priors for  $r$  – the baseline model incorporates a uniform prior  $U[0; 0.106]$  for C1, and an informative prior for C3 provided by the posterior for this parameter from a Bayesian assessment for breeding stock A. Sensitivity tests explore here are:

- a) Uniform prior where  $r$  for C1 and C3 are the same. The population trajectory of stock C3 will thus be informed by trend information for stock C1.
- b) Uniform prior with  $r$  estimated separately for C1 and C3.

Test 5: Years of photo-ID capture-recapture data to be excluded besides those years already identified in the text which are excluded due to poor coverage.

Here we omit the C1 data. In equation (17), all the terms where the recapture area is C1 are omitted from the  $-\ln L$  term, i.e. if  $y' = C1$ , the term is omitted.

Test 6: Explore model sensitivity to exponent  $z$ . Here we examine the extremes of the range of  $z$  which would correspond to a maximum sustainable yield range of 0.5-0.8,

- a)  $z = 1.0$
- b)  $z = 11.2$

Test 7: Alternative Cape Vidal treatment – due to time constraints this sensitivity has not yet been explored.

## RESULTS

### *Baseline results*

The Bayesian resident, sabbatical, tourist and migrant model results are reported in Tables 4a and d respectively; their results are compared to direct estimates of abundance in Table 5. Figures 1-4 illustrate the model C1 and C3 population trajectories and fits to data. Figure 5a shows the sabbatical model C1 fit compared to all available sources of trend data. Figure 5b shows the sabbatical C1+C3 breeding ground population values along with the IDCR estimates for comparative purposes. Figures 5c and d compare the median C1 and C3 population trends estimated across the four models.

### *Sensitivity tests*

Tables 6a-h report the results of the various sensitivity tests. Table 7 provides a summary table of the median  $N_{2006}/K$  values for the four baseline interchange models, and for the various sensitivity tests.

## DISCUSSION

The  $N_{\min}$  constraint did not come into play for any of the four baseline models. The three of these models allowing interchange produce interchange rate probability estimates which are small: posterior medians of between 0.016 and 0.048 for C1 and between 0.011 and 0.020 for C3 (Tables 4a-d), though the 95%ile for C1 for the sabbatical model is somewhat larger at 0.165. Figures 1-4 show that for all baseline models the C1 trajectory is more precisely determined than that for C3. Cumulative tag recapture data are within Poisson variance levels of model predictions. For the years for which absolute abundance estimates can be generated independently, these are within the probability intervals for the model predictions, though barely so for C3 (see Table 5).

Figure 5a shows that the results for the sabbatical model are consistent with all other sources of relative abundance data except for CPUE's off Durban over 1920-28. Best (pers. commn) suggests that there was a switch to other species during this period, so that more of the effort was devoted to the offshore whaling ground at the end of this time series than at the beginning.

Figure 5b indicates that the IDCR-SOWER estimates of abundance at high latitudes are consistent with the sabbatical model results. Figures 5c and d demonstrate that there is little difference in results for the four baseline models, except that recovery of C3 takes place slightly sooner for the resident model.

Table 6 shows results for various sensitivity tests for the sabbatical model. Points of note are that probability intervals broaden for the sabbatical model (as might be expected) if the aerial or the C1 tag-recapture data are excluded (sensitivities 2 and 5) or a uniform prior is used in place of the informative prior for  $r$  (sensitivity 5). However if the  $r$  parameter for C3 is the same as for C1, the C3 sub-stock is estimated to be further recovered (sensitivity 4a). If density dependence acts on the combined abundance of both sub-stocks, the levels to which each recovers can differ from its pre-exploitation abundance (sensitivity 3a). The choice of value for the resilience  $z$  (and hence MSYL) has an

appreciable impact on the extent of recovery estimated. For higher MSYL, recovery is more advanced, and *vice versa* (sensitivities 6a and b).

Table 7 summarises results for present (2006) posterior median estimates relative to pre-exploitation levels for the four baseline and all the sensitivity tests. With single exceptions, these estimates all exceed 80% for C1 and 90% for C3.

## ACKNOWLEDGEMENTS

We thank Ken Findlay and Howard Rosenbaum and colleagues for provision of data and the South African National Research Foundation and IWC for funding support.

## REFERENCES

- Best, P. 2003. How low did they go? An historical comparison of indices of abundance for some baleen whales on the Durban whaling ground. Paper SC/55/SH18 submitted to the IWC Scientific Committee, 11pp.
- Butterworth, D.S. and Johnston, S.J. 2009. Report on discussions on modelling studies of possible interchange between the C1 and C3 breeding substocks of Southern Hemisphere humpback whales, Cape Town, December 2008. IWC document, SC/F09/SH1.
- Cerchio, S., Ersts, P., Pomilla, C., Loo, J., Razafindrakoto, Y., Leslie, M., Andrianravelo, N., Minton, G., Dushane, J., Murray, A., Collins, T. and Rosenbaum, H. (2008a) Revised estimation of abundance for breeding stock C3 of humpback whales, assessed through photographic and genotypic mark-recapture data from Antongil Bay, Madagascar, 2000-2006. IWC document SC/60/SH32.
- Cerchio, S., Findlay, K., Ersts, P., Minton, G., Bennet, D., Meyer, M.A., Razafindrakoto, Y., Kotze, P.G.H., Oosthuizen, H., Leslie, M., Andrianravelo, N. and Rosenbaum, H. 2008b. Initial assessment of exchange between breeding stocks C1 and C3 of humpback whales in the western Indian Ocean using photographic mark-recapture data, 2000-2006. IWC document SC/60/SH33.
- Findlay, K., Meyer, M., Elwen, S., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Siteo, S., Wilke, C., Kerwath, S., Swanson, S., Stavarees, L. and J. van der Westhuizen. (in press). Distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the coast of Mozambique, 2004. J. Cetacean Res. Manage. (Special Issue).
- Findlay, K. and P. Best. 2006. The migration of humpback whales past Cape Vidal, South Africa, and a preliminary estimate of the population increase rate. Paper SC/A06/HW16 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.
- IWC. 2007. Report of the international Whaling Commission, Annex H, Report of the Sub-Committee on Southern Hemisphere whale stocks. Annex H. *J.Cetacean Res.Manage. Suppl.*
- IWC. 2008. Report of the international Whaling Commission, Annex H, Report of the Sub-Committee on Southern Hemisphere whale stocks. Annex H. *J.Cetacean Res.Manage. Suppl.*
- IWC. 2009. Seattle humpback workshop Report.
- Rosenbaum, H.C., Pomilla, C., Olavarria, C., Baker, C.S., Leslie, M.C., Mendez, M.C., Caballero, S., Brassuer, M., Bannister, J., Best, P.B., Bonatto, S., Collins, T., Engel, M.H., Ersts, P.J., Findlay, K.P., Florez-Gonzalez, L., Garrigue, C., Hauser, C., Jenner, N., Meyer, M., Minton, G., Poole, M. and Y. Razafindrakoto. 2006. Paper SC/A06/HW59 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.
- Rubin, D.B. 1988. Using the SIR algorithm to simulate posterior distributions. Pp. 395-402. In: J.M. Bernardo, M.H. DeGroot, D.V. Lindley and A.F.M Smith (eds). *Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting*. June 1-5, 1987. Clarendon Press, Oxford. 805pp.
- Walters, C. and Ludwig, D. 1994. Calculation of Bayes posterior probability distributions for key population parameters. *Can. J. Fish. Aquat. Sci.* 51: 713-722.
- Zerbini, A.N. 2004. Status of the Southern Hemisphere humpback whale breeding stock A: preliminary results from a Bayesian assessment. Paper SC/56/SH17 presented to the IWC Scientific Committee, 18pp.

Table 1a: Historic catch series for sub-stocks C1 and C2+3 (Allison, pers. commn).

Season	C1 Breeding grounds	C3 Breeding grounds	C1+C3 Feeding grounds	Season	C1 Breeding grounds	C3 Breeding grounds	C1+C3 Feeding grounds	Season	C1 Breeding grounds	C3 Breeding grounds	C1+C3 Feeding grounds
1900	0	0	0	1926	124	0	0	1952	111	0	208
1901	0	0	0	1927	86	0	0	1953	89	0	66
1902	0	0	0	1928	62	0	0	1954	28	0	50
1903	0	0	0	1929	99	0	4	1955	49	0	28
1904	0	0	0	1930	134	0	150	1956	36	0	4
1905	0	0	0	1931	72	0	2	1957	34	0	66
1906	0	0	0	1932	307	0	38	1958	39	0	120
1907	0	0	0	1933	162	0	54	1959	38	0	152
1908	104	0	0	1934	514	0	554	1960	36	0	72
1909	149	0	0	1935	418	0	1870	1961	48	12	28
1910	632	0	0	1936	300	0	2684	1962	39	2	74
1911	1580	0	0	1937	242	1223	780	1963	39	1	40
1912	2313	25	0	1938	177	1752	0	1964	7	7	48
1913	1805	0	0	1939	200	1240	4	1965	5	4	76
1914	830	0	0	1940	176	0	0	1966	31	31	196
1915	334	0	0	1941	79	0	0	1967	41	41	66
1916	94	0	0	1942	156	0	0	1968	0	0	0
1917	7	0	0	1943	80	0	0	1969	0	0	0
1918	9	0	0	1944	115	0	0	1970	0	0	0
1919	91	0	0	1945	116	0	0	1971	0	0	0
1920	148	0	0	1946	93	0	0	1972	0	0	0
1921	251	0	0	1947	89	0	0	1973	1	0	0
1922	285	0	0	1948	182	0	34	1974	0	0	0
1923	183	0	0	1949	190	1333	396	1975	0	0	0
1924	187	0	0	1950	151	714	74				
1925	372	0	0	1951	103	0	212				

Table 1b

Absolute abundance estimates considered in analyses for sub-stocks C1 and C3

<b>Breeding sub-stock</b>	<b>Abundance estimate</b>	<b>Year applicable</b>	<b>Source</b>
C1	5965 (CV = 0.17)	2003	Findlay <i>et al.</i> (in press)
C3 lower	6737 (CV = 0.31)	2005	Cerchio <i>et al.</i> (2008a)
C3 upper	7715 (CV = 0.24)	2005	Cerchio <i>et al.</i> (2008a)

Table 2: Relative abundance trend data for sub-stock C1. For SPUE, effort is in hours and  $n^s$  is the number of whales sighted.

