# Further results from an AWMPlite-like assessment of the West Greenland minke whale population 

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#### Abstract

The method advanced in Brandão and Butterworth (2006) to estimate a lower confidence limit on the size of the West Greenland minke whale population by taking account of the continuing sex bias in the catch is modified slightly and applied to updated data. The lower 5 percentile estimated for the pre-exploitation size of the population is in the 25-35 000 range, depending on assumptions made about intrinsic population growth rate and the extent to which Greenland operations have remained comparable over time. However, a simulation test of the method suggests that it provides positively biased estimates of this lower 5 percentile, with the true value for the specific case investigated being some 17000 rather than 27000.


## INTRODUCTION

This paper builds on Brandão and Butterworth (2006) whose purpose was to present a simplified approach to that in Witting (2006a, b) to the assessment of West Greenland minke whales, to illustrate the essence of those computations. Briefly this is that (under certain assumptions), given the preponderance of females in the catches, the female ratio in catches would have decreased over time, and the size of the observed decrease enables estimates of abundance to be made. The paper then proceeds to simulation test the basis used to estimate the lower $5 \%$ confidence estimate for pre-exploitation abundance for possible bias.

## DATA

The data used in Brandão and Butterworth (2006) which were obtained from Witting (2006a), have been updated, and a further year's catches have also become available. These updated data, kindly provided by Lars Witting (pers. commn) are given in Tables 1-2.

## METHODS

The methodology used is the same as that of Brandão and Butterworth (2006); however, previous errors in equations (6) and (7) have been corrected and a separate overdispersion parameter ( $\sigma_{i}$ ) is fitted to each of the whaling periods (as fits to the data indicated clear inter-period differences).

## Population dynamics

A sex-structured age-aggregated model is used:

$$
\begin{align*}
& N_{y+1}^{m}=N_{y}^{m}+\frac{r}{2} N_{y}^{t}\left(1-\left(\frac{N_{y}}{K}\right)^{2.39}\right)-C_{y}^{m}  \tag{1}\\
& N_{y+1}^{f}=N_{y}^{t}+\frac{r}{2} N_{y}^{t}\left(1-\left(\frac{N_{y}}{K}\right)^{2.39}\right)-C_{y}^{f} \tag{2}
\end{align*}
$$

where:
$N_{y}$ is the total number of minke whales in year $y$, which is given by:

$$
N_{y}=N_{y}^{m}+N_{y}^{f},
$$

$N_{y}^{m} \quad$ is the total number of male minke whales in year $y$,
$N_{y}^{t}$ is the total number of female minke whales in year $y$,
$K$ is the carrying capacity,
$C_{v}^{m} \quad$ is the number of male West Greenland minke whales caught in year $y$,
$C_{v}^{f} \quad$ is the number of female West Greenland minke whales caught in year $y$, and
$r$ is the intrinsic population growth rate, linked to the assumption of a 50:50 sex ratio at birth.

The number of male and female minke whales is assumed to be the same before exploitation so that $N_{1948}^{m}=N_{1948}^{f}=K / 2$. The values for $C_{y}^{m}$ and $C_{y}^{f}$ are taken from Table 2.

The total number of minke whales caught in the whaling period $i$ in year $y$ is given by:

$$
\begin{equation*}
C_{y}^{i}=C_{y}^{m(i)}+C_{y}^{f(i)} \tag{3}
\end{equation*}
$$

where:
$C_{y}^{m(i)}$ is the number of male minke whales caught in period $i$ by the fishery concerned, where the period/fishery $i$ represents:
$i= \begin{cases}I & \text { the period } 1955-1978 \text { by Greenlanic whalers } \\ \text { II } & \text { the period } 1968-1985 \text { by Norwegian whalers }, \text { and } \\ \text { III } & \text { the period } 1985-2005 \text { by Greenlanic whalers }\end{cases}$
$C_{y}^{f(i)}$
is the corresponding number of female minke whales caught in period/fishery i. The data for these catches are taken from Table 1.

The expected number of female minke whales caught by each period/fishery $i$ in year $y$ is given by:

$$
\begin{equation*}
\hat{C}_{y}^{f(i)}=C_{y}^{i} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{i} N_{y}^{m}} \tag{4}
\end{equation*}
$$

where:
$\lambda^{i} \quad$ is the selectivity of males relative to females for the period and fishery concerned, and is assumed to remain constant over that period, with equation (4) following from the associated assumptions that:

$$
\begin{equation*}
\hat{C}_{y}^{f(i)}=F_{y}^{(i)} N_{y}^{f} ; \hat{C}_{y}^{m(i)}=\lambda^{i} F_{y}^{(i)} N_{y}^{m} . \tag{5}
\end{equation*}
$$

