# A Bayesian approach to assess the status of Southern Hemipshere humpback whales (Megaptera novaeangliae) with an application to Breeding Stock G 

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#### Abstract

The Bayesian stock assessment methodology presently being applied in the Comprehensive Assessment of the Southern Hemisphere humpback whales, which uses a sex- and age-aggregated population model, is detailed. This methodology is applied to Breeding Stock G, which winters off the west coast of South America. This application takes into account the recently updated historic catch series, as well as the most recent estimates of absolute abundance and population trend information.

KEYWORDS: HUMPBACK WHALE; BAYESIAN ASSESSMENT; SOUTHERN HEMISPHERE; MODELLING


## INTRODUCTION

Humpback whales (Megaptera novaeangliae) were heavily exploited by commercial whaling in the Southern Hemisphere (Tønnessen and Johnsen, 1982). It is estimated that nearly 200,000 whales were captured in both wintering and feeding grounds (Findlay, 2000). Currently, seven Southern Hemisphere humpback whale breeding stocks are recognised by the International Whaling Commission (IWC, 1998; 2011). Breeding Stock G corresponds to whales wintering off the eastern coast of Central and South America, between Peru and Costa Rica (Acevedo-Gutiérrez and Smultea, 1995; Félix and Haase, 2001; Flórez-González et al., 1998; Rasmussen et al., 2007; Scheidat et al., 2000). Whales from this population migrate to two likely discrete feeding grounds in the Magellan Strait, Chile (Acevedo et al., 2007), and near the Antarctic Peninsula (Rasmussen et al., 2007; Stevick et al., 2004; Stone et al., 1990).

The history of exploitation of Breeding Stock G is poorly known before the beginning of modern whaling (post-1900). During this period, whales were taken only in wintering grounds and migratory routes off Panama, Colombia, Ecuador, Peru, Chile and near the Archipelagos of Galapagos and Juan Fernandez (Townsend, 1935). The total pre-1900 catch is unknown, but estimated to be at least 4,000 whales in the 1800s (Smith et al., 2006). Modern whaling catches in the wintering grounds totaled nearly 2,300 whales (Allison, 2006). Most catches were taken from land bases on the coast of Chile, but about 330 whales were taken by a factory ship that followed migrating whales to Peru, Ecuador and Colombia (Findlay, 2000). These catches were of relatively small scale (an annual average of 37 whales from 1908-68 and no more than 270 catches in a single year). Whaling in the feeding grounds was of greater magnitude, with nearly 15,000 whales taken between 1905 and 1961 (Findlay, 2000). The peak of catches occurred between 1905 and 1915, when over 11,000 whales were captured (Allison, 2006).

During the Comprehensive Assessment of Southern Hemisphere humpback whales, it has been customary to use a sex- and age-aggregated dynamic production model, with a surplus production function of the Pella-Tomlinson form, to assess population status. The reason more complex population models have not been employed is the relatively coarse nature of much of the available data, and in particular the methods used to allocate catches on the feeding grounds in the far south to stocks which breed in lower latitudes (fig. 1 in IWC, 2011). Earlier applications of this approach estimated the two parameters of the population model (the intrinsic growth rate $r$ and pre-exploitation abundance $K$ ) by having the population trajectory hit a recent survey estimate of absolute abundance, and also replicate the trend shown by some time series of population estimates (for example from coastal surveys) or alternatively fixing $r$ at a value estimated for another breeding stock. Examples of this approach may be found in Findlay et al. (2000), Findlay and Johnston (2001) and Johnston et al. (2001).

The approach was subsequently refined and cast in a Bayesian framework to provide improved indications of the precision of the estimates obtained (Zerbini, 2004, in an application to Breeding Stock A). This refinement has since been applied to assessments of other breeding stocks, making allowance also in some cases for the use of abundance estimates from surveys of the feeding grounds, and also mixing of breeding stocks on these grounds (Johnston and Butterworth, 2005a; 2005b; Johnston and Butterworth, 2006).

This paper documents this Bayesian methodology, as recently adapted and agreed (IWC, 2011), and then applies it to Breeding Stock G.

Due to the difficulty in allocating past catches to breeding stocks, applications of this assessment methodology generally considers sensitivity of results to three different options for this allocation of catches south of $40^{\circ} \mathrm{S}$ (allocation of catches north of $40^{\circ} \mathrm{S}$ being straightforward by comparison). The 'core' and the 'fringe' options can be

[^0]considered as two extremes, the former reflects the smallest longitudinal range (and hence lowest catches) considered certain to correspond to the breeding stock under consideration, while the latter covers the greatest range considered plausible. The 'overlap' option defines longitudinal ranges for the stock under consideration and the two on either side. Eighty percent of the catch from the central of these three ranges and $10 \%$ of the catches from the ranges on either side, are assumed to reflect removals from the stock being assessed.

