IS THE LENGTH DISTRIBUTION OF C1 AND C3 HUMPBACK WHALE CATCHES CONSISTENT WITH AN AGE-STRUCTURED VERSION OF THE RESIDENT MODEL?

ANDREA MÜLLER, DOUG S. BUTTERWORTH AND SUSAN J. JOHNSTON

Contact email: andrea.muller@uct.ac.za

ABSTRACT

A sex- and age-structured BALEEN II population model is fitted to population abundance and trend as well as photo-id capture-recapture data for the C1 and C3 humpback whale breeding sub-stocks. The model is of the "Resident" type, i.e. no interchange between breeding grounds, though the whales do mix on the feeding grounds. Uniform selectivity on the 1+ population is assumed for both regions. A particular aim is to address the question of whether length distribution differences between the two regions are a reflection of different levels of past exploitation. Comparison with length distribution data for both regions does however indicate a greater proportion of larger males than anticipated in the C3 catches, and the reverse effect for both males and females in the C1 catches.

INTRODUCTION

Historic catch-length frequency data for humpback whales in the lower latitudes of the western Indian Ocean (Breeding Stock C) are available for 1936-1937 and 1949-1950. This document builds on previous humpback assessments (Johnston and Butterworth 2009, and references therein) which have been based on age-aggregated models, and introduces a sex- and age-structured model. The purpose of this investigation is not to incorporate the length data in the estimation processes at this stage, but rather to compare the model-predicted catch-length frequencies with those on record.

A particular motivation underlying this analysis is the discussion that arose at the February 2009 Intersessional Meeting on Southern Hemisphere Humpback Whale Assessment Methodology (IWC, 2009) in relation to a contribution by Best (2009) which argued, *inter alia*, that differences in the length distributions of whales caught off the east African and the Madagascar coasts were indicative of the effect of what had been differing levels of past exploitation on essentially discrete populations. The Meeting had suggested that this hypothesis be tested by means of the development of a simple age-structured population model.

The document provides an outline of the data used in the analysis, a description of the model implemented, and the results of the investigation.

DATA

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
- ii) Catches south of 40°S

These are described in more detail in the Appendix, which gives the method used to obtain the sex-disaggregated catch series used in this analysis (shown in Tables A.1-3 in the Appendix).

Absolute abundance data

The absolute abundance data considered in these analyses are presented in Table 1. For breeding stock C1, an estimate of 5965 (CV = 0.17) for the 2003 season has been provided by Findlay *et al.* (in press).

Trend information

Cape Vidal sightings per unit effort data are 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.

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. 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.

Length-at catch data

Catch-length frequency data held by the IWC Secretariat are available for the periods 1936-1937 and 1949-1950 from the following sources:

- (i) Whale station at Durban (1936 and 1937)
- (ii) Uniwaleco expeditions in 1937 (Africa and Madagascar)
- (iii) AngloNorse expeditions in 1949 and 1950.

Plots of these data accumulated over years for Africa (C1) and Madagascar (C3) are shown split by sex in Figures 2a-d. The "stretching" of whales above the 35 ft size limit of the period for the C3 catches is very evident. For this reason model implementations for C3 group all lengths below 36 ft into a single "36-" group..

METHODS

In this assessment the generalized BALEEN II population dynamics model is used as in the HITTER-FITTER package (Punt 1996).

Basic Dynamics

BALEEN II is age- and sex-structured, and considers animals as being either recruited or unrecruited. It assumes that all whaling takes place at the start of the year, and that all animals are recruited (and have reached the age at first parturition) by the age m-1. The dynamics of the population are assumed to be governed by the equations:

$$N_{y+1,a}^{C1,s} = \begin{cases} 0 & \text{if } a = 0 \\ (N_{y,a-1}^{C1,s} - C_{y,a-1}^{C1,s})S_{y,a-1}^{s} + U_{y,a-1}^{C1,s}S_{y,a-1}^{s}\delta_{a}^{s} & \text{if } 1 \le a \le m-1 \\ (N_{y,m}^{C1,s} - C_{y,m}^{C1,s})S_{y,m}^{s} + (N_{y,m-1}^{C1,s} - C_{y,m-1}^{C1,s})S_{y,m-1}^{s} & \text{if } a = m \end{cases}$$

$$U_{y+1,a}^{C1,s} = \begin{cases} 0.5P_{y+1}^{C1,m}f_{y+1}^{C1} & \text{if } a = 0 \\ U_{y,a-1}^{C1,s}S_{y,a-1}^{s}(1-\delta_{a}^{s}) & \text{if } 1 \le a \le m-1 \end{cases}$$

$$N_{y+1,a}^{C3,s} = \begin{cases} 0 & \text{if } a = 0 \\ (N_{y,a-1}^{C3,s} - C_{y,a-1}^{C3,s})S_{y,a-1}^{s} + U_{y,a-1}^{C3,s}S_{y,a-1}^{s}\delta_{a}^{s} & \text{if } 1 \le a \le m-1 \\ (N_{y,m-1}^{C3,s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} + (N_{y,m-1}^{C3,s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} & \text{if } a = m \end{cases}$$

