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# A reassessment of Greenland walrus populations

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ABSTRACT

We use recent abundance estimates, historical catches and an age- and sex-structured population dynamic model with density regulation to perform Bayesian assessments of the three populations of Atlantic walrus (*Odobenus rosmarus rosmarus*) that occur in Greenland. We estimate that the West Greenland/Baffin Island population declined from 9000 (CI:5900-14000) walruses in 1900 to 3200 (CI:1790–5430) in 1960, where after it remained relatively stable with a local maximum of 4500 (CI:3650-5550) walruses in 1993 and a somewhat lower abundance 3200 (CI:2300-4400) in 2010. We estimate a 2010 depletion ratio of .33 (CI:.19-.60) and a yearly replacement of 130 (CI:61-190) individuals. The Baffin Bay population is estimated to have declined almost linearly from 10000 (CI:6900-16000) walruses in 1900 to 2100 (CI:1500-3100) in 2010. This population is estimated to have a depletion ratio of .20 (CI:.11-.33) and a replacement of 84 (CI:31-140) walruses per year. We also estimate that East Greenland walruses declined from 1600 (CI:1000-2500) individuals in 1889 to a maximal depletion of 0.73 (CI:0.48-0.91) in 1909. The population has since increased slowly to a current depletion ratio of .96 (CI:.80-.99) and a corresponding abundance of 1500 (CI:940-2400) individuals. Given the low depletion, the current replacement is only 12 (CI:10-16) individuals per year. Our estimates of status are comparable with an earlier assessment (Witting and Born 2005) for the East Greenland population only. Owing primarily to updated abundance estimates, but also to an improved abundance prior, our estimates of current status have improved greatly for the West Greenland/Baffin Island and the Baffin Bay populations since the assessment in 2005.

## INTRODUCTION

There are three populations of Atlantic walrus (*walwlat*) that occur in Greenland. West Greenland/Baffin Island walruses occur from fall to spring at the edge of the Baffin Bay pack ice from c. 66° 30N to 70° 30 N (Born et al. 1994; Born et al. 1995), while they are found mainly around Baffin Island during open water season. Further north in Baffin Bay and Smith Sound, walruses occur almost year-round in the North Water polynya and adjacent areas. They are, however, absent from the coastal areas of NW Greenland in August and September when they summer along the eastern and southern coast of Ellesmere Island (Canada) and in the Canadian High Arctic archipelago (Born et al. 1995). We refer to walruses in these areas as the Baffin Bay population. Walruses occur year-round along the eastern coast of Greenland where they mainly are distributed inside the National Park of North and Northeast Greenland north of the entrance to Scoresby Sound (c. 71°N) (Born et al. 1995, 1997). There is only limited exchange between the East Greenland and neighbouring populations, i.e., West Greenland, Baffin Bay and the Svalbard-Franz Joseph Land populations (Born et al. 1995; Andersen et al. 1998; Born et al. 2001). In conclusion, information on distribution and migration (Born et al. 1994, 1995, 1997) and genetics (Andersen et al. 1998; Andersen and Born 2000; Born et al. 2001) indicates that the three aggregations of walrus in Greenland represent relative separate population units and therefore should be managed separately.

The three populations have been subject to exploitation for centuries. First at a limited scale by Inuit, and then by European whalers and sealers who tolled heavily on the populations. From the beginning of the 20th Century Inuit hunted walrus with increasing efforts after the introduction of fire-arms and motorized vessels. The populations are still exploited for subsistence purposes in Greenland and Canada, with an additional small scale sport hunt in Canada.

A population model based assessment in 2005 indicating that both the West Greenland/Baffin Island and the Baffin Bay populations were likely over-exploited (Witting and Born 2005). While the assessment in 2005 was based on the best available data at that time, our data knowledge has since increased. Based on satellite tracking, it is now clear that walruses of West Greenland are part of a larger population that summers primarily around Baffin Island (Dietz et al. 2009). And while the assessment in 2005 was based primarily on best guess-estimates of abundance, we have now more solid abundance estimates for all populations (Heide-Jørgensen et al. 2009; Born et al. 2009; Heide-Jørgensen and Burt Hansennammco:sc:17:wwg14; Stewart and Born Dunnnammco:sc:17:wwg11). Hence, we update the assessment to obtain better estimates of the current status of the three populations.

In this paper we summarize the walrus catch history for West Greenland, the Baffin Bay and East Greenland for the last century, including Canadian catches from 1977 onwards. We apply the catch information, and recent abundance estimates, in the density regulated and age and sex structure model of Witting and Born (2005) to (1) reconstruct the historical dynamics of the three populations, (2) evaluate their current status, and (3) determine sustainable yield levels.

Our model is based on a Bayesian statistical simulation method (Berger 1985; Press 1989) that is particular useful when faced with limited or uncertain information. The major data uncertainties in this paper are the usual uncertainty associated with abundance estimates and catch histories, including unknown loss and reporting rates. Many of the historical catches for the Baffin Bay are model constructed and, thus, associated with a much larger degree of uncertainty than the catch histories from the two other populations. Please note that our description of the dynamics of the three populations rest on the available data and our population dynamic model. Hence, they provide only our best estimates of the dynamics and certainly not a complete and true description of the dynamic history and present status of the three walrus populations.

| Abun | $\mathbf{N^w}$ | *cv* | $\mathbf{N^{ii}}$ | *cv* | $\mathbf{N^n}$ | *cv* | $\mathbf{N^n}$ | *cv* | $\mathbf{N^e}$ | *cv* |
|---|---|---|---|---|---|---|---|---|---|---|
| Age | *N* | | *N* | | *N* | | *N* | | *N* | |
| 1981 | - | - | 114 | 75 | - | - | - | - | - | - |
| 1982 | - | - | 4 | 41 | - | - | - | - | - | - |
| 1984 | - | - | 39 | 32 | - | - | - | - | - | - |
| 1990 | - | - | 125 | 40 | - | - | - | - | - | - |
| 1991 | - | - | 182 | 21 | - | - | - | - | - | - |
| 1993 | - | - | 55 | 27 | - | - | - | - | - | - |
| 1994 | - | - | 48 | 26 | - | - | - | - | - | - |
| 1998 | - | - | 142 | 21 | - | - | - | - | - | - |
| 1999 | - | - | 43 | 37 | - | - | - | - | - | - |
| 2006 | 2791 | 51 | 7 | 43 | - | - | - | - | - | - |
| 2007 | 3030 | 20 | - | - | - | - | - | - | - | - |
| 2008 | 3240 | 68 | 88 | 35 | - | - | - | - | - | - |
| 2009 | - | - | - | - | 2676 | 32 | 1616 | 31 | 1429 | 43 |

Table 1: The sets with abundance estimates, their *cv* in %, and age component (*N* includes all age-classes). The sets of abundance estimates include corrected estimates from off West Greemland and and Baffin Island 2006 t ($\mathbf{N^w}$), the West Greenland index series (south of Disko) ($\mathbf{N^{ii}}$), the corrected North Water survey from 2009 ($\mathbf{N^n}$), the corrected North Water survey from 2009 ($\mathbf{N^n}$), and the corrected East Greenland survey from 2009 ($\mathbf{N^e}$).

## METHOD

### Data

### Abundance

***West Greenland/Baffin Island*** The assessment in 2005 was based on a fully corrected abundance estimate of 938 (CV:0.48) wintering walruses off Central West Greenland in 1990 (Witting and Born 2005). Since there have been two additional line-transect surveys in this areas in 2006 and 2008 with fully corrected estimates of $2,790$ (CV:0.51) and $3,240$ (CV:0.68) walruses (Heide-Jørgensen et al. 2009). On the Canadian side, hall-out counts from Baffin Island give minimum estimates of 1,000 walruses in 2007 (Stewart et al. 2009), increasing here to $3,030$ (CV:0.20) when corrected for walruses not hauled out.

Apart from the fully corrected abundance estimates there is a time-series of the relative abundance of wintering walruses off Central West Greenland based on the sighting rates in 11 surveys conducted from 1981 to 2008 (Heide-Jørgensen et al. 2009). This times-series is given both for a northern (west of Disko Island) and a southern (south of Disko Bay) wintering ground in Central West Greenland, with the relative abundance on the northern ground being correlated with sea ice and the relative abundance on the southern ground being independent of ice. We use the time-series for the southern areas as an index of the relative abundance of the West Greenland/Baffin Island population of walruses.