## DATA AND METHODS

## The data related to Breeding Stock G

## Historic catch data

The historic catch records for Southern Hemisphere humpback whales, which have recently (May 2006) been updated by Cherry Allison (IWC Secretariat) can be conveniently separated into catches taken north of $40^{\circ} \mathrm{S}$ and those taken south of that latitude. The updated catch records for whales caught north of $40^{\circ} \mathrm{S}$ are reported in Table 1a. Catches south of $40^{\circ} \mathrm{S}$ are reported in Table 1 b for the 'core', 'fringe' and 'overlap' models as recently re-defined (IWC, 2011). The fringe catch series, together with the differences in the core and overlap catches compared to the fringe model catches are shown in Fig. 1. Table 1b also reports catches taken off the Falkland Islands which are used in a sensitivity test.
The longitudinal boundaries that correspond to the hypotheses above for apportionment of the catch are as follows for Breeding Stock G:

Core: $\quad 50^{\circ} \mathrm{W}-100^{\circ} \mathrm{W}$
Fringe: $50^{\circ} \mathrm{W}-100^{\circ} \mathrm{W}+50 \%$ of catches from $100^{\circ} \mathrm{W}-$ $120^{\circ} \mathrm{W}$

The overlap series consists of $80 \%$ of the catch from the range of $60^{\circ} \mathrm{W}-110^{\circ} \mathrm{W}$ associated with the original naïve catch allocation model (as described in IWC, 1998) for Breeding Stock G, and $10 \%$ from each of the ranges associated with the naïve catch allocation models for Breeding Stocks A and F (the two stocks to the east and west of Breeding Stock G) which are taken to be $20^{\circ} \mathrm{W}-60^{\circ} \mathrm{W}$ and $110^{\circ} \mathrm{W}-170^{\circ} \mathrm{W}$ respectively (see fig. 8 of IWC, 2011).

## Absolute abundance data

The estimates of recent absolute stock abundance for Breeding Stock $G$ which are considered here are reported in Table 2a, along with their associated estimated CVs. The estimate of 6,504 provided by Felix et al. (2011) for 2006, which relates to the breeding area, was selected by the recent humpback workshop (IWC, 2011) as being the most reliable, and is used here for the Reference Case (RC). This estimate is based on the Petersen estimator. A test of sensitivity to using the Felix et al. (2011) Jolly-Seber abundance estimate of 5,456 for 2006 is also conducted. The other two abundance estimates are for the feeding areas - these being the most recent IDCR/SOWER estimate of 3,310 whales (in 1996) provided by Branch (2011) from the third circumpolar set of IDCR/SOWER surveys, and 6,991 whales (in 2000) provided by Hedley et al. (2001) from a joint CCAMLRIWC survey that year. These estimates are used under the assumption that each is unbiased and representative of the complete population.

## Trend information

Abundance estimates which can be used to provide information on trends for Breeding Stock G are available

Table 1a
Catches taken north of $40^{\circ} \mathrm{S}$ for Southern Hemisphere humpback whales for BS G (C. Allison, pers. comm.). There are no catches after 1973.

| Year | Catch | Year | Catch |
| :---: | :---: | :---: | :---: |
| 1900 | 0 | 1937 | 28 |
| 1901 | 0 | 1938 | 6 |
| 1902 | 0 | 1939 | 7 |
| 1903 | 0 | 1940 | 0 |
| 1904 | 0 | 1941 | 0 |
| 1905 | 0 | 1942 | 0 |
| 1906 | 0 | 1943 | 0 |
| 1907 | 0 | 1944 | 0 |
| 1908 | 16 | 1945 | 0 |
| 1909 | 44 | 1946 | 15 |
| 1910 | 62 | 1947 | 19 |
| 1911 | 92 | 1948 | 5 |
| 1912 | 86 | 1949 | 6 |
| 1913 | 45 | 1950 | 5 |
| 1914 | 195 | 1951 | 26 |
| 1915 | 30 | 1952 | 27 |
| 1916 | 15 | 1953 | 29 |
| 1917 | 15 | 1954 | 106 |
| 1918 | 23 | 1955 | 7 |
| 1919 | 24 | 1956 | 10 |
| 1920 | 21 | 1957 | 5 |
| 1921 | 21 | 1958 | 0 |
| 1922 | 19 | 1959 | 3 |
| 1923 | 16 | 1960 | 2 |
| 1924 | 34 | 1961 | 3 |
| 1925 | 248 | 1962 | 4 |
| 1926 | 277 | 1963 | 1 |
| 1927 | 40 | 1964 | 35 |
| 1928 | 36 | 1965 | 143 |
| 1929 | 26 | 1966 | 58 |
| 1930 | 33 | 1967 | 0 |
| 1931 | 53 | 1968 | 3 |
| 1932 | 21 | 1969 | 1 |
| 1933 | 11 | 1970 | 0 |
| 1934 | 13 | 1971 | 0 |
| 1935 | 31 | 1972 | 0 |
| 1936 | 18 | 1973 | 0 |

from IDCR/SOWER sightings surveys in the feeding grounds, as reported by Branch (2011). Those of Branch's estimates which have been corrected to represent comparable areas for the three circumpolar sets of surveys are used. These are listed in Table 2b.