$$U_{y+1,a}^{C3,s} = \begin{cases} 0.5P_{y+1}^{C3,m}f_{y+1}^{C3,s} & \text{if } 1 \le a \le m-1 \\ (N_{y,m-1}^{C3,s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} & \text{if } a = m \end{cases}$$

$$U_{y+1,a}^{C3,s} = \begin{cases} 0.5P_{y+1}^{C3,m}f_{y+1}^{C3,s} & \text{if } a = m \\ (N_{y,a-1}^{C3,s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} - C_{y,m-1}^{C3,s})S_{y,m-1}^{s} & \text{if } a = m \end{cases}$$

$$U_{y+1,a}^{C3,s} = \begin{cases} 0.5P_{y+1}^{C3,m}f_{y+1}^{C3,s} & \text{if } a = m \\ U_{y+1,a}^{C3,s} = \begin{cases} 0.5P_{y+1}^{C3,m}f_{y+1}^{C3,s} & \text{if } a = m \\ U_{y,a-1}^{C3,s}S_{y,a-1}^{s}(1-\delta_{a}^{s}) & \text{if } 1 \le a \le m-1 \end{cases}$$

where

 $N_{ta}^{C1,s}$ is the number of recruited animals of age a and sex s (m/f) at the start of year y for the C1 sub-stock,

- $U_{va}^{C1,s}$ is the number of unrecruited animals of age a and sex s at the start of year y for the C1 sub-stock,
- $N_{ta}^{C3,s}$ is the number of recruited animals of age a and sex s(m/f) at the start of year y for the C3 sub-stock,
- $U_{va}^{C3,s}$ is the number of unrecruited animals of age a and sex s at the start of year y for the C3 sub-stock,
- δ_a^s is the proportion of unrecruited animals of sex s which recruit at age a,
- S_{va}^{s} is the annual survival rate of animals of sex s and age a during year y,

 $C_{v,a}^{C1,s}$ is the total catch (in terms of animals) in year y for sex s and age a from breeding population C1,

 $C_{y,a}^{C3,s}$ is the total catch (in terms of animals) in year y for sex s and age a from breeding population C3,

 $P_{y}^{C1,M}$ is the number of C1 females which have reached the age at first parturition by the start of year y,

 f_v^{C1} is pregnancy rate during year y for sub-stock C1,

 $P_v^{C3,M}$ is the number of C3 females which have reached the age at first parturition by the start of year y,

- f_{v}^{C3} is pregnancy rate during year y for sub-stock C3, and
- m is the maximum (lumped) age-class (all animals of ages m and m-l are assumed to be recruited and to have reached the age at first parturition).

The annual survival rate is given by:

$$S_{y,a}^{s} = \exp(-M) \tag{2}$$

where M is the instantaneous rate of natural mortality for animals of sex s and age a in year y.

Density dependence

Density dependence on fecundity can be achieved by writing the pregnancy rate, f_y , as follows:

$$f_{y}^{C1} = f_{-\infty} \left[1 + A_{f} \left\{ 1 - \left(P_{y}^{C1,D} / K^{C1,D} \right)^{z_{f}} \right\} \right]$$
(3)

where

- A_f is the resilience parameter;
- Z_f is the degree of compensation
- $P_y^{C1,D}$ is the size, at the start of year y, of the component of the population to which density dependence is functionally related, taken to be the number of females which have reached the age at first parturition $P_y^{C1,M}$, where

$$P_{y}^{C1,M} = \sum_{a=a_{\min}}^{m} \beta_{a} \left(N_{y,a}^{C1,f} + U_{y,a}^{C1,f} \right)$$
(4)

where

 a_{min} is the minimum age that a female can reach first parturition,

- $f_{-\infty}$ is the pregnancy rate at the pre-exploitation equilibrium,
- β_a is the fraction of females of age *a* which have reached the age at first parturition, and
- K^{D} is the pre-exploitation equilibrium size of the component of the population to which density dependence is functionally related.

Recruitment and maturity

The fraction of unrecruited animals of sex s and age a which recruit at age a+1, δ_{a+1}^{s} , is given by:

SC/61/SH29

$$\delta_{a+1}^{s} = \begin{cases} \left(\alpha_{a+1}^{s} - \alpha_{a}^{s}\right) / \left(1 - \alpha_{a}^{s}\right) & \text{if } \alpha_{a}^{s} < 1 \\ 1 & \text{if } \alpha_{a}^{s} = 1 \end{cases}$$
(5)

where

 α_a^s is the proportion of animals of sex s and age a which would be recruited if the population were at preexploitation equilibrium:

$$\alpha_{a}^{s} = \begin{cases} 0 & \text{if } a = 0\\ \left[1 + \exp\left\{-\left(a - r_{50}^{s}\right) / \sigma_{r}^{s}\right\}\right]^{-1} & \text{if } 1 \le a \le m - 2\\ 1 & \text{if } a \ge m - 1 \end{cases}$$
(6)

where

 r_{50}^{s} is the age at 50% recruitment for animals of sex s, and

(

(

 σ_r^s is the parameter which determines the width of the recruitment ogive for animals of sex s.