***Baffin Bay*** Based on aerial counts of terrestrial hall-outs, a multiplication factor for walruses in the water, and a multiplication factor for areas not covered, an estimate of 1500 walruses was applied in the 2005 assessment for the population of walruses in the Baffin Bay. Two fully corrected line-transect surveys in the Baffin Bay estimated respectively 2,676 (CV:0.32) walruses in May 2009 (Heide-Jørgensen and Burt Hansennammco:sc:17:wwg14) and 1,616 (CV:0.31) in August 2009 (Born et al. 2009). We use both estimates to represent the number of walruses in the Baffin Bay population in 2009.

***East Greenland*** Based on opportunistic and systematic observations, the East Greenland population of walruses was sat to number 1000 individuals in the 2005 assessment. Given an aerial survey of the coast from Clavering Island to the northern border of the Northeast Water, there is now a fully corrected summer estimate of 1,429 (CV:0.43) walruses in East Greenland in 2009 (Born et al. 2009).

All the abundance estimates that are used in our modeling are listed in Table 1.

### Catch data and loss rates

We estimated two catch histories for each population. A low catch history based on reported or landed catch (and in some years estimates of the catch), and a high catch history that included also estimates of non-reported loss, i.e., animals that were struck and lost, and animals that were landed and not reported.

***West Greenland/Baffin Island*** Catch data were extracted from official catch statistics and written sources (Born et al. 1994; COSEWIC 2006). The catch history of our model (**W**) includes all West Greenland catches south of Qaanaaq, plus Canadian catches after 1977 from Qikiqtarjuaq, Iqaluit and Pangnirtung.

Losses were assumed to average 5% (1 lost for every 10 killed) from 1900 until 1930. During this period walruses were mainly taken by traditional means close to the coast and primarily at the terrestrial haul-outs. From 1930 onwards when walruses increasingly were hunted by use of motorized vessels operating in the offshore pack ice (Born et al. 1994) losses were assumed to average 30%. Loss rates of 20-30% are not uncommon during walrus hunts based on small-type vessels (cf. Born et al. 1995 and references therein; Gjertz et al. 1998).

An even sex ratio is applied to all historical catches, and the catch history with losses is shown in Table **??**. For future catches we apply two models with a female fraction of 0.68 or 0.20, to represent respectively the estimated proportion of females in recent catches (0.68 estimated from samples from 2006 and 2007) and an alternative case with a strong male bias in the catches.

***Baffin Bay*** Generally, the catch data from the Thule area of NW Greenland are insufficient in particular prior to 1950 (Teilmann and Kapel 1998). To obtain estimates for the early period, catches were inferred from the trend in growth of the human population in the area. Inferred from Gilberg (1976: fig 19), the Inuit population in the Thule area increased gradually with a rate of ca. 0.8% per year from about 200 at 1900 to about 300 around 1950. If assuming a proportional relationship between (1) the size of the human population, (2) the fraction of hunters (29-34% of the human population were men aged 15-64 years; Gilberg (1976: table 25)) in this population, and (c) the number of walrus caught per hunter, the annual catch of walrus during 1900-1950 was back-calculated from an average of about 200 in 1939-1940 (Vibe 1950): Catch ($c$) in year $x - 1 = c_x 0.9918$.

Canadian catches from Grise Fjord after 1977 are included in our model (**N**) of this population (COSEWIC 2006).

Losses were assumed to average 5% from 1900 until 1950. During this period walruses were mainly taken by traditional means and only few motorized vessels were available for hunting. Furthermore, the walruses were harpooned before being shot. For the period 1951-1969, a loss rate of 15% was applied taking into account an increased use of vessels during the open water period where walruses hauling out on ice flakes can be shot at before they are harpooned. After 1970, an overall loss rate of 30% was used based on observations in the late 1970s (Born et al. 1995).

An age-structured catch (Table **??**) is available from a sample of the Greenlanders catch of walruses (0-29 years of age) in the North Water (1987-1991). The sex ratio in this sample ($F$: $n = 179$; $M$: $n = 197$), did not differ from unity ($\chi^2 = 0.43$, $p = 0.512$, $df = 1$). We apply an even sex ratio to all the catches from this population, and the base case catch history with loss included is shown in Table **??**. For future catces, we apply to model that assume either an even sex ratio or a male biased sex ratio with a female fraction on only 0.20.

***East Greenland*** Catches for our East Greenland model (**E**) were extracted from Born et al. (1997); Table **??**. An average loss rate of 30% was applied to the catch by the European sealing vessels, while the loss rate of Greenlanders was set to 5% until 1949, where after a loss rate of 23% was applied (Born et al. 1997).

Information is not available on the sex ratio in the catches taken by European sealers prior to 1956 when walruses were completely protected in NE Greenland north of ca. 72°N (Born et al. 1997) - effectively prohibiting the catch of walrus in East Greenland by foreigners. Hence for the period 1889-1955 an even sex ratio in the catch was assumed. South of 72°N the recent catch consists of ca. 90% male walrus (Born et al. 1997), and we therefore applied a $0.9M : 0.1F$ ratio for the catch in East Greenland after 1956. For future catches we assume 90% males.

*Additional variance*

Following Butterworth et al. (1993) and Wade (2002), an additional variance term may be added to the abundance estimates in order to estimate variance that are not accounted for by the variance estimates of the abundance estimates. The cause for the additional variance is treated as unknown, with no attempt being made to model processes that can generate additional variance.

The additional variance is parameterised as a coefficient of variation that is considered constant across years. It is also assumed that the variance has a Gaussian distribution so that the total coefficient of variation in an abundance estimate $N_t^x$ for year $t$, with $x \in \{ii\}$, can be given

| Age | $m$ | $f$ | Age | $m$ | $f$ | Age | $m$ | $f$ | Age | $m$ | $f$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 0.26 | 0.52 | 4 | 0.17 | 0.33 | 8 | 0.17 | 0.67 | 12 | 0.43 | 0.81 |
| 1 | 0.26 | 0.14 | 5 | 0.30 | 0.38 | 9 | 0.78 | 0.62 | 13 | 0.70 | 0.33 |
| 2 | 0.22 | 0.19 | 6 | 0.39 | 0.81 | 10 | 1.00 | 1.00 | 14 | 0.52 | 0.14 |
| 3 | 0.17 | 0.38 | 7 | 0.48 | 0.33 | 11 | 0.74 | 1.00 | 0 | 0.00 | 0.00 |

Table 2: **The age structured catch** for male ($m$) and female ($f$) West Greenland/Baffin Island walrus.

as

$$cv_t^x = \sqrt{(cv_{n,t}^x)^2 + (cv_{ad}^x)^2} \tag{1}$$

where $cv_{n,t}^x$ is the coefficient of variation of the abundance estimate $N_t^x$ and $cv_{ad}^x$ is the additional coefficient of variation.

### Population dynamic model

Let the number of animals in age classes larger than zero be

$$\begin{array}{ll} N_{t+1,a+1}^{m/f} = (N_{t,a}^{m/f} - C_{t,a}^{m/f})s_a & 0 \le a \le x-2 \\ N_{t+1,x}^{m/f} = (N_{t,x}^{m/f} - C_{t,x}^{m/f})s_x + (N_{t,x-1}^{m/f} - C_{t,x-1}^{m/f})s_{x-1} & \end{array} \tag{2}$$

where $s_a$ is age specific annual survival, $N_{t,a}^{m/f}$ is the number of males/females of age $a$ at the start of year t, $C_{t,a}^{m/f}$ is the catch of males/females of age $a$ during year $t$, with the relative age distribution of the catches being sex specific, the same in all years, and given by Table 2, provided that the catch will not exceed the abundance in any age class. If instead the catch exceeds the abundance in an age class, the catch in that age class is set to the abundance of that class. This distribution of catches is continued until it is possible to distribute the remaining catches in accordance with the age-structure in Table 2.

Let the annual survival rate $s_a$ of animals of age $a$ be

$$s_a = \begin{cases} s_{juv}s_{ad} & \text{if } a = 0 \\ s_{juv} & \text{if } 1 \le a \le a_{ad} \\ s_{ad} & \text{if } a > a_{ad} \end{cases} \tag{3}$$

where $s_{juv}$ is the survival rate for 'juveniles', $s_{ad}$ is the survival rate for adults, $a_{ad}$ is the greatest age at which the 'juvenile' survival rate applies, and $x$ is the lumped age-class (all animals in this and the $x-1$ class have reached the age of reproductive maturity). In this paper $a_{ad} = 2$ and $x = 14$.