<b>Year</b>	<b>Cape Vidal (Findlay and Best 2006)</b>	<b>Year</b>	<b>Aircraft SPUE and effort from Durban 1954-75</b>		
			<b>SPUE</b>	<b><math>n^s</math></b>	<b>Effort</b>
<b>1988</b>	358	<b>1954</b>	2.868	5	174.35
<b>1989</b>	249	<b>1957</b>	0	0	325.49
<b>1990</b>	359	<b>1958</b>	0	0	423.40
<b>1991</b>	587	<b>1959</b>	0.223	1	448.58
<b>2002</b>	1673	<b>1960</b>	0	0	585.00
		<b>1961</b>	1.289	9	698.22
		<b>1962</b>	0.257	2	779.71
		<b>1963</b>	0.180	2	1119.99
		<b>1964</b>	0.197	2	1016.33
		<b>1965</b>	0	0	1102.26
		<b>1966</b>	1.336	13	972.86
		<b>1967</b>	0.710	6	844.95
		<b>1968</b>	0.294	2	681.36
		<b>1969</b>	1.254	9	717.87
		<b>1970</b>	0.536	4	745.83
		<b>1971</b>	0.426	3	704.31
		<b>1972</b>	0.966	7	724.51
		<b>1973</b>	1.720	11	639.23
		<b>1974</b>	1.514	8	528.32
		<b>1975</b>	1.871	10	534.35

**Table 3a: Photographic capture-recapture data from BS C1 – from SC/60/SH33 (Cerchio *et al.* 2008b)**

[ $n$  = number of different individuals sighted each year,  $m$  = total recaptures between pairs of years]

$n$								
	2000	2001	2002	2003	2004	2005	2006	2007
	3	24	49	115	21	134	112	167

$M$								
	2000	2001	2002	2003	2004	2005	2006	2007
2000	X	0	0	0	0	0	0	0
2001		X	1	0	0	0	0	0
2002			X	1	1	0	0	1
2003				X	0	0	0	1
2004					X	1	0	0
2005						X	2	3
2006							X	1

**Table 3b Photographic capture-recapture data from C3 – from SC/60/SH33 (Cerchio *et al.* 2008a)**

[ $n$  = number of different individuals sighted each year,  $m$  = total recaptures between pairs of years]

$N$							
	2000	2001	2002	2003	2004	2005	2006
	89	159	16	126	151	144	158

$m$							
	2000	2001	2002	2003	2004	2005	2006
2000	X	2	1	3	1	0	1
2001		X	1	3	3	3	2
2002			X	3	0	0	0
2003				X	2	1	3
2004					X	4	3
2005						X	4
2006							X

**Table 3c: Photographic capture-recapture data between C1 and C3 – from SC/60/SH33 (Cerchio *et al.* 2008a)**

[ $n$  = number of different individuals sighted each year,  $m$  = total recaptures between pairs of years; the entries above the diagonal in the matrix reflect animals first seen in C3 and later re-sighted in C1, whereas entries below the diagonal reflect the reverse, animals first seen in C1 and later re-sighted in C3.

$n$		2000	2001	2002	2003	2004	2005	2006
C1		89	159	16	126	151	144	158
	C3	3	24	49	115	21	134	112
Total								

$m$		C1						
		2000	2001	2002	2003	2004	2005	2006
C3	2000	X	0	0	0	0	0	0
	2001	0	X	0	0	0	0	0
	2002	0	0	X	0	0	0	0
	2003	0	0	0	X	0	0	0
	2004	0	0	0	0	X	0	0
	2005	0	0	0	0	0	X	0
	2006	0	0	0	1	0	0	X

Note: In line with the methods of analysis used, these Tables are structured such that if a whale is recaptured twice, say, the second recapture is linked only to the first recapture treated as a new capture.



Table 4a: **Resident** model assessment results (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C2+3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data*	“All” photo-ID data*
<i>r</i>	0.092 [0.072; 0.104]	0.065 [0.020; 0.089]
<i>K</i>	8402 [8058; 9270]	11 173 [9311; 16 058]
<i>α</i>	-	-
<i>N<sub>min</sub></i>	343 [254; 690]	2793 [1077; 6591]
<i>N<sub>2006</sub></i>	7493 [6577; 8137]	10 303 [7901; 13 951]
<i>η<sub>2006</sub></i>	7493 [6577; 8137]	10 303 [7901; 13 951]
<i>N<sub>min</sub>/K</i>	0.041 [0.031; 0.075]	0.256 [0.111; 0.440]
<i>N<sub>2006</sub>/K</i>	0.893 [0.743; 0.973]	0.992 [0.589; 1.000]
<i>N<sub>2020</sub>/K</i>	0.996 [0.971; 0.999]	0.999 [0.709; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.999; 1.000]	1.000 [0.849; 1.000]
<i>ROI</i> 2000-2006	0.037 [0.015; 0.054]	0.002 [0.000; 0.026]

\* As per the decision of IWC (2008), these exclude data from the years 2000 and 2004 for C1, and 2002 for C3, because of poor temporal coverage of capture effort. Further, for the resident model, the one recapture that reflects movement between C1 and C3 is excluded.

Table 4b **Sabbatical** model assessment results (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C2+3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture data</b>	“All” photo-ID data	“All” photo-ID data
<i>r</i>	0.091 [0.063; 0.105]	0.068 [0.030; 0.090]
<i>K</i>	8031 [6831; 9327]	10694 [9021; 14874]
<i>α</i>	0.048 [0.005; 0.165]	0.018 [0.002; 0.078]
<i>N<sub>min</sub></i>	431 [272; 1101]	2164 [732; 5208]
<i>N<sub>2006</sub></i>	7231 [6008; 8210]	9981 [7390; 12809]
<i>η<sub>2006</sub></i>	6995 [6056; 7933]	10056 [7572; 13022]
<i>N<sub>min</sub>/K</i>	0.055 [0.036; 0.125]	0.199 [0.081; 0.375]
<i>N<sub>2006</sub>/K</i>	0.912 [0.743; 0.991]	0.988 [0.636; 1.000]
<i>N<sub>2020</sub>/K</i>	0.996 [0.966; 1.000]	0.999 [0.805; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.999; 1.000]	1.000 [0.953; 1.000]
<i>ROI</i> 2000-2006	0.031 [0.005; 0.051]	0.004 [0.000; 0.032]

Table 4c: **Tourist** model assessment results (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data	“All” photo-ID data*
<i>r</i>	0.090 [0.064; 0.104]	0.067 [0.028; 0.090]
<i>K</i>	8078 [6956; 9135]	10795 [9206; 14577]
<i>γ</i>	0.028 [0.003; 0.094]	0.020 [0.001; 0.075]
<i>N<sub>min</sub></i>	377 [259; 973]	2143 [807; 4791]
<i>N<sub>2006</sub></i>	7188 [6041; 8069]	10075 [7728; 12748]
<i>η<sub>2006</sub></i>	7144 [6307; 8011]	1002 [7816; 12785]
<i>N<sub>min</sub>/K</i>	0.048 [0.033; 0.112]	0.196 [0.087; 0.357]
<i>N<sub>2006</sub>/K</i>	0.903 [0.744; 0.982]	0.980 [0.652; 1.000]
<i>N<sub>2020</sub>/K</i>	0.996 [0.965; 1.000]	0.998 [0.801; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.999; 1.000]	1.000 [0.939; 1.000]
<i>ROI</i> 2000-2006	0.032 [0.009; 0.052]	0.006 [0.000; 0.029]

Table 4d **Migrant** model assessment results (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture data</b>	“All” photo-ID data	“All” photo-ID data
<i>r</i>	0.066 [0.023; 0.101]	0.073 [0.028; 0.092]
<i>K</i>	8026 [6304; 9959]	11005 [9451; 15157]
<i>β</i>	0.016 [0.003; 0.058]	0.011 [0.002; 0.042]
<i>N<sub>min</sub></i>	352 [257; 1079]	2085 [999; 4699]
<i>N<sub>2006</sub></i>	6815 [5613; 7838]	10182 [8407; 12134]
<i>η<sub>2006</sub></i>	6836 [5659; 7843]	10178 [8429; 12127]
<i>N<sub>min</sub>/K</i>	0.044 [0.032; 0.128]	0.182 [0.101; 0.323]
<i>N<sub>2006</sub>/K</i>	0.875 [0.653; 0.979]	0.957 [0.627; 0.995]
<i>N<sub>2020</sub>/K</i>	0.985 [0.866; 0.999]	0.992 [0.789; 1.000]
<i>N<sub>2040</sub>/K</i>	0.999 [0.970; 1.000]	0.992 [0.789; 1.000]
<i>ROI</i> 2000-2006	0.027 [0.007; 0.043]	0.008 [0.001; 0.029]

Table 5: Comparison between population estimates reported in Table 2b with the model estimates showing 1.65s.e as 90% confidence intervals for the Table 1b estimates on the left, and 90% probability intervals for the model estimates on the right.