The proportion of females of age at which have reached the age at first parturition is given by:

$$\beta_{a} = \begin{cases} 0 & \text{if } a < a_{\min} \\ \left[1 + \exp\left\{-\left(a - p_{50}\right) / \sigma_{p}\right\}\right]^{-1} & \text{if } a_{\min} \le a \le m - 2 \\ 1 & \text{if } a \ge m - 1 \end{cases}$$
(7)

where

 p_{50} is the age at 50% maturity plus one year, and

 σ_r^s is the parameter which determines the width of the maturation ogive.

The parameter values are given in Table 4 (note that the parameter values are chosen such that the recruitment and maturity-at-age vectors are knife-edge).

The applications in this paper assume that MSYL=0.6 and MSYR refer to the total (1+) component of the population, and that density dependence acts on the mature female component. Values of the A_f and z_f parameters for different MSYR values and the biological parameters applicable were obtained from the HITTER-FITTER package (C. de Moor, pers. comm) and are listed in Table 5. Estimation was effected by liner interpolation between these values.

Catches

The total yearly catch by sex is given by:

$$C_{y}^{C1,s} = C_{y}^{C1,s,B} + C_{y}^{C1,s,F}$$

$$C_{y}^{C3,s} = C_{y}^{C3,s,B} + C_{y}^{C3,s,F}$$
(8)

where

 $C_{\nu}^{C1,s}$ is the total catch (in terms of animals) in year y from breeding population C1,

 $C_{\nu}^{C3,s}$ is the total catch (in terms of animals) in year y from breeding population C3,

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

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

 $C_y^{C3,s,B}$ are the catches of animals in year *y* for sex *s* from the C3 sub-stock in either breeding area, and $C_y^{C3,s,F}$ are the catches of animals in year *y* for sex *s* from the C3 sub-stock in the feeding area.

To split the feeding ground catch, it is assumed that the catches from each sub-stock 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:

$$C_{y}^{C1,s,F} = C_{y}^{s,F} \frac{N_{y}^{C1,s}}{\left(N_{y}^{C1,s} + N_{y}^{C3,s}\right)} \quad \text{and} \quad C_{y}^{C3,s,F} = C_{y}^{s,F} \frac{N_{y}^{C3,s}}{\left(N_{y}^{C1,s} + N_{y}^{C3,s}\right)}$$
(9)

where

 $N_{v}^{C1,s}$ is the total number of recruited C1 animals of sex s at the start of the year y, and

 $N_{v}^{C3,s}$ is the total number of recruited C3 animals of sex s at the start of the year y

given by:

$$N_{y}^{C1,s} = \sum_{a=1}^{m} N_{y,a}^{C1,s}$$
, and $N_{y}^{C3,s} = \sum_{a=1}^{m} N_{y,a}^{C3,s}$ (10)

The catch at age is assumed to be taken non-selectively across all recruited animals and is calculated as follows:

$$C_{y,a}^{C1,s} = C_y^{C1,s} N_{y,a}^{C1,s} / N_y^{C1,s} , \text{ and}$$

$$C_{y,a}^{C3,s} = C_y^{C3,s} N_{y,a}^{C3,s} / N_y^{C3,s}$$
(11)

Growth curves and catch-at-length

Chittleborough (1965) provides sex-specific length-at-age data from the 1950's. These were used to obtain separate growth curves for males and females. Owing to a relatively poor fit to the von Bertalanffy growth curve, an alternative approach has been taken in which four straight lines are fit to the data, with parameters estimated to give best possible fit to the data (see Figures 1a and b).

These growth curves can be used to obtain catch-at-length estimates from the catch-at-age estimates provided by the BALEEN II model. Given the catches-at-age, $C_{y,a}^{Ci,s}$, where $i = \{1,3\}$, these can be converted into proportions of the catch of age *a*:

$$p_{y,a}^{Ci,s} = C_{y,a}^{Ci,s} / \sum_{a'} C_{y,a'}^{Ci,s}$$
(12)

Using the above-mentioned growth curves, these proportions at age can be converted to proportions at length, under the assumption that the length-at-age distributions remain constant over time:

$$p_{y,\ell}^{Ci,s} = \sum_{a} p_{y,a}^{Ci,s} A_{a,\ell}^{Ci,s}$$
(13)

where $A_{a,\ell}^{Ci,s}$ is the proportion of animals of age *a* and sex *s* that fall into length group ℓ for sub-stock C*i*, where $i = \{1,3\}$. The *A* matrix has been calculated under the assumption for each age *a* the length-at-age is normally distributed about a mean length given by the above-mentioned growth curves. The standard deviation used for this normal distribution is a function of age and proportional to the mean length:

$$\sigma_a^{Ci,s} = 0.05 \overline{\ell}_a^{Ci,s} \tag{14}$$

where $\overline{\ell}_a^{Ci,s}$ is the mean length for age *a*, sex *s* and sub-stock Ci ($i = \{1,3\}$) obtained from the growth curve. Note that with mean lengths of typically 30-40 ft, this means that 95% of the length at age distribution varies between ± 3 and ± 4 ft.

Estimation process

Difficulties experienced in estimating the MSYR value (largely due to number of catches exceeding number of whales in certain age and sex cells) led to the following estimation approach: MSYR is set at a range of values and for each such value K^{C1} and K^{C3} (referring to the 1+ population) are estimated using the simplex minimisation routine to maximise the likelihood described below.

