

Lower confidence bound on population status from catch sex ratio: applied to minke whales off West Greenland

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ABSTRACT

We develop a frequentist statistical simulation framework to estimate the lower bound on the status of harvested populations from time series of the sex ratio of harvested individuals. The method is appropriate when the sex ratio of the harvest is biased relative to the sex ratio of the population, and the catch sex ratio depends upon the population sex ratio. It is applied to common minke whales (*Balaenoptera acutorostrata*) off West Greenland, where the female fraction in fetuses is around $1/2$, and the fraction in the catches has varied around $3/4$ since the beginning of the hunt in 1948, a difference that reflects segregation where females tend to occur in other areas than males. By fitting an age- and sex-structured population dynamic model with density regulation to the sex ratios of the historical catches, for an assumed *msyr* of 2%, we obtain a lower 5%-tile confidence limit of current abundance between 9,100 (95% CI: 7,400 – 10,400) and 12,300 (95% CI: 0 – 13,900) whales, a carrying capacity between 19,300 (95% CI: 18,300 – 20,300) and 21,500 (95% CI: 0 – 22,700) whales, and a current depletion ratio between 0.47 (95% CI: 0.40 – 0.51) and 0.56 (95% CI: 0 – 0.60). These estimates are negatively biased owing to the inclusion of non-converging optimizations. With non-converging optimizations excluded, the corresponding estimates are 10,400 (95% CI: 9,300 – 12,400) to 16,800 (95% CI: 15,800 – 18,100) whales for current abundance, 20,200 (95% CI: 19,500 – 21,700) to 24,800 (95% CI: 24,100 – 25,900) whales for carrying capacity, and 0.51 (95% CI: 0.47 – 0.56) to 0.68 (95% CI: 0.65 – 0.69) for the depletion ratio. These estimates are higher than all estimates obtained from aerial surveys, and they suggest that minke whales off West Greenland are only a fraction of a larger more widespread population.

KEYWORDS: SEX RATIO, REMOVAL METHOD, MODELING, ATLANTIC OCEAN, WHALING - ABORIGINAL, LIKELIHOOD, SIMULATION

1 INTRODUCTION

Most methods for status assessment of natural populations are heavily dependent upon abundance estimates from surveys. But reliable survey estimates may not necessarily exist, and nor may they easily be generated. If this is the case for a harvested population the development of alternative assessment methods can be crucial in order to ensure a sustainable exploitation. In this paper we develop an assessment method where population status and abundance can be estimated from time-series of sex specific harvest statistics only.

The proposed method will not work for all populations because it requires that the catch

sex ratio is biased relative to the sex ratio of the whole population, and that the sex ratio of the harvest depends upon the population sex ratio. An overexploitation will then show up differentially in the two sexes, with a trend in the catch sex ratio carrying a data signal on the exploitation level, abundance, and productivity of the population.

Our method is a variant of the removal method (Moran 1951). As Hirst (1994) we base our confidence bounds on the likelihood function. We focus on the differential removal of individuals by sex, and do not need to assume the population to be closed to recruitment and other mortality as must be done for the ordinary removal method. About 3/4 of the removed common minke whales off West Greenland are females, while the sex ratio is even among recruits. Our estimate of abundance is related to the slope in the time series of the fraction of females in the catch. The smaller the population, the more the female fraction is expected to slope down. The observed female fractions are however rather stable, and the maximum likelihood estimate of abundance is infinite. But even for this most difficult situation we show that it is possible to use classical frequentist statistics to estimate the lower confidence bounds of abundance and population status. As precautionary management is based on lower bounds, instead of point estimates and upper confidence limits, the proposed method should be generally applicable for management, as we illustrate by applying it to the harvest of common minke whales (*Balaenoptera acutorostrata*) off West Greenland.

1.1 Common minke whales off West Greenland

In the North Atlantic the common minke whale is sex segregated with females tending to occur further to the north than males (Jonsgård 1962; Larsen and Øien 1988; Øien 1988; Horwood 1989). In the eastern North Atlantic, females are found to dominate the catches in the Barents Sea, while males predominate the catches around the British Isles and on the Norwegian coast including Finnmark (Øien 1988). The same pattern was found in the Norwegian catches in the western North Atlantic, where males dominated the catches in the southern areas with the percentage of females increasing going northwards along East Greenland and West Greenland (Larsen and Øien 1988; Laidre et al. 2008). Females have also been found to dominate the catches in West Greenland early in the season with their proportion tending to decline thereafter (Larsen and Øien 1988; Simon et al. 2007).

Catches of common minke whales off West Greenland has occurred regularly since 1948, with the annual take having a maximum of four to five hundred individuals in the early 1970s, and a current take of approximately 175 individuals per year. Throughout the period the catch has been predominately of females. The average proportion of females in the catch from 1948 to 2004 is 0.74, which differs significantly from a foetal sex ratio that is not significantly different from even [40% females among 43 fetuses from the Norwegian hunt (Larsen and Kapel 1982), and 54% females among 544 fetuses from the Greenland hunt (Simon et al. 2007)].

It is most likely the geographical sub-structuring of the two sexes during summer that determines the female bias in the West Greenland catch of common minke whales. An alternative explanation is sex specific harvest selectivity combined with an even or uneven dispersal of males and females. This hypothesis may also explain the female biased catch, but it is unlikely true as female common minke whales cannot generally be distinguished from males at distance.

Owing to the female biased catches, the continuity of the reported catch history for the whole period of the fishery, and abundance surveys that cover only some fraction of the whole

population, for the common minke whale off West Greenland an assessment based on the catch sex ratio may provide a more accurate result than a traditional assessment based on abundance data.

2 METHOD

2.1 Catch statistics

Catch reports from Greenland with information on sex fall into three major sets: Inshore catches taken by Greenlandic whalers from 1955 to 1978, and from 1985 to the present, and offshore catches taken by Norwegian whalers from 1968 to 1985. Greenlandic whalers also took common minke whales from 1948 to 1954 and again from 1979 to 1984, but sex specific reporting is almost absent in these years. The three time series of sex specified catches are listed in Table 1.

A best estimate of a sex specific time series of the total removal of male and female common minke whales off West Greenland was constructed. The sex ratio of the sex specific reporting in any year t from a specific fishery was assumed to apply to the total number of whales landed and struck and loss by that fishery in that year. And for years with no or almost no sex information on the removals by Greenlandic whalers (1948-54; 1979-84), the sex specific removals were estimated from the sex ratio of the reported removals in that fishery over all years with sex specific reporting. The estimated sex specific removals of the different fisheries were then added to provide a time series of total sex specific removal (Table 3).

Nearly all the Norwegian catches were reported with sex, while the proportion reported with sex was generally below 50% for the Greenlandic catches from 1955 to 1978, with the proportion declining to approximately 10% toward the end of the period. The absolute number of sex reports remained relatively stable over the period, with the decline in the proportion reflecting mainly an increase in the absolute number of catches. From 1985 and onwards sex specific reporting was generally high in the Greenlandic catches, with the fraction of sex specific reporting being above 90% in most of the years since 1993.

The sex ratio of the sex specific reporting has fluctuated over the years but there is no apparent trend in the sex ratio of the three data sets, and nor do any of the three time series of catch data have significant autocorrelation in the fraction of females (tested for lags from one to 12 years). The average yearly sex ratio of reported caught males (\dot{C}^m) over reported caught females (\dot{C}^f) varies only little between the three data sets (geometric mean of 0.30 for Greenlandic whalers from 1955 to 1978, 0.32 for Greenlandic whalers from 1985 to 2006, and 0.44 for Norwegian whalers from 1968 to 1985), while the three sets differ more substantial in the variation (cv for $\ln \phi$ of 0.62 for Greenlandic whalers from 1955 to 1978, 0.23 for Greenlandic whalers from 1985 to 2006, and 0.96 for Norwegian whalers from 1968 to 1985).

The offshore Norwegian catches show a significant, and apparent continuous, increase in the female fraction with latitude, while the female fraction in the inshore late Greenlandic catches is nearly constant with latitude (Larsen and Øien 1988; Laidre et al. 2008). If the late Greenlandic catches are separated into northern (above 63 degrees North) and southern catches (Table 2) they even show a reversed sex ratio pattern. During the first half of the late Greenlandic period (1987-1996), the female fraction was highest in the southern catches [0.83 ($n = 303$) in southern catches, and 0.72 ($n = 558$) in northern catches]. The female fraction in the southern area, however, has shown a significant decline during the late Greenlandic period

with the female fraction during the second half of the period (1997-2006) resembling the female fraction in the northern area [0.76 ($n = 482$) in southern catches, and 0.74 ($n = 1,025$) in northern catches]. Owing to a general lack of sex specific catch data from the southern area during the early Greenlandic period; it is unclear whether the female fraction in the southern area was abnormally high during the first half of the late Greenlandic period, or whether it is now abnormally low for that area. The general sex segregation of common minke whales in the North Atlantic, as well as the increasing female fraction with latitude for the Norwegian catches offshore West Greenland, however, indicate that the female fraction during the first half of the late Greenlandic period may have been abnormally high in the southern area.

2.2 Population model

While a potential over-exploitation of the minke whale stock that supports the Greenlandic harvest is expected to result in a sex ratio shift towards a higher fraction of males in the catches, the observed increased male fraction in the southern area may more likely be due to other causes. The change in the female fraction in the southern area is correlated with changes in sea temperature (Laidre et al. 2008), indicating that the sex ratio may be influenced by oceanographic changes in the Irminger current; the major controller of the sea temperature in South West Greenland. This warm current originates in the waters off Southeast Greenland, where males predominated the Norwegian catches of common minke whales (Christensen 1976; Larsen and Øien 1988). An influx of warm water may induce an influx of male minke whales to West Greenland waters.

The presence of a small non-significant and recent increase in the fraction of females in the catches from the northern area (Laidre et al. 2008) is also not in agreement with a stock that is depleted for females. The apparent presence of opposite sex ratio trends between the two areas suggests a change in the segregation of males and females between the two areas over time. The variation and trends in the catch sex ratio in West Greenland may thus likely reflect not only the sex specific harvest, but also the relative distribution of the two sexes along the West Greenland coast, together with variation and trends in the influx of male minke whales to especially the southern area.

In this study we apply two models of population structure to cope with the sex ratio changes in our attempt to estimate lower bounds on the status of the minke whale stock that supports the harvest in West Greenland. A *closed model* assumes no influx of additional males to the southern area from the East, but only that the female fraction in the northern and southern area may change owing to the females biased catch and a differential segregation of the two sexes between the two areas. A second *influx model* assumes instead that the trend in the sex ratio in the southern area reflects exploitation and oceanographic changes, while for the northern area, that is less affected by the Irminger current, a sex ratio trend would reflect the sex specific degree of exploitation only.