## The likelihood function

The likelihood is calculated assuming that the observed female catches are distributed about their expected value according to an overdispersed Poisson model. The negative of the approximate log-likelihood (ignoring constants) which is minimised in the fitting procedure is thus given by:

$$
\begin{equation*}
-\ln L=\sum_{i=1}^{\text {III }} \sum_{y=y_{i}^{\prime}}^{y_{i}}\left\{\frac{1}{\sigma_{i}^{2}} \frac{\left(C_{y}^{f(i)}-\hat{C}_{y}^{f(i)}\right)^{2}}{\left(2 \hat{C}_{y}^{f(i)}\right)}+\ln \sigma_{i}+\ln \sqrt{\hat{C}_{y}^{f(i)}}\right\} \tag{6}
\end{equation*}
$$

where
$y_{i}^{1} \quad$ is the first year of catches for period i ,
$y_{i}^{*} \quad$ is the last year of catches for period i ,
$\sigma_{i} \quad$ measures overdispersion of the distribution of catches compared to a Poisson distribution for which the variance is equal to the expected catch for the period and fishery concerned, whose maximum likelihood estimate is given by:

$$
\begin{equation*}
\hat{\sigma}_{i}=\sqrt{\frac{1}{n_{i}} \sum_{i=1}^{\prime \prime \prime} \sum_{y=y_{i}^{\prime}}^{y_{i}}\left\{\frac{\left(C_{y}^{f(i)}-\hat{C}_{y}^{f(i)}\right)^{2}}{\hat{C}_{y}^{f(i)}}\right\}} \tag{7}
\end{equation*}
$$

$n_{i} \quad$ is the total number of years in the summation of each whaling period.

Note that the formulation of equation (6) assumes that the Poisson-like catch distribution can be approximated by a normal distribution of the same variance. The estimable parameters of this model are $\lambda^{\prime}, \lambda^{\prime \prime}, \lambda^{\prime \prime \prime}, \sigma_{I}, \sigma_{I I}, \sigma_{I I}$ and $K$.

## Sensitivity test

As a sensitivity test, the possibility of a sex bias in reproduction (or, effectively, in natural mortality), and hence in the population was introduced in the modelling procedure; thus in this instance equations (1) and (2) become:

$$
\begin{align*}
& N_{y+1}^{m}=N_{y}^{m}+\frac{r}{2} N_{y}^{f}(1-\mu)\left(1-\left(\frac{N_{y}}{K}\right)^{2.39}\right)-C_{y}^{m}  \tag{8}\\
& N_{y+1}^{f}=N_{y}^{f}+\frac{r}{2} N_{y}^{f}(1+\mu)\left(1-\left(\frac{N_{y}}{K}\right)^{2.39}\right)-C_{y}^{f} \tag{9}
\end{align*}
$$

A value of $\mu=0.1$ was used, which would lead to a $45: 55$ male:female ratio.

## RESULTS

## Model fit

The available data are such as indicate a maximum likelihood estimate of $K \rightarrow \infty$ (i.e. there is no upward trend in the male:female ratio in the catches over time).

Hence the approach taken here has been to estimate the lowest value of $K$ that remains statistically compatible with the $K \rightarrow \infty$ best estimate (approximated numerically here by $K=500000$ ) at the $5 \%$ level. This is taken to correspond approximately to the value of $K$ for which the value of $-\ell \mathrm{nL}$ increases by 1.92 over its value at $K=500000$ (effectively $\infty$ given the size of the catches).

Results for such values of $K$ are shown for three fixed input values of $r$ in Table 3. Note that MSYR $=0.705 r$ for this model, so that the choices for $r$ correspond to MSYR (effectively MSYR ${ }_{1+}$ ) values of $1.4 \%, 3.5 \%$ and $5.6 \%$. Two scenarios are explored, corresponding to whether or not the selectivity of males relative to females is the same for Greenlandic whalers in the 1955-1978 and 1985-2005 periods. Table 4 shows the corresponding results for current depletion, both for both sexes combined and for females only.

Trajectories for total population corresponding to the six scenarios examined are shown in Figure 1. Figure 2 compares observed and expected catches of females for one of these scenarios, and also contrasts expected trends in the proportion of females in the catch under $K=500000$ and the lower 5\% level shown in Table 3.

Allowing for the possibility of a sex bias ( $\mathrm{m}: \mathrm{f}=45: 55$ ) in the unexploited population does not change the results appreciably (Tables 3 and 4 ).

Table 5 shows the estimates of overdispersion and the selectivity of males relative to females for the period and fishery concerned for various population growth rates and for the case of $K=500000$.

## Simulation testing

The particular reason for simulation testing of the confidence interval estimation procedure is that the process used assumes asymptotic behaviour of the likelihood (and associated $\chi^{2}$ distributional properties) in circumstances where a true maximum of the likelihood does not exist.

The Appendix sets out the process used to generate the data for this exercise. This is complex because allowance has to be made for the fact that not all whales caught are sampled. Figure 3 shows the proportion sampled for sex by the Greenland fishery (under the assumption that the Norwegian fishery sampled all whales caught). The under-sampling is quite substantial in the earlier years of the fishery.