Likelihood contributions

The data used in the likelihood are the SPUE estimates from Cape Vidal (indexing the C1 population), the absolute abundance estimate from the sighting survey (C1) and the capture-recapture data (both C1 and C3).

Cape Vidal SPUE estimates

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

$$I_{y}^{C1} = \boldsymbol{q}^{C1} \boldsymbol{N}_{y}^{C1} \boldsymbol{e}^{\varepsilon_{y}}$$
(15)

where

 I_{v}^{C1} is the survey-based relative abundance (or SPUE index) for year y for breeding sub-stock C1,

 q^{C1} is the catchability coefficient for that index for breeding sub-stock C1,

 N_v^{C1} is the model estimate of the observed population size at the start of year y for breeding sub-stock C1, and

$$\varepsilon_{y}$$
 is from $N\left(0, \left(\sigma_{SPUE, VIDAL}^{C1}\right)^{2}\right)$

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

$$\sigma_{SPUE,VIDAL}^{C1} = \sqrt{1/\overline{n}_{SPUE,VIDAL}^{C1}} \sum_{y} \left(\ln I_{SPUE,VIDAL,y}^{C1} - \ln q_{SPUE,VIDAL}^{C1} - \ln N_{y}^{C1} \right)^{2}$$
(16)

where

 $\overline{n}_{SPUE,VIDAL}^{C1}$ 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:

$$\ln \hat{q}_{SPUE,VIDAL}^{C1} = 1/\overline{n}_{SPUE,VIDAL}^{C1} \sum_{y} \left(\ln I_{SPUE,VIDAL,y}^{C1} - \ln N_{y}^{C1} \right)$$
(17)

Absolute abundance estimate

This is treated in the same way as the SPUE indices above, except that q is set to 1 (the estimate is considered to be unbiased) and the σ value is taken to be the CV estimate for the survey and input.

Capture-recapture:

Tables 3a and 3b report the capture-recapture data, namely

 n_{y}^{Ci} , the number of animals captured in breeding region Ci in year y, and

 $m_{y,y'}^{Ci}$, the number of Ci animals captured in year y that were recaptured in year y', where i = 1,3.

If p_y^{Ci} is the probability a Ci animal is seen year y, then the number of Ci animals captured in year y is given by:

$$n_{y}^{Ci} = p_{y}^{Ci} N_{y,1+}^{Ci}$$
(18)

where $N_{y,l+}^{Ci}$ is the total (1+) Ci population. The model predicted number of animals in Ci captured in year y that were recapture in year y' is given by

$$\hat{m}_{y,y'}^{Ci} = p_{y'}^{Ci} p_{y}^{Ci} N_{y,1+}^{Ci} e^{-M(y'-y)} \qquad i = 1,3$$
(19)

where M is the natural mortality rate (which is taken to be 0.03 yr⁻¹).

The probability of a model-predicted $\hat{m}_{y,y'}^{Ci}$, given the observed $m_{y,y'}^{Ci}$, is derived assuming a Poisson distribution, and the likelihood contribution is given by:

$$L_{capture-recapture} = \frac{\left(\hat{m}_{y,y'}^{Ci}\right)^{m_{y,y'}^{Ci}}}{m_{y,y'}^{Ci}!} e^{-\hat{m}_{y,y'}^{Ci}}$$
(20)

The likelihood

The negative log-likelihood function taking all the data contributions into account is:

$$-\ln L = \left[\overline{n}_{SPUE,VIDAL}^{C1} \ln \sigma_{SPUE,VIDAL}^{C1} + \sum_{y} \left(\ln I_{SPUE,VIDAL,y}^{C1} - \ln q_{SPUE,VIDAL}^{C1} - \ln N_{y}^{C1} \right)^{2} \right] + \left[\frac{1}{2CV^{2}} \left(\ln N_{target}^{C1,obs} - \ln N_{target}^{C1} \right)^{2} \right] + \sum_{y=y_{0}}^{y_{f}-1} \sum_{y=y_{0}}^{y_{f}} \sum_{y'=y+1}^{y_{f}} \left[-m_{y,y'}^{Ci} \ln \hat{m}_{y,y'}^{Ci} + \hat{m}_{y,y'}^{Ci} \right]$$
(21)

where y_0 is the first year of captures, y_f is the last year of captures and i = 1,3

Sensitivity test

As a sensitivity test, the K^{C1} and K^{C3} obtained for the resident model in Johnston and Butterworth are used as fixed inputs for the 1+ population numbers to run the model fitting to MSYR.

RESULTS

Table 4 shows parameter values fixed for the analyses – note that an unselective harvest from age 1 and above is assumed. The results for the main analysis are reported in Table 6a, and Figures 3a and b illustrate the population trajectories and data fits. Figures 4a-d compare the model predicted catch-length frequencies with those reported.

The sensitivity test results are reported in Table 6b, and are illustrated in Figures 5 and 6.

DISCUSSION

Table 6a for the main analysis shows a smaller MSYR value than usual for the age- and sex-aggregated assessments of particularly the C1 population, and consequently lesser current depletion levels. The constraint that precludes a better fit to the trend information is that that would require a smaller population size in the 1960s, and there are then too few males to have admitted the male catches made at that time. A higher value of MSYR (and higher current depletion levels) follow if K values are increased as in the sensitivity test.