<b>C1 (2003)</b>	
Findlay <i>et al.</i> (in press): 5965 [4292; 7638]	Resident Model $\eta_{2003}^{C1}$ : 6508 [5415; 7698]
	Sabbatical Model $\eta_{2003}^{C1}$ : 6854 [5703; 7837]
	Migrant Model $\eta_{2003}^{C1}$ : 6347 [5212; 7594]
	Tourist Model $\eta_{2003}^{C1}$ : 6657 [5589; 7743]
<b>C3 (2005)</b>	
Cerchio (2008a) lower estimate: 6737 [3291; 10183]	Resident Model $\eta_{2005}^{C3}$ : 10029 [7353; 12955]
Cerchio (2008a) upper estimate: 7115 [4660; 10770]	Sabbatical Model $\eta_{2005}^{C3}$ : 10268 [7699; 13951]
	Migrant Model $\eta_{2003}^{C1}$ : 10114 [8260; 12077]
	Tourist Model $\eta_{2003}^{C1}$ : 9978 [7632; 12750]

Table 6a: **Sensitivity Test 1 – inclusion of IDCR data in the likelihood for the sabbatical model**  
(posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data	“All” photo-ID data*
<i>r</i>	0.091 [0.066; 0.104]	0.062 [0.025; 0.886]
<i>K</i>	8069 [6841; 9104]	10709 [9064; 14488]
<i>α</i>	0.049 [0.005; 0.165]	0.018 [0.001; 0.079]
<i>N<sub>min</sub></i>	378 [259; 851]	1901 [774; 4580]
<i>N<sub>2006</sub></i>	7209 [5975; 8032]	9626 [7359; 12068]
<i>η<sub>2006</sub></i>	6969 [5976; 7802]	9777 [7649; 12369]
<i>N<sub>min</sub>/K</i>	0.058 [0.033; 0.101]	0.176 [0.084; 0.338]
<i>N<sub>2006</sub>/K</i>	0.907 [0.748; 0.982]	0.943 [0.569; 1.000]
<i>N<sub>2020</sub>/K</i>	0.996 [0.968; 1.000]	0.993 [0.743; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.999; 1.000]	1.000 [0.902; 1.000]
<i>ROI</i> 2000-2006	0.033 [0.011; 0.051]	0.012 [0.000; 0.032]

Table 6b **Sensitivity Test 2 – exclusion of aerial sighting index data in the likelihood for the sabbatical model** (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data	“All” photo-ID data
<i>r</i>	0.072 [0.020; 0.100]	0.067 [0.029; 0.089]
<i>K</i>	8664 [6822; 15475]	10037 [8062; 14073]
<i>α</i>	0.047 [0.005; 0.166]	0.031 [0.003; 0.111]
<i>N<sub>min</sub></i>	656 [271; 3358]	1501 [495; 4949]
<i>N<sub>2006</sub></i>	7055 [5593; 8891]	8904 [6680; 12194]
<i>η<sub>2006</sub></i>	6925 [5891; 8533]	8919 [6931; 12230]
<i>N<sub>min</sub>/K</i>	0.077 [0.035; 0.232]	0.149 [0.057; 0.382]
<i>N<sub>2006</sub>/K</i>	0.814 [0.455; 0.968]	0.936 [0.624; 1.000]
<i>N<sub>2020</sub>/K</i>	0.982 [0.583; 0.999]	0.994 [0.816; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.768; 1.000]	0.999 [0.948; 1.000]
<i>ROI</i> 2000-2006	0.033 [0.009; 0.052]	0.014 [0.000; 0.038]

Table 6c: **Sensitivity Test 3a –density dependence operates on the sum of the abundances of the two stocks for the sabbatical model** (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data	“All” photo-ID data*
<i>r</i>	0.096 [0.071; 0.105]	0.038 [0.011; 0.069]
<i>K</i>	9552 [7760; 10813]	8592 [4845; 16056]
<i>α</i>	0.056 [0.006; 0.179]	0.025 [0.002; 0.107]
<i>N<sub>min</sub></i>	474 [296; 1194]	2401 [970; 6050]
<i>N<sub>2006</sub></i>	7817 [5923; 10353]	7980 [5824; 10557]
<i>η<sub>2006</sub></i>	7539 [5969; 9625]	8168 [6390; 10726]
<i>N<sub>min</sub>/K</i>	0.051 [0.032; 0.114]	0.282 [0.180; 0.419]
<i>N<sub>2006</sub>/K</i>	0.824 [0.616; 1.121]	0.935 [0.494; 1.608]
<i>N<sub>2020</sub>/K</i>	0.978 [0.655; 1.605]	0.994 [0.524; 1.654]
<i>N<sub>2040</sub>/K</i>	0.998 [0.659; 1.743]	0.999 [0.530; 1.659]
<i>ROI</i> 2000-2006	0.034 [0.003; 0.063]	0.011 [0.002; 0.020]

Table 6d **Sensitivity Test 3b – density dependence is on the number of animals present on the breeding grounds for the sabbatical model** (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
<b><i>r</i> prior</b>	U[0, 0.106]	Post BS(A)
<b>Historic catch</b>	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
<b>Recent abundance</b>	5965 (2003)	None
<b>Trend information</b>	Cape Vidal and aircraft SPUE trend data only	None
<b>Capture-recapture Data</b>	“All” photo-ID data	“All” photo-ID data
<i>r</i>	0.092 [0.066; 0.104]	0.067 [0.027; 0.089]
<i>K</i>	7809 [6828; 8966]	10767 [9094; 14626]
<i>α</i>	0.048 [0.005; 0.171]	0.019 [0.002; 0.093]
<i>N<sub>min</sub></i>	436 [272; 1014]	2223 [833; 5267]
<i>N<sub>2006</sub></i>	7307 [5967; 8171]	9808 [7391; 12516]
<i>η<sub>2006</sub></i>	7028 [6098; 8038]	9960 [7630; 12605]
<i>N<sub>min</sub>/K</i>	0.056 [0.036; 0.121]	0.209 [0.088; 0.371]
<i>N<sub>2006</sub>/K</i>	0.931 [0.755; 1.098]	0.949 [0.610; 1.044]
<i>N<sub>2020</sub>/K</i>	1.013 [0.897; 1.169]	0.966 [0.761; 1.051]
<i>N<sub>2040</sub>/K</i>	1.019 [0.904; 1.181]	0.979 [0.843; 1.068]
<i>ROI</i> 2000-2006	0.031 [0.006; 0.051]	0.004 [0.000; 0.031]

Table 6e: Sensitivity Test 4a – uniform prior for  $r$  which is the same for C1 and C3 for the sabbatical model (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
$r$ prior	U[0, 0.106]	U[0, 0.106] (same value as for C1)
Historic catch	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
Recent abundance	5965 (2003)	None
Trend information	Cape Vidal and aircraft SPUE trend data only	None
Capture-recapture Data	“All” photo-ID data	“All” photo-ID data*
$r$	0.090 [0.066; 0.104]	0.090 [0.066; 0.104]
$K$	8196 [7211; 9283]	9644 [8658; 11939]
$\alpha$	0.051 [0.007; 0.157]	0.018 [0.001; 0.085]
$N_{min}$	367 [254; 871]	1894 [653; 4352]
$N_{2006}$	7245 [6081; 8037]	9628 [8522; 11938]
$\eta_{2006}$	6962 [6037; 7886]	9819 [8462; 12304]
$N_{min}/K$	0.045 [0.032; 0.100]	0.199 [0.074; 0.367]
$N_{2006}/K$	0.890 [0.739; 0.980]	0.999 [0.942; 1.000]
$N_{2020}/K$	0.995 [0.966; 1.000]	1.000 [0.995; 1.000]
$N_{2040}/K$	1.000 [0.999; 1.000]	1.000 [1.000; 1.000]
ROI 2000-2006	0.035 [0.010; 0.032]	0.000 [0.000; 0.017]

Table 6f Sensitivity Test 4b – uniform prior for  $r$  for C1 and C3, but this estimated separately, for the sabbatical model (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	BS C1	BS C3
$r$ prior	U[0, 0.106]	U[0, 0.106]
Historic catch	Feeding grounds split proportional to abundance	Feeding grounds split proportional to abundance
Recent abundance	5965 (2003)	None
Trend information	Cape Vidal and aircraft SPUE trend data only	None
Capture-recapture Data	“All” photo-ID data	“All” photo-ID data
$r$	0.091 [0.065; 0.104]	0.054 [0.009; 0.106]
$K$	8066 [6968; 9262]	11416 [8788; 18935]
$\alpha$	0.048 [0.006; 0.156]	0.014 [0.001; 0.081]
$N_{min}$	366 [256; 882]	2501 [893; 6795]
$N_{2006}$	7229 [6089; 8004]	9461 [7219; 12427]
$\eta_{2006}$	6963 [6071; 7745]	9658 [7219; 12581]
$N_{min}/K$	0.046 [0.033; 0.098]	0.111 [0.092; 0.384]
$N_{2006}/K$	0.908 [0.753; 0.979]	0.906 [0.439; 1.000]
$N_{2020}/K$	0.996 [0.966; 1.000]	0.984 [0.489; 1.000]
$N_{2040}/K$	1.000 [0.999; 1.000]	0.999 [0.571; 1.000]
ROI 2000-2006	0.033 [0.011; 0.051]	0.009 [0.000; 0.030]