The algorithm used to generate the sampled Greenland data first generates the total Greenland catch by sex under the distributional assumptions of the estimator, and then generates the sexsampled subset by random selection without replacement from the first data set generated. However for the early (1955-1978) Greenland series, this was found to generate sampled data for which the $\sigma$ overdispersion values were negatively biased compared to the actual sampled data. In consequence, an autocorrelation $\rho$ was added to this second stage data generation algorithm for the early Greenland series (only). It was found that a value of $\rho=0.5$ roughly removed the bias (see Table 6 and Figure A.3), which was likely related to the small proportional sampling over this period.

Model fit negative log-likelihood ( $-\ell \mathrm{nL}$ ) values for various values of true $K$ and the corresponding $95^{\text {th }}$ percentile of the $-\ell \mathrm{nL}$ distribution obtained by simulation for the two methods considered (see Appendix) are shown in Table 7. The probability calculated from the simulations corresponding to the negative log-likelihood of the fit is also given. Figure 4 shows the observed negative loglikelihood function and $95^{\text {th }}$ percentiles calculated by simulation. Under "Method 1" (see Appendix), a lower $5 \%$ confidence limit is given by $K=17000$. For "Method 2", as $K$ decreases both the -loglikelihood function and the percentiles increase with no intersection even at very lows values of $K$.

Although we have shown results for "Method 2", we do not consider it appropriate. Our understanding is that the parameters generating the data for the simulation should be independent
of the value of $K$ assumed for comparability for different $K$ values, and further that these parameters are most appropriately set to those corresponding to the "best" fit obtainable to the original data (here $K=500000$ taken to represent $K \rightarrow \infty$ ). Were "Method 2" to be used, the $\sigma$ values used to generate data increase as $K$ decreases as a reflection of an increasing systematic lack of fit, which seems a bias that should not be reflected in the process of generating the simulated data.

## CONCLUSIONS

The lower $5^{\text {th }}$ percentile estimated for pre-exploitation size of the population output by the method advanced is in the 25-35 000 range, depending on assumptions made about intrinsic population growth rate and the extent to which Greenland operations have remained comparable over time. However, a simulation test of the method suggests that it provides positively biased estimates of this lower $5^{\text {th }}$ percentile, with the true value for the specific case investigated being some 17000 rather than 27000.

## ACKNOWLEDGMENTS

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Table 1. Annual reported catches of male and female common minke whales by Greenlandic and Norwegian whalers (source: L. Witting, pers.commn).

| Year | Greenlandic whalers <br> (1955-1978) |  | $\begin{aligned} & \text { Norwegian } \\ & \text { whalers } \\ & (1968-1985) \\ & \hline \end{aligned}$ |  | Greenlandic whalers (1985-2006) |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | male | female | male | female | male | female |
| 1955 | 7 | 8 |  |  |  |  |
| 1956 | 5 | 15 |  |  |  |  |
| 1957 | 6 | 18 |  |  |  |  |
| 1958 | 5 | 6 |  |  |  |  |
| 1959 | 2 | 17 |  |  |  |  |
| 1960 | 2 | 15 |  |  |  |  |
| 1961 | 7 | 9 |  |  |  |  |
| 1962 | 17 | 43 |  |  |  |  |
| 1963 | 32 | 47 |  |  |  |  |
| 1964 | 26 | 37 |  |  |  |  |
| 1965 | 19 | 30 |  |  |  |  |
| 1966 | 24 | 49 |  |  |  |  |
| 1967 | 7 | 42 |  |  |  |  |
| 1968 | 10 | 47 | 7 | 13 |  |  |
| 1969 | 14 | 42 | 119 | 46 |  |  |
| 1970 | 12 | 20 | 74 | 52 |  |  |
| 1971 | 6 | 25 | 86 | 177 |  |  |
| 1972 | 6 | 40 | 32 | 91 |  |  |
| 1973 | 8 | 39 | 67 | 154 |  |  |
| 1974 | 6 | 34 | 43 | 209 |  |  |
| 1975 | 1 | 17 | 11 | 91 |  |  |
| 1976 | 2 | 20 | 38 | 149 |  |  |
| 1977 | 15 | 39 | 21 | 54 |  |  |
| 1978 | 2 | 13 | 10 | 65 |  |  |
| 1979 |  |  | 31 | 44 |  |  |
| 1980 |  |  | 13 | 62 |  |  |
| 1981 |  |  | 15 | 46 |  |  |
| 1982 |  |  | 24 | 42 |  |  |
| 1983 |  |  | 25 | 42 |  |  |
| 1984 |  |  | 20 | 49 |  |  |
| 1985 |  |  | 28 | 24 | 59 | 163 |
| 1986 |  |  |  |  | 38 | 107 |
| 1987 |  |  |  |  | 14 | 29 |
| 1988 |  |  |  |  | 6 | 34 |
| 1989 |  |  |  |  | 14 | 32 |
| 1990 |  |  |  |  | 15 | 63 |
| 1991 |  |  |  |  | 22 | 66 |
| 1992 |  |  |  |  | 18 | 72 |
| 1993 |  |  |  |  | 25 | 74 |
| 1994 |  |  |  |  | 22 | 78 |
| 1995 |  |  |  |  | 44 | 103 |
| 1996 |  |  |  |  | 36 | 120 |
| 1997 |  |  |  |  | 42 | 99 |
| 1998 |  |  |  |  | 39 | 118 |
| 1999 |  |  |  |  | 34 | 123 |
| 2000 |  |  |  |  | 36 | 102 |
| 2001 |  |  |  |  | 32 | 91 |
| 2002 |  |  |  |  | 33 | 88 |
| 2003 |  |  |  |  | 58 | 117 |
| 2004 |  |  |  |  | 44 | 129 |
| 2005 |  |  |  |  | 34 | 130 |
| 2006 |  |  |  |  | 38 | 135 |