For the main analysis, only the average observed C3 female length distribution is well fitted by the model. For C3 males there is a greater proportion of larger whales caught than the model predicts. The reverse is true for the C1 population, where the proportion of smaller males and even more so smaller females is appreciably greater than the model predicts (see Figure 5). These features do not change qualitatively for the sensitivity test (see Figure 6).

The February 2009 Intersessional Meeting on Southern Hemisphere Humpback Whale Assessment Methodology (IWC, 2009) offered four alternative explanations or desired analyses in relation to a contribution by Best and Brandao (2009) which argued, *inter alia*, that differences in the length distributions of whales caught off the east African and the Madagascar coasts were indicative of differing levels of past exploitation on essentially discrete populations.

- (1) A test of the hypothesis using a simple age-based model with knife-edged selectivity was proposed. This is pursued in the analyses of this paper, which demonstrate that differential past exploitation alone is not sufficient to account for the (quite appreciable) differences in catch-at-length distributions off the African mainland and around Madagascar.
- (2) IWC (2009) suggests the possibility of distribution patterns differing with age. The comment in IWC (2009) that the Madagascar catches occurred mainly near the southern tip of the island is not correct, as these catches extended quite far north on both the eastern and western sides of the island. However the analyses of this paper do suggest that the catches off the African mainland are not representative of the complete C1 population, given the "over-representation" of smaller animals. Since catches along that coast were consistent in terms of age and sex, and the operations from which the length data were obtained were conducted identically to those off Madagascar, the most likely explanation seems to be that older C1 animals are preferentially located further offshore on migrations or do not all migrate very far north every year.
- (3) IWC (2009) suggests that body sizes might be different in the two regions because of selection between habitats, though interchange between the regions is not low. An initial impression from the modelling conducted is that this effect would have to be extremely strong to account for what are relatively substantial observed differences. Further this suggested mechanism seems unlikely given that feeding is primarily in the Antarctic where the two groups of whales would be highly mixed.
- (4) The suggestion that whaling selectivity differs between the two regions is responded to in (2) above.

ACKNOWLEDGEMENTS

We thank Peter Best for discussions. Financial support from the South African National Research Foundation is gratefully acknowledged.

REFERENCES

Best, P.B. and Brandão, A. 2009. Humpback whaling at Madagascar, 1910-1950. IWC document SC/F09/SH2. 19pp.

- Cerchio, S, Ersts, P., Pomilla, C., Loo, J., Razafindrakoto, Y., Leslie, M., Andrianrivelo, 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., Andrianarivelo, 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.
- Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. mar. Freshwat* 16: 33-128.
- 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.
- Findlay, K., Meyer, M, Elwen, S., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Sitoe, 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).
- Johnston, S.J. and Butterworth, D.S. 2009. Bayesian assessments using models which allow for interchange on the breeding grounds of Southern Hemisphere humpback whale breeding sub-stocks C1 and C3. IWC document SC/61/SH27.

- IWC. 2009. Report of the intersessional meeting on Southern Hemisphere humpback whale assessment methodology. IWC document SC/61/REP?.
- Punt, A.E. 1996. The effects of assuming that density dependence in the HITTER-FITTER model acts on natural mortality rather than fecundity. *Rep. int. Whal. Commn* 46: 629-636.

Table 1

Table 1: Absolute abundance estimate considered in analyses for sub-stocks C1

Breeding sub-stock	Abundance estimate	Year applicable	Source
C1	5965 (CV = 0.17)	2003	Findlay et al. (in press)

Year	Cape Vidal CPUE (Findlay and Best 2006)
1988	358
1989	249
1990	359
1991	587
2002	1673

Table 2: Relative abundance trend data for sub-stock C1.

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]	

Ν								
	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	Х	0	0	0	0	0	0	0
2001		X	1	0	0	0	0	0
2002			Х	1	1	0	0	1
2003				Х	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		Х	1	3	3	3	2
2002			X	3	0	0	0
2003				Х	2	1	3
2004					Х	4	3
2005						Х	4
2006							X

Table 4: Model parameters fixed on input

General population parameters					
т	Max age	50			
М	Natural mortality rate	0.03			
a_r	Age at recruitment	1			
a_m	Age at maturity	5			
Paramet	er values for equations 6	and 7			
<i>r</i> ₅₀ ^{<i>m</i>}	1				
r_{50}^{f}	1				
σ_r^m	0				
σ_r^f	0				
$ ho_{50}$	5				
$\sigma_{ ho}$	0				

Table 5: A_f and z_f values for fixed MSYR(1+)

MSYR	A_{f}	Z _f
0	0	2.389
0.005	0.27379	2.18054
0.01	0.57504	1.98889
0.015	0.90781	1.81291
0.02	1.27699	1.65091
0.025	1.68853	1.50143
0.03	2.14976	1.3632
0.035	2.66974	1.23511
0.04	3.25991	1.11618
0.045	3.93485	1.00557
0.05	4.71345	0.9025
0.055	5.62065	0.80632
0.06	6.69007	0.71643
0.065	7.9681	0.63228
0.07	9.52069	0.55341
0.075	11.44478	0.47938
0.08	13.88899	0.40982
0.085	17.09332	0.34437
0.09	21.47216	0.28273
0.095	27.80782	0.22461
0.1	37.77536	0.16974

