

# 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 foetuses 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, dependent upon the choice of ecological model, it is estimated that there is less than a 5% probability that the current abundance is below 10,000 to 12,000 whales, that the carrying capacity is below 16,000 to 20,000 whales, and that the current depletion ratio is below 0.72 to 0.50. The lower limit of the current abundance estimate obtained from our analysis is at least 2.4 times higher than the lower limit of the highest and fully corrected survey estimate for common minke whales off West Greenland. This suggests that the aggregation of common minke whales off West Greenland is only some fraction of a larger more widespread population.

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

## 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 sex ratios in the catch. The smaller the population is, the more is the sex ratio expected to slope down. The observed sex ratios 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.

### **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.

## METHOD

### Catch statistics

Catch reports 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 ( $\phi = \dot{C}^m / \dot{C}^f$ ) 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.

## 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 thus 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 obviously in agreement with a stock that is depleted for females. The apparent presence of opposite sex ratio trends between the two areas suggests instead 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 a differential segregation of the two sexes between the two areas. A second *influx model* assumes instead that the variation in the sex ratio in the southern area reflect oceanographic changes, while for the northern area, that is less affected by the variation in the Irminger current, variation in the sex ratio should reflect primarily the sex specific degree of exploitation.

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, with the aggregations included in the modelling being the early Greenlandic inshore fishery along the entire West Greenland coast (denoted by  $e$ ), the late Greenlandic inshore fishery in the northern ( $l_n$ ) and southern ( $l_s$ ) areas, and the Norwegian offshore fishery in the northern ( $n_n$ ) and southern ( $n_s$ ) areas.

#### *Influx model*

For the influx model the abundance ( $A$ ) of male ( $m$ ) and female ( $f$ ) minke whales of age-class  $a$  in aggregation  $i \in \{e, l_n, n_n, n_s\}$  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  $\beta_t$  parameter that is the fraction of the females in the total population that are present in the West Greenland aggregation for age classes where  $G_a = 1$  ( $\beta_t$  is a dummy parameter that is not estimated by the model), and an increased average tendency  $\vartheta^i > 1$  by which female minke whales migrate to aggregation  $i$  relative to male minke whales. For aggregation  $l_s$ , the southern area of the late Greenlandic fishery, the sex biased migration factor  $\vartheta^{l_s}$  is given as a linear function of time

$$\vartheta_t^{l_s} = \vartheta_0 + (t - 1987)\alpha \quad (2)$$

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

The expected sex ratio in the catch from aggregation  $i$ th in year  $t$  is then

$$\phi_t^i = \frac{\sum_{a=1}^x A_{t,a}^{i,m}}{\sum_{a=1}^x A_{t,a}^{i,f}} \quad (3)$$

#### *Closed model*

To allow for opposite sex ratio trends in the northern and southern areas for the late Greenlandic fishery, the distribution of the two sexes between the two areas in the closed model are given as

$$\begin{aligned} A_{t,a}^{N,m} &= r_t^m A_{t,a}^{G,m}, & A_{t,a}^{S,m} &= (1 - r_t^m) A_{t,a}^{G,m} \\ A_{t,a}^{N,f} &= r_t^f A_{t,a}^{G,f}, & A_{t,a}^{S,f} &= (1 - r_t^f) A_{t,a}^{G,f} \end{aligned} \quad (4)$$

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

$$\begin{aligned} r_t^m &= \frac{e^{\alpha^m + \beta^m t}}{1 + e^{\alpha^m + \beta^m t}} \\ r_t^f &= \frac{e^{\alpha^f + \beta^f t}}{1 + e^{\alpha^f + \beta^f t}} \end{aligned} \quad (5)$$

For the early Greenlandic, the northern Norwegian, and southern Norwegian catches the relative abundance of the two sexes were given by Eq. (1). The expected sex ratio from an aggregation was then given by Eq. (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. As is explained in Appendix B the chi-square method 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  $\alpha$  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  $\alpha$ . The upper confidence limit is infinite.

The applied statistics should be familiar, at least when applied to the profile deviance function  $D(K) = 2 \ln \left( L(\widehat{K}) / L(K) \right)$ . 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  $\theta$ , e.g.,  $\theta = \{\vartheta^e, \vartheta^G, \vartheta^{n_n}, \vartheta^{n_s}, \alpha^m, \beta^m, \alpha^f, \beta^f\}$  for the closed model, was first estimated by maximum likelihood over the original data, with the maximum likelihood estimate, denoted  $\widehat{\theta}$ , being given for  $K = \infty$  (approximated here as  $K = 200,000$ ), and the conditional maximum likelihood estimate  $\widehat{\theta}(K)$  being given for each  $K$ . The profile deviance function of  $K$  is then  $D(K) = 2 \ln \left( L(\infty, \widehat{\theta}) / L(K, \widehat{\theta}(K)) \right)$  with likelihood ( $L$ ) being estimated as described below.

Given the original catch histories and the age-structured parameterisation in the appendix, the parameter vector  $\{K, \widehat{\theta}(K)\}$  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  $\theta$  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  $\theta^*$ , is not necessarily at  $K = \infty$ , and thus the joint maximum likelihood estimate  $\{K^*, \theta^*\}$  required a joint optimisation over  $K$  and  $\theta$ . The deviance on the simulated data was then given as  $D^*(K) = 2 \ln (L(K^*, \theta^*) / L(K, \theta^*(K)))$ ,

where  $\theta^*(K)$  is the  $K$ -conditional maximum likelihood estimate. The quantiles over  $K$  for the 1000 replicate values  $D^*(K)$  were then calculated. The lower confidence bound for  $K$  is then 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.

In order to simulate the female fraction in the catches, the sex ratio expectations of the maximum likelihood data trajectory  $[\phi_t^i$  from Eq. (3) given  $\hat{\theta}$ ] were first used to obtain estimates of the additional variance in the catch sex ratio for the different fisheries. The  $cv$  of the sampling variation on the sex ratio estimate  $\phi_t^i$  in year  $t$  for fishery  $i$  was given by the binominal reporting of males and females

$$cv_{bin,t}^i = \sqrt{1/\dot{C}_t^{m,i} + 1/\dot{C}_t^{f,i}} \quad (6)$$

with  $\dot{C}_t^i = \dot{C}_t^{m,i} + \dot{C}_t^{f,i}$  being the total sex specific reporting for fishery  $i$  in that year. An estimate  $\hat{\sigma}_{ad}^{i,2}$  of the additional variance for fishery  $i$  was then given as

$$\hat{\sigma}_{ad}^{i,2} = \max \left\{ 0, \sum_{t=1987}^{2006} \left( [\ln(\hat{\phi}_t^i / \phi_t^i)]^2 - cv_{bin,t}^{i,2} \right) / n \right\} \quad (7)$$

where  $\hat{\phi}_t^i = \dot{C}_t^{m,i} / \dot{C}_t^{f,i}$  is the sex ratio of the original data,  $\phi_t^i$  the expected sex ratio [Eq. (3)] given  $\hat{\theta}$ , and  $n$  the number of years with reported sex ratios. These estimates of additive variance were maintained for all other simulations.