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

$$B_t = \sum_{a=a_m}^{x} B_{t,a} \tag{4}$$

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

$$B_{t,a} = b_t M_{t,a}^f \tag{5}$$

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

$$M_{t,a}^f = \begin{cases} 0 & \text{if } a_m > a \\ N_{t,a}^f & \text{if } a_m \leq a \end{cases} \tag{6}$$

Let the component of the population that imposes density-regulation be the one plus component

$$\hat{N} = \sum_{a=1}^{x} N_a^f + N_a^m \tag{7}$$

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

$$b_t = b^* + [b_{max} - b^*][1 - (\hat{N}_t / \hat{N}^*)^\gamma] \tag{8}$$

where $b^*$ is the birth rate at population dynamic equilibrium $N^*$, $b_{max}$ is the maximal birth rate, and $\gamma$ the level of density dependence.

Although not explicit parameters of the model, the maximum sustainable yield level (msyl) and the maximum sustainable yield rate (msyr) are treated as parameters in the analysis. The msyl depends mainly to the compensation parameter $\gamma$, and to speed computation the three parameters are defined relative to the mature component of the population, denoted by $\tilde{}$. Hence, the birth rate is

$$b = b^* + (b_{max} - b^*)(1 - \tilde{d}^\gamma) \tag{9}$$

where $\tilde{d} = M/M^*$ is the depletion ratio of the mature component. Assuming that the sex ratio of the mature component is equal to the sex ratio at birth, the sustainable yield is

$$\mathrm{s\tilde{y}} = M[s_m \vartheta b - (1 - s_{ad})] \tag{10}$$

where $s_m = \prod_{i=0}^{a_m - 1} s_i$ is survival from birth to age of reproductive maturity. The $s\tilde{y}r$ relative to the deplection ratio $\tilde{d}$ is then

$$\mathrm{s\tilde{y}r} = \tilde{d}[s_m \vartheta b_{max} - s_m \vartheta (b_{max} - b^*)\tilde{d}^\gamma - (1 - s_{ad})] \tag{11}$$

Solving $d\mathrm{s\tilde{y}r}/d\tilde{d} = 0$ for $\tilde{d}$, the $\mathrm{m\tilde{s}yl}$ is

$$\mathrm{m\tilde{s}yl} = \left( \frac{s_m \vartheta b_{max} - (1 - s_{ad})}{s_m \vartheta (b_{max} - b^*)(1 + \gamma)} \right)^{1/\gamma} \tag{12}$$

with $\mathrm{m\tilde{s}yr}$ being the $\mathrm{s\tilde{y}r}$ at the $\mathrm{m\tilde{s}yl}$.

### Assessment models

**W:** West Greenland/Baffin Island, with 68% females in future catches.

**W$_m$:** West Greenland/Baffin Island, with 80% females in future catches.

**N:** Baffin Bay with 50% males in future catches.

**N$_m$:** Baffin Bay with 80% males in future catches.

**E:** East Greenland

| Model | $s_{ad}$ | $s_{juv}$ | $b_{max}$ | $a_m$ | $\vartheta$ | msyl | $N^*$ | $\kappa$ | $\beta^{ii}$ | $cv_{ad}^{ii}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| **W** | $.95, .99^u$ | $.71, .95^u$ | $.33, .5^u$ | $5, 9^i$ | $.5^p$ | $.5, .7^u$ | $9, 4\text{e-}4^l$ | $0, 1^u$ | $1\text{e-}4, .025^u$ | $.5, 2.5^u$ |
| $\mathbf{W}_m$ | $.95, .99^u$ | $.71, .95^u$ | $.33, .5^u$ | $5, 9^i$ | $.5^p$ | $.5, .7^u$ | $9, 4\text{e-}4^l$ | $0, 1^u$ | $1\text{e-}4, .025^u$ | $.5, 2.5^u$ |
| **N** | $.95, .99^u$ | $.71, .95^u$ | $.33, .5^u$ | $5, 9^i$ | $.5^p$ | $.5, .7^u$ | $10, 4\text{e-}4^l$ | $0, 1^u$ | - | - |
| $\mathbf{N}_m$ | $.95, .99^u$ | $.71, .95^u$ | $.33, .5^u$ | $5, 9^i$ | $.5^p$ | $.5, .7^u$ | $11, 4\text{e-}4^l$ | $0, 1^u$ | - | - |
| **E** | $.95, .99^u$ | $.71, .95^u$ | $.33, .5^u$ | $5, 9^i$ | $.5^p$ | $.5, .7^u$ | $1.6, 4\text{e-}4^l$ | $0, 1^u$ | - | - |

Table 3: **Prior distributions** for the different assesment models. The list of parameters: $s_{ad}$ is adult survival, $s_{juv}$ juvenile survival, $b_{max}$ the maximal birth rate, $a_m$ the age of reproductive maturity, $\vartheta$ the fraction of females at birth, msyl the maximum sustainable yield level, $N^*$ the equilibrium abundance (given in thousands), $\kappa$ the low/high catch parameter, $\beta^{ii}$ the bias of abundance estimates $\mathbf{N^{ii}}$, and $cv_{ad}^{ii}$ the additional variance of abundance estimates $\mathbf{N^{ii}}$. The type of probability distribution is given by superscripts; $u$=uniform, $i$=discrete uniform, $l$=ln normal, and $p$ a parameter with fixed value. The first number of an entry in the table is the min value if $pd = u$ or $pd = i$, the mode if $pd = l$, and a fixed parameter value if $pd = p$. The second number is the max value if $pd = u$ or $pd = i$, and the sd of the corresponding normal distribution if $pd = l$.

## Statistical methods

The population dynamic models were fitted to the abundance data by projecting the population under the influence of the historical catches, with the initial abundance reflecting a pre-harvested population in dynamic equilibrium. A Bayesian statistical method (e.g, Berger 1985; Press 1989) was used, and posterior estimates of the model parameters and other management related outputs were calculated. This implied an integration of the product between a prior distribution for each parameter and a likelihood function that links the probability of the data to the different parameterisations of the model.

### *Prior distributions*

The values and prior ranges of the different parameters for all the assessment models are listed in Table 3. Prior probability distributions were assigned to adult survival ($s_{ad}$), juvenile survival ($s_{juv}$), the maximal birth rate ($b_{max}$), the age of reproductive maturity ($a_m$), the maximum sustainable yield level (msyl), the equilibrium abundance ($N^*$), the low/high catch parameter ($\kappa$), the bias of abundance estimates $\mathbf{N^{ii}}$ ($\beta^{ii}$), and the additional variance of abundance estimates $\mathbf{N^{ii}}$ ($cv_{ad}^{ii}$). The fraction of females at birth ($\vartheta$) was set to the fixed value of 0.5 in all runs.

Most of the priors were uniform. The age of reproductive maturity was a discrete variable, while all other priors were continuous. The range of values for the priors (Table 3), together with the value for the fraction of females at birth, were based on various studies of walrus populations and previous modelling of walrus population dynamics (Fay 1982; DeMaster 1984; Fay et al. 1989, 1997; Chivers 1999). The annual natural survival rate of adults ($s_{ad}$) was set in this study to range between 0.95 and 0.99 with constant survival rate for all adult age classes. The juvenile annual survival rate ($s_{juv}$) was set to 0.71-0.95.

The maximal birth rate ($b_{max}$), i.e, the maximal number of offspring per female per year, was set to range between 0.33 and 0.50 (Mansfield 1958; Fay 1982; Born 2001), reflecting the assumption that each female produces one offspring every second or third year. The age of reproductive maturity ($a_m$) is set to 5-9, and the maximum sustainable yield level (msyl) to 0.50-0.70. The prior for the equilibrium abundance was log normal, with parameters being set by trial and error so that the prior was slightly wider than the posterior and the mode of the prior and the posterior coincided with one another.

The $\kappa$ parameter sets a uniform prior on the catch history, where the catch history that is applied in a give parameterised iteration $\theta_i$ is given by a linear scaling between the low and the high catch histories. Here the catch in year $t$ of parameterisation $\theta_i$ is

$$c_{t,i} = c_{l,t}(1 - \kappa_i) + c_{h,t}\kappa_i \tag{13}$$

where $c_{l,t}$ is the low catch and $c_{h,t}$ is the high catch. Thus, the low catch history is applied when $\kappa = 0$, and the high catch history when $\kappa = 1$.