	BS C1	BS C2+3		
Historic catch	Feeding grounds split	Feeding grounds split		
	proportional to abundance	proportional to abundance		
Recent abundance	5965 (2003)	None		
Trend information	Cape Vidal	None		
Capture-recapture data	"All" photo-ID data*	"All" photo-ID data*		
MSYR	0.034	0.034		
K (1+)	9910	8916		
K (mat)	8790	7908		
N _{min}	1168	1031		
N _{min} /K	0.1179	0.1156		
N ₂₀₀₆ (1+)	7162	7662		
N ₂₀₀₆ (mat)	5670	6329		
N ₂₀₀₆ /K (1+)	0.7227	0.8594		
N ₂₀₀₆ /K (mat)	0.6452	0.8003		

Table 6a: Assessment results (model fitted to both *K*'s and to MSYR)

* 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.

	BS C1	BS C2+3		
Historic catch	Feeding grounds split	Feeding grounds split		
Recent abundance	5965 (2003)	None		
Trend information	Cape Vidal	None		
Capture-recapture data	"All" photo-ID data*	"All" photo-ID data*		
MSYR	0.045	0.045		
K (1+)	8402	11173		
K (mat)	7462	9910		
N _{min}	547	3845		
N _{min} /K	0.0651	0.3442		
N ₂₀₀₆ (1+)	7488	11079		
N ₂₀₀₆ (mat)	6097	9817		
N ₂₀₀₆ /K (1+)	0.8912	0.9916		
N ₂₀₀₆ /K (mat)	0.8182	0.9907		

 Table 6b: Sensitivity test results (K's fixed from Johnston and Butterworth (2009) Resident model and MSYR estimated)



Figure 1a: Length-age data from Chittleborough (1965) with fitted growth curves, for male animals

Figure 1b: Length-age data from Chittleborough (1965) with fitted growth curves, for female animals







Figure 2b: Original catch-length data for C1 female catches (1936 and 1937 combined)



C1 female catches

15

Figure 2c: Original catch-length data for C3 male catches (1937, 1949 and 1950 combined)



Figure 2d: Original catch-length data for C3 female catches (1937, 1949 and 1950 combined)





Figure 3a: Population model fit to C1 trend data (Cape Vidal), capture-recapture data and the 2003 abundance estimate for C1



Figure 3b: Population model fit toC3, capture-recapture data



Figure 4a: Comparison of the model-predicted **C1 male** catches-at-length to observed catches (accumulated for the years 1936 and 1937)



Figure 4b: Comparison of the model-predicted **C1 female** catches-at length to observed catches (accumulated for the years 1936 and 1937)



Figure 4c: Comparison of the model-predicted **C3 male** catches-at-length to observed catches (accumulated for the years 1937, 1949 and 1950)



Figure 4d: Comparison of the model-predicted C3 female catches-at-length to observed catches (accumulated for the years 1937, 1949 and 1950)



19

Figure 5a: Sensitivity results (*K*'s fixed based on Johnston and Butterworth (2009) resident model results) for C1 population trajectory



Figure 5b: Sensitivity results for C3 population trajectory







Figure 6b: Comparison of the model-predicted C1 female catches-at-length to observed catches for the sensitivity case



C1 Females

Figure 6c: Comparison of the model-predicted C3 male catches-at-length to observed catches for the sensitivity case



Figure 6d: Comparison of the model-predicted C3 female catches-at-length to observed catches for the sensitivity case



APPENDIX

The sex-disaggregation of humpback catches from breeding stocks C1 and C3

Catches North of 40°S

Catches from the C1 and C3 breeding stocks are reported as combined (male+female) catches. For C1 we combine catches reported for Southern Cape, Natal and Mozambique, and the C3 catches are from Western Indian Ocean. Russian catches caught between $10^{\circ} - 60^{\circ}$ E are split equally and added to the C1 and C3 catch database.

C1 Catches

For certain periods the catches have been either totally or partially sexed. Figure A.1a shows the percentages of the total catch that have been sexed. Figure A.1b shows the actual sex ratio – here the percentages of the sexed-catch that are males is illustrated.

In order to produce a sex-disaggregated catch series for the full time period, the following rules were applied:

- Use the observed sex ratio in years these are available
- For years for which there is no sex-ratio information, the following apply:
- 1. 1900-1930 period use the average of available sex ratio data from 1918-1930 for the missing years (=55.71% male). Note that when calculating the average, we use (total males/total whales) over the 1900-1930 period.
- 2. 1939-1945 period use the average sex ratio reported for the five years before and five years after this period (=53.14% male).
- 3. 1968+ period: for years with no sex ratio data, use the average of the 1955-1967 period (=58.67%).

The final sex-disaggregated catch series for C1 is reported in Table A.1.

C3 Catches

As with C1, for certain periods the catches have been either totally or partially sexed. Figure A.2a shows the percentages of the total catch that have been sexed. Figure A.2b shows the actually sex ratio – here the percentage of the sexed-catch that are males is illustrated.