We assume an age- and sex-structured population with dynamics that is regulated by a Pella-Tomlinson form of density dependence on the reproductive rate (appendix A). Initially, prior to the first harvest in 1948, the population is assumed to be at carrying capacity (K). Hereafter it develops in response to the age- and sex-structured catches that have been taken off West Greenland until today. For the purpose of our analysis, the catches are divided into three time-series; the early Greenlandic (1948-1984), the late Greenlandic (1985-2006), and the

Norwegian (1968-1985) catches, with the Norwegian and late Greenlandic catches being spatially separated into a northern (above 63 degrees North) and a southern aggregation (Table 2).

As there is no evidence of a female biased catch caused by hunter selectivity, and as there is plenty of evidence that show that minke whales in the North Atlantic are sex segregated with females occurring further to the north than males, the population model is best seen as being geographically sub-structured, although the applied mathematics is realistic also for a female selective hunt. The harvest is thus best seen as being taken from aggregations that have a female biased sex ratio relative to the sex ratio of the total population.

The aggregations of minke whales that are included in the modeling are the early Greenlandic inshore fishery along the entire West Greenland coast (denoted by e), the late Greenlandic inshore fishery in the northern area (l_n), the southern area (l_s), and the along the entire coast ($l_w = l_n + l_s$), as well as the Norwegian offshore fishery in the northern (n_n) and southern (n_s) areas.

The abundance (A) of male (m) and female (f) minke whales of age-class a in aggregation i at time t

$$\begin{aligned} A_{t,a}^{i,m} &= \beta_t G_a N_{t,a}^m / \vartheta^i \\ A_{t,a}^{i,f} &= \beta_t G_a N_{t,a}^f \end{aligned} \quad (1)$$

reflects the total gender (g) specific abundance for that age-class $N_{t,a}^g$, the relative age-specific migration G_a of individuals in age-class a ($G_a = 1$ for at least one age-class), a β_t parameter that is the fraction of the females in the total population that are present in the West Greenland aggregation for age classes where $G_a = 1$ (β_t is a dummy parameter that is not estimated but set equal to 1), and an increased average tendency $\vartheta^i > 1$ by which female minke whales migrate to aggregation i relative to male minke whales.

The expected fraction of females in the catch from aggregation i in year t is then

$$\theta_t^i = \frac{\sum_{a=1}^x A_{t,a}^{i,f}}{\sum_{a=1}^x A_{t,a}^{i,f} + A_{t,a}^{i,m}} \quad (2)$$

with the one plus abundance of female and male minke whales being $A_t^{i,f} = \sum_{a=1}^x A_{t,a}^{i,f}$ and $A_t^{i,m} = \sum_{a=1}^x A_{t,a}^{i,m}$.

2.2.1 Influx model

For the influx model it is the abundance in aggregations e , l_n , l_s , n_n and n_s that are given by Eq. (1), expect that for aggregation l_s , the southern area of the late Greenlandic fishery, the sex biased migration factor ϑ^{l_s} is given as a linear function of time

$$\vartheta_t^{l_s} = \vartheta_0 + (t - 1987)\beta \quad (3)$$

in order to capture a time change in the influx of males to the southern area.

An old version of the closed model with an additional parameter is described in Appendix D.

2.2.2 Closed model

For the closed model it is the abundance in aggregations e , l_w , n_n and n_s that are given by Eq. (1). The l_w abundance is then split between l_n and l_s in order to allow for opposite sex ratio

trends in the northern and southern areas for the late Greenlandic fishery. This split is done by letting the female fraction in the southern area be

$$\theta_t^{l_s} = \frac{e^{\alpha+\beta(t-1987)}}{1 + e^{\alpha+\beta(t-1987)}} \quad (4)$$

and the number of age class a females in the southern area be

$$A_{t,a}^{l_{s,f}} = p^{l_{s,f}} A_{t,a}^{l_{w,f}} \quad (5)$$

where $p^{l_{s,f}}$ is the proportion of the female minke whales in West Greenland that are in the southern area. For the southern area we may insert Eq. (5) into Eq. (2), set Eq. (2) equal to Eq. (4) and find that the one plus abundance of males in the southern area is

$$A_t^{l_{s,m}} = A_t^{l_{s,f}} / e^{\alpha+\beta(t-1987)} \quad (6)$$

The proportion of the male minke whales in West Greenland that are in the southern area is then

$$p^{l_{s,m}} = A_t^{l_{s,m}} / A_t^{l_{w,m}} \quad (7)$$

with $A_t^{l_{w,m}}$ obtained from Eq. (1), and the abundance of age class a males

$$A_{t,a}^{l_{s,m}} = p^{l_{s,m}} A_{t,a}^{l_{w,m}} \quad (8)$$

Hence, the number of age class a female and male minke whales in the northern area is

$$\begin{aligned} A_{t,a}^{l_{n,f}} &= A_{t,a}^{l_{w,f}} - A_{t,a}^{l_{s,f}} \\ A_{t,a}^{l_{n,m}} &= A_{t,a}^{l_{w,m}} - A_{t,a}^{l_{s,m}} \end{aligned} \quad (9)$$

assuming that West Greenland minke whales are either in the northern or the southern area ($A_t^{l_w} = A_t^{l_n} + A_t^{l_s}$).

2.3 One-sided confidence bounds

We use simulation and likelihood analysis to make inference on the population parameters. We face the problem that the likelihood function has no maximum within the parameter space; for carrying capacity, e.g., the maximum is at $K = \infty$. By simulation we are however able to find the distribution of the profile likelihood and thereby we can obtain a one-sided confidence interval on the lower bound of abundance and other status related parameters.

The log likelihood ratio curve, called the deviance curve, provides confidence intervals through the chi-square distribution in standard applications. The chi-square method, however, must be modified when the parameter is restricted to an interval, or when a transformation is needed to make the maximum likelihood estimator approximately normal and the transformed parameter is restricted. In our rather complex model it is difficult to evaluate the quality of the chi-square approximation, and we have found it necessary to estimate the distribution of the deviance by simulation. Our maximum likelihood estimate of carrying capacity is infinite. The deviance function is therefore decreasing, and it crosses the curve of quantiles at level α only once. Above the point of crossing the deviance curve is below the curve of quantiles. The point of crossing is therefore a lower confidence limit at level α . The upper confidence limit is infinite.

The applied statistics should be familiar, at least when applied to the profile deviance function $D(K) = 2 \ln(L(\widehat{K})/L(K))$. In regular models the deviance has approximately a chi-square distribution at the true value in repeated samples, and a confidence set is obtained as $\{K : D(K; D_{obs}) < q_{.95}\}$. The fortunate thing here is that the approximate null distribution is the same for all values of the parameter. This standard construction, as well as the slightly more general construction we will use applies to parameters of any dimension.

To estimate the one-sided confidence bound, two types of projections were run for each carrying capacity: data trajectories where the original catches were subtracted from the projected population, and simulated data trajectories where catches with simulated female fractions were subtracted. The parameter vector \mathbf{V} , e.g., $\mathbf{V} = \{\vartheta^e, \vartheta^{lw}, \alpha, \beta, p^{ls,f}, \sigma^e, \sigma^{ls}, \sigma^{ln}\}$ for our base case version of the closed model, was first estimated by maximum likelihood over the original data, with the maximum likelihood estimate, denoted $\widehat{\mathbf{V}}$, being given for $K = \infty$ (approximated here as $K = 200,000$), and the conditional maximum likelihood estimate $\widehat{\mathbf{V}}(K)$ being given for each K . The profile deviance function of K is then $D(K) = 2 \ln(L(\infty, \widehat{\mathbf{V}})/L(K, \widehat{\mathbf{V}}(K)))$ with likelihood (L) being estimated as described below.

Given the original catch histories and the age-structured parameterisation in the appendix, the parameter vector $\{K, \widehat{\mathbf{V}}(K)\}$ specifies the population trajectory completely and allows hypothetical catch data for the three fisheries to be simulated. For each K we simulated 1000 sex specific catch series for each fishery, and for each of the simulated series the \mathbf{V} parameters were re-estimated by the same maximum likelihood method as applied for the original catch data. For the simulated data the maximum likelihood estimate, denoted \mathbf{V}^* , is not necessarily at $K = \infty$, and thus the joint maximum likelihood estimate $\{K^*, \mathbf{V}^*\}$ required a joint optimisation over K and \mathbf{V} . The deviance on the simulated data was then given as $D^*(K) = 2 \ln(L(K^*, \mathbf{V}^*)/L(K, \mathbf{V}^*(K)))$, where $\mathbf{V}^*(K)$ is the K -conditional maximum likelihood estimate. The quantiles over K for the 1000 replicate values $D^*(K)$ were then calculated, and the lower confidence bound for K was found as the intercept between the quantile curve and the profile deviance function $D(K)$.

As, for a given msyr, the carrying capacity for the given model is monotonically related to the current abundance (N) and the current depletion ratio ($dr = N/K$) lower bounds on the latter parameters were estimated by similar methods.

We assume the likelihood to be over-dispersed binomial in order to reflect the binomial sampling of males and females in the catch, letting the reported catch of females $\dot{C}_t^{f,i}$ from aggregation i in year t be distributed as a normal variate rounded to the nearest integer between zero and \dot{C}_t^i ; the total catch with reported sex for that aggregation that year. To obtain a simple model of over-dispersion, let the normal variate have mean $\mu = \dot{C}_t^i p_t^i$ and variance $\sigma_i^2 \dot{C}_t^i p_t^i (1 - p_t^i)$, with p_t^i being the expected proportion of females, and $\sigma_i > 1$ being over-dispersion in the reported female catch from aggregation i . The log likelihood for the catch in aggregation i is then

$$\ln L = \sum_t -\frac{1}{2} \left[\frac{(\dot{C}_t^{f,i} - \dot{C}_t^i p_t^i)^2}{\sigma_i^2 \dot{C}_t^i p_t^i (1 - p_t^i)} + \ln(\dot{C}_t^i p_t^i (1 - p_t^i)) + 2 \ln \sigma_i \right] \quad (10)$$

with p_t^i being a function of the model and its parameters. These are estimated by maximizing the log likelihood (appendix C), with the ML-estimator for σ_i^2 being

$$\hat{\sigma}_i^2 = \max \left\{ 1, \frac{1}{n^i} \sum_t \frac{(\dot{C}_t^{f,i} - \dot{C}_t^i p_t^i)^2}{\dot{C}_t^i p_t^i (1 - p_t^i)} \right\} \quad (11)$$

where n^i is the number of years with sex specific catch data for aggregation i .

Given parameter estimates from the original data, catches are simulated as

$$\begin{aligned}\tilde{C}_t^{f,i} &= \text{round} \left(C_t^i \hat{p}_t^i + Z \hat{\sigma}_i \sqrt{C_t^i \hat{p}_t^i (1 - \hat{p}_t^i)} \right) \\ \tilde{C}_t^{m,i} &= C_t^i - \tilde{C}_t^{f,i}\end{aligned}\tag{12}$$

with $Z \sim N(0, 1)$.

For some n_f cases of the 1000 simulated data sets for a given value of k , it was impossible to obtain a deviance value because one or both of the log likelihood optimizations failed to converge to an optimum. We solved this problem by assigning all such cases the largest deviance value that was found among the remaining 1000- n_f deviance values. Hence, we expect that the variance in our distributions of deviance values was increased relative to the true variance, and consequently our abundance estimates should be negatively biased.