Table 6g: **Sensitivity Test 5 – omit C1 photo-ID data from the likelihood for the sabbatical model**  
(posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	<b>BS C1</b>	<b>BS C3</b>
<b><i>r</i> prior</b>	<b>U[0, 0.106]</b>	<b>Post BS(A)</b>
<b>Historic catch</b>	<b>Feeding grounds split proportional to abundance</b>	<b>Feeding grounds split proportional to abundance</b>
<b>Recent abundance</b>	<b>5965 (2003)</b>	<b>None</b>
<b>Trend information</b>	<b>Cape Vidal and aircraft SPUE trend data only</b>	<b>None</b>
<b>Capture-recapture Data</b>	<b>omitted</b>	<b>“All” photo-ID data*</b>
<i>r</i>	0.090 [0.066; 0.105]	0.068 [0.023; 0.091]
<i>K</i>	8100 [6883; 9311]	10833 [9164; 14991]
$\alpha$	0.034 [0.003; 0.150]	0.015 [0.001; 0.071]
<i>N<sub>min</sub></i>	406 [266; 942]	2356 [882; 5505]
<i>N<sub>2006</sub></i>	7062 [5743; 8050]	10102 [7567; 12932]
$\eta_{2006}$	6917 [5732; 7795]	10145 [7713; 13139]
<i>N<sub>min</sub>/K</i>	0.050 [0.034; 0.109]	0.222 [0.090; 0.381]
<i>N<sub>2006</sub>/K</i>	0.882 [0.683; 0.984]	0.990 [0.599; 1.000]
<i>N<sub>2020</sub>/K</i>	0.995 [0.954; 0.999]	0.999 [0.750; 1.000]
<i>N<sub>2040</sub>/K</i>	1.000 [0.999; 1.000]	1.000 [0.908; 1.000]
<i>ROI</i> 2000-2006	0.037 [0.009; 0.056]	0.003 [0.000; 0.031]

Table 6h **Sensitivity Test 6a –  $z = 1.0$  for the sabbatical model** (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	<b>BS C1</b>	<b>BS C3</b>
<b><i>r</i> prior</b>	<b>U[0, 0.106]</b>	<b>Post BS(A)</b>
<b>Historic catch</b>	<b>Feeding grounds split proportional to abundance</b>	<b>Feeding grounds split proportional to abundance</b>
<b>Recent abundance</b>	<b>5965 (2003)</b>	<b>None</b>
<b>Trend information</b>	<b>Cape Vidal and aircraft SPUE trend data only</b>	<b>None</b>
<b>Capture-recapture Data</b>	<b>“All” photo-ID data</b>	<b>“All” photo-ID data</b>
<i>r</i>	0.096 [0.069; 0.105]	0.067 [0.029; 0.089]
<i>K</i>	9006 [7488; 10553]	11902 [9636; 15874]
$\alpha$	0.050 [0.005; 0.159]	0.021 [0.002; 0.089]
<i>N<sub>min</sub></i>	662 [394; 1460]	2315 [857; 5298]
<i>N<sub>2006</sub></i>	6998 [5625; 8392]	9357 [6689; 12673]
$\eta_{2006}$	6830 [5693; 8147]	9420 [6992; 12677]
<i>N<sub>min</sub>/K</i>	0.074 [0.047; 0.148]	0.191 [0.088; 0.352]
<i>N<sub>2006</sub>/K</i>	0.787 [0.636; 0.909]	0.806 [0.522; 0.956]
<i>N<sub>2020</sub>/K</i>	0.936 [0.837; 0.978]	0.917 [0.629; 0.986]
<i>N<sub>2040</sub>/K</i>	0.991 [0.956; 0.997]	0.979 [0.756; 0.997]
<i>ROI</i> 2000-2006	0.025 [0.012; 0.038]	0.014 [0.004; 0.025]

Table 6i **Sensitivity Test 6b** –  $z = 11.2$  for the sabbatical model (posterior medians with 5<sup>th</sup> and 95<sup>th</sup> percentiles in parenthesis).

	<b>BS C1</b>	<b>BS C3</b>
<b><math>r</math> prior</b>	<b>U[0, 0.106]</b>	<b>Post BS(A)</b>
<b>Historic catch</b>	<b>Feeding grounds split proportional to abundance</b>	<b>Feeding grounds split proportional to abundance</b>
<b>Recent abundance</b>	<b>5965 (2003)</b>	<b>None</b>
<b>Trend information</b>	<b>Cape Vidal and aircraft SPUE trend data only</b>	<b>None</b>
<b>Capture-recapture data</b>	<b>“All” photo-ID data</b>	<b>“All” photo-ID data</b>
$r$	0.086 [0.060; 0.103]	0.073 [0.031; 0.090]
$K$	7458 [6609; 8622]	9649 [8240; 13189]
$\alpha$	0.045 [0.004; 0.158]	0.019 [0.001; 0.083]
$N_{min}$	392 [258; 1063]	2410 [944; 5375]
$N_{2006}$	7290 [6354; 8187]	9492 [7899; 12086]
$\eta_{2006}$	7107 [6281; 7950]	9647 [8081; 12559]
$N_{min}/K$	0.052 [0.037; 0.141]	0.025 [0.103; 0.431]
$N_{2006}/K$	0.998 [0.864; 1.000]	1.000 [0.741; 1.000]
$N_{2020}/K$	1.000 [1.000; 1.000]	1.000 [0.987; 1.000]
$N_{2040}/K$	1.000 [1.000; 1.000]	1.000 [1.000; 1.000]
$ROI$ 2000-2006	0.049 [0.000; 0.075]	0.000 [0.000; 0.041]



Table 7: Summary table of median  $N_{2006}/K$  values for the four interchange models, and for the various sensitivity tests. The sensitivity tests are all for the sabbatical model.

	<b>C1 <math>N_{2006}/K</math></b>	<b>C3 <math>N_{2006}/K</math></b>
Resident	0.893	0.992
Sabbatical	0.912	0.988
Migrant	0.875	0.957
Tourist	0.903	0.980
Test 1 (inclusion of IDCR data)	0.907	0.943
Test 2 (exclusion of aerial sightings index }	0.814	0.936
Test 3a (density dependence – sum of abundances)	0.824	0.935
Test 3b (density dependence – based on breeding grounds)	0.931	0.949
Test 4a ( $r$ priors both uniform - C1 and C3 the same)	0.890	0.999
Test 4b ( $r$ priors both uniform – C1 and C3 estimated separately)	0.908	0.906
Test 5 (omit C1 photo-ID data)	0.882	0.990
Test 6a ( $z = 1.0$ )	0.787	0.806
Test 6b ( $z = 11.2$ )	0.998	1.000

Figure 1a: **Resident** model fit to C1 trend data (Cape Vidal and aircraft SPUE), as well as the recent abundance estimate (2003). The model trajectory is the Bayesian posterior median values of  $\eta_y^{C1}$ , the whales in the C1 breeding grounds. The vertical line shows 2006.

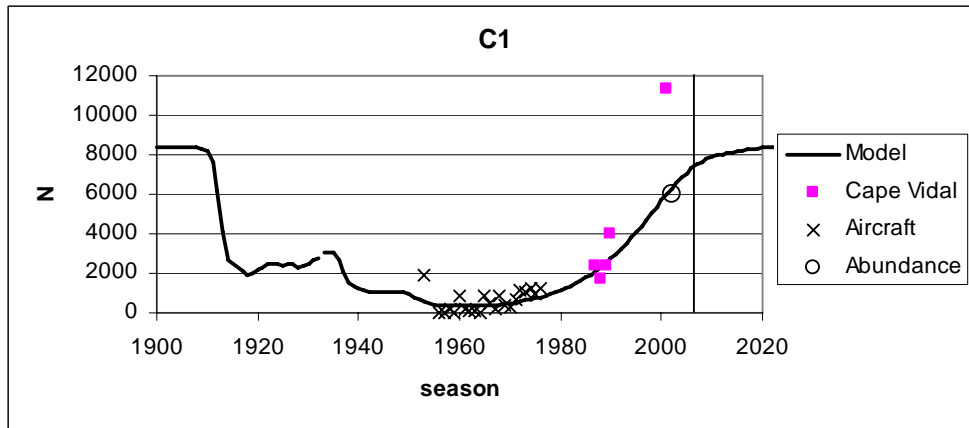


Figure 1b: **Resident** model C1 population ( $N_y^{C1}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

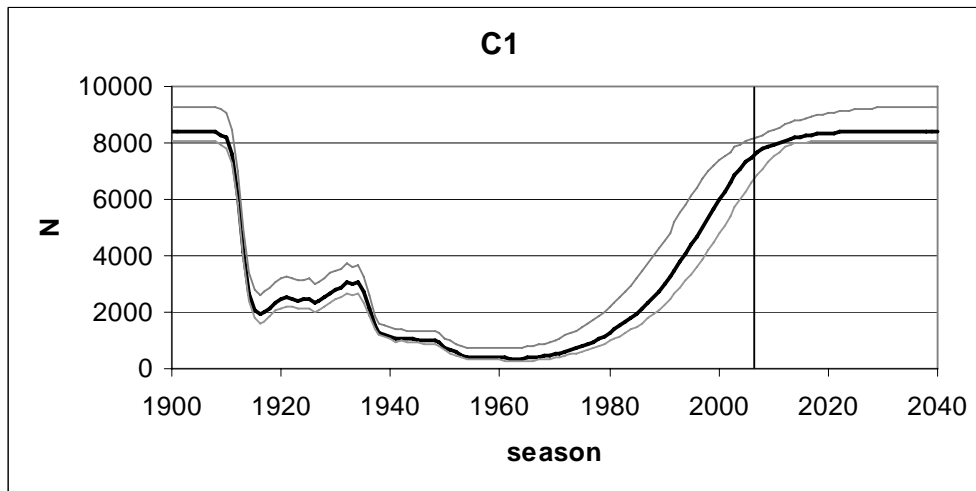


Figure 1c: **Resident** model trajectories of is the Bayesian posterior median values of  $\eta_y^{C3}$ , the whales in C3 breeding grounds. The vertical line shows 2006. The squares show the upper and lower abundance estimates from Cerchio (2008a) for comparative purposes – these estimates are not used in fitting the model because the capture-recapture data underlying them are used instead.