Table 2. Annual catches of male and female West Greenland common minke whales, as reconstructed from total reported catch and reporting on caught males and females (source: L. Witting, pers.commn).

| Year | males | females | Year | males | females |
| ---: | ---: | ---: | ---: | ---: | ---: |
| $\mathbf{1 9 4 8}$ | 1 | 3 | $\mathbf{1 9 7 8}$ | 70 | 209 |
| $\mathbf{1 9 4 9}$ | 1 | 4 | $\mathbf{1 9 7 9}$ | 119 | 240 |
| $\mathbf{1 9 5 0}$ | 2 | 7 | $\mathbf{1 9 8 0}$ | 84 | 255 |
| $\mathbf{1 9 5 1}$ | 4 | 12 | $\mathbf{1 9 8 1}$ | 70 | 195 |
| $\mathbf{1 9 5 2}$ | 8 | 24 | $\mathbf{1 9 8 2}$ | 90 | 226 |
| $\mathbf{1 9 5 3}$ | 8 | 24 | $\mathbf{1 9 8 3}$ | 106 | 258 |
| $\mathbf{1 9 5 4}$ | 6 | 16 | $\mathbf{1 9 8 4}$ | 85 | 228 |
| $\mathbf{1 9 5 5}$ | 9 | 13 | $\mathbf{1 9 8 5}$ | 95 | 187 |
| $\mathbf{1 9 5 6}$ | 6 | 16 | $\mathbf{1 9 8 6}$ | 38 | 107 |
| $\mathbf{1 9 5 7}$ | 6 | 18 | $\mathbf{1 9 8 7}$ | 25 | 61 |
| $\mathbf{1 9 5 8}$ | 10 | 20 | $\mathbf{1 9 8 8}$ | 23 | 86 |
| $\mathbf{1 9 5 9}$ | 12 | 43 | $\mathbf{1 9 8 9}$ | 18 | 45 |
| $\mathbf{1 9 6 0}$ | 12 | 44 | $\mathbf{1 9 9 0}$ | 18 | 71 |
| $\mathbf{1 9 6 1}$ | 12 | 23 | $\mathbf{1 9 9 1}$ | 27 | 82 |
| $\mathbf{1 9 6 2}$ | 21 | 51 | $\mathbf{1 9 9 2}$ | 21 | 82 |
| $\mathbf{1 9 6 3}$ | 55 | 111 | $\mathbf{1 9 9 3}$ | 27 | 80 |
| $\mathbf{1 9 6 4}$ | 52 | 110 | $\mathbf{1 9 9 4}$ | 23 | 81 |
| $\mathbf{1 9 6 5}$ | 58 | 138 | $\mathbf{1 9 9 5}$ | 46 | 107 |
| $\mathbf{1 9 6 6}$ | 64 | 161 | $\mathbf{1 9 9 6}$ | 38 | 126 |
| $\mathbf{1 9 6 7}$ | 60 | 185 | $\mathbf{1 9 9 7}$ | 44 | 104 |
| $\mathbf{1 9 6 8}$ | 90 | 252 | $\mathbf{1 9 9 8}$ | 41 | 125 |
| $\mathbf{1 9 6 9}$ | 192 | 247 | $\mathbf{1 9 9 9}$ | 34 | 123 |
| $\mathbf{1 9 7 0}$ | 142 | 202 | $\mathbf{2 0 0 0}$ | 39 | 108 |
| $\mathbf{1 9 7 1}$ | 136 | 323 | $\mathbf{2 0 0 1}$ | 38 | 102 |
| $\mathbf{1 9 7 2}$ | 68 | 214 | $\mathbf{2 0 0 2}$ | 39 | 100 |
| $\mathbf{1 9 7 3}$ | 142 | 366 | $\mathbf{2 0 0 3}$ | 61 | 124 |
| $\mathbf{1 9 7 4}$ | 97 | 373 | $\mathbf{2 0 0 4}$ | 46 | 133 |
| $\mathbf{1 9 7 5}$ | 66 | 258 | $\mathbf{2 0 0 5}$ | 34 | 132 |
| $\mathbf{1 9 7 6}$ | 85 | 293 | $\mathbf{2 0 0 6}$ | 39 | 137 |
| $\mathbf{1 9 7 7}$ | 97 | 263 |  |  |  |