The simulated sex specific catch reports did not account for all catches; for the periods 1948-1954 and 1979-1984, for example, there were basically no sex specific reporting from the Greenland fishery. In order to simulate a complete catch history, which could be used to subtract from the population dynamics of the simulated data trajectories, and additional run of catch sampling was carried out to account for catches with no reported sex, and late Greenlandic catches with no reported area. For a given year, late Greenlandic catches with no reported area were distributed between the two areas in proportion to the number of catches reported from each area. The total number of aggregation specific catches with no reported sex was then binomially sampled for sex using the procedure for sex reporting described above. Having sampled both sex specific catches with sex specific reports and sex specific catches with no reported sex for each fishery, all the catches for all fisheries were added to obtain the complete simulated catch history for minke whales taken of West Greenland.

3 RESULTS

Table 4 shows the *cv* of the female fraction in the catch from the early Greenlandic fishery and the northern and southern areas of the late Greenlandic fishery for the original data and simulated data given the ML-estimates of the influx and closed models with *msy*-rates of one and two percent. On average the *cv* of the simulated data were 10% higher than the *cv* of the original data, with the *cv* of the simulated data being higher than the *cv* of the original data in 9 out of 12 cases. It is thus unlikely that our simulation approach will give positively biased abundance estimates due to an underrepresentation of variation in the original data; if anything we expect instead the estimates to be negatively biased.

Table 5 shows the maximum ln likelihood and Akaike's information criterion (Akaike 1974) corrected for small sample size (AICc) for the different models. The maximum ln likelihood value of the closed model is 0.8 higher than the value for the influx model, but when corrected for the additional parameter the AICc value for the closed model is 1.1 higher than the AICc value for the influx model. The old version of the closed model has a ln likelihood value that is slightly smaller than the new version, but with yet an additional parameter the old version of the closed model has a AICc value that is 3.0 higher than the AICc value for the new version of the model.

Given the AICs values, the influx model is best at explaining the data with a minimum of parameters. But as the AICc values of the influx and the closed model are relatively similar, and as they represent different hypotheses that both are ecologically plausible, we give results from both models. The old version of the closed model, however, is inferior because even with an additional parameter it provides a less good fit than the new version of the closed model.

The old version of the closed model had the additional problem that between 11% and 44% of the log likelihood optimizations on the simulated data failed to converge to an optimum (Table 9). With average conversion failure rates between 0.4 and 2.3% for all other models (Table 9), the conversion problem was corrected in these cases by the method described in Section 2.3.

The Maximum Likelihood fits of the closed and influx models to the female fraction in the catch data are shown in Figure 1 for the early Greenlandic fishery, and the northern and southern areas of the late Greenlandic fishery. There is hardly any trend in the sex ratio data for the early Greenlandic hunt, while there is a decline in the female fraction in the southern area during the late Greenlandic fishery and for the closed model, a somewhat smaller increase in the northern area during the same period. Normal probability plots are shown in Figure 2 for the standardized residuals of the MLE models.

For MLE optimizations, Figure 3 shows the distribution of estimated k values and their median as a function of the true k of the simulated data. Many of the distributions are bimodal and there is a generally good agreement between the median of the distribution and the true value of k .

For the closed and influx models with a $msyr$ of 2%, the deviance functions for the 2007 abundance and carrying capacity are shown in Figure 4 and 5, together with the 5%, 10% and 50% percentiles based on 1000 sets of simulated data and the cumulated distribution of simulated deviances near the 5%-tile estimate.

The estimated lower confidence limits for the 2007 abundance, carrying capacity, and 2007 depletion ratio are shown in Table 7 with non converging optimizations included as described above, and in Table 8 with non converging optimizations excluded. The inclusion of the non converging optimizations result in lower estimates especially for the 5%-tile and the closed models. It was, e.g., impossible to get a reasonable estimate of the lower confidence limit of the 5%-tile estimate for the 2%-closed model owing to its relatively high conversion failure rate of 2.3%.

The closed model gives slightly higher estimates than the influx model. With conversion failures included, for a $msyr$ of 2%, the 5%-tile estimates of the 2007 abundance and carrying capacity are 12,300 (95% CI: 0 – 13,900) and 21,500 (95% CI: 0 – 22,700) minke whales for the closed model, and 9,100 (95% CI: 7,400 – 10,400) and 19,300 (95% CI: 18,300 – 20,300) whales for the influx model. The associated 5%-tile estimates of the 2007 depletion ratio are 0.56 (95% CI: 0 – 0.60) and 0.47 (95% CI: 0.40 – 0.51). These estimates are negatively biased due to the way the non converting optimizations are included in the estimate. Excluding conversion failures, the 2007 abundance estimates become 16,800 (95% CI: 15,800 – 18,100) and 10,400 (95% CI: 9,300 – 12,400) for the two models, the carrying capacities 24,800 (95% CI: 24,100 – 25,900) and 20,200 (95% CI: 19,500 – 21,700), and the depletion ratios 0.68 (95% CI: 0.65 – 0.69) and 0.51 (95% CI: 0.47 – 0.56).

The estimates above incorporate the sampling variability of the data into the estimate, and incorporate the simulation uncertainty (not infinitely many simulations, only 1000) into

the estimated confidence intervals. Alternatively both processes can be incorporated into a single confidence estimate (Appendix E). Given linear interpolation, for the influx and closed models with a *msyr* of 2%, this results in 5%-tile abundance estimates of 7,920 and 7,070, of carrying capacity of 18,700 and 18,100 and of the depletion ratio of 0.48 and 0.38. The corresponding 10%-tile estimates are 17,800 and 19,600 for abundance, 25,800 and 27,300 for carrying capacity, and 0.69 and 0.71 for the depletion ratio. Again we note that the 5%-tile estimates for the closed model are negatively affected by the relatively high rate of non converting optimizations.

Some sensitivity results are described in Appendix G.

4 DISCUSSION

4.1 Population structure

In order to explain the high female fraction in the catches, we have assumed a widespread population with a sex specific dispersal of males and females to West Greenland waters. This implies a source-sink type of dispersal dynamics with West Greenland acting as a sink where a relative depletion induces an inflow of whales from other areas. Such a dispersal pattern is well supported by data where the continued female biased catches are in disagreement with abundance data from surveys off West Greenland unless there is an influx of whales from a larger area (Witting 2005). An influx may occur relatively directly in response to a local depletion within a given year, or it may occur more indirectly with a one-year time lag when the whales redistribute themselves in relation to food abundance during the spring migration period.

There are, however, at least two other mechanisms that might theoretically explain the apparent inconsistency between the sex ratio and the abundance data. The first is differential natural mortality between females and males. This mechanisms could explain the sex ratio in the catches if, for annual female survival rates of 0.90, 0.95 and 0.98, the annual mortality rate in male minke whales would be respectively 2.3, 2.5 and 2.7 times higher than the mortality rate in females (assuming constant survival with age, no catches of animals that are younger than one year, and a non selective catch of animals older than one year). But there is no evidence that male baleen whales have natural mortality rates that are more than twice the natural mortality in females.

The second mechanism is a sex specific catch selectivity that has changed over time so that the sex ratio in the catches has remained constant while at the same time the sex ratio in a local West Greenland population has become more and more male biased. The generally unsupported hypothesis of sex selective catches in minke whales, however, becomes even more implausible if selectivity has to change over time in a so accurately timed manner that its effects on the catch sex ratio is cancelled out by an increasing fraction of male minke whales in West Greenland. In conclusion our underlying assumption of a source-sink dispersal pattern seems well supported.

4.1.1 Sex ratio changing with depletion

Another essential assumption for our assessment method is that the sex ratio in the West Greenland area will change with a change in the sex ratio of the overall population. Unless the separation between the two sexes are basically complete, this is generally expected when individuals of the two sex have different dispersal, simply because a change in the sex ratio

of the overall population will imply a change in the relative abundance of the two sexes that are available for dispersal. One potential exception to this rule, however, is a purely socially determined dispersal where males are found in West Greenland only because some males follow the dispersing females with the number of males per female in West Greenland being independent of the number of males that are available per female.

Such a social structure would require that the proportion of males that follow females should be approximately one male per 2.7 female. This might, for example, be the case if either a pregnant or a non-pregnant female is associated with a single male, and the ratio of pregnant to non-pregnant females is 1:1.7 or 1.7:1. But the fraction of pregnant to non-pregnant females among 1,392 female minke whales that were caught off West Greenland is only 1.06:1 (Simon et al. 2007), suggesting that this mechanism would allow for only two females per male. Off course, if only 3/4 of the pregnant, or non-pregnant, females would be associated with a male it would be possible to have one male per 2.7 female. But in this case it seems reasonable to assume that the fraction of the pregnant, or non-pregnant, females that are associated with a male would reflect the overall number of males per female. A West Greenland female fraction that tracks changes in the female fraction of the total population is also generally expected if the 1 to 2.7 ratio arises from a social structure where it is females that follow males. This is because it is difficult, if not impossible, to imagine a biologically plausible mechanism that would cause the number of females that will associate themselves with a male to be 2.7 independently of the relative availability of females per male.

At least theoretically a 1 to 2.7 ratio could also arise if the only males that are found off West Greenland are one-year old males that follow their mother. This hypothesis would be supported if the ratio of male to female size for the minke whales caught off West Greenland would be smaller than the general ratio for minke whales. The ratio of male to female length for 2,074 minke whales (68% females) caught by Norwegian whalers off West Greenland is 0.99 (Larsen and Øien 1988), and the ratio for 1,282 minke whales (77% females) caught by Greenlanders is 0.97 (Witting 2000). This is similar, or slightly larger, than a ratio of 0.97 for 106,023 minke whales (52% females) caught by Norwegian whalers in the eastern North Atlantic (Øien 1988). There is also no sign of young male dominance in the complete length distributions of 663 male and 1,411 female minke whales that were caught off West Greenland (Larsen and Øien 1988). Hence, there seems to be no support for the hypothesis that it is only young male minke whale that are caught off West Greenland.

4.1.2 Changes in southwest only

A first thought might suggest that a local overexploitation could cause the female fraction in southwest Greenland to decline, with the sex ratio to the north remaining constant because of individual site-fidelity that is so strong that it would hinder an inflow of whales to the southwest area. This hypothesis, however, it seems will generally not work because individual site-fidelity makes the distribution of whales geographically stationary so that an overexploitation will operate only locally. While this implies that the local abundance can more easily be depleted, it implies also that whales are harvested in proportion to the local availability of the two sexes and, thus, the local sex ratio will remain constant while the abundance is declining. Site-fidelity by itself is thus unable to explain a local change in sex ratio; in fact it operates against such changes.