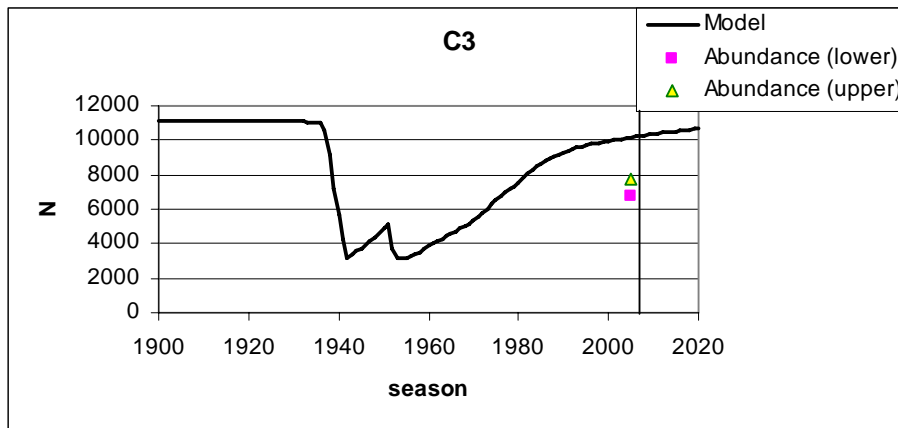


Figure 1d: **Resident** model C3 population ( $N_y^{C3}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

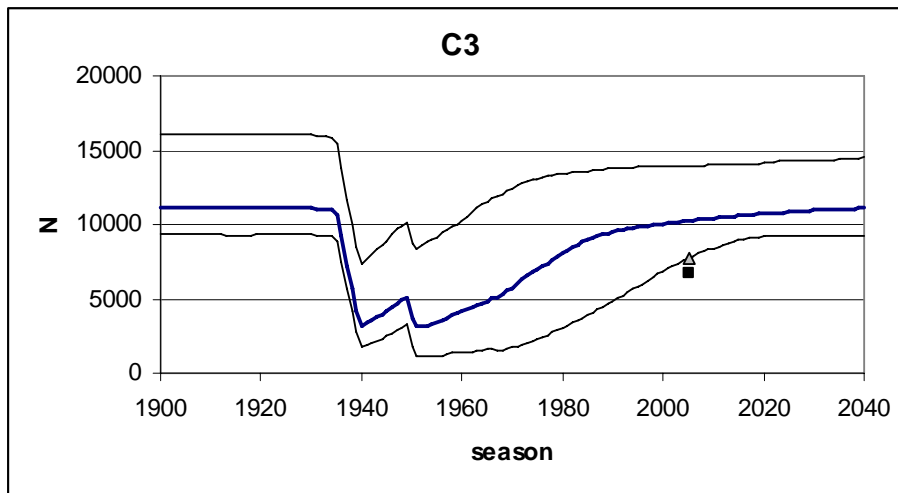


Figure 1e: The **Resident** model cumulative recaptures (c.r.) for each year for both the observed data (open circles), and for the model estimated posterior medians and 90% probability intervals.

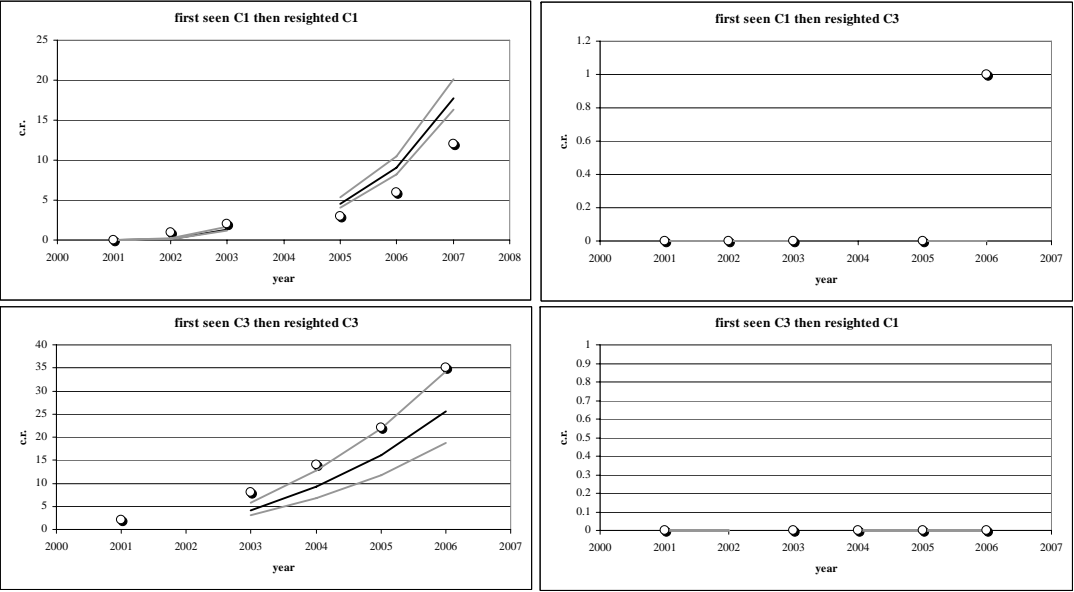


Figure 2a: **Sabbatical** model fit to C1 trend data (Cape Vidal and aircraft SPUE), as well as the recent abundance estimate (2003). The model trajectory is the Bayesian posterior median values of  $\eta_y^{C1}$ , the whales in C1 breeding grounds. The vertical line shows 2006.

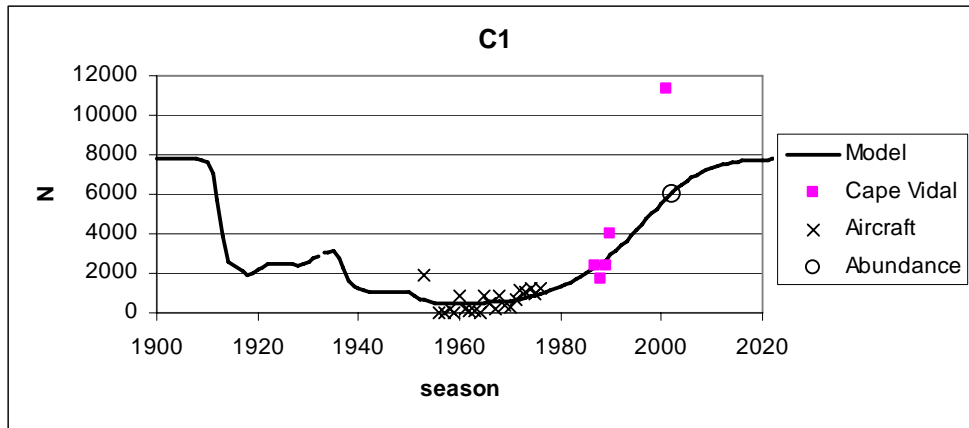


Figure 2b: **Sabbatical** model C1 population ( $N_y^{C1}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

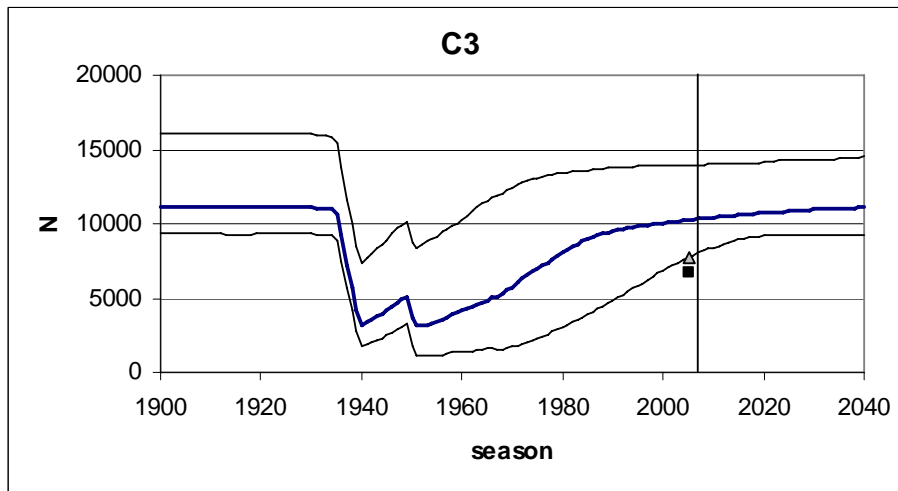


Figure 2c: **Sabbatical** model trajectories of is the Bayesian posterior median values of  $\eta_y^{C3}$ , the whales in the C3 breeding grounds. The vertical line shows 2006. The squares show the upper and lower abundance estimates from Cerchio (2008a) for comparative purposes – these estimates are not used in fitting the model because the capture-recapture data underlying them are used instead.