Having an estimate of the additional variability in the reported sex ratios, the data trajectories,  $\{K, \hat{\theta}(K)\}$  were run in order to generate simulated sex specific catch data. To simulate the time series of sex specific reporting, which were used for the calculation of likelihood, binominal catch sampling with sex specific reporting was carried out for each fishery, with the Norwegian and late Greenlandic fishery being split into catch reports sampled from the northern and the southern areas separately. 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  $\theta_t^i$  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

$$\phi_t^{i*} = \left( \frac{\dot{C}_t^{f,i*}}{\dot{C}_t^{m,i*}} \right) e^{\hat{\sigma}_{ad}^i Z} \quad (8)$$

where  $\dot{C}_t^{f,i*}$  and  $\dot{C}_t^{m,i*}$  are the simulated females and males sampled for the  $i$ th area in year  $t$ ,  $Z$  is a random draw from the standard normal distribution, and  $\hat{\sigma}_{ad}^i$  is the estimated sd for the additional variability in the catch sex ratio of fishery aggregation  $i$ .

The log likelihood of a data, or simulated data, trajectory was then calculated under the assumption of log-normally distributed errors

$$\ln L_\phi = \sum_t -[\ln(\hat{\phi}_t^i / \phi_t^i)]^2 / 2cv_t^{i,2} - \ln cv_t^i \quad (9)$$

where  $\phi_t^i$  is the sex ratio expected from Eq. (3) for the  $i$ th fishery,  $\hat{\phi}_t^i$  the sex ratio of the original, or simulated, data for that fishery, and  $cv_t^i$  the coefficient of variation of the sex ratio estimate of the  $i$ th fishery in year  $t$  including both sampling and additional variation. As shown in the

Appendix, the likelihood of a trajectory may be extended to depend also on abundance estimates from surveys.

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 fishery/area specific catches with no reported sex were then binomially sampled for sex using the procedure for sex reporting described above. Additional variation was added, using the same random draw for Eq. (8) as used in the reporting of sex. 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 then added to obtain the complete simulated catch history for minke whales taken of West Greenland.

### Estimation runs

The 1+ msyr for the common minke whale is often assumed to lie between 0.01 and 0.07. For both the influx and the closed model, we consider the precautionary range from 0.01 to 0.04, providing abundance estimates for the conservative limit assumption that the msyr is 0.01, for the conservative assumption that the msyr is 0.02, and for the moderate and likely more realistic assumption that the msyr is 0.04. For both the influx and closed model, our base case model was fitted only to the early and late Greenlandic data, while the Norwegian data were also included for the msyr 0.02 case as a sensitivity run. The main reason to exclude the Norwegian data from the base case analysis is that we are primarily interested in abundance estimates that relate directly to the inshore Greenlandic fishery.

## RESULTS

Given a msyr of 2%, the Maximum Likelihood fit of the closed model to the female/male ratio of the catch data is shown in Figure 1 for the early Greenlandic fishery, and for the northern and southern areas of the late Greenlandic fishery. Figure 2 shows the corresponding fit for the influx model. In agreement with the findings in Laidre et al. (2008), there is hardly any trend in the sex ratio data for the early Greenlandic hunt, while there is an decline in the female/male ratio in the southern area for the late Greenlandic harvest and, at least for the closed model, a somewhat smaller increase in the northern area during the same period. The residuals of all fits are shown in Figures 4 to 6; none of the residuals have significant autocorrelation (tested for lags from one to 12 years).

Given a msyr of 2%, the deviance function for the carrying capacity is shown in Figure 3 for the closed and the influx model, together with the 5%, 10% and 50% quantiles based on 1000 sets of simulated data.

The estimated lower confidence limits are shown in Table 4 for the abundance in 2006, the carrying capacity, and the depletion ratio in 2006. Both models give practically identical estimates for a msyr of 2%, that is, 5% quantile estimates of the abundance in 2006 of 10, 100



whales, of the carrying capacity of 19,900 whales, and of the 2006 depletion ratio of 0.49. The msyr 1% estimates of the 2006 abundance are slightly smaller, while the msyr 1% estimates of the carrying capacity are slightly larger, while the opposite is the case for the msyr 4% estimates. The influx model with a 2% msyr was also applied with the Norwegian data split into a northern and southern area. This gave slightly smaller abundance estimates [2006 abundance of 9.080 whales and carrying capacity of 19.200 for the 5% quantile] than the corresponding influx 2% msyr model with no fit to Norwegian data.

The Maximum Likelihood estimates of the sd for the additional variance were 0.55, 0.29, 0.00, 0.69 and 3.1 for the early Greenlandic, late northern Greenlandic, late southern Greenlandic, northern Norwegian, and southern Norwegian catch series independently of the applied model. The averages of the corresponding sd's for the additional variance of the simulated data were stable across models and carrying capacity, having average values of 0.48, 0.23, 0.05, 0.49 and 3.2.

## DISCUSSION

### 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, 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.

### *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 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 seem 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.

### *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, will not work because individual site-fidelity makes the distribution of whales geographically stationary so that an overexploitation will operate only

locally. While this imply that the local abundance can more easily be depressed, it also implies 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 (refs), 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, including West Greenland, 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. All of 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. The occurrence of two independent minke whale populations in West Greenland, however, 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. Genetic studies have also failed to detect any signal of population structure within West Greenland.

Hence, in order to account for the sex ratio patterns in the West Greenland fisheries, we considered the most plausible hypothesis of 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.

## Estimates

The estimates of population status obtained by the sex ratio model are considerable higher than the number of minke whales that have been estimates by aerial surveys off West Greenland. In 1988 an aerial survey estimated 3266 (95% CI: 1,700 – 5,710) minke whales (IWC 1990) off West Greenland, while a similar survey in 1993 estimated 8,371 (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 increasing to 10,790 (90% CI: 4,290 – 27,160) when corrected for perception bias (Heide-Jørgensen et al. 2007). Hence, with the lower 5% confidence limit of the most optimistic aerial survey being of 4,290 whales in 2005, the more realistic (msyr of 0.04 and 0.02) runs of both the closed and the influx model suggest a lower bound estimate that is 2.4 to 2.9 times higher than the highest number accounted for by aerial surveys off West Greenland.

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 sex ratio model suggests that the true abundance of the stock that supplies the West Greenland harvest is considerably higher than 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 larger more widespread population that number at least 10,000 whales.

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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	-	-
1990	13	32	1996	31	76	2002	21	60	2008	-	-

Late Greenlandic catches; 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>
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	-	-
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											
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	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	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$
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.

		$N$			$K$			$d$		
	msyr	2.5%	5%	10%	2.5%	5%	10%	2.5%	5%	10%
closed	0.01	8,050	8,230	9,510	22,300	22,500	23,500	0.36	0.36	0.40
	0.02	9,740	10,100	10,500	19,700	19,900	20,100	0.49	0.50	0.52
	0.04	11,600	12,300	13,000	16,500	16,900	17,200	0.68	0.72	0.75
influx	0.01	7,080	7,090	11,600	21,600	21,600	25,200	0.33	0.33	0.45
	0.02	9,730	10,100	14,000	19,700	19,900	22,700	0.49	0.51	0.61
	0.04	8,850	10,800	12,900	15,100	16,000	17,100	0.54	0.64	0.75

Table 4: **Estimates** of the 2.5%, 5% and 10% quantile for the abundance in 2006 ( $N$ ), the carrying capacity ( $K$ ), and the depletion ratio in 2006 ( $d$ ), for the closed and the influx model.