Only if site-fidelity is coupled with the alternative hypothesis that the skewed catch sex ratio is not reflecting the local sex ratio, but instead a catch selectivity where hunters prefer females to males would site-fidelity and a local overexploitation result in a more and more male biased catch. But as catches throughout the North Atlantic, and within West Greenland, show relatively consistent geographical patterns in the catch sex ratio, both within and across different types of fisheries, and as female minke whales are generally impossible to distinguish from males at distance because there is only a mean size difference of 3% between the two sexes and no sex specific characteristics, there is really no indication that the catch sex ratio is reflecting anything but random sampling over the local availability of the two sexes.

Furthermore, it seems that strong site-fidelity is not an issue for minke whales, at least not on a scale where it can hinder source-sink dispersal or other distributional shifts in the abundance between years. While there is some evidence of site-fidelity to the degree that some minke whales visit the same area in different years (Dorsey et al. 1990), we have already seen that there is also evidence for an influx of whales to the West Greenland area because otherwise the continued skewed sex ratio is not self-consistent with the abundance of minke whales in West Greenland. Surveys of minke whales in the North Atlantic (NAMMCO 2010), including West Greenland (Heide-Jørgensen and Laidre 2008), also show shifts in the distribution of minke whales between years, and the distribution of female fractions in West Greenland over months and latitude (Laidre et al. 2008) indicate a pattern with spring and fall migration of whales through the West Greenland area towards, and from, northern and more offshore areas. This suggests a connection between the whales in the whole West Greenland area as indicated also by genetic studies that have found no evidence of stock structure within West Greenland.

Another model that might allow for a local change in the sex ratio in the southwest only, is a two-stock hypothesis with independent source-sink dynamics for each population, so that a southwest Greenland population of minke whales can be exploited independently of a population in the central and northern West Greenland. But the occurrence of two independent minke whale populations in West Greenland is unlikely. First of all, the two populations would have to co-exist on the same banks, with no distance between them, and with no indication of an abundance decline in the transition zone between the two populations. While two populations can be separated by a borderline with no geographical barrier, this is known to occur only in relation with hybrid zones with a fitness cost to hybrids, a scenario that evidently does not apply for minke whales. In order to explain the declining female fraction in the southern area, the two-stock hypothesis requires that the southern area is heavily depleted relative to the northern area (Brandão and Butterworth 2009), and this is not in agreement with the most recent survey, which found that the highest concentration of minke whales off West Greenland is in the southern area (Heide-Jørgensen et al. 2009).

In order to account for the sex ratio patterns in the West Greenland fisheries, we considered that the most plausible hypothesis is a single widespread population with a sex differential source-sink type of dispersal. To account for the different trends in the southern and the northern areas we considered two scenarios where either there is a trend in the relative distribution of males and females between the southern and northern areas, or there is a time-trend in the influx of whales to the southern area.

4.2 Abundance estimates

The estimates of population abundance obtained in this paper are higher than all the estimates obtained by aerial surveys off West Greenland. In 1988 an aerial survey estimated 3,300 (95% CI: 1,700 – 5,710) minke whales (IWC 1990) off West Greenland, while a similar survey in 1993 estimated 8,370 (95% CI: 2,410 – 16,900) whales (Larsen 1995), with a later reanalysis suggesting 6,340 (95% CI: 2,940 – 13,900) whales (Hedley et al. 1997). A preliminary estimate of 3,470 (95% CI: 1,570 – 7,700) minke whales from 2005 (Heide-Jørgensen et al. 2006a,b) was later reanalysed to 4,860 (95% CI: 1,910 – 12,350); and increased to 10,790 (90% CI: 4,290 – 27,160) when corrected for perception bias (Heide-Jørgensen et al. 2007). Another fully corrected estimate from 2007 resulted in the highest survey abundance ever, with two alternative approaches suggesting an abundance of either 17,300 (95% CI: 7,630 – 39,300) or 23,000 (95% CI: 8,400 – 62,400) minke whales off West Greenland (Heide-Jørgensen et al. 2009).

With a negatively biased (for conversion failures) lower 5%-tile estimate between 9,100 and 12,300 for the 2007 abundance (given a $msyr$ of 2%), the lower estimate of the proposed method for one-sided confidence bounds is higher than the lower bound of all the aerial surveys that have been conducted off West Greenland. If we assume that the current sex ratio in the population is even (which is likely conservative owing to the female bias of the hunt), that the fraction of females in the survey area resemble the average fraction in the harvest from 1984 to 2007, and that all females in the population was present in the survey area during the survey, the true population abundance is 1.48 times the survey estimate. Hence, from the 2007 survey we expect a population of at least 25,600 minke whales with a 95% confidence interval between 11,300 and 58,100 whales. The lower bound of this estimate is basically the same as the average 5%-tile-estimates of 10,300 minke whales from our simulation approach (assuming a $msyr$ of 2%).

Given the continued skewed sex ratio of the catches in West Greenland, and the continued relative high catch of minke whales when compared to the number of whales that can be counted off West Greenland, it is not surprising that the population dynamic modeling in this paper suggests that the true abundance of the stock that supplies the West Greenland harvest is considerably higher than most of the numbers indicated by aerial surveys. Taken together the sum of point estimates from minke whale surveys in the Central and Western North Atlantic, excluding areas to the West and Southwest of West Greenland, is around 100,000 whales, based on the 1997 estimate from the CM area (Skaug et al. 2002), the 2001 estimate from the CIC area (Borchers et al. 2003), the 2001 estimate from the CG and CIP areas (Gunnlaugsson et al. 2003), and the 2005 estimate from West Greenland (Heide-Jørgensen et al. 2007). As the estimated 100,000 whales is negatively biased owing to submerged whales, whales at the surface not seen by observers, and uncovered areas it is certainly not unrealistic that minke whales off West Greenland is a fraction of a much larger and more widespread population.

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Greenlandic whalers 1955 to 1978											
Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>
1955	7	8	1961	7	9	1967	7	42	1973	8	39
1956	5	15	1962	17	43	1968	10	47	1974	6	34
1957	6	18	1963	32	47	1969	14	42	1975	1	17
1958	5	6	1964	26	37	1970	12	20	1976	2	20
1959	2	17	1965	19	30	1971	6	25	1977	15	39
1960	2	15	1966	24	49	1972	6	40	1978	2	13
Greenlandic whalers 1985 to 2005											
1985	59	163	1991	22	66	1997	42	102	2003	58	117
1986	38	107	1992	18	75	1998	42	123	2004	44	129
1987	12	38	1993	25	74	1999	37	131	2005	34	135
1988	5	35	1994	22	78	2000	36	102	2006	44	127
1989	16	34	1995	46	105	2001	32	91	2007	38	121
1990	15	63	1996	38	125	2002	33	96	2008	-	-
Norwegian whalers 1968 to 1985											
1968	7	13	1973	67	154	1978	10	65	1983	25	42
1969	117	50	1974	43	209	1979	31	44	1984	20	49
1970	74	52	1975	11	91	1980	14	65	1985	28	23
1971	89	182	1976	38	149	1981	15	46	1986	-	-
1972	94	142	1977	21	54	1982	24	42	1987	-	-

Table 1: **Yearly reporting** of male (*m*) and female (*f*) common minke whales caught by Greenlandic whalers from 1955 to 1978, and from 1985 to 2005, and by Norwegian whalers from 1968 to 1985.

Late Greenlandic catches; Northern area											
Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>
1985	-	-	1991	10	38	1997	33	70	2003	34	59
1986	-	-	1992	9	44	1998	33	81	2004	26	88
1987	6	9	1993	22	44	1999	26	86	2005	20	93
1988	4	27	1994	14	50	2000	17	57	2006	34	106
1989	12	13	1995	36	68	2001	25	56	2007	30	97
1990	13	32	1996	31	76	2002	21	60	2008	-	-
Late Greenlandic catches; Southern area											
1985	-	-	1991	9	25	1997	9	31	2003	22	57
1986	-	-	1992	9	30	1998	9	42	2004	18	39
1987	1	3	1993	3	26	1999	11	45	2005	14	42
1988	1	8	1994	6	27	2000	8	24	2006	10	19
1989	4	21	1995	10	37	2001	5	30	2007	8	22
1990	1	27	1996	7	48	2002	11	36	2008	-	-
Norwegian catches; Northern area											
Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>
1968	1	3	1973	42	144	1978	10	65	1983	22	42
1969	40	19	1974	42	209	1979	31	44	1984	20	49
1970	68	44	1975	8	85	1980	13	62	1985	17	20
1971	74	172	1976	38	149	1981	15	46	1986	-	-
1972	8	63	1977	21	54	1982	24	42	1987	-	-
Norwegian catches; Southern area											
1968	6	10	1973	25	10	1978	-	-	1983	3	0
1969	77	31	1974	1	0	1979	-	-	1984	-	-
1970	6	8	1975	3	6	1980	1	3	1985	11	3
1971	15	10	1976	-	-	1981	-	-	1986	-	-
1972	86	79	1977	-	-	1982	-	-	1987	-	-

Table 2: **Yearly reporting** of male (*m*) and female (*f*) common minke whales caught in the northern (above 63 degrees North) and southern area.

Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>	Year	<i>m</i>	<i>f</i>
1948	1	3	1960	7	49	1972	114	278	1984	80	225	1996	40	130
1949	1	4	1961	15	20	1973	114	383	1985	87	186	1997	43	105
1950	2	7	1962	20	52	1974	76	393	1986	38	107	1998	43	126
1951	4	12	1963	67	99	1975	23	301	1987	21	65	1999	38	134
1952	8	24	1964	67	95	1976	55	323	1988	14	95	2000	38	107
1953	8	24	1965	76	120	1977	100	260	1989	20	43	2001	36	103
1954	6	16	1966	74	151	1978	34	221	1990	17	72	2002	36	103
1955	10	12	1967	35	209	1979	95	230	1991	28	81	2003	62	124
1956	6	16	1968	62	273	1980	80	257	1992	21	89	2004	46	133
1957	6	18	1969	184	252	1981	67	198	1993	28	84	2005	35	141
1958	14	16	1970	152	181	1982	88	228	1994	23	81	2006	47	134
1959	6	49	1971	127	340	1983	94	242	1995	47	108	2007	40	127

Table 3: **Yearly catch** of male (*m*) and female (*f*) West Greenland common minke whales, as reconstructed from the total reported catch and the reporting on caught males and females.

Fishery	data	influx 2%	influx 1%	closed 2%	closed 1%
Early	0.169	0.182	0.191	0.181	0.191
Late N	0.111	0.097	0.157	0.097	0.109
Lats S	0.093	0.107	0.113	0.104	0.111

Table 4: **CV of female fraction** in the early Greenlandic fishery and the northern and southern areas of the late Greenlandic fishery, for original catch data and simulated data given the ML-estimate of the different models.