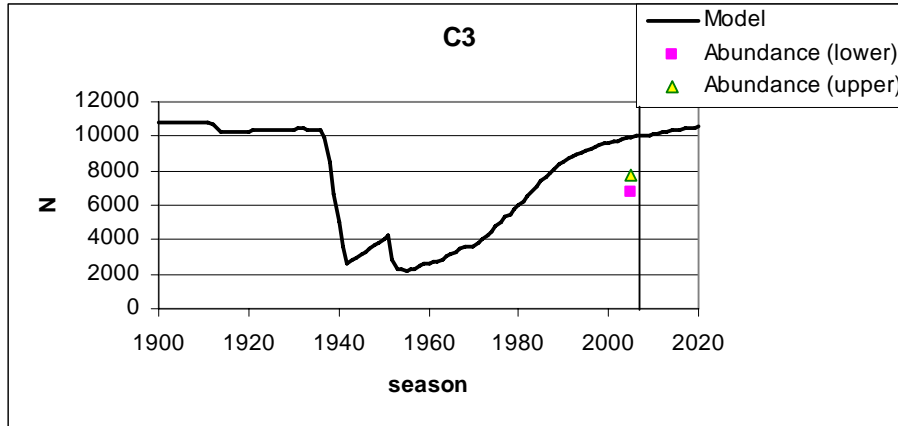


Figure 2d: **Sabbatical** model C3 population ( $N_y^{C3}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

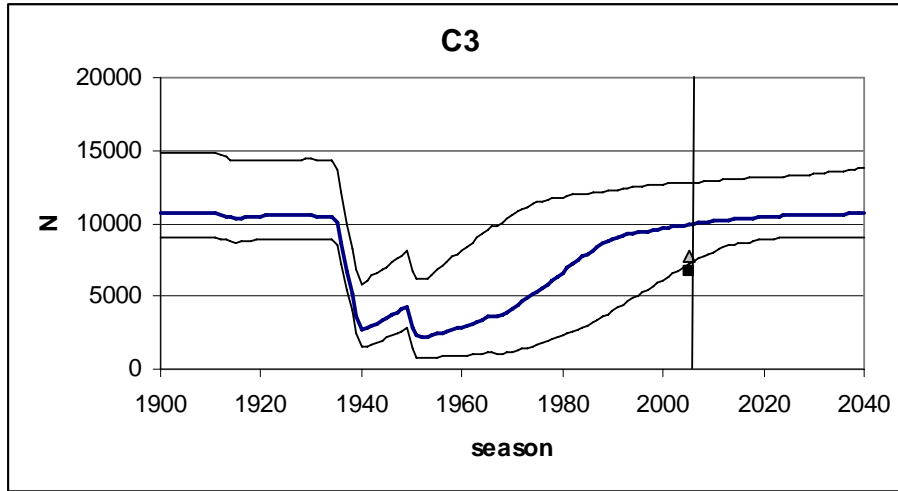


Figure 2e: The **Sabbatical** model cumulative recaptures (c.r.) for each year for both the observed data (open circles), and for the model estimated posterior medians and 90% probability intervals.

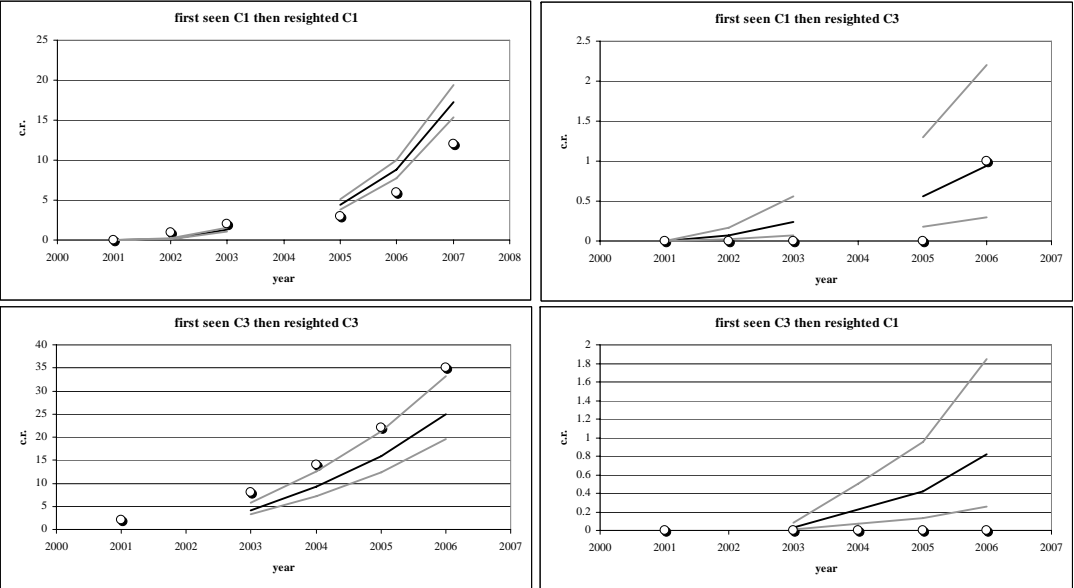


Figure 3a: **Tourist** model fit to C1 trend data (Cape Vidal and aircraft SPUE), as well as the recent abundance estimate (2003). The model trajectory is the Bayesian posterior median values of  $\eta_y^{C1}$ , the whales in C1 breeding grounds. The vertical line shows 2006.

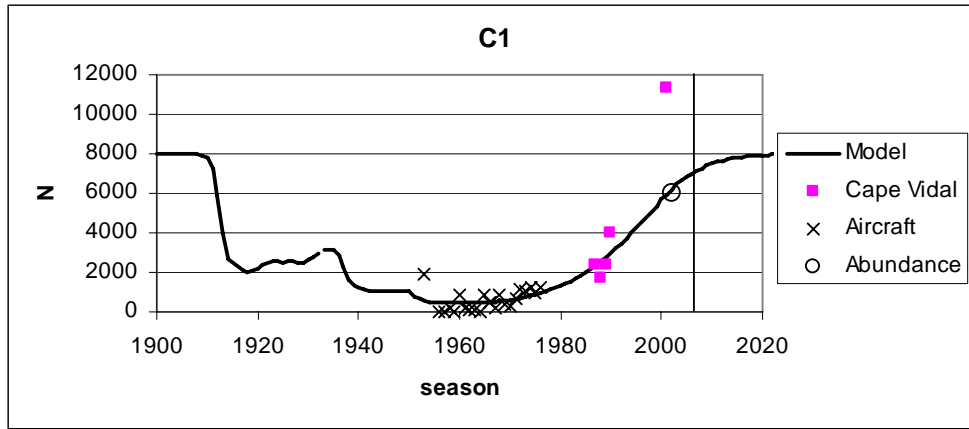


Figure 3b: **Tourist** model C1 population ( $N_y^{C1}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

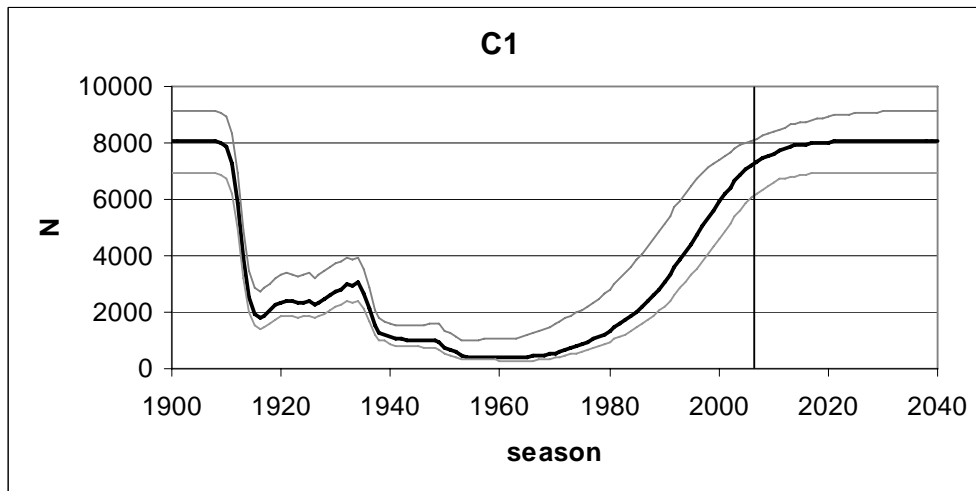




Figure 3c: **Tourist** model trajectories of is the Bayesian posterior median values of  $\eta_y^{C3}$ , the whales in the C3 breeding grounds. The vertical line shows 2006. The squares show the upper and lower abundance estimates from Cerchio (2008a) for comparative purposes – these estimates are not used in fitting the model because the capture-recapture data underlying them are used instead.