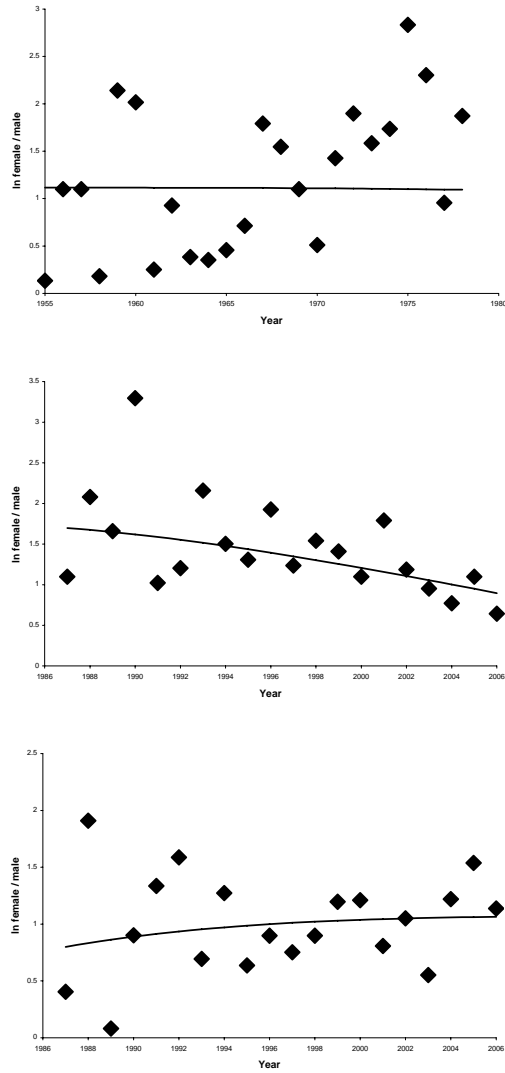


Figure 1: The ln female/male ratio over time in the early Greenlandic (upper figure), and southern (middle figure) and northern (lower figure) late Greenlandic fisheries, together with the MLE estimates (curves) for the closed model (msyr of 2%).

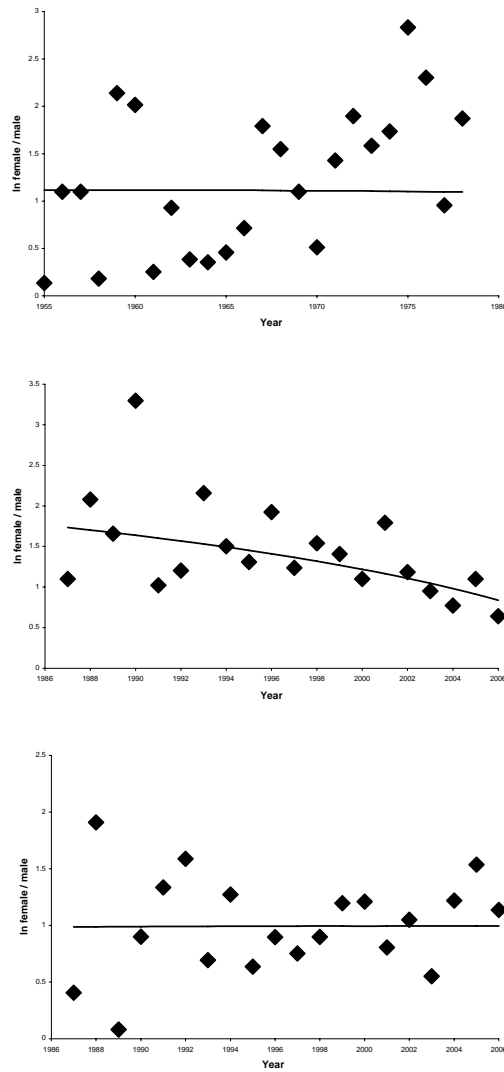


Figure 2: The ln female/male ratio over time in the early Greenlandic (upper figure), and southern (middle figure) and northern (lower figure) late Greenlandic fisheries, together with the MLE estimates (curves) for the influx model (msyr of 2%).

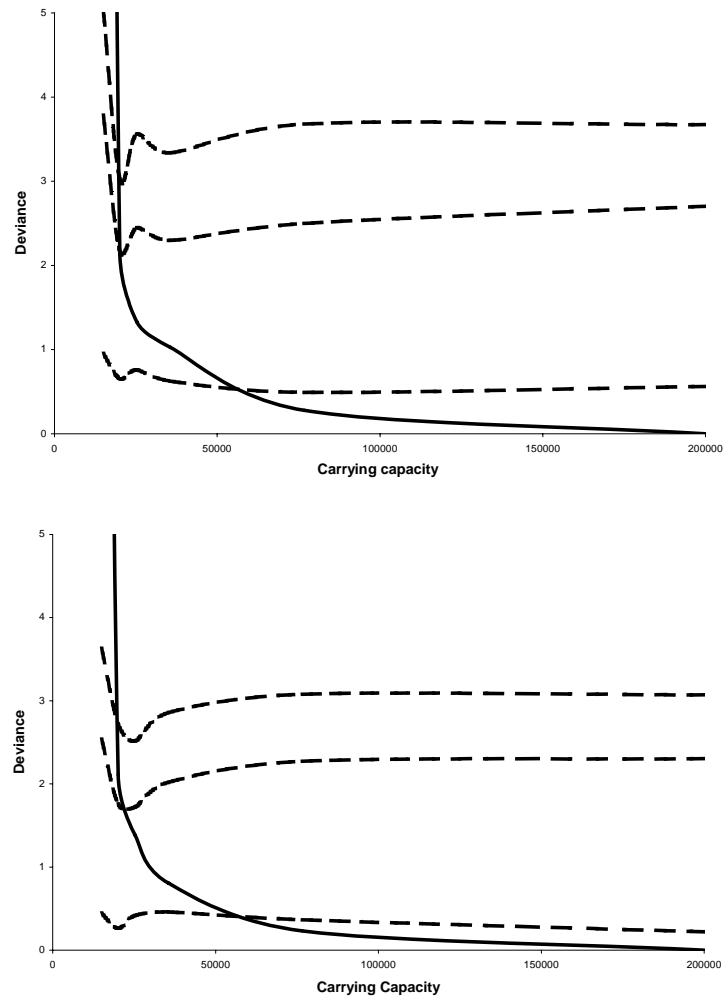


Figure 3: The deviance function for the data (solid curve), and the 5%, 10% and 50% quantiles based on 1000 simulations of the closed model (upper figure) and 1000 simulations of the influx model (lower figure).