Model:	influx 2%	influx 1%	closed 2%	closed 1%	old closed 2%	old closed 1%
$\ln(L)$:	-113.2	-113.2	-112.4	-112.4	-112.5	-112.6
AICc:	245.0	245.0	246.1	246.1	249.1	249.1

Table 5: **Maximum ln likelihood and AICc** for the different models ($AICc = 2[k - \ln(L)] + (k(k + 1))/(n - k - 1)$), where L is the maximum likelihood, k is the number of parameters (8,9,10), and n the number of data points (66)).

model	k_1	k_2	k_3	k_4	k_5	k_6	k_7
influx 2%	1.1	0.9	0.7	0.1	0.0	0.0	0.0
influx 1%	3.2	1.7	0.3	0.1	0.0	0.0	0.0
closed 2%	3.6	3.0	2.3	2.2	2.0	1.4	1.3
closed 1%	5.8	2.8	1.1	0.8	1.1	0.8	1.1
old closed 2%	44.4	35.9	33.2	20.5	16.9	13.7	14.7
old closed 1%	41.7	11.0	37.9	23.4	17.2	12.3	14.2

Table 6: **Convergence.** The percent of the log likelihood optimizations that failed to converge to an optimum for the different models, given simulated data based on seven different k -values [k in thousands: influx 2% $k_1 = 16.5; k_2 = 17.3; k_3 = 19.7; k_4 = 24.6; k_5 = 33.6; k_6 = 50; k_7 = 200$; influx 1% $k_1 = 18.5; k_2 = 19.3; k_3 = 21.7; k_4 = 26.5; k_5 = 35; k_6 = 50; k_7 = 200$; closed 2% $k_1 = 16.8; k_2 = 17.5; k_3 = 20; k_4 = 24.9; k_5 = 33.8; k_6 = 50; k_7 = 200$; closed 1% $k_1 = 19.5; k_2 = 20.2; k_3 = 22.7; k_4 = 27.4; k_5 = 35.6; k_6 = 50; k_7 = 200$]; old closed 2% $k_1 = 16.3; k_2 = 16.5; k_3 = 17.9; k_4 = 22.2; k_5 = 34.3; k_6 = 69.6; k_7 = 200$; old closed 1% $k_1 = 20.0; k_2 = 20.2; k_3 = 21.8; k_4 = 26.7; k_5 = 39.6; k_6 = 75.8; k_7 = 200$].

		2%		1%		2%		1%	
		Closed	CI	Closed	CI	Influx	CI	Influx	CI
	5%	12.3	0.0–13.9 0.0–14.3	11.5	10.1–13.1 10.0–13.3	9.1	7.4–10.4 5.5–11.0	9.6	8.7–10.5 8.5–10.6
	10%	19.5	18.2–20.2 18.0–20.3	17.0	16.0–18.1 15.9–18.2	17.7	15.9–20.3 15.7–20.7	16.3	14.7–17.7 14.3–18.0
N	50%	182.8	181.5–184.2 181.1–184.4	173.2	171.7–174.8 171.3–175.0	172.4	169.6–174.9 168.8–175.2	170.8	169.0–172.5 168.7–172.8
	5%	21.5	0.0–22.7 0.0–23.0	26.7	25.5–28.2 25.4–28.3	19.3	18.3–20.3 17.2–20.7	25.2	24.4–26.0 24.2–26.0
	10%	27.1	26.1–27.7 25.9–27.9	31.7	30.8–32.7 30.7–32.8	25.7	24.2–27.9 24.1–28.3	31.2	29.7–32.5 29.4–32.7
K	50%	187.5	186.2–188.9 185.8–189.1	185.8	184.3–187.4 184.0–187.6	177.2	174.4–179.7 173.7–180.0	183.6	181.7–185.3 181.5–185.5
	5%	0.56	0.00–0.60 0.00–0.61	0.43	0.39–0.46 0.39–0.46	0.47	0.40–0.51 0.32–0.52	0.38	0.35–0.40 0.34–0.41
	10%	0.71	0.69–0.72 0.69–0.72	0.53	0.51–0.54 0.51–0.55	0.68	0.65–0.72 0.65–0.72	0.51	0.48–0.54 0.48–0.54
D	50%	0.97	0.97–0.97 0.97–0.97	0.92	0.92–0.92 0.92–0.92	0.96	0.96–0.96 0.96–0.96	0.91	0.91–0.92 0.91–0.92

Table 7: **Estimates (including non-converging cases)** of the 5%, 10% and 50% percentile for the 2007 abundance (N), the carrying capacity (K), and the depletion ratio in 2007 (D), for the closed and influx models given a $msyr$ of one and two percent. The 95% and 90% confidence intervals due to simulation uncertainty are given as subscripts and superscripts (estimated from 3000 bootstraps of the deviance distributions from simulated data).

		2%		1%		2%		1%	
		Closed	CI	Closed	CI	Influx	CI	Influx	CI
N	5%	16.8	15.8–18.1 15.7–18.3	13.2	11.6–14.4 11.5–14.6	10.4	9.3–12.4 9.0–12.8	9.7	8.9–10.6 8.8–10.7
	10%	21.4	20.4–23.2 20.2–23.6	18.1	17.2–19.7 17.0–19.9	17.5	15.9–20.1 15.8–20.4	16.2	14.7–17.7 14.3–18.0
	50%	183.5	182.0–184.6 181.7–184.8	173.9	172.2–175.2 172.0–175.4	172.2	169.3–174.7 168.5–175.2	170.8	168.9–172.6 168.6–172.8
K	5%	24.8	24.1–25.9 24.0–26.1	28.3	26.8–29.3 26.7–29.5	20.2	19.5–21.7 19.3–22.0	25.3	24.6–26.0 24.5–26.1
	10%	28.8	27.9–30.4 27.8–30.7	32.7	31.9–34.2 31.7–34.4	25.5	24.2–27.7 24.1–28.0	31.1	29.7–32.4 29.4–32.7
	50%	188.2	186.7–189.3 186.4–189.5	186.5	184.9–187.8 184.6–188.0	177.0	174.2–179.5 173.4–180.0	183.6	181.7–185.4 181.4–185.6
D	5%	0.68	0.65–0.69 0.65–0.70	0.46	0.43–0.48 0.43–0.49	0.51	0.47–0.56 0.46–0.57	0.38	0.36–0.41 0.35–0.41
	10%	0.73	0.72–0.76 0.72–0.76	0.55	0.53–0.57 0.53–0.57	0.68	0.65–0.71 0.65–0.72	0.51	0.48–0.54 0.48–0.54
	50%	0.97	0.97–0.97 0.97–0.97	0.92	0.92–0.92 0.92–0.92	0.96	0.96–0.96 0.96–0.96	0.91	0.91–0.92 0.91–0.92

Table 8: **Estimates (excluding non-converging cases)** of the 5%, 10% and 50% percentile for the 2007 abundance (N), the carrying capacity (K), and the depletion ratio in 2007 (D), for the closed and influx models given a $msyr$ of one and two percent. The 95% and 90% confidence intervals due to simulation uncertainty are given as subscripts and superscripts (estimated from 3000 bootstraps of the deviance distributions from simulated data).

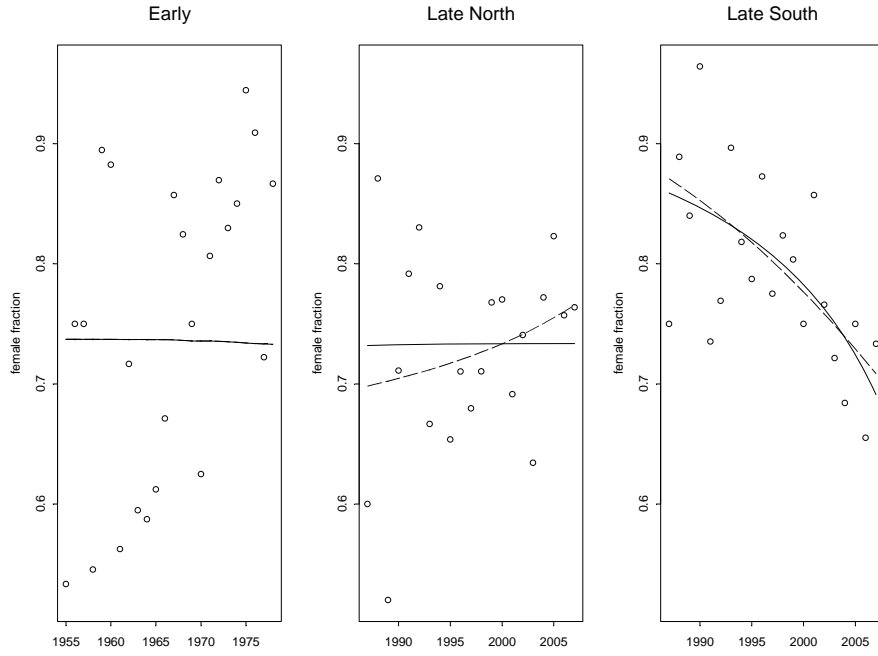


Figure 1: The female fraction in the West Greenlandic catches by year. The solid curves are for the influx model and the dashed curves for the closed model, both for a $msyr$ of 2%. The curves for $msyr = 1\%$ are indistinguishable from the curves shown.

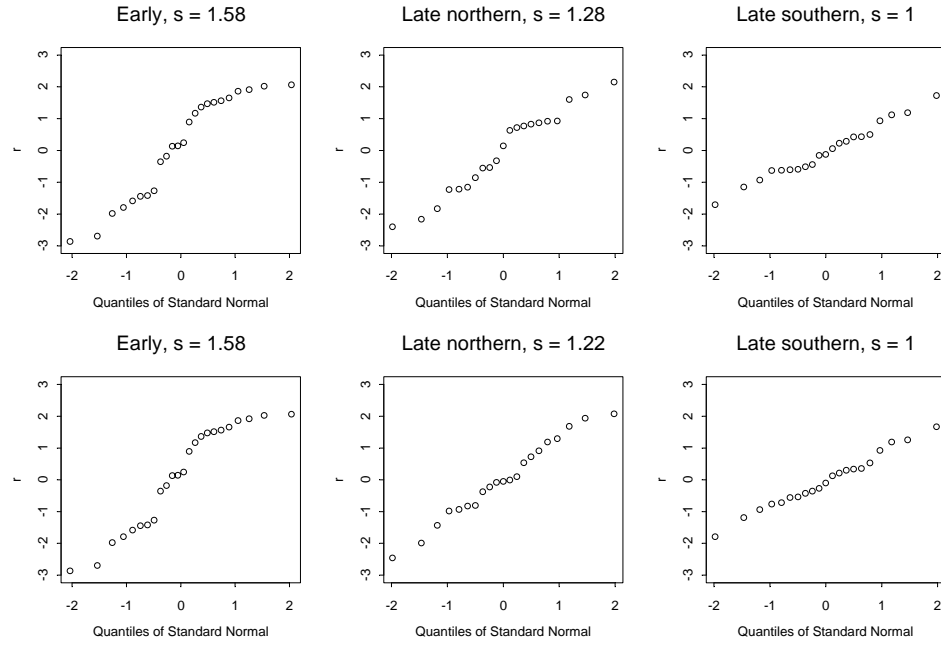


Figure 2: Normal probability plots for the standardized (by the binomial standard deviation) residuals. Upper plots: influx model, lower plots: closed model. Both at $msyr = 2\%$; results for $msyr = 1\%$ are identical. The degree of over-dispersion is estimated by $s = \max(1, \text{mean square standardized residual})$, as given in the titles.