Apart from the distributions given in Table 3, for each randomly selected parameter set, the upper bound on the juvenile survival rate was always set to be smaller than or equal to the randomly selected value for the adult survival rate.

Although the msyl is not an explicit parameter of the model, a uniform prior was assigned to it. This was possible since no prior distribution was assigned to the compensation parameter $\gamma$; given values for msyl and the other parameters of the model, a unique value is given for $\gamma$.

Realised priors, or post-model-pre-data probability distributions, were generated by discarding any parameterisation $\theta_i$ that would not generate a viable model with a maximal population dynamic growth rate above zero. In result the discarded parameterisations were given zero likelihood, and the $n_1$ sampled parameterisations include only realistic models with positive maximal growth rates.

### *Bayesian integration*

The Bayesian integration was obtained by the sampling-importance-resampling routine (Berger 1985; Rubin 1988), where $n_1$ random parameterisations $\theta_i$ ($1 \leq i \leq n_1$) are sampled from an importance function $h(\theta)$. This function is a probability distribution function from which a large number, $n_1$, of independent and identically distributed draws of $\theta$ can be taken. $h(\theta)$ shall generally be as close as possible to the posterior, however, the tails of $h(\theta)$ must be no thinner (less dense) than the tails of the posterior (Oh and Berger 1992). For each drawn parameter set $\theta_i$ the population was projected from the first year with a harvest estimate to the present. For each draw an importance weight, or ratio, was then calculated

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)} \tag{14}$$

where $L(\theta_i)$ is the likelihood given the data, and $h(\theta_i)$ and $p(\theta_i)$ are the importance and prior functions evaluated at $\theta_i$. In the present study the importance function is set to the joint prior, so that the importance weight is given simply by the likelihood. The $n_1$ parameter sets were then re-sampled $n_2$ times with replacement, with the sampling probability of the $i$th parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_1} w(\theta_j)} \tag{15}$$

This generates a random sample of the posterior distribution of size $n_2$. The resample of the posterior distribution was set to $n_2 = 2500$, and the $n_1$ sample from the joint prior being 1000000.

The method of de la Mare (1986) was used to calculate the likelihood $L$ under the assumption that observation errors were log-normally distributed (Buckland 1992). With a bias factor $\beta^x$ [where $N_t^x = \beta^x N_t$, $N_t^x$ is the point estimate and $N_t$ the iterated abundance of time series $\mathbf{N^x}$ at time $t$] that is constant over all years, and to be estimated for the abundance of time series two ($\mathbf{N^{ii}}$) the likelihood function is

$$L \quad = \quad \prod_t \exp\left(-\frac{[\ln(N_t^i/N_t)]^2}{2cv_t^2}\right)/cv_t \tag{16}$$

where $cv_t$ is the coefficient of variation of the abundance estimate at time $t$.

If the importance function is adequately specified, the mean of the importance sample for each parameter should approach the mean from the true posterior distribution, given a sufficiently large sample. To illustrate whether the sampled posterior quantities can be assumed to be representative of the true posterior distribution, convergence diagnostics were calculated. One such diagnostic is the maximum importance weight of a parameter set relative to the total summed importance weight over all $n_1$ draws. For example, McAllister et al. (2001) suggest that the maximum importance weight needs to have dropped below 1% of the total sum. And in line with Wade (2002), we also calculated the total number of unique parameter sets in the resample of $n_2$ parameter sets, as well the maximum number of occurrences of a unique parameter set in the resample.

### *Probability of meeting the objective*

The management objective was set to $N_{2020} > N_{2010}$ should the abundance be below the msyl, while a total take of 90% of the msy was allowed should the abundance be at or above the msyl.

Given the population dynamic model and the data, the probabilities that this objective be met by future catches are straightforwardly calculated from the Bayesian statistical method applied here. For each parameterisation $\theta_i$ of the random sample of the posterior distribution of size $n_2$, we have perfect knowledge of the status of the population for that parameterisation. Hence, for a given $\theta_i$-projection with future catches $c$ it can be determined whether the population objectives are met or not. This implies that the probability $p(ob)$ that the objectives be met can be determined by the following sum

$$\begin{aligned} p(ob) \quad &= \quad \sum_{i=1}^{n_2} g(\theta_i, c)/n_2 \qquad (17) \\ g(\theta_i, c) \quad &= \quad \begin{cases} 1 & \text{if objective met} \\ 0 & \text{if objective not met} \end{cases} \end{aligned}$$

over the complete random sample of the posterior distribution.

| Model | Sample | Weight | Unique | Max |
|---|---|---|---|---|
| $\mathbf{W}$ | 1000000 | 0.0 | 2335 | 4 |
| $\mathbf{W}_m$ | 1000000 | 0.0 | 2335 | 4 |
| $\mathbf{N}$ | 1000000 | 0.0 | 2402 | 3 |
| $\mathbf{N}_m$ | 1000000 | 0.0 | 2402 | 3 |
| $\mathbf{E}$ | 1000000 | 0.0 | 2500 | 1 |

Table 4: **Sampling statistics** for the Bayesian runs of the different assessments models. Sample is the number of draws from the importance function; Weight the maximum importance weight of a draw relative to the total importance weight of all draws (given in percent); Unique the number of unique parameter sets in the resample of 2500 parameter sets; and Max the maximum occurrence of a unique parameter set in the resample.

## RESULTS

### Posterior distributions

The maximum importance weight of a parameter set relative to the total sum of importance weights for all drawn parameter sets in an assessment was smaller than 0% for all assessments. And the number of unique parameter sets in a resample of 2500 parameter sets was not smaller than 2335 for any model, while the maximum occurrences of a unique parameter set in the resample across all models was 4. The model specific statistics are given in Table 4.

The posterior estimates and their 90 % credibility intervals are given in Table 5. The realized prior and posterior distributions are shown in Fig. 1 and 2 for all the parameters of the base case model of the West Greenland/Baffin Island population, and in Fig. 3 for selected parameters for base case Baffin Bay and East Greenland walruses.

Owing to the limited data on trends in all populations there is almost no updating of the posterior distributions relative to the realized priors. It is generally only the absolute abundance that is strongly updated by the model, although this is not very evident from the equilibrium abundance ($N^*$) distributions in the figures because the realized prior for this parameter was set by trial and error to be only slightly wider than the posterior distribution. From Fig. 2 we note that for the West Greenland/Baffin Island model with a time series of relative abundance estimates, there is not unsurprisingly a strong updating of the bias of the relative abundance estimates, but also a strong updating for the additional variance in the times series of relative abundance estimates.

### Population dynamics

*West Greenland/Baffin Island*

Our model suggest that the West Greenland/Baffin Island population of walrus declined from an equilibrium of 9000 (CI:5900-14000) walruses in 1900 to an abundance of 3200 (CI:1790–5430) individuals in 1960, where after the population has been relatively stable with a local maximum of 4500 (CI:3650-5550) walruses in 1993 and a lower 2010 abundance of 3200 (CI:2300-4400)

| Model | | $s_{ad}$ | $s_{juv}$ | $b_{max}$ | $a_m$ | $\gamma$ | msyr | msyl | $r$ | $N_0$ | $\kappa$ | $\beta^{ii}$ | $cv^{ii}_{ad}$ | $N_T$ | $d$ | $ry$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **W** | Med. | .98 | .83 | .42 | 7.0 | 1.6 | .03 | .58 | .05 | 9.0 | .46 | .01 | 1.2 | 3.2 | .33 | 130 |
| | 5th | .95 | .72 | .34 | 5.0 | .74 | .02 | .51 | .02 | 5.9 | .05 | .01 | .81 | 2.3 | .19 | 61 |
| | 95th | .99 | .94 | .49 | 9.0 | 3.8 | .05 | .68 | .08 | 14 | .95 | .02 | 1.9 | 4.4 | .60 | 190 |
| $\mathbf{W}_m$ | Med. | .98 | .83 | .42 | 7.0 | 1.6 | .03 | .58 | .05 | 9.0 | .46 | .01 | 1.2 | 3.2 | .33 | 130 |
| | 5th | .95 | .72 | .34 | 5.0 | .74 | .02 | .51 | .02 | 5.9 | .05 | .01 | .81 | 2.3 | .19 | 61 |
| | 95th | .99 | .94 | .49 | 9.0 | 3.8 | .05 | .68 | .08 | 14 | .95 | .02 | 1.9 | 4.4 | .60 | 190 |
| **N** | Med. | .98 | .81 | .41 | 7.0 | 1.5 | .03 | .57 | .04 | 10 | .51 | - | - | 2.1 | .20 | 84 |
| | 5th | .95 | .72 | .34 | 5.0 | .75 | .01 | .51 | .02 | 6.9 | .05 | - | - | 1.5 | .11 | 31 |
| | 95th | .99 | .93 | .49 | 9.0 | 3.8 | .04 | .68 | .07 | 16 | .95 | - | - | 3.1 | .33 | 140 |
| $\mathbf{N}_m$ | Med. | .98 | .81 | .41 | 7.0 | 1.5 | .03 | .57 | .04 | 10 | .51 | - | - | 2.1 | .20 | 84 |
| | 5th | .95 | .72 | .34 | 5.0 | .75 | .01 | .51 | .02 | 6.9 | .05 | - | - | 1.5 | .11 | 31 |
| | 95th | .99 | .93 | .49 | 9.0 | 3.8 | .04 | .68 | .07 | 16 | .95 | - | - | 3.1 | .33 | 140 |
| **E** | Med. | .97 | .84 | .42 | 7.0 | 2.0 | .03 | .60 | .05 | 1.6 | .50 | - | - | 1.5 | .96 | 12 |
| | 5th | .95 | .72 | .34 | 5.0 | .79 | .02 | .51 | .02 | 1.0 | .05 | - | - | .94 | .80 | 10 |
| | 95th | .99 | .94 | .49 | 9.0 | 4.0 | .05 | .69 | .08 | 2.5 | .94 | - | - | 2.4 | .99 | 16 |