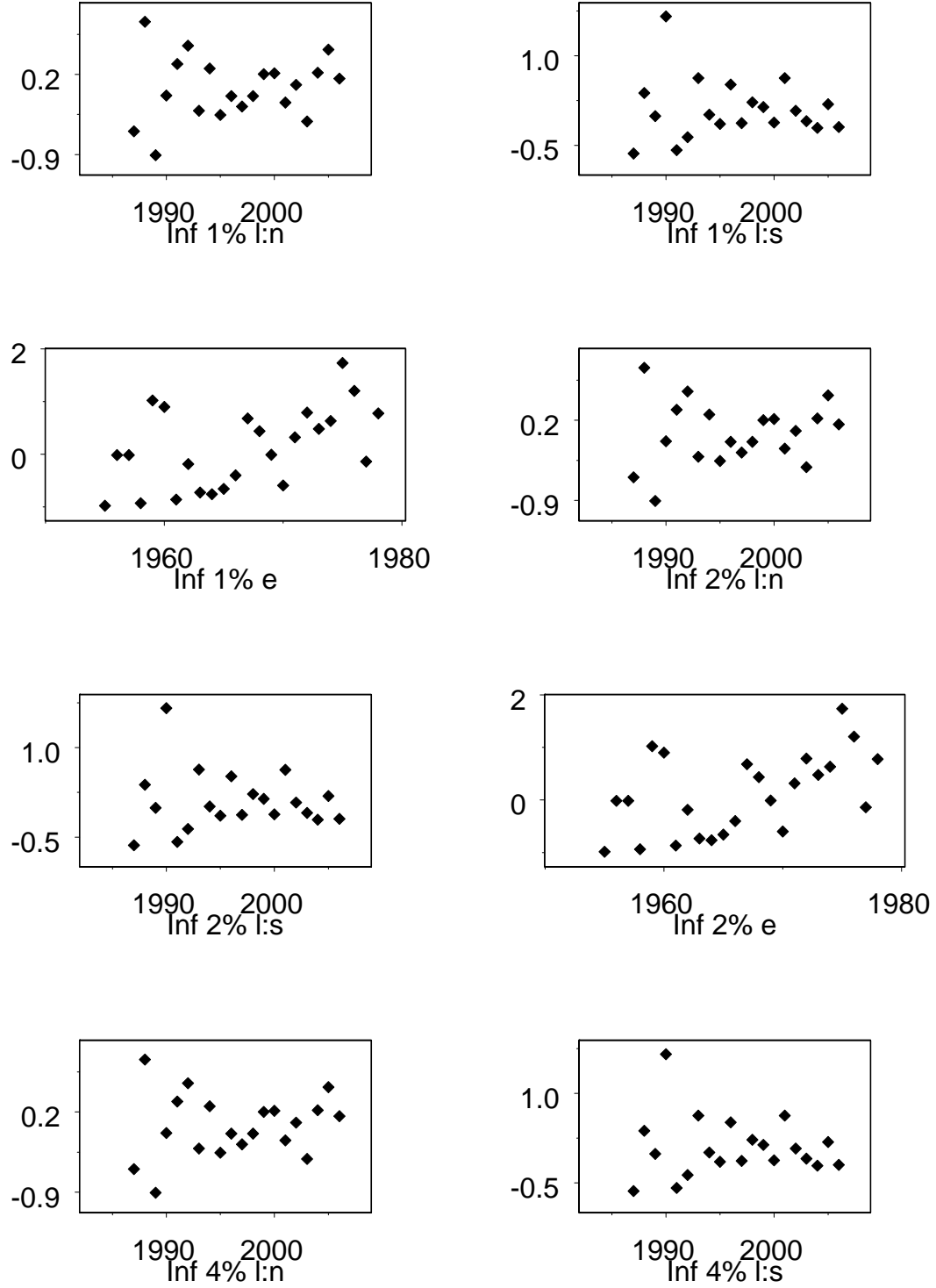


Figure 4: Residuals ( $\ln \hat{\phi} - \ln \phi$ ;  $\phi$ : expected sex ratio;  $\hat{\phi}$ : data sex ratio) across years for the Maximum Likelihood Estimates of the different models [influx (inf), closed (clo), msyr (1%, 2%, 4%)] to the different time series [early Greenlandic (e), late Greenlandic north (l:n) and south (l:s), Norwegian north (n:n) and south (n:s)].

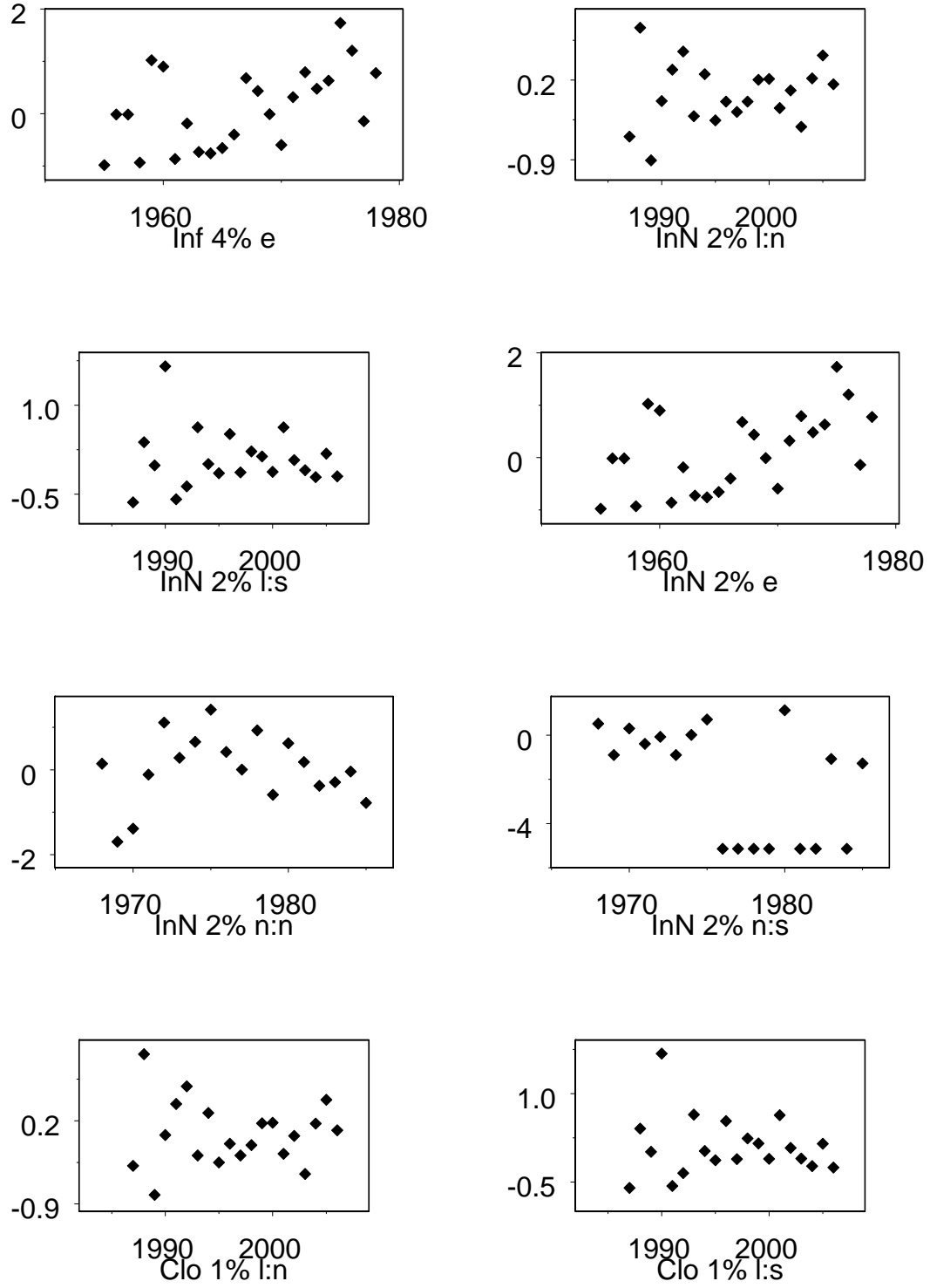


Figure 5: Residuals ( $\ln \hat{\phi} - \ln \phi$ ;  $\phi$ : expected sex ratio;  $\hat{\phi}$ : data sex ratio) across years for the Maximum Likelihood Estimates of the different models [influx (inf), closed (clo), msyr (1%, 2%, 4%)] to the different time series [early Greenlantic (e), late Greenlantic north (l:n) and south (l:s), Norwegian north (n:n) and south (n:s)].