In order to produce a sex-disaggregated catch series for the full time period, the following rules were applied:

- Use the observed sex ratio in years these are available
- For years for which there is no sex-ratio information,
- 1. For pre-1940 use the 1937 sex ratio (61.65% male)
- 2. For 1951+, use the average (over the 1951+ period) for the years for which sex ratio information is available (62.5% male)

The final sex-disaggregated catch series for C3 is reported in Table A.2.

Catches South of 40°S

These catches are from $10^{\circ} - 60^{\circ}$ E. There is no differentiation between C1 and C3. Figure A.3a shows the percentages of the total catch that have been sexed. Figure 3b shows the actually sex ratio – here the percentage of the sexed-catch that are males is illustrated. All but three years (1957-1959) have sex ratio information. For these three years, we use the average of the 1948-1967 period (42.5%). Table A.333 reports the final sex-disaggregated catch series for catches south of 40° S.

Table A.1: Sex disaggregated catches for breeding sub-stock C1 for catches taken north of 40°S.

Year	Total C1 annual catches	Total C1 animals sexed	C1 % male values	C1 male catches	C1 female catches
1900	0	0	55.71	0	0
1901	0	0	55.71	0	0
1902	0	0	55.71	0	0
1903	0	0	55.71	0	0
1904	0	0	55.71	0	0
1905	0	0	55.71	0	0
1906	0	0	55.71	0	0
1907	0	0	55.71	0	0
1908	104	0	55.71	58	46
1909	149	0	55.71	83	66
1910	632	0	55.71	352	280
1911	1580	0	55.71	880	700
1912	2313	0	55.71	1289	1024
1913	1805	0	55.71	1006	799
1914	830	0	55.71	462	368
1915	334	0	55.71	186	148
1916	94	0	55.71	52	42
1917	7	0	55.71	4	3
1918	9	2	100.00	9	0
1919	91	0	55.71	51	40
1920	148	50	50.00	74	74
1921	251	0	55.71	140	111
1922	285	285	62.46	178	107
1923	183	109	48.62	89	94
1924	187	187	57.22	107	80
1925	372	167	59.28	221	151
1926	124	124	49.19	61	63
1927	86	86	52.33	45	41
1928	62	62	41.94	26	36
1929	99	50	56.00	55	44
1930	134	131	56.49	76	58
1931	72	72	47.22	34	38
1932	307	307	55.70	171	136
1933	162	162	51.23	83	79

1934	514	514	53.31	274	240
1935	418	417	50.60	212	206
1936	300	300	50.33	151	149
1937	242	242	52.07	126	116
1938	177	177	50.28	89	88
1939	200	0	53.14	106	94
1940	176	0	53.14	94	82
1941	79	0	53.14	42	37
1942	156	0	53.14	83	73
1943	80	0	53.14	43	37
1944	115	0	53.14	61	54
1945	116	0	53.14	62	54
1946	93	93	61.29	57	36
1947	89	89	57.30	51	38
1948	182	182	57.69	105	77
1949	190	190	62.11	118	72
1950	151	151	46.36	70	81
1951	103	103	53.40	55	48
1952	111	111	51.35	57	54
1953	89	89	49.44	44	45
1954	28	27	48.15	13	15
1955	49	49	63.27	31	18
1956	36	36	50.00	18	18
1957	34	34	67.65	23	11
1958	39	39	64.10	25	14
1959	38	38	55.26	21	17
1960	36	36	50.00	18	18
1961	48	44	55.68	27	21
1962	39	37	50.00	20	20
1963	38.5	37.5	62.67	24	14
1964	6.5	3.5	28.57	2	5
1965	4.5	2.5	60.00	3	2
1966	31	31	54.84	17	14
1967	41	33	75.76	31	10
1968	0	0	58.67	0	0
1969	0	0	58.67	0	0
1970	0	0	58.67	0	0
1971	0	0	58.67	0	0
1972	0	0	58.67	0	0
1973	1	1	100.00	1	0
1974	0	0	58.67	0	0

1975	0	0	58.67	0	0
1976	0	0	58.67	0	0
1977	0	0	58.67	0	0
1978	0	0	58.67	0	0
1979	0	0	58.67	0	0

Table A.2: Sex disaggregated catches for breeding sub-stock C3 for catches taken north of 40°S.

Year	Total C3 annual catches	Total animals sexed	C3 % male	C3 male catches	C3 female catches
1900	0	0	61.65	0	0
1901	0	0	61.65	0	0
1902	0	0	61.65	0	0
1903	0	0	61.65	0	0
1904	0	0	61.65	0	0
1905	0	0	61.65	0	0
1906	0	0	61.65	0	0
1907	0	0	61.65	0	0
1908	0	0	61.65	0	0
1909	0	0	61.65	0	0
1910	0	0	61.65	0	0
1911	0	0	61.65	0	0
1912	25	0	61.65	15	10
1913	0	0	61.65	0	0
1914	0	0	61.65	0	0
1915	0	0	61.65	0	0
1916	0	0	61.65	0	0
1917	0	0	61.65	0	0
1918	0	0	61.65	0	0
1919	0	0	61.65	0	0
1920	0	0	61.65	0	0
1921	0	0	61.65	0	0
1922	0	0	61.65	0	0
1923	0	0	61.65	0	0
1924	0	0	61.65	0	0
1925	0	0	61.65	0	0
1926	0	0	61.65	0	0
1927	0	0	61.65	0	0
1928	0	0	61.65	0	0
1929	0	0	61.65	0	0
1930	0	0	61.65	0	0
1931	0	0	61.65	0	0
1932	0	0	61.65	0	0
1933	0	0	61.65	0	0