Table 3. Lower $5 \% K$ values for various intrinsic population growth rates $(r)$ under the scenario of different fishing patterns for all three groups/periods of whaling (i.e. all $\lambda$ 's different), and under the assumption of constant behaviour for Greenlandic whalers (i.e. $\left.\lambda^{\prime}=\lambda^{\prime \prime \prime}\right)$. Results for the case of a sex bias ( $\mu=0.1 \Rightarrow \mathrm{~m}: \mathrm{f}=45: 55$ ) in the unexploited population is also shown.

| $\boldsymbol{r}$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}$ | $\lambda^{\prime}=\lambda^{\prime \prime \prime} \neq \lambda^{\prime \prime}$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}, \mu=0.1$ |
| :---: | :---: | :---: | :---: |
| $\mathbf{0 . 0 2}$ | 30290 | 35200 | 28800 |
| $\mathbf{0 . 0 5}$ | 27170 | 32330 | 24430 |
| $\mathbf{0 . 0 8}$ | 25720 | 30550 | 22280 |

Table 4. Current depletion ( $N_{2007} / \mathrm{K}$ ) at the start of 2007 for intrinsic population growth rates ( $r$ ) under the scenario of different fishing patterns for all three groups/periods of whaling (i.e. all $\lambda$ 's different) and under the assumption of constant behaviour for Greenlandic whalers (i.e. $\left.\lambda^{\prime}=\lambda^{\prime \prime \prime}\right)$. Results for the case of a sex bias $(\mu=0.1 \Rightarrow \mathrm{~m}: f=45: 55)$ in the unexploited population is also shown.
a) All whales

| $N_{2007} / K$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}$ | $\lambda^{\prime}=\lambda^{\prime \prime \prime} \neq \lambda^{\prime \prime}$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}, \mu=0.1$ |
| :---: | :---: | :---: | :---: |
| $\mathbf{r}=0.02$ | 0.753 | 0.793 | 0.738 |
| $\mathbf{r}=0.05$ | 0.838 | 0.873 | 0.813 |
| $\mathbf{r}=0.08$ | 0.896 | 0.919 | 0.874 |

b) Females only

| $N_{2007} / K / 2$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}$ | $\lambda^{\prime}=\lambda^{\prime \prime \prime} \neq \lambda^{\prime \prime}$ | $\lambda^{\prime} \neq \lambda^{\prime \prime} \neq \lambda^{\prime \prime \prime}, \mu=0.1$ |
| :---: | :---: | :---: | :---: |
| $\mathbf{r}=0.02$ | 0.595 | 0.656 | 0.790 |
| $\mathbf{r}=0.05$ | 0.662 | 0.723 | 0.791 |
| $\mathbf{r}=\mathbf{0 . 0 8}$ | 0.710 | 0.760 | 0.795 |

Table 5. Parameter estimates for overdispersion and male selectivity relative to females for the case of $K \rightarrow \infty$ (approximated numerically here by $K=500000$ ) for various intrinsic population growth rates $(r)$.

| Parameter | $\boldsymbol{r}=\mathbf{0 . 0 2}$ | $\boldsymbol{r}=\mathbf{0 . 0 5}$ | $\boldsymbol{r}=\mathbf{0 . 0 8}$ |
| :---: | :---: | :---: | :---: |
| $\lambda^{\prime}$ (Greenland <br> 1955-1978) | 0.357 | 0.357 | 0.357 |
| $\lambda^{\prime \prime}$ (Norwegian) | 0.468 | 0.468 | 0.468 |
| $\lambda^{\prime \prime \prime}$ (Greenland <br> 1985-2006) | 0.334 | 0.334 | 0.334 |
| $\sigma_{l}$ (Greenland <br> $1955-1978)$ | 0.811 | 0.811 | 0.811 |
| $\sigma_{l \prime}$ (Norwegian) | 2.161 | 2.161 | 2.161 |
| $\sigma_{I \prime \prime}$ (Greenland <br> 1985-2006) | 0.496 | 0.496 | 0.496 |

Table 6. Model fit and simulation (median) parameter estimates of overdispersion $\sigma$ for the case of $K \rightarrow \infty$ (approximated numerically here by $K=500000$ ) for an intrinsic population growth rate of 0.05 , under different values of autocorrelation in the sampling procedure.

| Whaling period | autocorrelation | original | generated | ratio of <br> generated to <br> original |
| :---: | :---: | :---: | :---: | :---: |
| Greenland <br> (1955-1978) | $\boldsymbol{\rho = 0}$ | 0.811 | 0.597 | 0.736 |
| Norwegian <br> $(1968-1985)$ | $\boldsymbol{\rho}=\mathbf{0}$ | 2.161 | 0.824 | 1.016 |
| Greenland <br> $(\mathbf{1 9 8 5 - 2 0 0 6})$ | $\boldsymbol{\rho}=\mathbf{0}$ | 0.496 | 1.984 | 0.918 |

Table 7. Observed negative log-likelihood values for various values of true $K$ and the corresponding upper $5^{\text {th }}$ percentile obtained by simulation for the two methods considered. The probability corresponding to the fitted - log-likelihood is also shown.