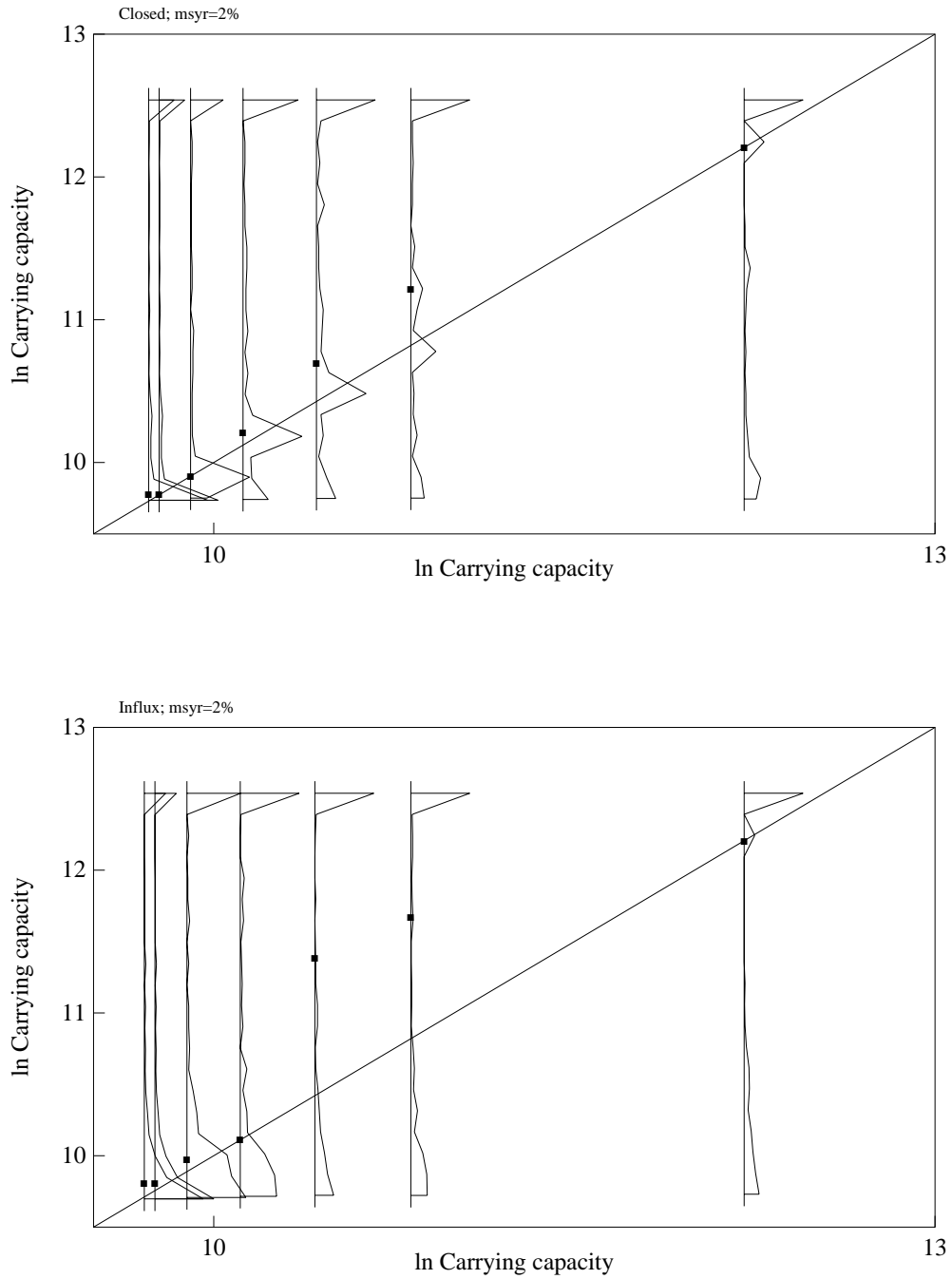


Figure 3: The distribution of estimated carrying capacities for the MLE optimizations on the simulated data as a function of the true carrying capacity of the simulation (on log scale), for the closed and influx model with a *msyr* of 2%. Dots show the median of the distribution. **Preliminary figure based on less than 200 replicates.**

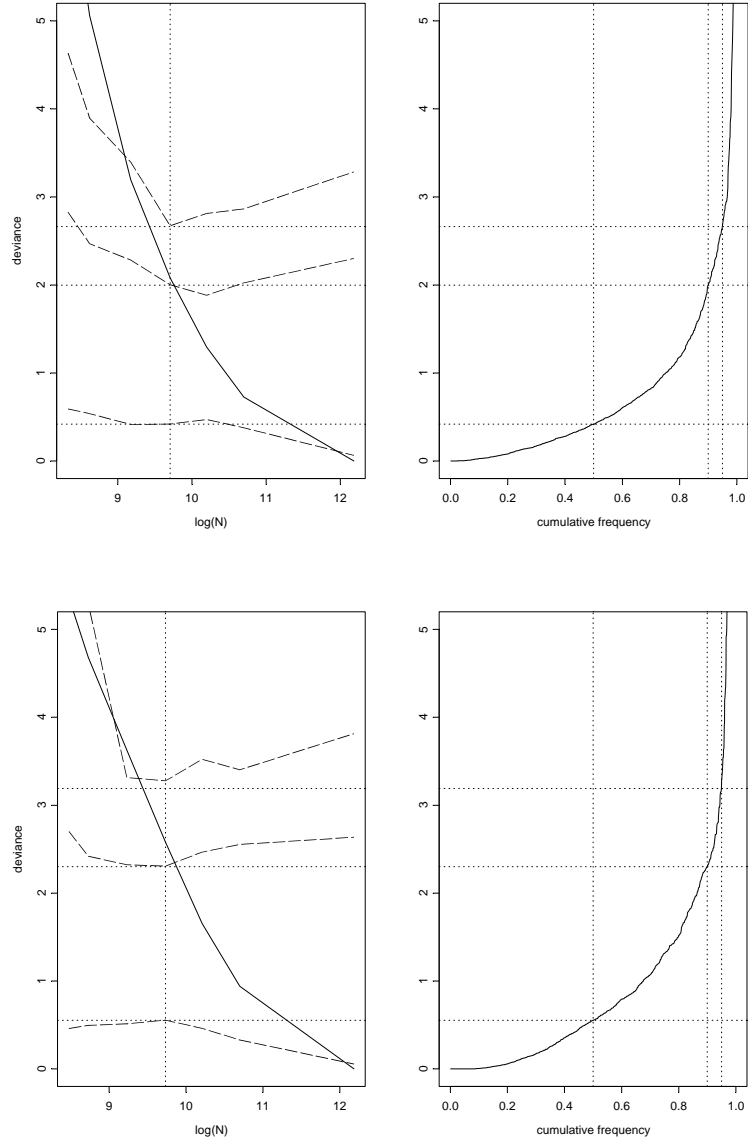


Figure 4: Left plots: deviance (solid line), and upper 5%, 10% and 50% curves from simulations (dashed, top to bottom) by log abundance. Dotted vertical line at $\ln(16,400) = 9.7$, where right plots show the cumulative distribution (rotated 90 degrees), with the upper 5%, 10% and 50% quantiles indicated by dotted horizontal lines in both plots. Upper plots: influx model, lower plots: closed model; both with $msyr = 2\%$.

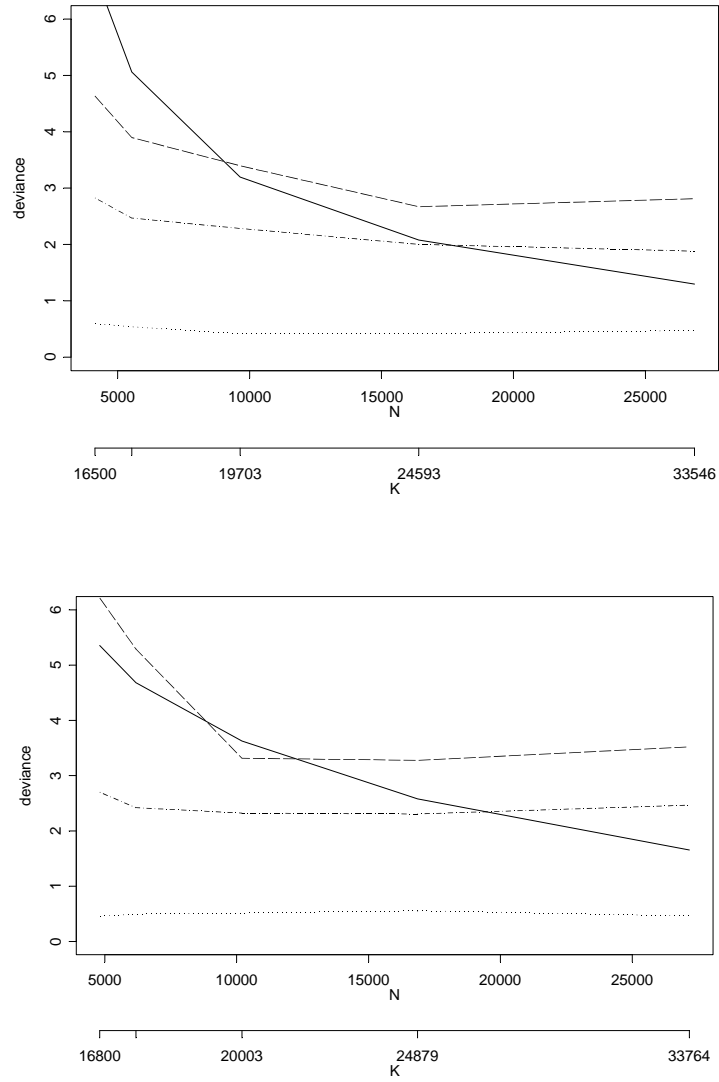


Figure 5: Close up of the deviance and the upper 5%, 10% and 50% quantile curves by abundance N and carrying capacity K . Upper plot: influx model, lower plot: closed model, both with $msyr = 2\%$.

APPENDIX

A POPULATION DYNAMIC MODEL

An age-structured model was applied with the number of animals in age classes larger than zero being

$$\begin{aligned} N_{t+1,a+1}^g &= (N_{t,a}^g - C_{t,a}^g)s_a & 0 \leq a \leq x-2 \\ N_{t+1,x}^g &= (N_{t,x}^g - C_{t,x}^g)s_x + (N_{t,x-1}^g - C_{t,x-1}^g)s_{x-1} \end{aligned} \quad (13)$$

where gender (g) is either male (m) or female (f), s_a is age specific annual survival, $N_{t,a}^g$ is the number of males/females of age a at the start of year t , $C_{t,a}^g$ is the catch of males/females of age a during year t , and x is the lumped age-class.