Table 5: **Parameter estimates** for the different assessment models denoted by the labels in Section . The estimates are given by the median and the 90% credibility intervals of the posterior distributions. Abundances ($N$) are given in thousands, and $N_T$ and $d$ are estimated for 2010.

(Fig. 4, top). This estimates a 2010 depletion ratio of .33 (CI:.19-.60) and a yearly replacement of 130 (CI:61-190) individual. The alternative high catch history give essentially the same results (Table 5).

*Baffin Bay*

The Baffin Bay population is projected to have declined almost linearly from an estimated equilibrium of 10000 (CI:6900-16000) individuals in 1900, to an abundance of 2100 (CI:1500-3100) walruses in 2010 (Fig. 4, middel). The population is predicted to have a current 2010 depletion ratio of .20 (CI:.11-.33) with a yearly replacement yield of 84 (CI:31-140). The alternative high catch history give essentially the same results (Table 5).

*East Greenland*

The model for East Greenland walruses suggests a population that declined from an equilibrium abundance of 1600 (CI:1000-2500) individuals in 1889 to a maximal depletion of 0.73 (CI:0.48-0.91) in 1909 (Fig. 4, bottom) . The population has since increased slow and steadily to an estimated depletion ratio of .96 (CI:.80-.99) in 2010 with a corresponding abundance of 1500 (CI:940-2400) individuals. Given the low depletion, the current yearly replacement yield is also low [12 (CI:10-16)].

### Meeting management objectives

Assuming that the fraction of females in the future catches is 0.68, we calculated the probabilities of meeting the management objectives given the different assessment models. This was done for

| Catch | $p_1$ | $p_2$ | $p_3$ | $p_4$ | $p_5$ |
|---|---|---|---|---|---|
| 5 | 1.0 | 1.0 | 1.0 | 1.0 | 1.0 |
| 15 | 1.0 | 1.0 | 1.0 | 1.0 | .88 |
| 25 | 1.0 | 1.0 | .98 | .99 | .53 |
| 35 | .99 | 1.0 | .95 | .98 | .27 |
| 45 | .98 | .99 | .90 | .95 | .13 |
| 55 | .94 | .99 | .82 | .91 | .05 |
| 65 | .90 | .98 | .73 | .86 | .02 |
| 75 | .84 | .96 | .60 | .79 | .01 |
| 85 | .75 | .93 | .48 | .72 | .00 |
| 95 | .65 | .90 | .34 | .62 | .00 |
| 105 | .54 | .85 | .24 | .52 | .00 |
| 115 | .43 | .80 | .15 | .44 | .00 |
| 125 | .32 | .73 | .10 | .34 | .00 |
| 135 | .21 | .65 | .06 | .26 | .00 |
| 145 | .12 | .57 | .03 | .19 | .00 |
| 155 | .07 | .49 | .02 | .14 | .00 |

Table 6: **Catch objective trade-off.** The probability $p_i$ of meeting the management objectives for annual total removals between 5 and 155 individuals in the period 2010 to 2020. The assessment models, denoted by subscript $i$ in $p_i$, are: $1 = \mathbf{W}$; $2 = \mathbf{W}_m$; $3 = \mathbf{N}$; $4 = \mathbf{N}_m$; $5 = \mathbf{E}$.

total annual removals of 5 to 150 individuals in the period from 2010 to 2020, with the results shown in Table 6.

Assuming a current loss rate of 30% the average total removals in 2007 and 2008 were 99 walruses from the West Greenland/Baffin Island population, 84 walruses from the Baffin Bay population, and 12 walruses from the population in East Greenland.

Given the estimates in Table 6, we find that the estimates of current removals coincide with a 60% probability of fulfilling the management objectives for the West Greenland/Baffin Island population of walruses, a 48% probability of fulfilling the management objectives for Baffin Bay walruses, and a 95% probability of fulfilling the management objectives for the East Greenland population of walruses.

## DISCUSSION

### Biological parameters

The ranges chosen by us for the various prior distributions were based on previous knowledge of the biology of Atlantic and Pacific walrus and estimates of their vital parameters. Although recognized as two geographically and taxonomically distinct subspecies (e.g. Fay 1985), the life history of Atlantic and Pacific walrus appears to be very similar. However, in both cases the segregation of different sex and age classes for most of the year, and the selective hunting pattern make it difficult to obtain unbiased samples for determining biological parameters (Fedoseev and Goltsev 1969; Fay 1982; DeMaster 1984). Our prior and posterior distributions of the biological parameters are generally in good agreement with estimates in other studies.

The sex ratio in walrus populations is not well known. On the assumption that walruses are polygynous, an adult sex ratio of 1 male to 3 females has been suggested in the population of Pacific walrus (Fay 1982; Fay et al. 1984; Sease and Chapman 1988). DeMaster (1984) adopted this sex ratio in his modelling of the dynamics of a hypothetical walrus population. The sex ratio in the Pacific walrus changed from (M:F) 1:1.7 to 1:3 between 1960 and 1985 during a period of population increase according to Fay et al. (1997), a pattern that might actually be expected from density and frequency dependent natural selection (Witting 1997, 2000). To our knowledge there are no indications of the sex ratio being severely skewed towards females in Atlantic walrus sub-populations, and we therefore assumed that it was even.

The natural mortality rate in walrus is not well established but is assumed to be low because productivity is low and longevity is relatively high (Fay 1982; Fay et al. 1997). Natural mortality rate has been estimated to be 3 to 5 % for the entire population of Pacific walrus (DeMaster 1984; Fay et al. 1989). Fay et al. (1994) suggested that natural mortality in adults was higher than 1% but probably not higher than 2% per year. A natural mortality rate of 1.5% per year was applied in simulations of Bering Sea walruses (Fay et al. 1997). Chivers (1999) used an estimate of survival in adults between 9 and 24 years to 0.98 (it then decreased until 40 years of age). We applied a uniform prior from 0.95 to 0.99 for adult mortality, and obtained a posterior estimate of .98 (CI:.95-.99) for West Greenland/Baffin and Baffin Bay walruses, and an estimate of .97 (CI:.95-.99) for walruses in East Greenland.

Survival in calves until their second year of life (during this year suckling ceases) has been estimated to range between 0.5 and 0.9 (Fay et al. 1997). We applied the corresponding uniform prior between 0.71 and 0.95 for the annual survival rate for walruses in age class zero and one, and obtained posterior estimates of .83 (CI:.72-.94) for West Greenland/Baffin walruses, of .81 (CI:.72-.93) for Baffin Bay walruses, and .84 (CI:.72-.94) for walruses in East Greenland.

Based on analyses of reproductive organs, rates of fecundity have been estimated at between 0.29 and 0.40 in walruses (Mansfield 1958; Fay 1982; Garlich-Miller and Stewart 1999; Born 2001). According to Mansfield (1958), the reproductive cycle of the female Atlantic walrus in Foxe Basin was basically biennial, but, to an unknown extent, older females may give birth at three or four year intervals. According to Fay (1982) female Pacific walruses tend to breed at 2-year intervals or less often, and hence maximum fecundity was thought to be 0.5 (Fay et al. 1997). Our prior of maximum annual fecundity ranged between 0.33 and 0.5 calf/mature female/year, and we obtained an posterior estimates of .42 (CI:.34-.49) for West Greeland/Baffin Island walruses, of .41 (CI:.34-.49) for Baffin Bay walruses, and .42 (CI:.34-.49) for walruses in east Greenland.