## The population dynamics model and Bayesian estimation framework

The population dynamics model described here is an aggregated (over both sex and age) model. The basic population dynamics equation is:

$$
\begin{equation*}
N_{y+1}=N_{y}+r N_{y}\left(1-\left(N_{y} / K\right)^{u}\right)-C_{y} \tag{1}
\end{equation*}
$$

where
$N_{y}$ is the total population size at the start of year $y$, and is set equal to $K$ in years prior to the onset of exploitation;

## $K$ is the pre-exploitation population size;

$r$ is the intrinsic or maximum growth rate (i.e. the maximum per capita rate the population can achieve when its size is very low);
$\mu$ is set at 2.39 , which fixes the MSY level, MSYL $=$ $0.6 K$, as conventionally assumed by the IWC Scientific Committee; and
$C_{y}$ is the total catch (in terms of number of animals) in year $y$.

Table 1b
Catches taken south of $40^{\circ} \mathrm{S}$ for Southern Hemisphere humpback whales for Breeding Stock G. Catches have been apportioned from feeding area catches advised by C. Allison (pers. comm.). These catches correspond to either the core, fringe or overlap catch allocation hypotheses (IWC, 2011). Catches off the Falkland Islands used in sensitivity 8 are also given. There are no catches after 1973.

| Year | Core | Fringe | Overlap | Falklands | Year | Core | Fringe | Overlap | Falklands |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1900 | 0 | 0 | 0 | 0 | 1937 | 0 | 0 | 24 | 0 |
| 1901 | 0 | 0 | 0 | 0 | 1938 | 0 | 0 | 0 | 0 |
| 1902 | 0 | 0 | 0 | 0 | 1939 | 0 | 0 | 0 | 0 |
| 1903 | 1 | 1 | 1 | 0 | 1940 | 0 | 0 | 4 | 0 |
| 1904 | 0 | 0 | 18 | 0 | 1941 | 0 | 0 | 1 | 0 |
| 1905 | 23 | 23 | 47 | 0 | 1942 | 0 | 0 | 0 | 0 |
| 1906 | 498 | 498 | 422 | 0 | 1943 | 0 | 0 | 0 | 0 |
| 1907 | 366 | 366 | 419 | 0 | 1944 | 0 | 0 | 6 | 0 |
| 1908 | 1,246 | 1,246 | 1,182 | 9 | 1945 | 0 | 0 | 24 | 0 |
| 1909 | 1,481 | 1,481 | 1,524 | 94 | 1946 | 0 | 0 | 3 | 0 |
| 1910 | 2,527 | 2,527 | 2,668 | 70 | 1947 | 0 | 0 | 2 | 0 |
| 1911 | 2,039 | 2,039 | 2,204 | 17 | 1948 | 0 | 0 | 3 | 0 |
| 1912 | 976 | 976 | 1,035 | 8 | 1949 | 0 | 0 | 7 | 0 |
| 1913 | 1,038 | 1,038 | 895 | 7 | 1950 | 271 | 271 | 317 | 0 |
| 1914 | 656 | 656 | 609 | 12 | 1951 | 0 | 0 | 6 | 0 |
| 1915 | 219 | 219 | 337 | 0 | 1952 | 0 | 0 | 4 | 0 |
| 1916 | 21 | 21 | 55 | 0 | 1953 | 0 | 0 | 27 | 0 |
| 1917 | 69 | 69 | 61 | 0 | 1954 | 0 | 0 | 37 | 0 |
| 1918 | 81 | 81 | 72 | 0 | 1955 | 14 | 14 | 53 | 0 |
| 1919 | 181 | 181 | 153 | 0 | 1956 | 600 | 666 | 551 | 3 |
| 1920 | 149 | 149 | 129 | 0 | 1957 | 59 | 90 | 73 | 0 |
| 1921 | 0 | 0 | 1 | 0 | 1958 | 52 | 52 | 1 | 52 |
| 1922 | 189 | 189 | 188 | 0 | 1959 | 201 | 282 | 218 | 0 |
| 1923 | 96 | 96 | 90 | 0 | 1960 | 88 | 88 | 348 | 6 |
| 1924 | 102 | 102 | 108 | 0 | 1961 | 1,167 | 1,265 | 1,201 | 1 |
| 1925 | 163 | 163 | 156 | 0 | 1962 | 278 | 321 | 269 | 32 |
| 1926 | 88 | 88 | 82 | 0 | 1963 | 0 | 0 | 0 | 0 |
| 1927 | 3 | 3 | 2 | 2 | 1964 | 0 | 0 | 0 | 0 |
| 1928 | 16 | 16 | 14 | 0 | 1965 | 0 | 0 | 53 | 0 |
| 1929 | 0 | 0 | 5 | 0 | 1966 | 0 | 0 | 24 | 0 |
| 1930 | 1 | 1 | 12 | 0 | 1967 | 0 | 0 | 11 | 0 |
| 1931 | 0 | 0 | 2 | 0 | 1968 | 0 | 0 | 0 | 0 |
| 1932 | 0 | 0 | 2 | 0 | 1969 | 0 | 0 | 0 | 0 |
| 1933 | 0 | 0 | 13 | 0 | 1970 | 0 | 0 | 0 | 0 |
| 1934 | 0 | 0 | 6 | 0 | 1971 | 0 | 3 | 0 | 0 |
| 1935 | 0 | 0 | 5 | 0 | 1972 | 0 | 0 | 0 | 0 |
| 1936 | 0 | 0 | 11 | 0 | 1973 | 0 | 0 | 0 | 0 |