| True K | Fit -loglikelihood$(-\ell \mathrm{nL})$ | "Method 1" |  | "Method 2" |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{gathered} 95^{\text {th }} \\ \text { percentile } \end{gathered}$ | Probability corresponding to fit -InL | $\stackrel{95^{\text {th }}}{\text { percentile }}$ | Probability corresponding to fit -InL |
| 500000 | 150.041 | 157.860 | 0.601 | 157.860 | 0.601 |
| 45000 | 150.974 | 156.517 | 0.692 | 159.250 | 0.555 |
| 30000 | 151.688 | 156.093 | 0.742 | 160.811 | 0.496 |
| 20000 | 153.454 | 155.593 | 0.872 | 164.444 | 0.377 |
| 18000 | 154.543 | 155.661 | 0.923 | 166.293 | 0.355 |
| 17000 | 155.463 | 155.332 | 0.952 | 167.336 | 0.333 |
| 16000 | 156.921 | 155.275 | 0.972 | 168.826 | 0.306 |
| 15000 | 159.489 | 155.378 | 0.996 | 172.028 | 0.259 |



Figure 1. Population trajectories for the lower $5 \% K$ case for various values of intrinsic population growth rate under the assumption of common hunting behaviour by the Greenlandic whalers during the two whaling periods 1955-1978 and 1985-2005 (denoted with " S " in the legend) and when different hunting behaviour is assumed (denoted with "D" in the legend").

Greenlandic whalers 1955-1978


Norwegian whalers 1968-1985


Greenlandic whalers 1985-2006

——obsened. \#- - estimated

Greenlandic whalers 1955-1978


- -I- - K=500000 工— lower $5 \% \mathrm{~K}$

Norwegian whalers 1968-1985


Greenlandic whalers 1985-2005

-- - K $=500000$ 乙—lower $5 \% \mathrm{~K}$

Figure 2. Observed and estimated proportion of females caught for the lower $5 \% K$ case (left), and the estimated proportion of females caught for the lower $5 \% K$ case compared to the case of $K=500000$ (right) by: i) the Greenlandic whalers during the period 1955-1978 (top), ii) the Norwegian whalers in the period 1968-1985 (middle) and iii) the Greenlandic whalers during the period 1985-2005 (bottom). Note that for clarity the scale of the plots on the right hand side are different


Figure 3. Proportion of minke whales sampled for sex by the Greenland whalers (assuming that the Norwegian whalers sampled all the whales that they caught).


Figure 4. Observed negative log-likelihood function and upper $5^{\text {th }}$ percentiles calculated by simulation.

## APPENDIX

## Simulation algorithm

A fixed intrinsic population growth rate $(r)$ of 0.05 was set for all simulations. For a given value of the true virgin biomass $(K)$, the model described in the text is fitted to the original data to obtain estimates for the overdispersion (os) and the selectivity of males relative to females ( $\lambda \mathrm{s}$ ) parameters for the period and whalers concerned (Table A.1). For each model fit the negative loglikelihood value is also obtained. Figure A. 1 shows model diagnostics for the original data (and for $K=500000$ ) and Figure A. 2 shows these for one of the simulations. Note that the standardised residuals in Figure A. 1 appear reasonably random and homoscedastic. Figure A. 3 shows the simulated distributions of the overdispersion parameters for the whaling periods, with the positions of the estimated overdispersion parameter from the original data also shown.

For each set of values of $K, r, \sigma_{i}$ and $\lambda_{i}$, the total annual catches $\left(C_{y}=C_{y}^{m}+C_{y}^{f}\right)$ and the annual reported total catches ( $C_{y}^{i}$ ), the following steps are taken:

1. Set $N_{1948}=K=N_{1948}^{f}+N_{1948}^{f}$.
2. Generate $C_{y}^{f}, C_{y}^{m}, C_{y}^{f(i)}$ and $C_{y}^{m(i)}$.
3. From $C_{y}$, project $N_{y}^{t}$ and $N_{y}^{m}$ forward one year (using equations (1) and (2)).
4. Repeat steps (2) and (3) until the end of the time period (i.e. 2006).
5. Fit model to the generated data to get $-\ell \mathrm{nL}$.
6. Repeat steps (2) to (5) 500 times.

## Data generation

The data generation has to take into account that not all whales are sampled for sex, and that there is a period over which both Norwegian and Greenlandic catches occurred. The assumption has been made that the Norwegian catch was always fully sampled, so that the sampled Greenland catch has to be generated from the total Greenland catch each year.

1] Period 1948-1954 (no sampling):

- Generate $C_{y}^{f}$ from the normal distribution given by:

$$
\begin{equation*}
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{l} N_{y}^{m}} C_{y}, \sigma_{l}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime} N_{y}^{m}} C_{y}\right), \tag{A.1}
\end{equation*}
$$

i.e. the $\lambda_{i}$ and $\sigma_{i}$ correspond to the Greenland (1955-1978) period.

- The total number of males is then given by $C_{y}^{m}=C_{y}-C_{y}^{f}$.