Mansfield (1958) found that the age at first ovulation varied from 5 to 10 years, but that the majority of females in his Canadian sample became sexually mature at the age of 7. Born (2001) found that the average age at sexual maturity was 6 years in Atlantic walruses from the North Water and stated that attainment of sexual maturity in female Atlantic walruses is similar to that in the Pacific subspecies. By the age of 6 years, two-thirds of the female Pacific walruses have ovulated at least once and by the 8th or 9th year practically all have ovulated (Fay 1982). Our prior for the age at maturity ranged between 5 and 9 years of age, and our posterior estimate was 7.0 (CI:5.0-9.0) for all three populations.

Our fixed parameter for sex ratio at birth (1:1) was in accordance with findings in Atlantic walrus from the North Water (Born 2001) and in Pacific walrus from the Bering Strait region (Fay 1982; Fay et al. 1984).

The population birth rate (fraction of neonates in the total population) has been estimated at 0.07 (Mansfield 1966) or 0.11 (Mansfield 1973) in Atlantic walrus and between 0.12 and 0.17 in Pacific walrus (Fedoseev and Goltsev 1969; Fay 1982). Instantaneous net growth rate of the population of Pacific walruses during the late 1950s to mid-1970s was estimated at 0.067 (Tavrovski 1971; Sease and Chapman 1988), indicating a finite growth rate of about 7% per year for a population in a phase of growth under favorable environmental conditions with no food limitations. Chivers (1999) modeled an annual maximum growth rate of 8% but stressed that because survival rates are unknown for walrus, the models growth rate should not be considered an estimate of maximum growth rate for walrus. We did not apply a prior to the maximal growth rate, but a realized prior was generated from the prior on other parameters, and we obtained a posterior estimate for the maximal growth rate of .05 (CI:.02-.08) for West Greenland/Baffin Island and East Greenland walruses, and an estimate of .04 (CI:.02-.07) for Baffin Bay walruses.

DeMaster (1984) estimated that the maximum sustainable yield of adult females (4 years and older) would be 5.1% of the total population of females. He suggested that an adult female harvest of 1 to 5% could be sustained. Fay (1985) suggested that an annual hunting mortality of 5 to 7% of the total population of walrus would be sustainable. Gjertz et al. (1998) suggested a net maximum recruitment rate of 5% to be the most plausible and in compliance with the estimates of current abundance of walruses at Franz Josef Land. We did not apply a prior to the msyr, but a realized prior was generated from the prior on other life history parameters, and we obtained a posterior estimate of .03 (CI:.02-.05) for West Greenland/Baffin Island walruses, an estimate of .03 (CI:.01-.04) for Baffin Bay walruses, and an estimate of .03 (CI:.02-.05) for walruses in East Greenland.

### Comparison to 2005 assessment

Our results for walruses in East Greenland are similar to the results in 2005 (Witting and Born 2005). The assessment in 2005 suggested a carrying capacity of 1,600 walruses, and that a total annual removal of 15 individuals would be sustainable with 85% probability. Today we estimate a carrying capacity of 1,500 individuals and that a total annual take of 16 walruses will be sustainable with 85% probability.

The populations of West Greenland/Baffin Island and Baffin Bay walruses, however, are estimated to be in much better shape than indicated in 2005. Given the catch history and the abundance estimate available in 2005 we projected extinction of West Greenland walruses around year 2000, and the population in the Baffin Bay was estimated to be depleted to two percent in 2010 given continued catches at 1999 level. The models in this paper suggest instead that the 2010 depletion is not smaller than .33 (CI:.19-.60) for the West Greenland/Baffin Island population of walruses and .20 (CI:.11-.33) for the population of Baffin Bay walruses.

When translated into sustainable removal levels, no removals were sustainable for West Greenland/Baffin Island walruses according to the assessment in 2005, while our current assessment estimates that a total annual removal of 72 walruses from this population is sustainable with 85% probability. The same probability of sustainability allowed only a total removal level of nine walruses from the Baffin Bay population in 2005, while this level is now estimated to 51 walruses.

The main reason for the much better status estimate for West Greenland/Baffin Island walruses is a change in abundance estimate. In 2005 we had only an older estimate of approximately 1000 (cv:0.48) walruses in 1990, while we now have an estimate that is three times as high and twice as precise for 2007. For Baffin Bay the improvement in the abundance estimates is somewhat lower.

Another reason for the current better status estimates is a change in the prior distribution for the equilibrium abundance from a uniform prior in 2005 to a log normal prior in this paper. It was found that a uniform prior on the equilibrium abundance imposes some negative bias in the growth rate during the updating of the realized prior to the posterior (Fig. 5). In result the equilibrium abundance is overestimated while the msyr, the maximal growth rate, and the depletion ratio are underestimated. While it may be argued that a smaller growth rate is desirable because it is precautionary, we have chosen a model approach that is neutral in the sense that it, to the extent possible, maintains our informed realized prior on the growth rate as it was deducted from our current knowledge and uncertainty on life history parameters in walruses. We agree that an updating of this prior would be beneficial; however, such updating should arise from informative trend data and not from constraints imposed by uninformative priors.

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| Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1900 | 5 | 5 | 1922 | 32 | 32 | 1944 | 175 | 175 | 1966 | 27 | 27 | 1988 | 81 | 81 |
| 1901 | 5 | 5 | 1923 | 101 | 101 | 1945 | 289 | 289 | 1967 | 12 | 12 | 1989 | 58 | 58 |
| 1902 | 5 | 5 | 1924 | 26 | 26 | 1946 | 321 | 321 | 1968 | 21 | 21 | 1990 | 81 | 81 |
| 1903 | 2 | 2 | 1925 | 37 | 37 | 1947 | 215 | 215 | 1969 | 64 | 64 | 1991 | 70 | 70 |
| 1904 | 5 | 5 | 1926 | 87 | 87 | 1948 | 174 | 174 | 1970 | 23 | 23 | 1992 | 64 | 64 |
| 1905 | 105 | 105 | 1927 | 71 | 71 | 1949 | 62 | 62 | 1971 | 29 | 29 | 1993 | 176 | 176 |
| 1906 | 13 | 13 | 1928 | 147 | 147 | 1950 | 25 | 25 | 1972 | 38 | 38 | 1994 | 222 | 222 |
| 1907 | 56 | 56 | 1929 | 87 | 87 | 1951 | 182 | 182 | 1973 | 39 | 39 | 1995 | 204 | 204 |
| 1908 | 13 | 13 | 1930 | 129 | 129 | 1952 | 182 | 182 | 1974 | 33 | 33 | 1996 | 122 | 122 |
| 1909 | 13 | 13 | 1931 | 117 | 117 | 1953 | 182 | 182 | 1975 | 53 | 53 | 1997 | 113 | 113 |
| 1910 | 6 | 6 | 1932 | 211 | 211 | 1954 | 186 | 186 | 1976 | 66 | 66 | 1998 | 111 | 111 |
| 1911 | 26 | 26 | 1933 | 55 | 55 | 1955 | 129 | 129 | 1977 | 79 | 79 | 1999 | 131 | 131 |
| 1912 | 34 | 34 | 1934 | 46 | 46 | 1956 | 267 | 267 | 1978 | 75 | 75 | 2000 | 150 | 150 |
| 1913 | 13 | 13 | 1935 | 62 | 62 | 1957 | 131 | 131 | 1979 | 108 | 108 | 2001 | 123 | 123 |
| 1914 | 53 | 53 | 1936 | 302 | 302 | 1958 | 126 | 126 | 1980 | 120 | 120 | 2002 | 125 | 125 |
| 1915 | 32 | 32 | 1937 | 351 | 351 | 1959 | 228 | 228 | 1981 | 152 | 152 | 2003 | 85 | 85 |
| 1916 | 53 | 53 | 1938 | 406 | 406 | 1960 | 74 | 74 | 1982 | 96 | 96 | 2004 | 78 | 78 |
| 1917 | 6 | 6 | 1939 | 339 | 339 | 1961 | 79 | 79 | 1983 | 77 | 77 | 2005 | 122 | 122 |
| 1918 | 8 | 8 | 1940 | 404 | 404 | 1962 | 75 | 75 | 1984 | 80 | 80 | 2006 | 69 | 69 |
| 1919 | 113 | 113 | 1941 | 353 | 353 | 1963 | 34 | 34 | 1985 | 58 | 58 | 2007 | 56 | 56 |
| 1920 | 16 | 16 | 1942 | 205 | 205 | 1964 | 46 | 46 | 1986 | 31 | 31 | 2008 | 44 | 44 |
| 1921 | 26 | 26 | 1943 | 196 | 196 | 1965 | 29 | 29 | 1987 | 72 | 72 | 2009 | 44 | 44 |