The following prior distributions for $r$ and an estimate of absolute abundance are considered:
(i) If the assessment model is fit to data with information on trend (from the IDCR/SOWER surveys) then $r \sim \mathrm{U}[0$, $0.106]$. If no such trend data are used in the model fit, then $r \sim$ posterior derived from an assessment of Breeding Stock A (Zerbini et al., 2011). The upper boundary of 0.106 corresponds to the maximum growth rate given a range of life history parameters observed for several humpback whale populations (Clapham et al., 2006).
(ii) $\ln N_{Y}^{X, \text { obs }} \sim \mathrm{U}\left[\ln \hat{N}_{Y}^{X, \text { obs }}-4 C V_{Y}, \ln \hat{N}_{Y}^{X, o b s}+4 C V_{Y}\right]$
where $N_{Y}^{X, \text { obs }}$ refers to the absolute abundance estimate for a humpback breeding stock $X$ in year $Y$.
Note that the prior distribution from which target absolute abundance estimates ( $N_{Y}^{X, o b s}$ ) are drawn at random is uniform on a natural logarithmic scale, corresponding to the conventional approach in the IWC Scientific Committee to make distributional assumptions for abundance estimates transformed in this way. The upper and lower bounds are set by adding and subtracting four times the CV of the survey estimate.

For each of $n_{1}$ replicates, values of $N_{Y}^{X, o b s}$ and $r$ are drawn from their prior distributions. A bisection method is used to calculate $K$ such that the model value of $N_{Y}^{X}$ is identical to the randomly drawn value $N_{Y}^{X, \text { obs }}$.

For each of the $n_{1}$ replicates, using the generated $r$ and calculated $K$ values, a negative $\log$ likelihood is then computed by comparing the population model output to observed data - these including the recent absolute abundance estimate, preferably from the breeding grounds (see Table 2a). The components of the negative log likelihood are calculated as follows for Breeding Stock G.

For the absolute abundance estimate, the negative loglikelihood component is:

$$
\begin{equation*}
-\ln L=\frac{1}{2 C V_{r}^{2}}\left(\ln \hat{N}_{r}^{x_{r}^{x, o k s}}-\ln N_{r}^{x}\right)^{2} \tag{2}
\end{equation*}
$$

where
$\hat{N}_{Y}^{X, o b s}$ and $C V_{Y}$ are the survey estimate of population size at the start of year $Y$ for breeding stock $X$ and the associated survey-sampling based coefficient of variation, and
$N_{Y}^{X}$ is the model value for population size at the start of year $Y$ for this breeding stock.

It is assumed that the abundance estimates used to provide trend information are log-normally distributed about their model values:

$$
\begin{equation*}
I_{y}^{X}=q^{X} N_{y}^{X} e^{\varepsilon_{y}} \tag{3}
\end{equation*}
$$

where
$I_{y}^{X}$ is the survey-based abundance index for year $y$,


Fig. 1. The fringe catch series together including the catches North of $40^{\circ}$ is shown in (a), with the differences in the core and overlap catches compared to the fringe model catches shown in (b) and (c) respectively.
$q^{X}$ is the constant of proportionality between that index and the absolute abundance of breeding stock $X$,
$N_{v}^{X}$ is the model value for population size at the start of year $y$ for breeding stock $X$, and
$\varepsilon_{y}$ is from $N\left(0, \sigma_{X}^{2}\right)$.
The contribution of these data to the negative of the loglikelihood function is then given by:

$$
\begin{equation*}
-\ln L=n^{x} \ln \sigma_{x}+\frac{1}{2 \sigma_{x}^{2}} \sum_{y}\left(\ln I_{y}^{x}-\ln q^{x}-\ln N_{y}^{x}\right)^{2} \tag{4}
\end{equation*}
$$

with the total negative log-likelihood thus being:

$$
\begin{align*}
-\ln L & =n^{X} \ln \sigma_{x}+\frac{1}{2 \sigma_{x}^{2}} \sum_{y}\left(\ln I_{y}^{X}-\ln q^{X}-\ln N_{y}^{X}\right)^{2} \\
& +\frac{1}{2 C V_{y}^{2}}\left(\ln \hat{N}_{Y}^{X, o b s}-\ln N_{y}^{X}\right)^{2} \tag{5}
\end{align*}
$$