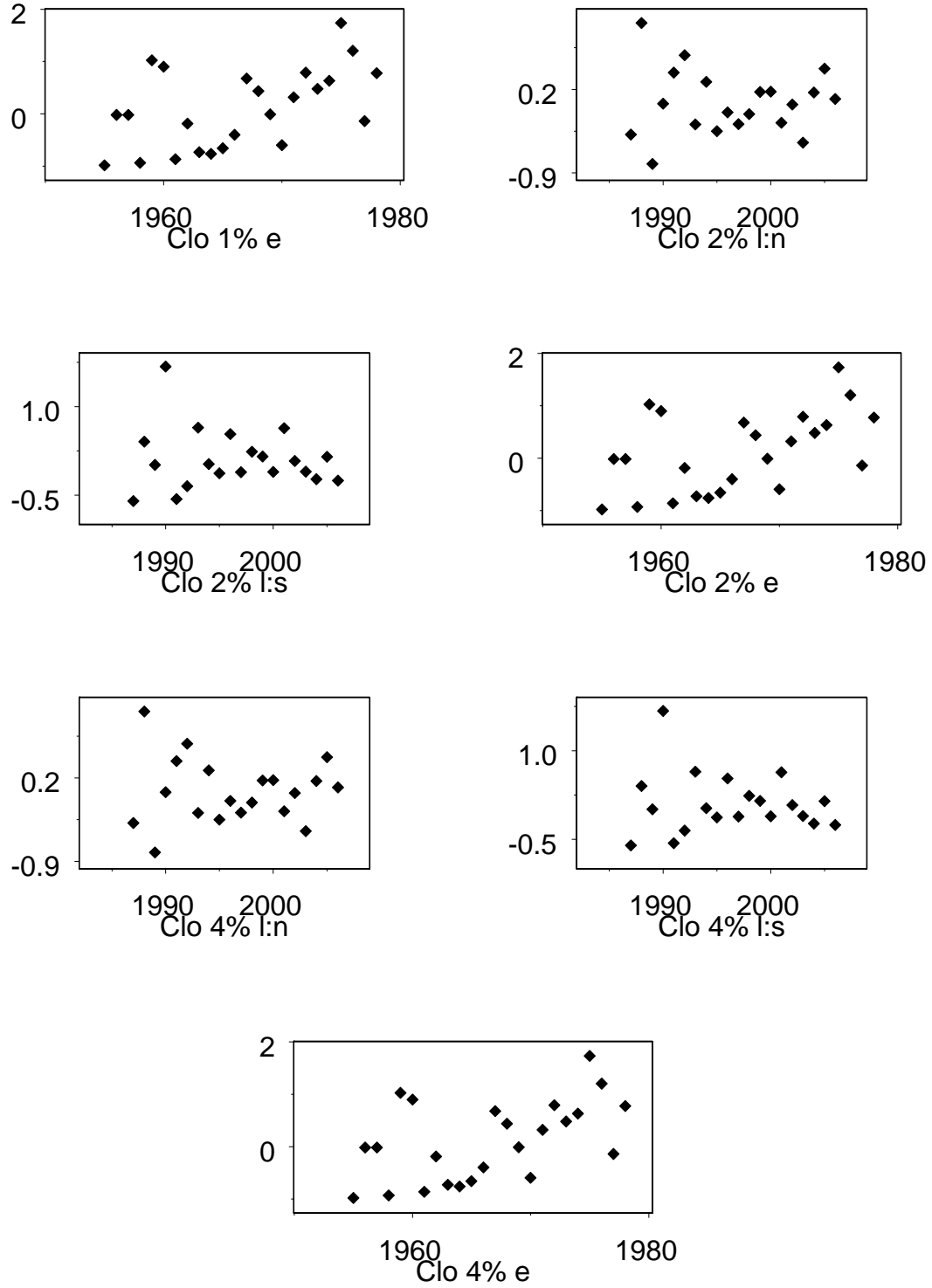


Figure 6: Residuals ( $\ln \hat{\phi} - \ln \phi$ ;  $\phi$ : expected sex ratio;  $\hat{\phi}$ : data sex ratio) across years for the Maximum Likelihood Estimates of the different models [influx (inf), closed (clo), msyr (1%, 2%, 4%)] to the different time series [early Greenlandic (e), late Greenlandic north (l:n) and south (l:s), Norwegian north (n:n) and south (n:s)].

## APPENDIX A

### POPULATION DYNAMIC MODEL

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

$$\begin{aligned} N_{t+1,a+1}^g &= (N_{t,a}^g - C_{t,a}^g)s_a & 0 \leq a \leq x-2 \\ N_{t+1,x}^g &= (N_{t,x}^g - C_{t,x}^g)s_x + (N_{t,x-1}^g - C_{t,x-1}^g)s_{x-1} \end{aligned} \quad (10)$$

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

$$C_{t,a}^g = \frac{G_a N_{t,a}^g C_t^g}{\sum_{a=0}^x G_a N_{t,a}^g} \quad (11)$$

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

$$s_a = \begin{cases} s_{juv}s_{ad} & \text{if } a = 0 \\ s_{juv} & \text{if } 1 \leq a \leq a_{ad} \\ s_{ad} & \text{if } a > a_{ad} \end{cases} \quad (12)$$

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

$$B_t = \sum_{a=a_m}^x B_{t,a} \quad (13)$$

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

$$B_{t,a} = b_t M_{t,a}^f \quad (14)$$

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

$$M_{t,a}^f = \begin{cases} 0 & \text{if } a_m > a \\ N_{t,a}^f & \text{if } a_m \leq a \end{cases} \quad (15)$$

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

$$N^{1+} = \sum_{a=1}^x N_a^f + N_a^m \quad (16)$$



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

$$b_t = b_k + [b_{max} - b_k][1 - (N_t^{1+}/K^{1+})^z] \quad (17)$$

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

$$Q1 = \min[\text{msyr}N^{f,1+}(1 + \vartheta)/\vartheta, 0.45\text{msy}(1 + \vartheta)/\vartheta] \quad (18)$$

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.

## 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

$$\ln L_a = 180 \ln[p(a_m)] + 82 \ln[1 - p(a_m)] \quad (19)$$

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

$$p(a_m) = \frac{\sum_{t=1979}^{1983} \sum_{a=a_m}^x G_a N_{t,a}^f}{\sum_{t=1979}^{1983} \sum_{a=1}^x G_a N_{t,a}^f} \quad (20)$$

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.