Table 7: **High yearly catch** of male ($m$) and female ($f$) West Greenland/Baffin Island walruss. Data from Born et al. (1994).

| Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1900 | 81 | 81 | 1922 | 97 | 97 | 1944 | 110 | 110 | 1966 | 85 | 85 | 1988 | 101 | 101 |
| 1901 | 82 | 82 | 1923 | 97 | 97 | 1945 | 110 | 110 | 1967 | 85 | 85 | 1989 | 100 | 100 |
| 1902 | 83 | 83 | 1924 | 98 | 98 | 1946 | 110 | 110 | 1968 | 85 | 85 | 1990 | 108 | 108 |
| 1903 | 83 | 83 | 1925 | 99 | 99 | 1947 | 110 | 110 | 1969 | 85 | 85 | 1991 | 101 | 101 |
| 1904 | 84 | 84 | 1926 | 100 | 100 | 1948 | 75 | 75 | 1970 | 85 | 85 | 1992 | 110 | 110 |
| 1905 | 85 | 85 | 1927 | 100 | 100 | 1949 | 474 | 474 | 1971 | 93 | 93 | 1993 | 180 | 180 |
| 1906 | 85 | 85 | 1928 | 101 | 101 | 1950 | 120 | 120 | 1972 | 100 | 100 | 1994 | 117 | 117 |
| 1907 | 86 | 86 | 1929 | 102 | 102 | 1951 | 826 | 826 | 1973 | 100 | 100 | 1995 | 87 | 87 |
| 1908 | 87 | 87 | 1930 | 103 | 103 | 1952 | 81 | 81 | 1974 | 100 | 100 | 1996 | 85 | 85 |
| 1909 | 87 | 87 | 1931 | 104 | 104 | 1953 | 71 | 71 | 1975 | 100 | 100 | 1997 | 56 | 56 |
| 1910 | 88 | 88 | 1932 | 104 | 104 | 1954 | 68 | 68 | 1976 | 96 | 96 | 1998 | 54 | 54 |
| 1911 | 89 | 89 | 1933 | 105 | 105 | 1955 | 156 | 156 | 1977 | 152 | 152 | 1999 | 69 | 69 |
| 1912 | 89 | 89 | 1934 | 131 | 131 | 1956 | 78 | 78 | 1978 | 166 | 166 | 2000 | 85 | 85 |
| 1913 | 90 | 90 | 1935 | 132 | 132 | 1957 | 122 | 122 | 1979 | 100 | 100 | 2001 | 113 | 113 |
| 1914 | 91 | 91 | 1936 | 108 | 108 | 1958 | 176 | 176 | 1980 | 104 | 104 | 2002 | 98 | 98 |
| 1915 | 91 | 91 | 1937 | 109 | 109 | 1959 | 85 | 85 | 1981 | 127 | 127 | 2003 | 109 | 109 |
| 1916 | 92 | 92 | 1938 | 109 | 109 | 1960 | 85 | 85 | 1982 | 117 | 117 | 2004 | 62 | 62 |
| 1917 | 93 | 93 | 1939 | 110 | 110 | 1961 | 85 | 85 | 1983 | 111 | 111 | 2005 | 52 | 52 |
| 1918 | 94 | 94 | 1940 | 110 | 110 | 1962 | 262 | 262 | 1984 | 163 | 163 | 2006 | 47 | 47 |
| 1919 | 94 | 94 | 1941 | 110 | 110 | 1963 | 85 | 85 | 1985 | 55 | 55 | 2007 | 46 | 46 |
| 1920 | 95 | 95 | 1942 | 110 | 110 | 1964 | 85 | 85 | 1986 | 100 | 100 | 2008 | 38 | 38 |
| 1921 | 96 | 96 | 1943 | 110 | 110 | 1965 | 85 | 85 | 1987 | 102 | 102 | 2009 | 48 | 48 |

Table 8: **High yearly catch** of male ($m$) and female ($f$) North Water walruss. Data from Born et al. (1994).

| Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ | Year | $m$ | $f$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1889 | 168 | 168 | 1914 | 1 | 1 | 1939 | 14 | 14 | 1964 | 1 | 0 | 1989 | 2 | 0 |
| 1890 | 1 | 1 | 1915 | 1 | 1 | 1940 | 4 | 4 | 1965 | 1 | 0 | 1990 | 8 | 1 |
| 1891 | 1 | 1 | 1916 | 1 | 1 | 1941 | 4 | 4 | 1966 | 1 | 0 | 1991 | 2 | 0 |
| 1892 | 1 | 1 | 1917 | 1 | 1 | 1942 | 4 | 4 | 1967 | 1 | 0 | 1992 | 2 | 0 |
| 1893 | 1 | 1 | 1918 | 1 | 1 | 1943 | 4 | 4 | 1968 | 1 | 0 | 1993 | 17 | 2 |
| 1894 | 1 | 1 | 1919 | 24 | 24 | 1944 | 4 | 4 | 1969 | 1 | 0 | 1994 | 11 | 1 |
| 1895 | 1 | 1 | 1920 | 6 | 6 | 1945 | 4 | 4 | 1970 | 1 | 0 | 1995 | 12 | 1 |
| 1896 | 1 | 1 | 1921 | 1 | 1 | 1946 | 4 | 4 | 1971 | 1 | 0 | 1996 | 8 | 1 |
| 1897 | 15 | 15 | 1922 | 6 | 6 | 1947 | 5 | 5 | 1972 | 1 | 0 | 1997 | 1 | 0 |
| 1898 | 84 | 84 | 1923 | 6 | 6 | 1948 | 5 | 5 | 1973 | 1 | 0 | 1998 | 8 | 1 |
| 1899 | 56 | 56 | 1924 | 2 | 2 | 1949 | 5 | 5 | 1974 | 1 | 0 | 1999 | 11 | 1 |
| 1900 | 27 | 27 | 1925 | 8 | 8 | 1950 | 4 | 4 | 1975 | 6 | 1 | 2000 | 8 | 1 |
| 1901 | 48 | 48 | 1926 | 47 | 47 | 1951 | 4 | 4 | 1976 | 1 | 0 | 2001 | 11 | 1 |
| 1902 | 19 | 19 | 1927 | 46 | 46 | 1952 | 4 | 4 | 1977 | 4 | 0 | 2002 | 38 | 4 |
| 1903 | 15 | 15 | 1928 | 5 | 5 | 1953 | 4 | 4 | 1978 | 2 | 0 | 2003 | 12 | 1 |
| 1904 | 7 | 7 | 1929 | 10 | 10 | 1954 | 5 | 5 | 1979 | 1 | 0 | 2004 | 4 | 1 |
| 1905 | 14 | 14 | 1930 | 8 | 8 | 1955 | 12 | 12 | 1980 | 1 | 0 | 2005 | 18 | 2 |
| 1906 | 34 | 34 | 1931 | 10 | 10 | 1956 | 4 | 0 | 1981 | 12 | 1 | 2006 | 6 | 1 |
| 1907 | 3 | 3 | 1932 | 43 | 43 | 1957 | 1 | 0 | 1982 | 13 | 1 | 2007 | 11 | 1 |
| 1908 | 50 | 50 | 1933 | 4 | 4 | 1958 | 2 | 0 | 1983 | 21 | 2 | 2008 | 10 | 1 |
| 1909 | 4 | 4 | 1934 | 7 | 7 | 1959 | 2 | 0 | 1984 | 12 | 1 | 2009 | 10 | 1 |
| 1910 | 4 | 4 | 1935 | 5 | 5 | 1960 | 1 | 0 | 1985 | 26 | 3 | 2010 | - | - |
| 1911 | 1 | 1 | 1936 | 7 | 7 | 1961 | 1 | 0 | 1986 | 4 | 0 | 2011 | - | - |
| 1912 | 2 | 2 | 1937 | 6 | 6 | 1962 | 1 | 0 | 1987 | 11 | 1 | 2012 | - | - |
| 1913 | 1 | 1 | 1938 | 3 | 3 | 1963 | 1 | 0 | 1988 | 8 | 1 | 2013 | - | - |

Table 9: **High yearly catch** of male ($m$) and female ($f$) East Greenland walruss. Data from Born et al. (1997).