The Bayesian approach applied also requires integration over priors for $\sigma_{X}$, the standard deviation of the residuals about the data used for trend information, and the constant of proportionality $q^{X}$. Taking these priors to be respectively

Table 2a
Recent absolute abundance estimate considered for assessments of Breeding Stock G.

| Year | Abundance estimate | Area | Source |
| :---: | :---: | :---: | :--- |
| 2006 | $6,504(\mathrm{CV}=0.21)$ | Breeding | Felix et al. (2011): Petersen\# |
| 2006 | $5,456(\mathrm{CV}=0.21)^{@}$ | Breeding | Felix et al. (2011): Jolly-Seber |
| 1996 | $3,310(\mathrm{CV}=0.21)$ | Feeding | Branch (2011)* |
| 2000 | $6,991(\mathrm{CV}=0.32)$ | Feeding | Hedley et al. $(2001)^{+}$ |

[^1]Table 2b
Abundance estimates for Breeding Stock G from the IDCR-SOWER sighting surveys for comparable areas (Branch, 2011) that are used to provide information on population trend.

| Year | Abundance estimate |
| :---: | :---: |
| 1982 | $1,452(\mathrm{CV}=0.65)$ |
| 1989 | $2,817(\mathrm{CV}=0.38)$ |
| 1996 | $3,310(\mathrm{CV}=0.21)$ |

proportional to $\sigma_{X}^{-3}$ and uniform in log-space allows the integration over these parameters to be performed analytically, with the resultant negative logarithm of the marginal likelihood of the same form as equation (5) with $\sigma_{X}$ and $q^{X}$ each substituted by their maximum likelihood estimates for the values of $r$ and under consideration [see proof in Geromont and Butterworth (1995) from a generalisation of the results of Walters and Ludwig (1994)]:

$$
\begin{equation*}
\hat{\sigma}_{X}=\sqrt{1 / n \Sigma\left(\ln I_{y}^{X}-\ln q^{X}-\ln \hat{N}_{y}^{X}\right)^{2}} \tag{6}
\end{equation*}
$$

where
$n$ is the number of data points in the abundance series, and
$q^{X}$ is the constant of proportionality for the index of abundance which is substituted by its maximum likelihood estimate:

$$
\begin{equation*}
\ln \hat{q}^{x}=1 / n \sum_{y}\left(\ln I_{y}^{x}-\ln N_{y}^{x}\right) \tag{7}
\end{equation*}
$$

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 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 and stored. This process is repeated until an initial sample of $n_{1} \theta_{i} s$ is generated. This sample is then re-sampled with replacement $n_{2}$ times with probability equal to weight $w_{j}$, where:

$$
\begin{equation*}
w_{j}=\frac{L\left(\theta_{j} / \text { data }\right)}{\sum_{k=1}^{n_{i}} L\left(\theta_{k} / \text { data }\right)} \tag{8}
\end{equation*}
$$

The resample is thus a random sample of size $n_{2}$ from the joint posterior distribution of the parameters (Rubin, 1988).

The value of $n_{1}$ (the original number of replicates) used is 500,000 and of $n_{2}$ (number of re-samples) is 5,000 . Convergence is checked by examining results for different random number seeds, and ensuring that no sample contributes more than $0.001 \%$ of the total weight.
$N_{\text {min }}$ constraint
It has been suggested (Jackson et al., 2006) that genetic constraints be used in the assessment of humpback whale populations, given the observed genetic diversity. This idea had previously been discussed by Baker and Clapham (2004), who advocated that demographic and genetic approaches should be integrated to better describe whale population dynamics. In the application of this assessment
methodology to Breeding Stock G, this approach has been used to determine how low the minimum population size of the humpback whales from Breeding Stock G could have been, given their observed genetic diversity. Baker and Clapham (2004) suggested that the number of extant haplotypes sampled in a population which has undergone a recent bottleneck provides an absolute minimum bound on the number of mature females in the population at the time of the bottleneck. Jackson et al. (2006) suggested a correction factor of four to scale the number of sampled haplotypes (minimum number of mature females) to the total $(1+)$ population size when the population was at its minimum. The rationale behind this correction factor is that the number of haplotypes must be multiplied by two to account for the male population (assuming an even sex ratio) and also by a further two to correct the minimum effective population size to a lower estimate of total population size [as described by Nunney (1993) and used in Roman and Palumbi (2003)]. Jackson et al. (2006) point out that this correction factor is normally too small, but nevertheless remains useful to provide a minimum population number.

In the application to Breeding Stock G, the minimum population size () of 108 whales (in any year) is set as such a constraint. This is four times the total number of mtDNA haplotypes (27) observed for this breeding stock (Rosenbaum et al., 2006).