2] Period 1955-1967 (only Greenland catch, which is sampled):

- Generate $C_{y}^{f}$ and $C_{y}^{m}$ as in 1] above.
- Sample $C_{y}^{\prime}$ without replacement and with autocorrelation $\rho$ from $C_{y}$ with sex split given by $C_{y}^{f}$ and $C_{y}^{m}$, to get sampled numbers $C_{y}^{f(l)}$ and $C_{y}^{m(l)}$.

3] Period 1968-1978 (both Greenland and Norwegian catches, both sampled):

- Generate the Norwegian catch $C_{y}^{f(1)}$ from the normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}, \sigma_{\| \prime}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}\right)
$$

- The total number of males caught by the Norwegians is then given by $C_{y}^{m(I I)}=C_{y}^{\prime \prime}-C_{y}^{f(I I)}$.
- Note that the Greenland catch is $C_{y}-C_{y}^{\prime \prime}$, to be comprised of $C_{y}^{f(l)^{*}}$ females and $C_{y}^{m(l)^{*}}$ males.
- Generate $C_{y}^{f(l)^{*}}$ from the normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right), \sigma_{I}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right)\right)
$$

- The total number of males caught by Greenland is then given by $C_{y}^{m(l)^{*}}=\left(C_{y}-C_{y}^{\prime \prime}\right)-C_{y}^{f(l)^{*}}$.
- Sample without replacement and with autocorrelation from $C_{y}-C_{y}^{\prime \prime}$ with sex split given by $C_{y}^{f(l)^{*}}$ and $C_{y}^{m(l)^{*}}$, to give the whales caught and sampled by Greenland $C_{y}^{f(l)}$ and $C_{y}^{m(l)}$.
- Add the $C_{y}^{f(l)^{*}}$ and $C_{y}^{m(l)^{*}}$ to the Norwegian generated catches to get the total catches by sex (e.g. $\left.C_{y}^{f}=C_{y}^{f(I I)}+C_{y}^{f(l)^{*}}\right)$.

4] Period 1979-1984 (both Greenland and Norwegian catches; the former is not sampled, but is assumed to be governed by the parameters for the first (1955-1978) period of sampled Greenland catches):

- Generate the Norwegian catch $C_{y}^{f(1)}$ from the normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}, \sigma_{I I}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}\right)
$$

- The total number of males caught by the Norwegians is then given by $C_{y}^{m(I I)}=C_{y}^{\prime \prime}-C_{y}^{f(I I)}$.
- Note that the Greenland catch is $C_{y}-C_{y}^{\prime \prime}$, to be comprised of $C_{y}^{f(l)^{*}}$ females and $C_{y}^{m(l)^{*}}$ males.
- Generate $C_{y}^{f(l)^{*}}$ from the normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right), \sigma_{I}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right)\right)
$$

- The total number of males caught by Greenland is then given by $C_{y}^{m(l)^{*}}=\left(C_{y}-C_{y}^{\prime \prime}\right)-C_{y}^{f(l)^{*}}$.
- Add the $C_{y}^{f(l)^{*}}$ and $C_{y}^{m(l)^{*}}$ to the Norwegian generated catches to get the total catches by sex (e.g. $\left.C_{y}^{f}=C_{y}^{f(I I)}+C_{y}^{f(l)^{*}}\right)$.

5] Period 1985 (both Greenland and Norwegian catches, both sampled):

- Generate the Norwegian catch $C_{y}^{f(1 I)}$ from the normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}, \sigma_{I I}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime} N_{y}^{m}} C_{y}^{\prime \prime}\right)
$$

- The total number of males caught by the Norwegians is then given by $C_{y}^{m(I I)}=C_{y}^{\prime \prime}-C_{y}^{f(I)}$.
- Note that the Greenland catch is $C_{y}-C_{y}^{\prime \prime}$, to be comprised of $C_{y}^{f(l)^{*}}$ females and $C_{y}^{m(l)^{*}}$ males.
- Generate $C_{y}^{f(I I I)^{*}}$ from the normal distribution given by:

$$
N\left(\frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime \prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right), \sigma_{I I \prime}^{2} \frac{N_{y}^{t}}{N_{y}^{t}+\lambda^{\prime \prime \prime} N_{y}^{m}}\left(C_{y}-C_{y}^{\prime \prime}\right)\right)
$$

- The total number of males caught by Greenland is then given by $C_{y}^{m(I I I)^{*}}=\left(C_{y}-C_{y}^{I \prime}\right)-C_{y}^{f(I I)^{*}}$.
- Sample randomly without replacement from $C_{y}-C_{y}^{\prime \prime}$ with sex split given by $C_{y}^{f(I I)^{*}}$ and $C_{y}^{m(I I I)^{*}}$, to give the whales caught and sampled by Greenland $C_{y}^{f(I I I)}$ and $C_{y}^{m(I I I)}$.
- Add the $C_{y}^{f(I I I)^{*}}$ and $C_{y}^{m(I I I)^{*}}$ to the Norwegian generated catches to get the total catches by sex (i.e. $C_{y}^{f}=C_{y}^{f(I I)}+C_{y}^{f(I I I)^{*}}$ ).