The catch of gender g from age class a in year t is

$$C_{t,a}^g = \frac{G_a N_{t,a}^g C_t^g}{\sum_{a=0}^x G_a N_{t,a}^g} \quad (14)$$

where C_t^g is the total catch of that gender in year t , and $0 \leq G_a \leq 1$ is the age-specific differentiation of the catch relative to the age composition of the overall population, reflecting, e.g., age-specific migration to West Greenland waters or age-specific hunting selectivity, or both. Data from the Norwegian hunt indicate that the fraction of mature individuals in the hunt may be higher than the fraction in the population (REF), which suggests that G_a should be monotonically increasing with age. We define G_a by a linear increase where $G_0 = 0$, as no age-class zero individuals are taken in the hunt, and G_a increases linearly to $G_i = 1$ for $i \geq a_c$.

The annual survival rate s_a of animals of age a is

$$s_a = \begin{cases} s_{juv}s_{ad} & \text{if } a = 0 \\ s_{juv} & \text{if } 1 \leq a \leq a_{ad} \\ s_{ad} & \text{if } a > a_{ad} \end{cases} \quad (15)$$

where s_{juv} is the survival rate for ‘juveniles’, s_{ad} is the survival rate for adults, and $a_{ad} = 1$ is the greatest age at which the ‘juvenile’ survival rate applies.

The number of births at the start of year t , B_t , is

$$B_t = \sum_{a=a_m}^x B_{t,a} \quad (16)$$

where a_m is age of reproductive maturity, and $B_{t,a}$, the number of births in age class a , is

$$B_{t,a} = b_t M_{t,a}^f \quad (17)$$

where b_t is the fecundity rate for mature females at time t , and $M_{t,a}^f$ is the number of mature females in age class a at the start of year t , defined as

$$M_{t,a}^f = \begin{cases} 0 & \text{if } a_m > a \\ N_{t,a}^f & \text{if } a_m \leq a \end{cases} \quad (18)$$

The component of the population that imposes density-regulation is assumed to be the one plus component

$$N^{1+} = \sum_{a=1}^x N_a^f + N_a^m \quad (19)$$

and the density-regulation on the fecundity rate b_t to take the Pella-Tomlinson form

$$b_t = b_k + [b_{max} - b_k][1 - (N_t^{1+}/K^{1+})^z] \quad (20)$$

where b_k is the birth rate at carrying capacity K , b_{max} is the maximal birth rate, and z the strength of density dependence.

Although not explicit parameters of the model, the maximum sustainable yield level (msyl) and the maximum sustainable yield rate (msyr) were treated as parameters in the analysis, with both parameters relating to the one plus component of the population. The msyl depends mainly on the compensation parameter z , with the relationship between z and the msyl being solved numerically.

An estimate (Q) of sustainable harvest was set to reflect the sustainable yield should the abundance be below msyl, and to reflect 90% of the maximum sustainable yield (msy) should the abundance be above the msyl (Wade and Givens 1997). Basing this estimate on the one plus component of the population, and correcting for the female bias of the catch we obtained the following estimate

$$Q1 = \min[\text{msyr}N^{f,1+}(1 + \vartheta)/\vartheta, 0.45\text{msy}(1 + \vartheta)/\vartheta] \quad (21)$$

assuming that $\vartheta = 2.9$ to reflect the average increased tendency by which female minke whales migrate to the waters of the current fishery relative to male minke whales.

B PARAMETERISATION

The productivity potential of the population can to a large extent be summarised by the msyr for the one-plus component of the population, although it is ultimately determined by the age-structured life history parameters, where there are infinitely many combinations of parameter values that give the same msyr. While the available data might be able to determine the productivity potential of the population, it is almost certain that they cannot differentiate the underlying life history that defines the production. We thus assume that the age-structured life history resembles that of the best available estimates in the literature for minke whales, while we summarise the production potential by a msyr that is estimated by our model (given the constraint $0.01 \leq \text{msyr} \leq 0.07$).

Larsen (1991) summarised estimates of biological parameters in North Atlantic common minke whales. An annual natural survival rate of 0.90 was estimated by Horwood (1989) for the central North Atlantic, and a rate of 0.91 for the eastern North Atlantic was given by Ugland (1977). Given adult survival (s_{ad}), a msyl of 0.6, and the other parameter values given below, we calculated a juvenile survival (s_{juv}) that would match a given msyr between 0.01 and 0.07, given that $s_{juv} < s_{ad}$. The latter constraint allowed a s_{ad} of 0.91 for a msyr between 0.01 and 0.04 (s_{juv} between 0.65 and 0.89). For a msyr > 0.04 , s_{ad} had to be larger than 0.91 to allow $s_{juv} < s_{ad}$. Choosing, for a given msyr > 0.04 , the smallest s_{ad} with three decimal accuracy that allowed $s_{juv} > s_{ad}$, s_{ad} increased to a maximum of 0.952 at a msyr of 0.07, where s_{juv} was solved to 0.941.

Various studies have found annual pregnancy rates between 0.86 and 0.99 for North Atlantic common minke whales (Sergeant 1963; Mitchell and Kozicki 1975; Christensen 1981; Larsen and Kapel 1983; Sigurjonsson 1988), and we fixed it at 0.94; the value for the most inclusive estimate for West Greenland including 109 individuals from 1979 to 1981 (Larsen and Kapel 1982, 1983).

The age of reproductive maturity has been estimated to lie between six and nine years from readings of laminations in the ear bone (Mitchell and Kozicki 1975; Christensen 1981; Sigurjonsson 1988), with the average estimate from Larsen (1991) being seven years. This method may though severely underestimate age (Olsen 1997). The alternative method of aspartic acid racemization in eye-lenses, however, gave similar estimates of seven or nine years, with the best \pm SE interval ranging from four to ten years (Olsen and Sunde 2002). The age of reproductive maturity was fixed at seven years in our study.

The fraction of females in the fetuses of pregnant females caught off West Greenland has been estimated to 0.41 (Larsen and Kapel 1982; Larsen 1984) and 0.54 (Simon et al. 2007), and a rather similar fraction of 0.48 had been found for East Canadian minke whales (Mitchell 1974). As none of these values differed significantly from an even sex ratio, the female fraction at birth was fixed at 0.50.

The fraction of mature individuals in the female minke whales caught by the Norwegian whalers between 1979 and 1983 was used to obtain a maximum likelihood estimate for the age-specific catch as represented by the a_c parameter.

Out of 262 examined females from the Norwegian catch, 180, or 69%, were sexually mature (Larsen and Kapel 1982, 1983). Thus, following binominal sampling of mature and non-mature females, we get a log likelihood of

$$\ln L_a = 180 \ln[p(a_m)] + 82 \ln[1 - p(a_m)] \quad (22)$$

where the probability that a female caught in the Norwegian fishery is mature is equal to the availability of mature females to the West Greenland hunt

$$p(a_m) = \frac{\sum_{t=1979}^{1983} \sum_{a=a_m}^x G_a N_{t,a}^f}{\sum_{t=1979}^{1983} \sum_{a=1}^x G_a N_{t,a}^f} \quad (23)$$

under the assumption that no age class zero females are caught. By applying the joint likelihood function $\ln L = \ln L_\phi + \ln L_a$, a maximum likelihood estimate of the age-specific hunt was obtained from the joint maximum likelihood estimate $\{\hat{\theta}, \hat{a}_c\}$ given the original data and $K = 200,000$. This estimate, $\hat{a}_c = 5$, was then applied to all simulations.

C LOG LIKELIHOOD OPTIMISATION

The log likelihood optimization was done with the Multidimensional Variable Metric Method using gradients (*dfpmin* routine in Press et al. 1986), with the convergence criterion being an average gradient less than 0.004 across all the parameters in the optimization. If no convergence was found within 70 loops of the optimization routine, the Multidimensional Downhill Simplex Method (*amoeba* routine in Press et al. 1986) was allowed to run over 70 loops from the original starting point, where after the Variable Metric Method was rerun from the endpoint of the Downhill Simplex Method. An alternative long optimization (with 500 loops of the Variable Metric Method and no used of the Downhill Simplex Method) was run occasionally when convergence was difficult.

Multiple staring points were applied for all optimizations on simulated data. One standard starting point (\mathbf{V}_a) had $\beta = 0$, another \mathbf{V}_o was the k -conditional ML-estimate from the original

data, a third \mathbf{V}_c the k -conditional ML-estimate for simulated data (applied only to the ML-estimate of simulated data), and a fourth \mathbf{V}_m the ML-estimate for the simulated data (applied only as a final check for the k -conditional ML-estimate of simulated data).

For given simulated data the optimization was first run to find the k -conditional estimate. Here the optimization routine was initialized first by \mathbf{V}_o and then by \mathbf{V}_a . If no convergence was found, the long optimization was applied for \mathbf{V}_o and then \mathbf{V}_a . Finally, after having run optimizations for the ML-estimate, the k -conditional optimization was rerun with the ML-estimate as the starting point, except that k was maintained at its condition.

For ML-estimates the optimization was first initialized by the k -conditional estimate \mathbf{V}_c . Then it was initialized by \mathbf{V}_a for five different values of k in the interval from $k_{min}/1.1$ to $1.1k_{max}$, and if for each of these optimization there was no convergence the optimization routine was re-initialized by \mathbf{V}_o , and if no convergence then by \mathbf{V}_c . If no converging optima was found after all these runs, the long optimization routine was applied over the five different values of k ; first with \mathbf{V}_a , then \mathbf{V}_o , and finally \mathbf{V}_c . Long optimizations were stopped as soon as one converging optima had been found.

The optimization with the highest log likelihood was chosen as the output of the optimization routine, even if this optimization was non-converging and there were converging optimizations with smaller log likelihoods. If, however, the absolute difference in log likelihood between a converging and a non-converging optimum was less than 0.0001 the converging optimum was always chosen as output.

D CLOSED MODEL; OLD VERSION

The old version of the closed model uses four parameters (α^m , β^m , α^f , and β^f), instead of the three parameters α , β , and $p^{l,s,f}$ in the new version (Section 2.2.2), to allow for linked sex ratios in the northern and southern areas of the late Greenlandic fishery.

In the old version the distribution of the two sexes between the two areas in the closed model are given as

$$\begin{aligned} A_{t,a}^{N,m} &= r_t^m A_{t,a}^{G,m}, & A_{t,a}^{S,m} &= (1 - r_t^m) A_{t,a}^{G,m} \\ A_{t,a}^{N,f} &= r_t^f A_{t,a}^{G,f}, & A_{t,a}^{S,f} &= (1 - r_t^f) A_{t,a}^{G,f} \end{aligned} \quad (24)$$

where $A_{t,a}^{G,g}$ is the abundance of gender g in the overall West Greenland area (G) that encompasses both the northern and the southern areas (given by Eq. (1) for an overall aggregation G), and $0 \leq r_t^m \leq 1$ and $0 \leq r_t^f \leq 1$ give the fraction of the West Greenland male and female individuals that are present in the northern area as a function of time. We assume these probabilities to change smoothly according to the logistic model

$$\begin{aligned} r_t^m &= \frac{e^{\alpha^m + \beta^m(t-1987)}}{1 + e^{\alpha^m + \beta^m(t-1987)}} \\ r_t^f &= \frac{e^{\alpha^f + \beta^f(t-1987)}}{1 + e^{\alpha^f + \beta^f(t-1987)}} \end{aligned} \quad (25)$$

For the early Greenlandic, the northern Norwegian, and southern Norwegian catches the relative abundance of the two sexes were given by Eq. (1).