The methodology as currently agreed and applied in the Scientific Committee then excludes any population trajectory which violates this constraint (see also comments in the final section of this paper). Generally this has the effect of excluding some of the trajectories with higher $r$ values.

## Reference case and sensitivity tests

The Reference Case (RC) assessment uses inputs and makes assumptions as follows:
(a) The fringe catch allocation hypothesis is assumed for the historic catch.
(b) The Felix et al. (2011) Petersen estimate of 6,504 in 2006 (from the breeding grounds) is used as the absolute abundance estimate.
(c) The trend information from IDCR/SOWER surveys as reported in Branch (2011) is used.
(d) The prior for $r$ is $r \sim \mathrm{U}[0,0.106]$.

The following sensitivities are explored:
Sensitivity 1: The most recent abundance estimate from the IDCR/SOWER information (3,310 in 1996, Branch, 2011) is used in place of the Felix et al. (2011) Petersen estimate for the recent absolute abundance estimate (though note that the Branch estimate corresponds to a slightly different longitudinal range to that which the fringe catch allocation prescription applies).
Sensitivity 2: The abundance estimate from Hedley et al. (2001) is used in place of the Felix et al. (2011) Petersen estimate for the recent absolute abundance estimate.

Sensitivity 3: The Petersen estimate for abundance is replaced by the open population estimate of 5,456 for 2006 provided by Felix et al. (2011). This estimate is based on a Jolly-Seber analysis with a survival rate adjusted to be the same for transient and non-transient animals.

Sensitivity 4: The model fits to the RC breeding ground abundance estimate as well as to the two abundance estimates from the feeding grounds in Table 2a. This involves adding further terms to equation (2).

Sensitivity 5: The model fits to the Felix et al. (2011) Petersen estimate only, and replaces data with trend information by an informative $r$ prior taken from the $r$ posterior for Breeding Stock A (as estimated by Zerbini et al., 2011).

Sensitivity 6: The core catch allocation hypothesis replaces the fringe hypothesis.
Sensitivity 7: The overlap catch allocation hypothesis replaces the fringe hypothesis.

Sensitivity 8: The catches made off the Falkland Islands (reported in Table 1b) are included in the total catch history.

Note that the purpose of many of these sensitivities is to provide a broad indication of how dependent key outputs are to certain inputs. Thus, for example, sensitivities 1 and 2 are intended to provide only some sense of the possible range for recent abundance, rather that to suggest that these abundance estimates from the feeding grounds correspond exactly to the breeding stock being modelled.

## Projections

In this study, the population is projected into the future (to 2040) assuming that no future catches are taken.

## RESULTS AND DISCUSSION

Table 3 reports results for the RC and eight sensitivity tests. Posterior medians with the $5^{\text {th }}$ and $95^{\text {th }}$ percentiles (in parentheses) are reported. These results show that for Breeding Stock G there is very little sensitivity of results to the alternate historic catch series used (sensitivity tests 6-8). There is far greater sensitivity to the estimates of current abundance selected, with the Felix et al. (2011) Petersen estimate producing results which show Breeding Stock G to be currently around 0.56 K , while the use of the IDCR/SOWER current abundance estimate for the feeding grounds (sensitivity 1) produces results which are less optimistic, with a current abundance estimate of 0.49 K . The use of the Hedley et al. (2001) estimate (sensitivity 2) from the feeding grounds produces a more optimistic result however, with a current abundance estimate of 0.78 K . When all three recent estimates of abundance are fit instead of only one (sensitivity 4), precision is improved with the width of the $90 \% \mathrm{PI}$ on current depletion reduced by about one third. Excluding the trend data, and using a prior for $r$ from the posterior from Breeding Stock A (sensitivity 5) produces similar results to those for the RC. For all nine models explored here, the lowest population size $N_{\text {min }}$ does not drop below the bound deduced from genetics data of 108 for any of the trajectories simulated.

Table 3
Breeding Stock G model parameter estimates. Posterior medians with the 5 th and 95 th percentiles (in parentheses) are reported. An $N_{\text {min }}$ constraint $>108$ is imposed for all models. Headers in italics reflect choices differing from those for the Reference Case.