1934	0	0	61.65	0	0
1935	0	0	61.65	0	0
1936	0	0	61.65	0	0
1937	1223	1223	61.65	754	469
1938	1752	0	61.65	1080	672
1939	1240	0	61.65	764	476
1940	0	0	61.65	0	0
1941	0	0	61.65	0	0
1942	0	0	61.65	0	0
1943	0	0	61.65	0	0
1944	0	0	61.65	0	0
1945	0	0	61.65	0	0
1946	0	0	61.65	0	0
1947	0	0	61.65	0	0
1948	0	0	61.65	0	0
1949	1333	1333	61.37	818	515
1950	714	707	34.37	245	469
1951	0	0	62.50	0	0
1952	0	0	62.50	0	0
1953	0	0	62.50	0	0
1954	0	0	62.50	0	0
1955	0	0	62.50	0	0
1956	0	0	62.50	0	0
1957	0	0	62.50	0	0
1958	0	0	62.50	0	0
1959	0	0	62.50	0	0
1960	0	0	62.50	0	0
1961	12	8	56.25	7	5
1962	2	1	50.00	1	1
1963	1	1	100.00	1	0
1964	7	4	28.57	2	5
1965	4	3	60.00	2	1
1966	31	31	54.84	17	14
1967	41	33	75.76	31	10
1968	0	0	62.50	0	0
1969	0	0	62.50	0	0
1970	0	0	62.50	0	0
1971	0	0	62.50	0	0
1972	0	0	62.50	0	0
1973	0	0	62.50	0	0
1974	0	0	62.50	0	0

SC/61/SH29

1975	0	0	62.50	0	0
1976	0	0	62.50	0	0
1977	0	0	62.50	0	0
1978	0	0	62.50	0	0
1979	0	0	62.50	0	0

Table A.3: Breeding stock C sex disaggregated catches for south of 40°S.

	South annual catches	Total animals sexed	% male	South male catches	South female catches
1900	0	0		0	0
1901	0	0		0	0
1902	0	0		0	0
1903	0	0		0	0
1904	0	0		0	0
1905	0	0		0	0
1906	0	0		0	0
1907	0	0		0	0
1908	0	0		0	0
1909	0	0		0	0
1910	0	0		0	0
1911	0	0		0	0
1912	0	0		0	0
1913	0	0		0	0
1914	0	0		0	0
1915	0	0		0	0
1916	0	0		0	0
1917	0	0		0	0
1918	0	0		0	0
1919	0	0		0	0
1920	0	0		0	0
1921	0	0		0	0
1922	0	0		0	0
1923	0	0		0	0
1924	0	0		0	0
1925	0	0		0	0
1926	0	0		0	0
1927	0	0		0	0
1928	0	0		0	0
1929	4	3	66.67	3	1
1930	150	113	45.13	68	82
1931	2	2	100.00	2	0
1932	38	37	45.95	17	21
1933	54	54	62.96	34	20
1934	554	541	47.69	264	290
1935	1870	1868	45.77	856	1014
1936	2684	2683	51.99	1396	1288
1937	780	774	43.93	343	437
1938	0	0		0	0
1939	4	4	25.00	1	3

1940	0	0		0	0
1941	0	0		0	0
1942	0	0		0	0
1943	0	0		0	0
1944	0	0		0	0
1945	0	0		0	0
1946	0	0		0	0
1947	0	0		0	0
1948	34	7	14.29	5	29
1949	396	195	38.97	154	242
1950	74	20	45.00	33	41
1951	212	14	28.57	61	151
1952	208	14	35.71	74	134
1953	66	18	27.78	18	48
1954	50	29	31.03	16	34
1955	28	14	35.71	10	18
1956	4	3	33.33	1	3
1957	66	0	42.50	28	38
1958	120	0	42.50	51	69
1959	152	0	42.50	65	87
1960	72	46	39.13	28	44
1961	28	28	53.57	15	13
1962	74	74	41.89	31	43
1963	40	28	42.86	17	23
1964	48	48	29.17	14	34
1965	76	74	60.81	46	30
1966	196	195	48.72	95	101
1967	66	66	39.39	26	40
1968	0	0		0	0
1969	0	0		0	0
1970	0	0		0	0
1971	0	0		0	0
1972	0	0		0	0
1973	0	0		0	0
1974	0	0		0	0
1975	0	0		0	0
1976	0	0		0	0
1977	0	0		0	0
1978	0	0		0	0
1979	0	0		0	0
1980	0	0		0	0





Figure A.1b: The percentage of the C1 sexed catches that are male.



Figure A.2a: The percentage of the C3 catches that have been sexed.



Figure A.2b: The percentage of the C3 sexed catches that are male.





Figure A.3a: The percentage of the catches south of 40°S that have been sexed.

Figure A.3b: The percentage of the catches south of 40°S that are male.