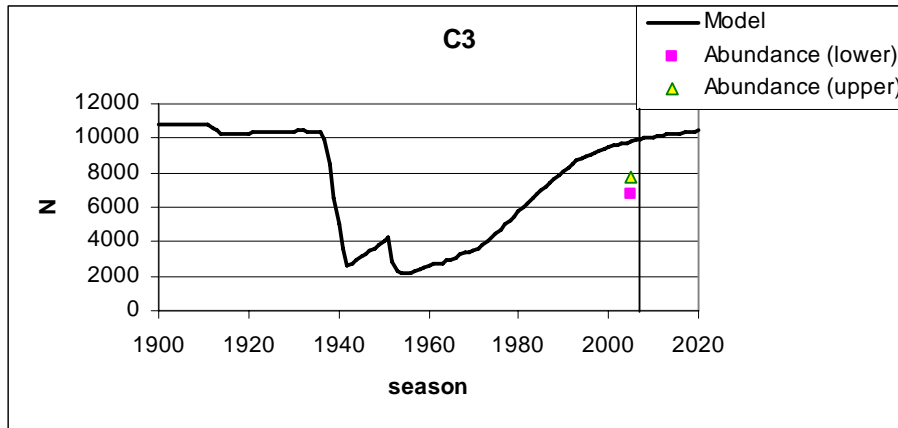


Figure 3d: **Tourist** model C3 population ( $N_y^{C3}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

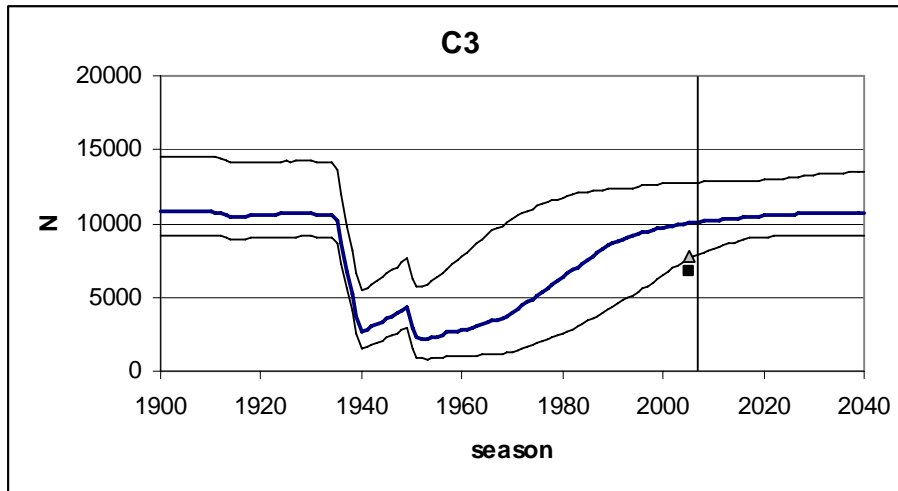


Figure 3e: The **Tourist** model cumulative recaptures (c.r.) for each year for both the observed data (open circles), and for the model estimated posterior medians and 90% probability intervals.

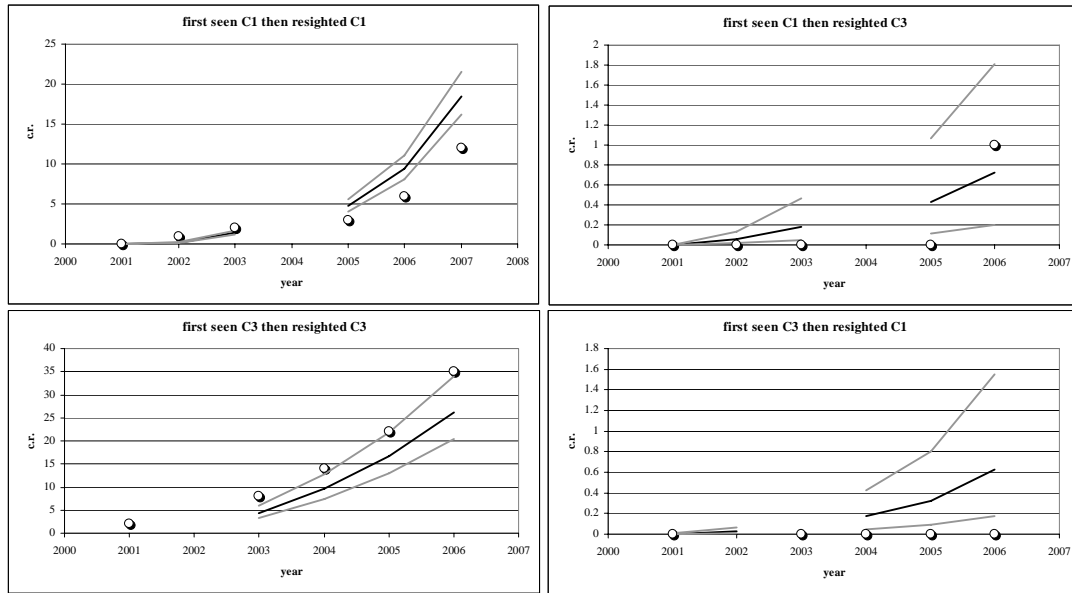


Figure 4a: **Migrant** model fit to C1 trend data (Cape Vidal and aircraft SPUE), as well as the recent abundance estimate (2003). The model trajectory is the Bayesian posterior median values of  $\eta_y^{C1}$ , the whales in C1 breeding grounds. The vertical line shows 2006.

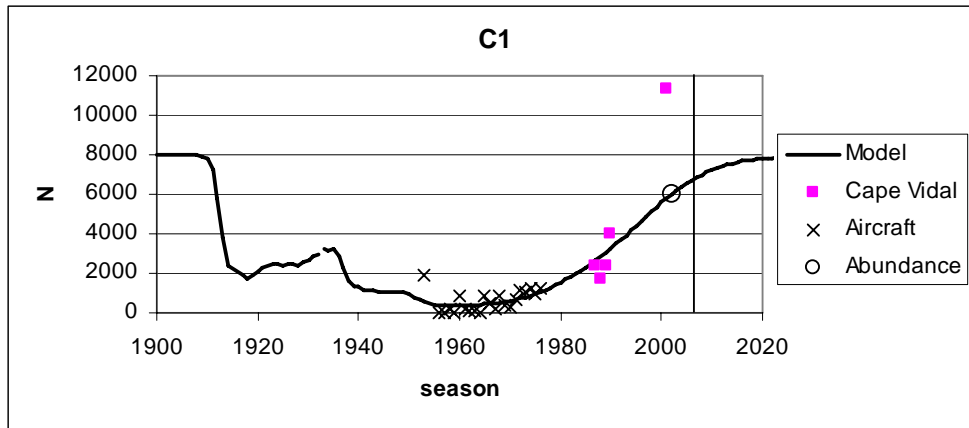


Figure 4b: **Migrant** model C1 population ( $N_y^{C1}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

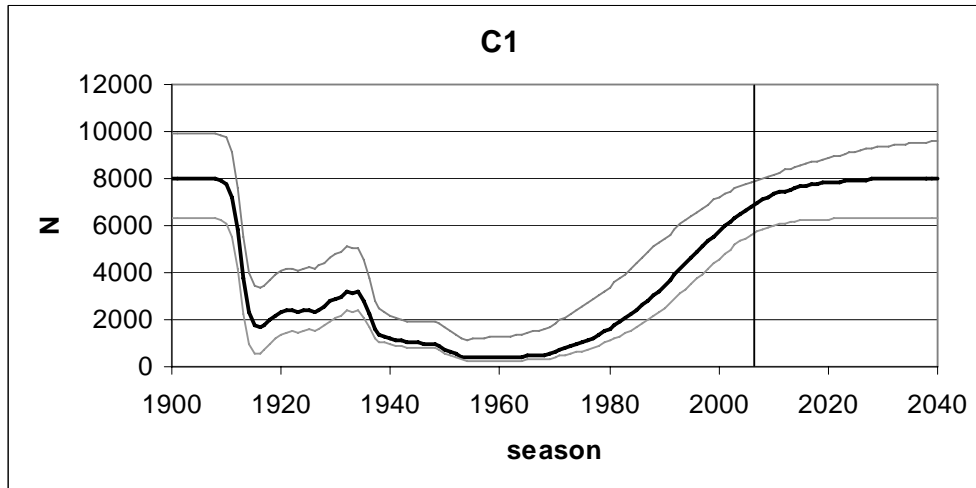


Figure 4c: **Migrant** model trajectories of is the Bayesian posterior median values of  $\eta_y^{C3}$ , the whales in the C3 breeding grounds. The vertical line shows 2006. The squares show the upper and lower abundance estimates from Cerchio (2008a) for comparative purposes – these estimates are not used in fitting the model because the capture-recapture data underlying them are used instead.

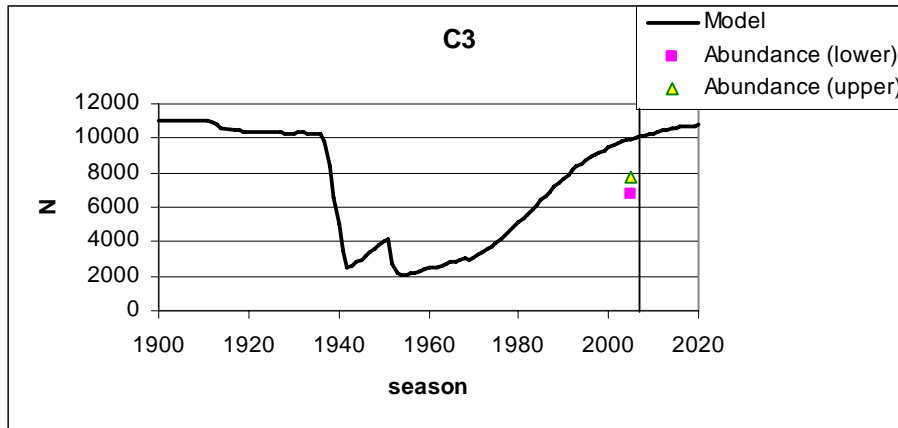


Figure 4d: **Migrant** model C3 population ( $N_y^{C3}$ ) trajectories, showing the median and 90% probability envelopes. The vertical line shows 2006.