| $r$ prior | Reference Case | Sensitivity 1 | Sensitivity 2 |
| :---: | :---: | :---: | :---: |
| Historic catch | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \mathrm{U}[0,0.106]$ |
| Recent abundance | Fringe | Fringe | Fringe |
| Trend information | Felix et al. (2011): Petersen | IDCR/SOWER | Hedley et al. (2001) |
|  | IDCR/SOWER | IDCR/SOWER | IDCR/SOWER |
| $r$ | 0.063 [0.023; 0.093] | 0.062 [0.024; 0.092] | 0.068 [0.029; 0.099 |
| K | 11,584 [10,590; 14,878] | 11,617 [10,610; 14,363] | 11,382 [10,424; 14,123] |
| $N_{\text {min }}$ | 731 [238; 2959] | 608 [266; 1758] | 760 [414; 2843] |
| $N_{2006}$ | 6,579 [4,698; 9,817] | 5,736 [3,757; 8,135] | 9,004 [5,699; 10,798] |
| $N_{\text {min }}{ }^{\text {I }}$ / | 0.063 [0.022; 0.198] | 0.052 [0.028; 0.125] | 0.067 [0.040; 0.200] |
| $N_{2006} / K$ | 0.561 [0.376; 0.833] | 0.493 [0.281; 0.723] | 0.783 [0.450; 0.987] |
| $N_{2020} / K$ | 0.885 [0.575; 0.988] | 0.829 [0.422; 0.979] | 0.972 [0.692; 1.000] |
| $N_{2040} / K$ | 0.994 [0.818; 1.000] | 0.990 [0.660; 1.000] | 0.999 [0.913; 1.000] |
| $r$ prior | Sensitivity 3 | Sensitivity 4 | Sensitivity 5 |
| Historic catch | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \operatorname{post}$ ( $A$ ) |
| Recent abundance | Fringe | Fringe | Fringe |
| Trend information | Felix et al. (2011): Jolly-Seber IDCR/SOWER | $R C+\operatorname{Sen} 1+\operatorname{Sen} 2$ IDCR/SOWER | Felix et al. (2011): Petersen <br> None |
| $r$ | 0.062 [0.023; 0.090] | 0.065 [0.036; 0.093] | 0.066 [0.025; 0.089] |
| K | 11,619 [10,655; 14,813] | 11,500 [10,594; 13,162] | 11,480 [10,695; 14,457] |
| $N_{\text {min }}$ | 586 [204; 2334] | 647 [283; 1615] | $655[244 ; 3150]$ |
| $N_{2006}$ | 5,504 [3,885; 7,970] | 6,557 [5,210; 8,162] | 6,539 [4,634; 9,361] |
| $N_{\text {min }} / K$ | 0.051 [0.019; 0.163] | 0.056 [0.026; 0.123] | 0.057 [0.023; 0.211] |
| $N_{2006} / K$ | 0.468 [0.317; 0.695] | 0.568 [0.419; 0.742] | 0.557 [0.375; 0.813] |
| $N_{2020} / \mathrm{K}$ | 0.820 [0.496; 0.961] | 0.893 [0.660; 0.981] | 0.891 [0.570; 0.984] |
| $N_{2040} / K$ | 0.989 [0.734; 1.000] | 0.995 [0.991; 1.000] | 0.996 [0.784; 1.000] |
| $r$ prior | Sensitivity 6 | Sensitivity 7 | Sensitivity 8 |
| Historic catch | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \mathbf{U}[0,0.106]$ | $r \sim \mathbf{U}[0,0.106]$ |
| Recent abundance | Core | Overlap | Fringe+Falklands |
| Trend information | Felix et al. (2011): Petersen IDCR/SOWER | Felix et al. (2011): Petersen IDCR/SOWER | Felix et al. (2011): Petersen IDCR/SOWER |
| $r$ | 0.063 [0.024; 0.092] | 0.062 [0.025; 0.092] | 0.063 [0.027; 0.092] |
| K | 11,569 [10,601; 14,589] | 11,887 [10,866; 14,956] | 11,785 [10,804; 14,475] |
| $N_{\text {min }}$ | 719 [242; 2922] | 749 [252; 2831] | 720 [246; 2662] |
| $N_{2006}$ | 6,573 [4,630; 9,694] | 6,620 [4,678; 9,742] | 6,634 [4,723; 9,579] |
| $N_{\text {min }} / K$ | 0.062 [0.023; 0.197] | 0.062 [0.023; 0.189] | 0.061 [0.023; 0.185] |
| $N_{2006} / \mathrm{K}$ | 0.561 [0.376; 0.824] | 0.550 [0.370; 0.808] | 0.554 [0.378; 0.810] |
| $N_{2020} / K$ | 0.887 [0.585; 0.986] | 0.877 [0.575; 0.985] | 0.881 [0.593; 0.985] |
| $N_{2040} / K$ | 0.994 [0.820; 1.000] | 0.994 [0.820; 1.000] | 0.994 [0.832; 1.000] |



Fig. 2. Estimated population trends for Breeding Stock G, with projected trajectories which assume a continued zero catch. The posterior medians with $90 \%$ probability interval envelopes are illustrated. The vertical lines at 2006 separate assessments from projections. The scenarios shown are the Reference Case and Sensitivities 1, 2 and 5 (which explore fitting to the IDCR/SOWER recent estimate as the recent abundance data and to the Hedley et al.(2001)) estimate from the feeding grounds, and then omitting the IDCR/SOWER trend data by using an informative prior for the intrinsic growth rate parameter $r$ obtained from the assessment of Breeding Stock A (Zerbini et al., 2011). The single dots show the recent abundance estimate fitted by each model which replaces the Felix et al. (2011) Petersen estimate of recent abundance by those from the IDCR/SOWER surveys or from Hedley et al. (2001) for the feeding grounds for sensitivities 1-2.