6] Period 1986-2006 (only Greenland catch, which is sampled):

- Generate $C_{y}^{f}$ from normal distribution given by:

$$
\mathrm{N}\left(\frac{N_{y}^{f}}{N_{y}^{t}+\lambda^{\prime \prime \prime} N_{y}^{m}} C_{y}, \sigma_{I I}^{2} \frac{N_{y}^{t}}{N_{y}^{f}+\lambda^{I \prime \prime} N_{y}^{m}} C_{y}\right)
$$

- The total number of males is then given by $C_{y}^{m}=C_{y}-C_{y}^{f}$.
- Sample $C_{y}^{\prime \prime \prime}$ randomly without replacement from $C_{y}$ with sex split given by $C_{y}^{f}$ and $C_{y}^{m}$, to get sampled numbers $C_{y}^{f(I I I)}$ and $C_{y}^{m(I I I)}$.

In the data generation algorithm described above, in instances in which a negative catch was generated for one of the sexes, the catch for that sex was set to zero and consequently the catch for the opposite sex was set to the total number being sampled (as otherwise in this case, a catch greater than the number being sampled would have been generated to compensate for the negative generated catch).

## Simulation confidence limits

Two methods of obtaining simulation confidence limits were used. In "Method 1", the parameter estimates used for data generation in the simulation algorithm described above were the ones obtained for the "best" fit (i.e. for $K=500000$ ). In "Method 2", for each true $K$ in the simulation, the parameter estimates obtained for that fit were used to generate the data.

Table A. 1 Parameter estimates used in the generation of data for the simulation testing algorithm.
For "Method 1" only the "best" fit parameter estimates (shown in italics corresponding to $K=500000$ ) are used to generate data.

| $\boldsymbol{K}$ | $\boldsymbol{\sigma}_{\boldsymbol{I}}$ | $\boldsymbol{\sigma}_{I I}$ | $\boldsymbol{\sigma}_{I I}$ | $\boldsymbol{\lambda}^{\prime}$ | $\boldsymbol{\lambda}^{\prime \prime}$ | $\boldsymbol{\lambda}^{\prime \prime \prime}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathbf{5 0 0} \mathbf{0 0 0}$ | 0.811 | 2.161 | 0.496 | 0.357 | 0.468 | 0.334 |
| $\mathbf{4 5 0 0 0}$ | 0.831 | 2.184 | 0.450 | 0.344 | 0.433 | 0.279 |
| $\mathbf{3 0 0 0 0}$ | 0.843 | 2.200 | 0.505 | 0.337 | 0.412 | 0.247 |
| $\mathbf{2 0 0 0 0}$ | 0.866 | 2.231 | 0.525 | 0.324 | 0.377 | 0.194 |
| $\mathbf{1 8 0 0 0}$ | 0.875 | 2.244 | 0.543 | 0.319 | 0.365 | 0.174 |
| $\mathbf{1 7 0 0 0}$ | 0.881 | 2.253 | 0.560 | 0.316 | 0.357 | 0.161 |
| $\mathbf{1 6 0 0 0}$ | 0.887 | 2.263 | 0.591 | 0.312 | 0.347 | 0.145 |
| $\mathbf{1 5 0 0 0}$ | 0.895 | 2.277 | 0.653 | 0.308 | 0.336 | 0.125 |




$$
\varlimsup_{\text {Observed }-\ldots \text { Estimated }}
$$



Year



year




Figure A.1. Model diagnostics for the original data and for $K=500000$ corresponding to i) the Greenlandic whalers during the period 1955-1978 (left), ii) the Norwegian whalers in the period 1968-1985 (middle) and iii) the Greenlandic whalers during the period 1985-2005 (right).


Observed - . . Estimated



Year



Figure A.2. Model diagnostics for one of the simulations and for $K=500000$ corresponding to i) the Greenlandic whalers during the period 19551978 (left), ii) the Norwegian whalers in the period 1968-1985 (middle) and iii) the Greenlandic whalers during the period 1985-2005 (right).




Figure A.3. Simulated distributions of the overdispersion parameter $\sigma$ for i) the Greenlandic whalers during the period 1955-1978 (top), ii) the Norwegian whalers in the period 1968-1985 (middle) and iii) the Greenlandic whalers during the period 1985-2005 (bottom). The position of the estimated overdispersion parameter for the original data is shown ("observed") as well as the median of the simulated data.

## ADDENDUM

The same assessment as presented in this paper was attempted on catch data for West Greenland fin whales. However, there was no differentiation in the negative log-likelihood function for different values of $K$. Figure 5Add1 shows the proportion of female catches for the fin whales. For comparison the same is shown for the minke whales. This clearly shows that there is not much contrast in the sex ratio of catches for fin whales (average of 0.523 ), while for the minke whales considerably more females were caught (average proportion of 0.723 ).


Figure 5Add1. Comparison of the proportion of fin and minke whales females caught. The horizontal line is at 0.5 .