## ABUNDANCE DATA

A second likelihood contribution can be given by abundance data from aerial surveys in West Greenland, where the number of whales in the area covered by a survey represent either the whole West Greenland aggregation or a fraction  $\beta_t^s$  thereof. If we assume that a sex biased catch is caused by differential migration of the two sexes to West Greenland waters and that an age biased catch is caused by harvest selectivity, following Eq. (1) the total abundance of one plus animals in the whole West Greenland aggregation in year  $t$  is

$$N_t^G = \beta_t \sum_{a=1}^x \left( N_{t,a}^f + \frac{N_{t,a}^m}{\vartheta} \right) \quad (21)$$

As we have no information on  $\beta_t$  it is arbitrarily set to one so that we make the conservative assumption that all the females in the whole population are present in the West Greenland

aggregation. Assuming then that the survey estimate in year  $t$ ,  $\hat{N}_t^G$ , is log normally distributed with mean  $\ln(\beta_t^s N_t^G)$  and error coefficient of variation  $cv_t$  we have the likelihood component

$$\ln L_n = \sum_t -(\ln[\hat{N}_t^G / \beta_t^s N_t^G])^2 / 2cv_t^2 - \ln cv_t \quad (22)$$

that, under the restriction  $\beta_t^s \leq 1$ , is maximised by

$$\hat{\beta}_t^s = \min(1, \hat{N}_t^G / N_t^G) \quad (23)$$

Note here that  $L_n$  only works as a soft lower bound on the abundance estimate of the total population, and that the assumption of age bias by harvest selectivity, if anything, provides a conservative, i.e., smaller, abundance estimate relative to the assumption of age bias by age differential migration, where the  $G_a$  function would have to be included in Eq. (21). The overall log likelihood can then be calculated as a joint likelihood  $\ln L = \ln L_\phi + \ln L_n$  from the sex ratio of the catches and the abundance data.

# APPENDIX B

The problem of infinite maximum likelihood estimates of a key parameter, or the maximum likelihood estimate being at the boundary of its parameters space, might occur in many different situations. In the context of abundance estimation of natural populations, one might for example obtain no recaptures in a capture-recapture estimate. We first present some examples for illustration, and a bit of statistical theory. Then the West Greenland minke whale data are analysed in a model where the over-dispersion in sex ratios are modelled by the beta distribution. The purpose here is to provide a check on our other work.

## 1 Some simple examples

### 1.1 Normal data and a finite restriction

Let the parameter interval be  $(-\infty, 0)$ , and let the the maximum likelihood estimator be  $\hat{\theta} = \min(X, 0)$  where  $X \sim N(\theta, 1)$ . With  $I(X > 0)$  denoting the indicator function of the event  $X > 0$  the deviance function is  $D(\theta; X) = -2 \log \left( L(\theta; X) / L(\hat{\theta}; X) \right) = (X - \theta)^2 - X^2 I(X > 0)$ . For large negative values of  $\theta$  the distribution of  $D$  is the chi-square distribution with one degree of freedom. As the parameter tends towards the boundary,  $P(X > 0)$  increases towards 0.5, and at  $\theta = 0$  the distribution is a half-mixture of 0 and the chi-square, see Figure 1. For  $\theta = -\sqrt{q}$  with  $q$  the p-quantile of the chi-square 1 distribution,  $P(D(\theta) \leq q) = p$ . The observed deviance for  $\hat{\theta} = 0$  is  $D_{obs}(\theta) = q$ . The crossing of this deviance and the various quantile curves are in fact exactly where the quantile curves starts to curve downwards. The ordinary probability calibration of the deviance function by the chi-square 1 distribution is thus correct also in this normal case when the maximum likelihood estimate is at the boundary, and the lower confidence bounds in the restricted case are exactly the left confidence interval limits when  $\theta$  is unrestricted. Note also that the p-quantile of the half-mixture is the  $2p - 1$  chi-square quantile, as illustrated by the two horizontal lines in the figure.

In a more general setting let  $\theta$  be the primary parameter and let  $\chi$  be a vector of secondary parameters. Assume there exists a monotone transformations  $h$  such that  $h(\theta) > 0$  while  $h(\hat{\theta})$  is approximately normally distributed. If say  $\theta = \frac{c}{\beta}$  where  $\beta$  is an approximately normally distributed regression parameter the appropriate transformation is  $h(\theta) = \theta^{-1}$ . Assume the profile deviance to be approximately  $D(\theta) = \left( h(\hat{\theta}) - \theta \right)^2 - h(\hat{\theta})^2 I(h(\hat{\theta}) < 0)$ , which would be the case if there is a transformation  $g$  of the secondary parameter such that  $(h(\hat{\theta}), g(\hat{\chi}))$  approximately has a multinormal distribution. In this case an observed estimate at the boundary of the parameter space,  $h(\hat{\theta}_{obs}) = 0$ , would yield a profile deviance on the transformed scale much like Figure 1, but reflected

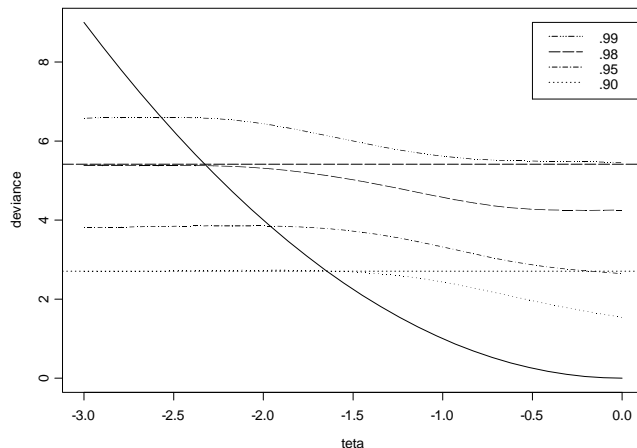


Figure 1: Deviance for normal data with maximum likelihood estimate at the boundary. Quantile curves for  $p = .9, .95, .98$  and  $.99$ . The two flat lines are at chi-square quantiles  $.9$  and  $.98$  ( $df=1$ ).

about the y-axis, and with probability calibration approximately obtained from the chi-square distribution with  $df = 1$ .

It is worth noting that the quantile curves provides the relevant cut-offs also when the maximum likelihood estimator is in the interior of the parameter space. If say  $\hat{\theta} = -1.64 = -\sqrt{q}$  for  $p = 0.90$ , proper confidence intervals are available up to level 0.95, and they will have their right limit to the left of what would have been obtained by a flat cut off at the relevant chi-square quantile. At level 0.95, the confidence interval is actually  $(-1.64 - 1.96, -1.64 + 1.64)$ . At higher levels only left confidence limits are available.