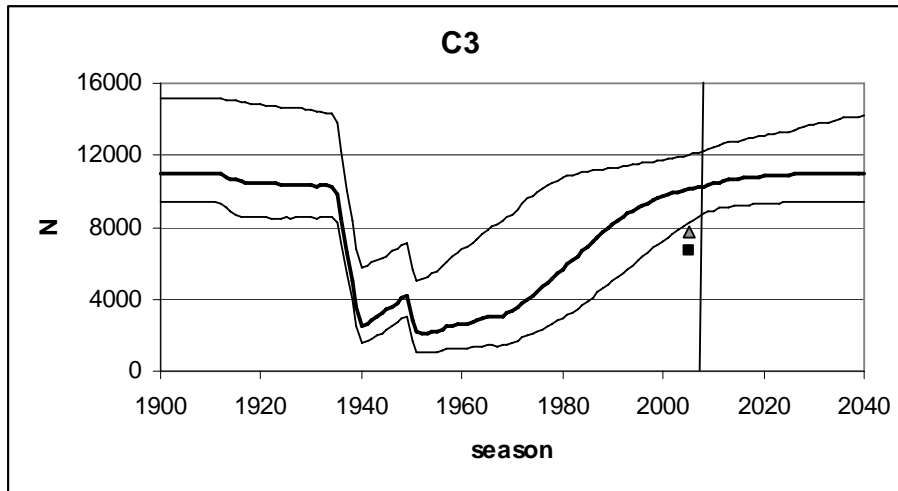


Figure 4e: The **Migrant** model cumulative recaptures (c.r.) for each year for both the observed data (open circles), and for the model estimated posterior medians and 90% probability intervals.

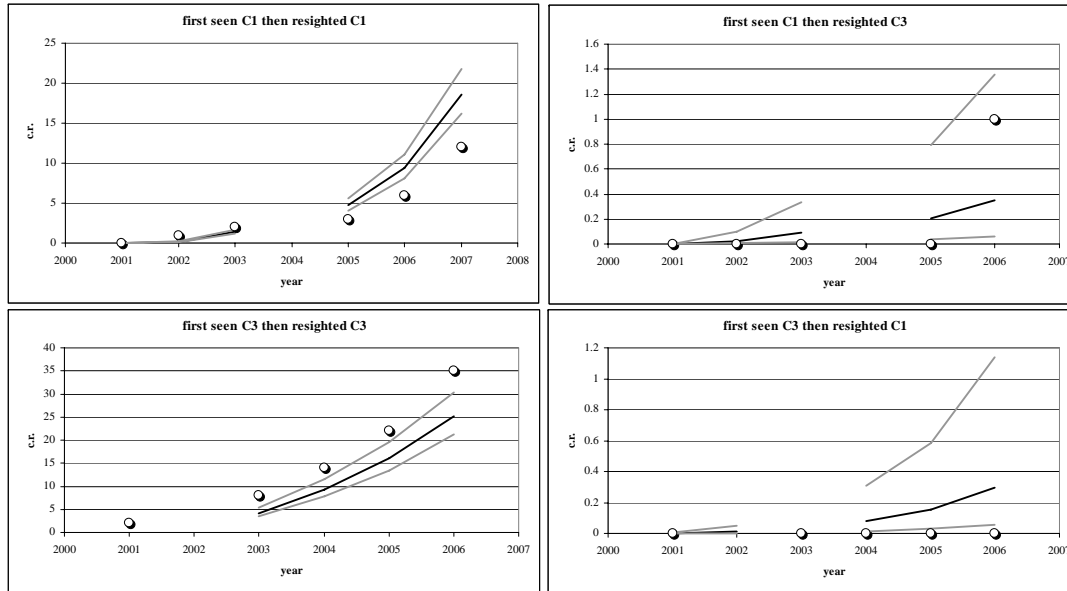


Figure 5a: Sabbatical model fit showing model values with values of all other C1 trend data approximately normalised.

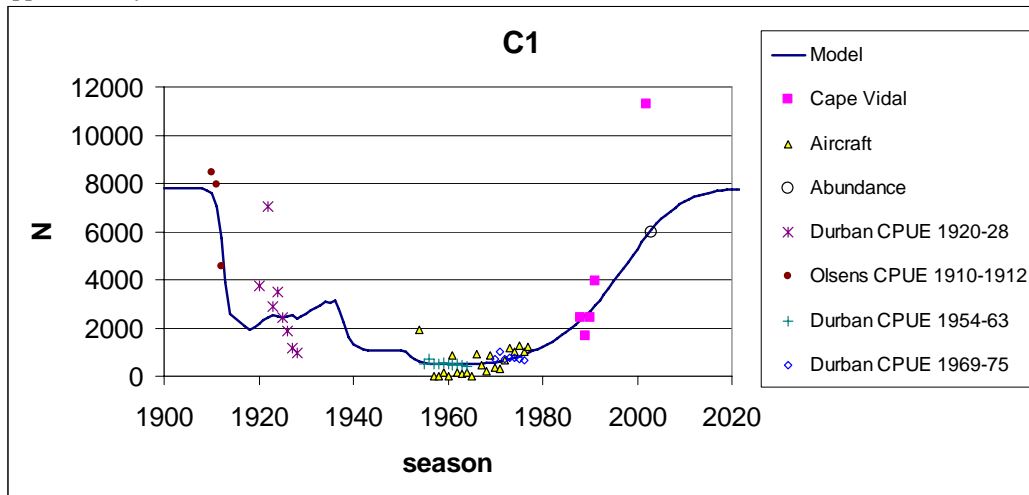


Figure 5b: Sabbatical model fit showing the C1+C3 feeding ground model values with IDCR abundance estimates. The median and 90% probability envelopes are shown, with the IDCR estimates shown as open circles.

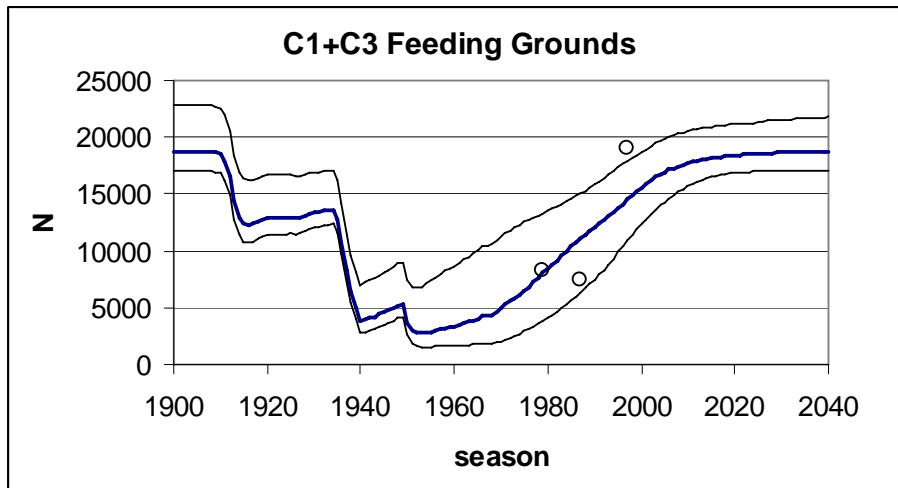


Figure 5c: Comparison between the sabbatical, resident, tourist and migrant model fits of C1 population trajectories (the Bayesian medians of  $N_y^{C1}$  are shown).

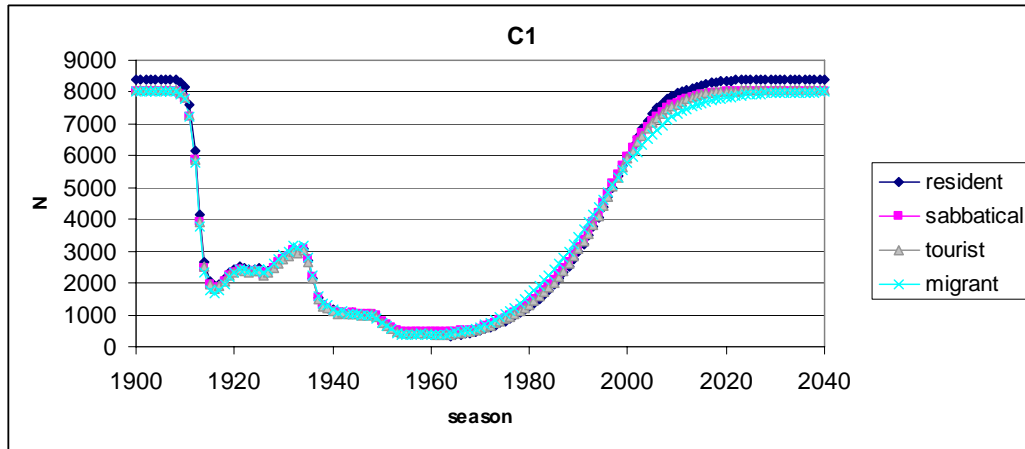


Figure 5d: Comparison between the sabbatical, resident, tourist and migrant model fits of C3 population trajectories (the Bayesian medians of  $N_y^{C3}$  are shown).