Fig. 2 shows the population abundance trends for the RC and for sensitivities 1,2 and 5 . These plots also show projected trajectories which assume a continued zero catch. The posterior medians together with the $90 \%$ PI envelopes are illustrated. Fig. 3 shows the RC model fit to the abundance data provided by the IDCR/SOWER sightings estimates to inform on trend. It is evident that the model is able to fit adequately to both the Felix et al. (2011) recent Petersen abundance estimate (Fig. 2), as well as to the abundance data series from the feeding grounds provided by the IDCR/SOWER survey sightings (Fig. 3).

Assuming future zero catches, the RC estimates the breeding stock (in median terms) to reach 0.89 K by 2020 and


Fig. 3. The RC model fit to the abundance data used to provide trend information, as obtained from the IDCR/SOWER sightings surveys. The dots show the abundance estimates from the surveys, together with their $90 \%$ confidence intervals, and the curve shows the model posterior medians. Note that the model estimates reflect the population abundance estimates adjusted by the estimated constant of proportionality $q$.
0.97 K by 2030. Slightly less optimistic projection estimates are obtained for sensitivity 1 (fitting to the IDCR/SOWER recent abundance estimate) for which the stock is estimated to reach 0.83 K by 2020 and 0.95 K by 2030 , and more optimistic estimates for sensitivity 2 (fitting to the Hedley et al., 2001 estimate) which reflects near full recovery $(0.97 \mathrm{~K})$ by 2020 .

## POSSIBLE FURTHER DEVELOPMENTS

This paper has documented the Bayesian methodology currently agreed for use in the Scientific Committee for Southern Hemisphere humpback stock status evaluation, and applied that to data for Breeding Stock G. There are some ways in which the method could be technically improved and/or further sensitivities explored, some specific to the Breeding Stock G case:
(a) when using feeding ground estimates of abundance, evaluate abundance for longitudinal ranges which correspond to the basis used to develop the historical catch series for higher latitudes;
(b) take account of the CVs for the abundance estimates in Table 2 b used to provide information on trend, rather than assume these to be the same (the $\sigma_{X}$ parameter);
(c) integrate over a prior distribution for the $\mu$ parameter (or equivalently MSYL) rather than fix this at a single value;
(d) apply alternative Bayesian population model approaches (note that the approach applied here corresponds to the 'Backwards' variant of the various approaches that have been applied in assessment of the Bering-ChukchiBeaufort bowhead whale population - see for example Punt and Butterworth (1999); and
(e) change to a population model which disaggregates by sex and age.
A number of these would require considerably extra work, e.g. the further survey abundance estimates required under (a), or the incorporation of additional variance and more complex integration over $q^{X}$ and $\sigma_{X}$ needed for (b). Thus given the relatively coarse nature of the abundance and trend information available, and that it seems unlikely that these factors listed would greatly impact results, such additional analyses do not seem an immediate priority, and reflect a level of sophistication perhaps more appropriate to the stage when the population model is refined to incorporate age- and sex-structure as suggested in (e). A higher priority is further information on trend, as the data available do not update the prior used for $r$ appreciably (see Fig. 4).

In the longer term a multi-stock procedure will be need, in particular so that proper account is taken of the co-


Fig. 4. Comparison of the uniform prior distribution (horizontal line) used for the intrinsic growth rate parameter $r$ and the associated posterior (histogram) for the RC model for Breeding Stock G.
variances that arise for the different catch allocation hypotheses because catches taken to come from one breeding stock need then to be precluded from coming also from neighbouring breeding stock.
In the application here, the $N_{\min }$ constraint played no role. However in instances where it does so, greater care needs to be exercised as this constraint effectively modifies the independent prior distributions for $r$ and absolute abundance by introducing covariance, and raises Borel's paradox difficulties (Brandon et al., 2007).

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[^1]:    ${ }^{\text {@ As no CV was provided for the Jolly-Seber estimate, the same CV is }}$ assumed as for the Petersen estimate. "Survey areas covered the wintering grounds off the coast of Ecuador, varying slightly amongst years but ranging approximately $01^{\circ} 26^{\prime} \mathrm{S}, 80^{\circ} 50^{\prime} \mathrm{W}$ to $02^{\circ} 10^{\prime} \mathrm{S}, 81^{\circ} 05^{\prime} \mathrm{W}$. *Survey area south of $60^{\circ}$ and between $110^{\circ} \mathrm{W}-50^{\circ} \mathrm{W}$. ${ }^{+}$Survey area around the Antarctic Peninsular of approximately between $60^{\circ} \mathrm{S}-65^{\circ} \mathrm{S}$ and between $70^{\circ} \mathrm{W}-50^{\circ} \mathrm{W}$.