## 1.2 Simple removal model

Let  $N$  be the size of a closed population subject to harvest at two points in time. Effort is identical for the two catches. The capture intensity is  $\lambda$  for each individual. Let  $C_1$  be the first catch, which is Poisson distributed with mean  $N\lambda$ , and  $C_2$  the second. Since the first catch is removed,  $C_2$  is Poisson distributed with mean  $(N - C_1)\lambda$ . The maximum likelihood estimate of  $N$  is finite when  $C_1 > C_2$  and infinite in the opposite case. Figure 2 shows profile deviance and quantile curves, as in Figure 1 in the case of an infinite maximum likelihood estimate of abundance. The lower confidence bounds are close to where the profile deviance equals the quantiles of the chi-square distribution with one degree of freedom. Note that the .95 quantile curve drops to the .9

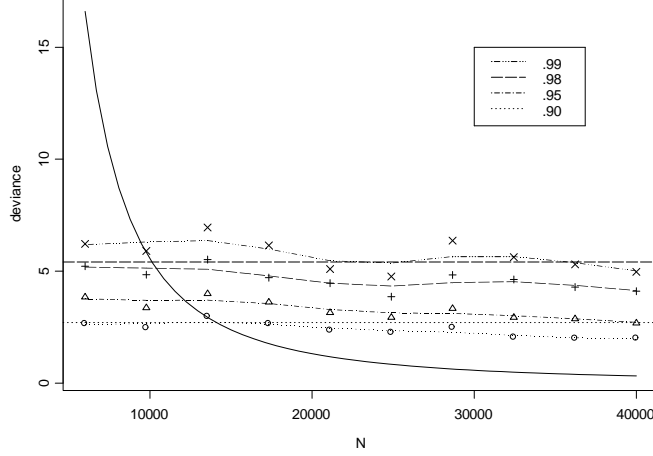


Figure 2: Profile deviance function for  $N$  for the simple removal model when  $C_1 = C_2 = 1000$ . The quantile curves are estimated by simulation and smoothing, with the simulated quantiles shown as points. Horizontal lines are chi-square 1 quantiles at level .9 and .98.

chi-square quantile. A similar pattern is seen for the .99 quantile curve.

In the data rich situation, with both  $C_1$  and  $C_2$  large, the maximum likelihood estimator is close to the moment estimator satisfying the equations  $\hat{N}\hat{\lambda} = C_1$  and  $(\hat{N} - C_1)\hat{\lambda} = C_2$  yielding  $\hat{N} = \frac{C_1^2}{C_1 - C_2}$  for  $C_2 < C_1$  and  $\hat{N} = \infty$  in the reverse case. In this model,  $\hat{N}^{-1}$  is approximately normally distributed, and the restriction  $N < \infty$  is simply  $N^{-1} > 0$ . The estimator of  $\lambda$  is also approximately normal for large values of  $N$ , and the situation is thus as described above. The probability calibration of the profile deviance is thus approximately obtained by the chi-square distribution with one degree of freedom, as illustrated in Figure 2.

### 1.3 Mark-recapture data

Consider the simple mark-recapture experiment of a closed population of  $N$  individuals of which  $m$  are marked, and where there are  $X$  marked individuals in a random sample of size  $n$ . The maximum likelihood estimate of  $N$  is infinite when  $X = 0$ . The deviance function is in this case  $D(N) = -2 \log(P_{hyp}(0; N, m, n))$  where  $P_{hyp}(x; N, m, n) = P(X = x)$  is the hypergeometric probability. The deviance is falling monotonically, but the quantile curves are problematic since the distribution of the deviance is highly discrete at high values of  $N$ . The max-

imum likelihood estimator has a distribution progressively more different from the normal distribution as  $N$  increases, and there is no transformation that yields a normal approximation, as in the previous example.

## 2 Common minke whales off West Greenland

The productivity of the population is assumed here to follow a lumped Pella-Tomlinson model with  $MSYL = 0.6$  and  $MSYR_{1+} = 0.01$ . The sex ratios by year have more variation than binomial variation, particularly in the two early periods. We use a beta binomial model to capture this extra variation. The distribution of the profile deviance in carrying capacity is estimated by simulation.

### 2.1 Model

Let  $N_{ta}^s$  be the number of individuals in the population by sex  $s = f, m$  and age  $a = 1, \dots, A$  in year  $t$ . The probability of an individual being caught in one or the five regions of Table B1 in year  $t$  depends on effort and spatial distribution of males and females. Region is denoted by  $r$ . We assume no selectivity by sex, and since we condition on the numbers caught, effort drops out of the equations for sex ratios. Let  $q_{tar}^s$  be the probability that an individual of sex  $s$  and age  $a$  is caught in region  $r$  in year  $t$ .

We will assume separability between age and sex, region and year,

$$q_{tar}^s = q_a q_{tr}^s.$$

This could come about if the migration by age to regions of whaling is the same for all years and both sexes. With a stable age distribution in the population, the probability that a caught individual is a female is then

$$\pi_{tr} = \frac{\sum_a N_{ta}^f q_{tar}^f}{\sum_a N_{ta}^f q_{tar}^f + \sum_a N_{ta}^m q_{tar}^m} = \frac{N_t^f}{N_t^f + N_t^m q_{tr}^m}, \quad (1)$$

where  $q$  is the mean of  $q_a$  over the age distribution, and where  $N_t^s$  is the number, say of the 1+ population, by sex.

Let the log sex ratio in the population be

$$b_t = \log \left( \frac{N_t^f}{N_t^m} \right),$$

and let

$$q \frac{q_{tr}^m}{q_{tr}^f} = e^{-\beta' x},$$

where  $x$  is a vector of covariates characterizing year and area with respect to catchability. Equation (1) is then a logistic regression model for the expected

sex ratio in the catch,

$$\log \left( \frac{\pi_{tr}}{1 - \pi_{tr}} \right) = b_t + \beta' x. \quad (2)$$

The number of males and females in the population, and thus  $b$ , depends on the history of sex-specific removals by harvest  $C_t^s$ , and the population dynamics of the population. We assume that reproduction and mortality follows the deterministic Pella-Tomlinson model lumped over ages with balance between the sexes,

$$N_{t+1}^s = N_t^s - C_t^s + \frac{1}{2} N_t^f \rho \left( 1 - \left( \frac{N_t^f + N_t^m}{K} \right)^z \right) \quad s = f, m. \quad (3)$$

The productivity parameter  $\rho$  and the shape parameter  $z$  are assumed given, as mentioned above. The term  $b_t$  might therefore be regarded as an offset term. There will also be an intercept in the regression  $\beta' x$ . The intercept is due to  $q$  and possibly a constant proportionality between  $q_{tr}^m$  and  $q_{tr}^f$ .

In addition to the regression vector  $\beta$  there are parameters of over-dispersion relative to binomial variation in the sex distribution in the catch,  $c$ . This parameter is discussed below. Lower confidence bounds for the carrying capacity is found by comparing the profile deviance function in  $K$  to its distribution given  $K$ . The deviance, or minus twice the log likelihood ratio, is based on the likelihood function  $L(K, \beta, c)$ ,

$$D(K) = -2 \ln \left( \frac{L(K, \hat{\beta}_K, \hat{c}_K)}{L(\hat{K}, \hat{\beta}, \hat{c})} \right), \quad (4)$$

where  $(\hat{K}, \hat{\beta}, \hat{c})$  is the maximum likelihood estimate of all the free parameters, and  $\hat{\beta}_K$  and  $\hat{c}_K$  are the values maximizing  $L(K, \beta, c)$  for fixed values of  $K$ .

Since the sex reporting is incomplete (Table B1) it is necessary to estimate the sex ratio in each catch from its subset with sex ratio recorded. This is done pro rata, with rounding to integer numbers of males and females, and such that the sex ratio in the catch is as close as possible to the sex-reported subset.

The reported sex ratios are over-dispersed relative to the binomial distribution. This is modeled by having the probability of a harvested whale being female  $p_{tr}$  being beta distributed with density proportional to  $p^{a-1} (1-p)^{b-1}$  and with  $a = \pi_{tr} c_{tr}$ ,  $b = (1 - \pi_{tr}) c_{tr}$  making  $Ep_{tr} = \pi_{tr}$  given by (2). Given their expectations,  $p_{tr}$  are independent across years and regions. We assume that the degree of over-dispersion is constant in each of the three fisheries, i.e. that the parameter  $c_{tr}$  is constant within each of them.