E CONFIDENCE INTERVALS

The traditional method of calculating confidence intervals, dating back to Jerzy Neyman, is to first determine the degree of confidence, and then to calculating the confidence limit. The standard CI based on the normal distribution for an estimate $\hat{\mu}$ with standard error s is for confidence level $1 - p$, as we know, $\hat{\mu} \pm z_{p/2}s$, where $z_{p/2}$ is the lower $p/2$ quantile of the standard normal distribution. Other statisticians (R.A. Fisher and A. Birnbaum) find it just as natural to fix the interval $\hat{\mu} \pm d$ and to calculate the confidence from the equation $p = 2\Phi(-d/s)$ where Φ is the cumulative distribution function of the normal.

This latter route is followed for various one-sided intervals for carrying capacity K and for the corresponding parameters abundance and depletion. The intervals are based on the deviance function D . For a chosen value $K = k$ the model is simulated $B = 1000$ times, and the deviance at k is calculated for each set of simulated data. If $K = k$, $D(k)$ and the B simulated deviances are independent draws from the same distribution. Let R be the rank of the observed value $D(k) = d$ among the $B + 1$ values. The observed value is $R = r$. Since the deviance is a decreasing function the obtained confidence is

$$\text{conf}(k \leq K) = P_{K=k}[D(k) \leq d] = P(R \leq r) = r/(B + 1) \quad (26)$$

This calculation is carried out for the various chosen values of K , and for each model variant.

As an example take the Closed model at 2% *msyr* and for $K = 20,003$. The observed deviance value is 3.63. Of the $B = 1000$ simulated deviances at the chosen value of K there are 43 cases larger than the observed. The rank is thus $1001 - 43 = 958$ and the confidence attached to the interval $(17,549, \infty)$ is $0.96 = 958/1001$. The confidence in this interval accounts for both the simulation uncertainty (not infinitely many simulations, only 1000), and the sampling variability in the observed data. The interval is shown in Figure 6 and Table 9 together with other intervals. It is a nuisance that the three intervals at levels of confidence .93, .95 and .96 come out as inconsistent. Consistency dictates a larger interval for a higher confidence, but these three intervals are nested in reverse order. Figure 7 illustrates the problem. The many points rising vertically at the upper end of the QQ-plot are due to 48 cases of convergence failures for $K = 17,549$. This clearly disrupts the confidence calculation.

C_I	N	K	D	C_C	N	K	D
0.969	4,145	16,500	0.25	0.934	4,809	16,800	0.29
0.961	5,543	17,248	0.32	0.948	6,179	17,549	0.35
0.942	9,645	19,703	0.49	0.957	10,198	20,003	0.51
0.909	16,413	24,593	0.67	0.925	16,855	24,879	0.68
0.840	26,854	33,546	0.80	0.832	27,164	33,764	0.80
				0.757	44,348	50,000	0.89
				0.035	195,382	200,000	0.98

Table 9: **Left confidence** limits for abundance (N), carrying capacity (K) and depletion (D) for various levels of confidence. Confidence limits for influx model (C_I) and closed model (C_C) are for *msyr* = 2%

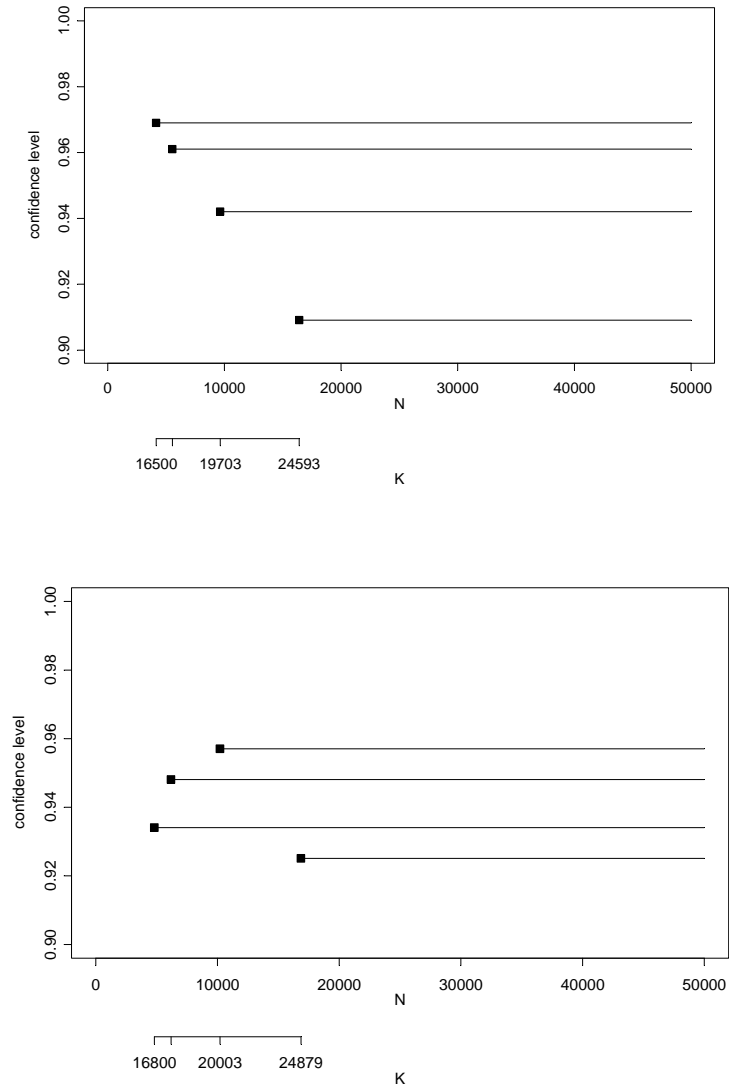


Figure 6: One-sided confidence intervals for abundance and carrying capacity at confidence levels 0.97, 0.96, 0.94 and 0.91 for the influx (upper plot) and closed (lower plot) models given a *msyr* of 2%.

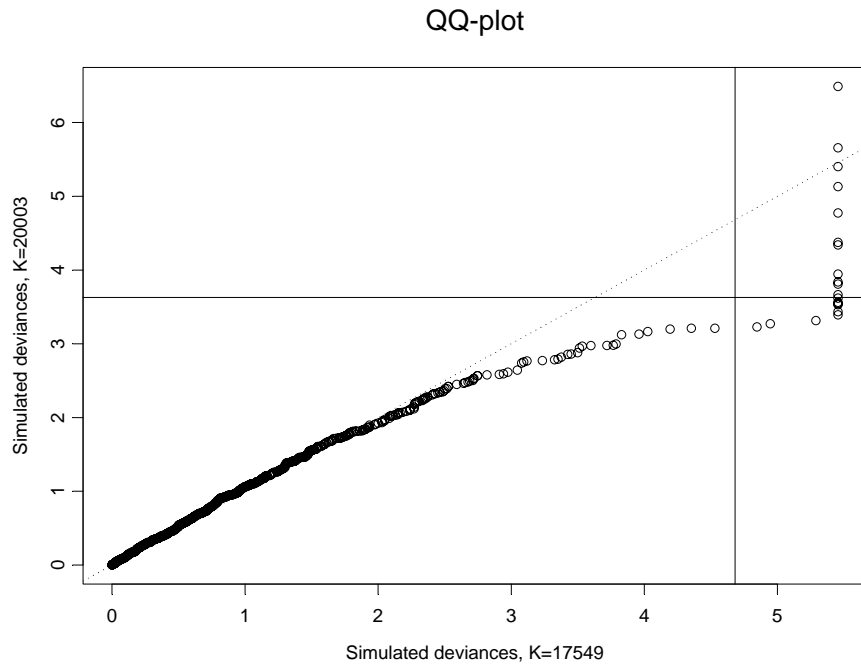


Figure 7: Simulated deviance distributions for two values of carrying capacity compared. Observed deviances at the two values shown by solid lines, the diagonal is dotted. Closed model with $msyr = 2\%$.

F SEX RATIO BASED LIKELIHOOD

An alternative likelihood estimator was based on the sex ratio

$$\phi_t^i = \frac{\dot{C}_t^{m,i} + 1}{\dot{C}_t^{f,i} + 1} \quad (27)$$

of the reported sex specific catches in the different fisheries. Assuming, as supported by data, that the sex ratio is log normally distributed, the log likelihood for the i th fishery/area was then

$$\ln L = \sum_t -[\ln(\hat{\phi}_t^i/\phi_t^i)]^2/2\sigma_t^{i,2} - \ln \sigma_t^i \quad (28)$$

where ϕ_t^i is the expected sex ratio, $\hat{\phi}_t^i$ the sex ratio of the original or simulated data, and σ_t^i the coefficient of variation of the sex ratio for the i th fishery in year t including both sampling and additional variation.

The parameters of the model were estimated by maximizing the log likelihood (appendix C), with the estimator for σ_t^i being

$$\hat{\sigma}_t^i = \sqrt{\sigma_{bin,t}^{i,2} + \sigma_{ad}^{i,2}} \quad (29)$$

where $\sigma_{bin,t}^i$ is the sampling variation on the sex ratio given by the binominal reporting of males and females

$$\sigma_{bin,t}^i = \sqrt{1/\dot{C}_t^{m,i} + 1/\dot{C}_t^{f,i}} \quad (30)$$

and the additional variance for fishery i being

$$\sigma_{ad}^{i,2} = \max \left\{ 0, \frac{1}{n^i} \sum_t [\ln(\hat{\phi}_t^i/\phi_t^i)]^2 - \sigma_{bin,t}^{i,2} \right\} \quad (31)$$

where n^i is the number of years with sex ratio data for fishery i .

Given parameter estimates from the original data, binominal catch sampling with sex specific reporting was simulated for each fishery/area. This was done by $\text{binom}(\dot{C}_t^i, \theta_t^i)$ where \dot{C}_t^i is the total number of catches with sex specific reporting in fishery/area i in year t and θ_t^i is the probability that a one-plus caught individual in fishery/area i in year t is a female. With additional variation added the simulated sex ratios of the catch reports were

$$\tilde{\phi}_t^i = \frac{\tilde{\dot{C}}_t^{m,i} + 1}{\tilde{\dot{C}}_t^{f,i} + 1} e^{\hat{\sigma}_{ad}^i Z} \quad (32)$$

where $\tilde{\dot{C}}_t^{f,i}$ and $\tilde{\dot{C}}_t^{m,i}$ are the simulated females and males sampled for the i th fishery/area in year t , $Z \sim N(0, 1)$, and $\hat{\sigma}_{ad}^i$ is the additional variability in the catch sex ratio of that fishery/area.

G SENSITIVITY ESTIMATES

Not yet ready.