The expected female probability is a function of the parameters,  $\pi_{tr} = \pi_{tr}(K, \beta)$ , where  $K$  acts through  $b_t$ . The probability of observing  $x$  females among  $n$  sexed individuals in a given year and region with female probability  $\pi$



is

$$\begin{aligned}
P(x; n, \pi, c) &= \int_0^1 \binom{n}{x} p^x (1-p)^{n-x} \frac{\Gamma(c\pi + c(1-\pi))}{\Gamma(c\pi) \Gamma(c(1-\pi))} p^{c\pi-1} (1-p)^{c(1-\pi)-1} dp \\
&\propto \frac{\Gamma(c)}{\Gamma(n+c)} \frac{\Gamma(x+c\pi) \Gamma(n-x+c(1-\pi))}{\Gamma(c\pi) \Gamma(c(1-\pi))},
\end{aligned}$$

where  $\Gamma$  is the gamma function. Conditioning on the numbers of sexed animals the log likelihood to be maximized is

$$l(K, \beta, c) = \sum_{t,r} \log(P(x_{tr}; n_{tr}, \pi_{tr}, c_{tr})) \quad (5)$$

where  $c$  is a vector holding the three distinct over-dispersion coefficients.

The estimate of abundance is closely related to the slopes in the sex ratio plots, with finite estimate in case of negative slopes and infinite estimate in the reverse case. The inverse abundance might thus be approximately proportional to a weighted mean of the estimated slopes, and thus approximately normally distributed. The inverse transformation might actually allow a normal approximation, and quantile curves with crossing of the profile deviance (for an infinite abundance estimate) at levels close to the chi-square quantiles ( $df = 1$ ) are to be expected.

## 2.2 Bootstrapping and inference

The simulation is carried out as follows. For each value of  $K$  we simulate the number of males and females in each of the 122 catch units by series, area and year. This is done forward in time. For year  $t$  the offset  $b_t^*$  is calculated from the given carrying capacity  $K$ , and the previous simulated catches of males and females. Then  $\pi_{tr}^*$  is calculated from  $b_t^*$  and  $\hat{\beta}_K$ , and a bootstrap value  $p_{tr}^*$  is drawn from the beta distribution with parameters  $a = \pi_{tr}^* \hat{c}_{tr}$ ,  $b = (1 - \pi_{tr}^*) \hat{c}_{tr}$ . Then a draw from the appropriate binomial distribution yields number of females and males in the sex-reported subset of the catch. The unreported remainder (unsexed in Table B1) is then divided into females and males by the same pro rata method that was used for the observed data. This process leads to a bootstrapped data set and consequently a bootstrapped value for the deviance  $D(K)^*$ . This simulated profile deviance is actually calculated on the simulated data in exactly the same way as the observed profile deviance, i.e. with both  $\beta$  and  $c$  as free parameters to be profiled out.

The simulation is repeated 1000 times for each selected value of  $K$ , providing estimated quantile curves  $d_\alpha(K)$  at various confidence levels  $\alpha$ . If  $K$  is the true carrying capacity and the simulation model is correct, the observed data would by chance yield a profile deviance value  $D(K)$  below  $d_\alpha(K)$  with probability  $\alpha$ . Thus, given the simulation model, the set  $\{K : D(K) \leq d_\alpha(K)\}$  is a confidence set with confidence level  $\alpha$ , which possibly is a half-open interval  $(\hat{K}_\alpha, \infty)$ .

### 2.3 Results

Computation are carried out by the package AD model builder. The maximum likely point estimates are given in Table B2. High values of  $c$  indicate little over-dispersion. There is thus some over-dispersion in the early coastal series and in the Norwegian series of off-shore catches, while the sex ratios in the late coastal catch show almost binomial variation. The probability of a caught whale being female is estimated to be around  $3/4$  except in the off-shore south ( $\exp(1)/(1 + \exp(1)) = 0.73$ ).

The profile deviance and the estimated quantile curves are shown in Figure 3. The quantile curves cross the profile deviance at  $K = 20000$  (99%), 21500 (95%) and 24000 (90%), which are the lower confidence bounds for carrying capacity.

	EC	NOS	NON	LC	LCS	LCN
females	241	234	494	124	168	426
males	672	160	1312	342	617	1157
unsexed	2910	0	2	264	0	0

Table B1. The total catch of 9123 minke whales from 1955 to 2006 off West Greenland, by reported sex, operation (early E, Norwegian N, and late L), coastal (C) or off shore (O), and region(south of 63 degrees: S, and north of 63 degrees: N).

	$K$	$\beta_{OS}$	$\beta_{ON}$	$\beta_C$	$\beta_{CS}$	$\beta_{CN}$	$c_{Early}$	$c_{Norwegian}$	$c_{Late}$
Estimate	$\infty$	0.00	0.89	1.07	1.36	1.04	22.65	9.68	246.02
se		0.00	0.21	0.15	0.25	0.24	11.75	3.13	281.59

Table B2. Maximum likelihood estimates for West Greenland minke whales.

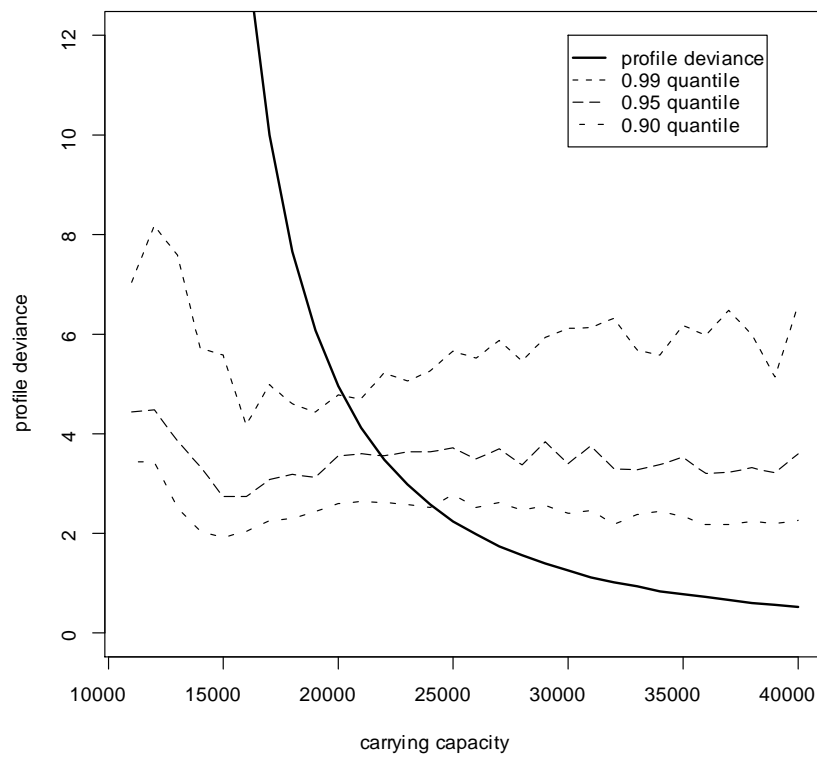


Figure 3: Profile deviance with quantile curves based on 1000 simulations at each of 30 values of carrying capacity.