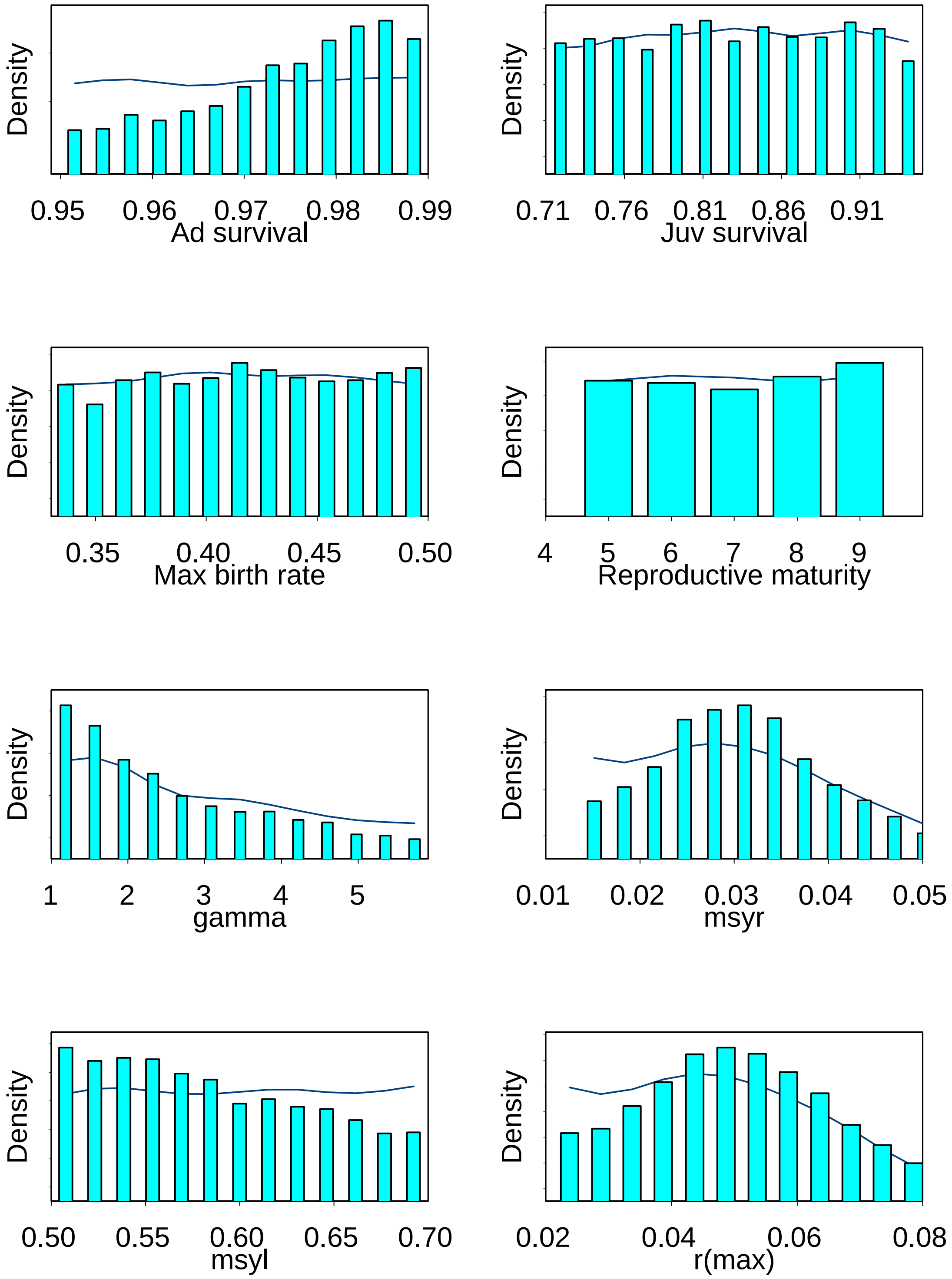

Figure 1: Posterior (bars) and realised prior (curve) distributions for the base case model of the West Greenland/Baffin Island population of walrus. (Not updated)

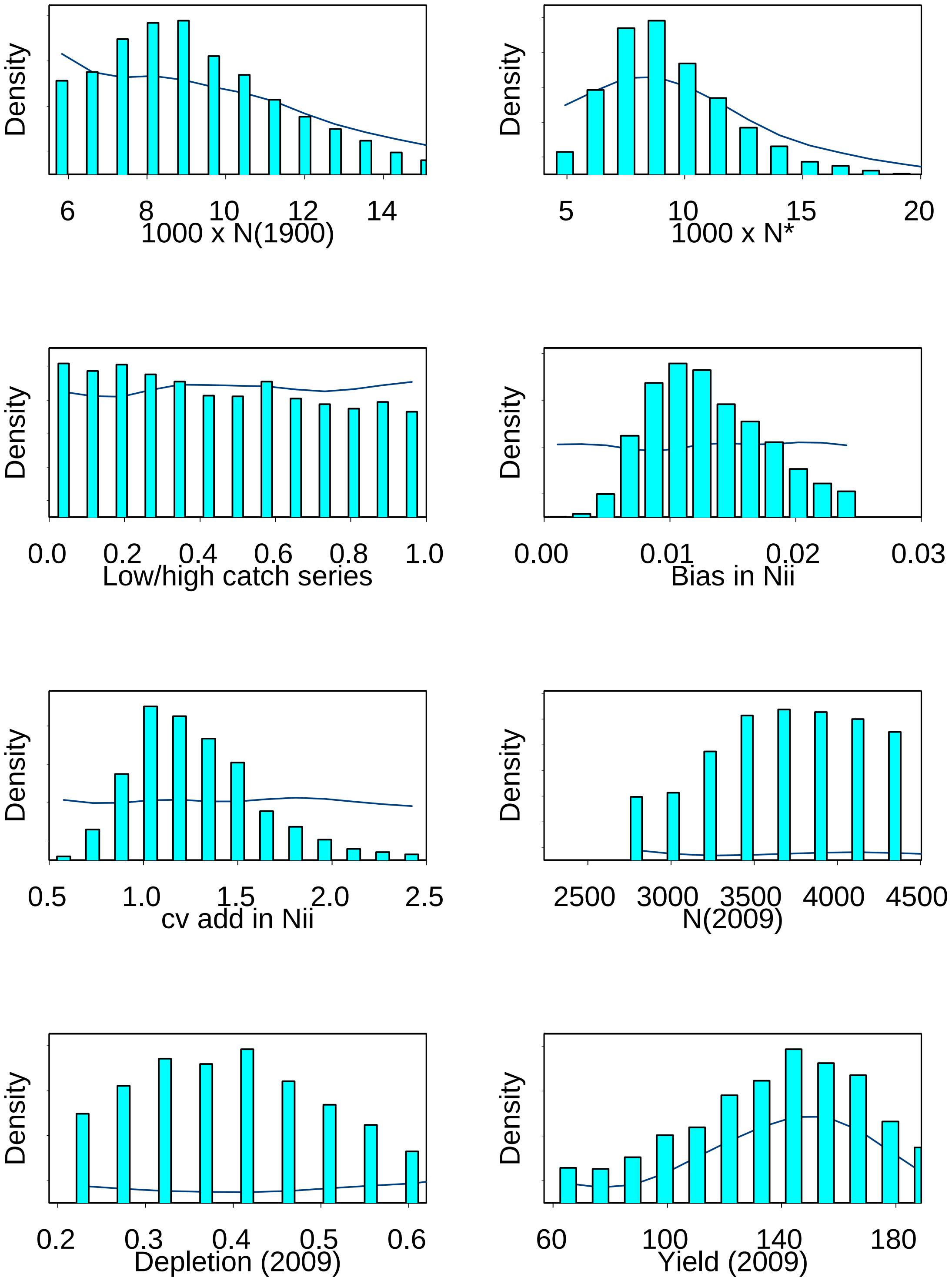

Figure 2: Posterior (bars) and realised prior (curve) distributions for the base case model of the West Greenland/Baffin Island population of walrus. (Not updated)

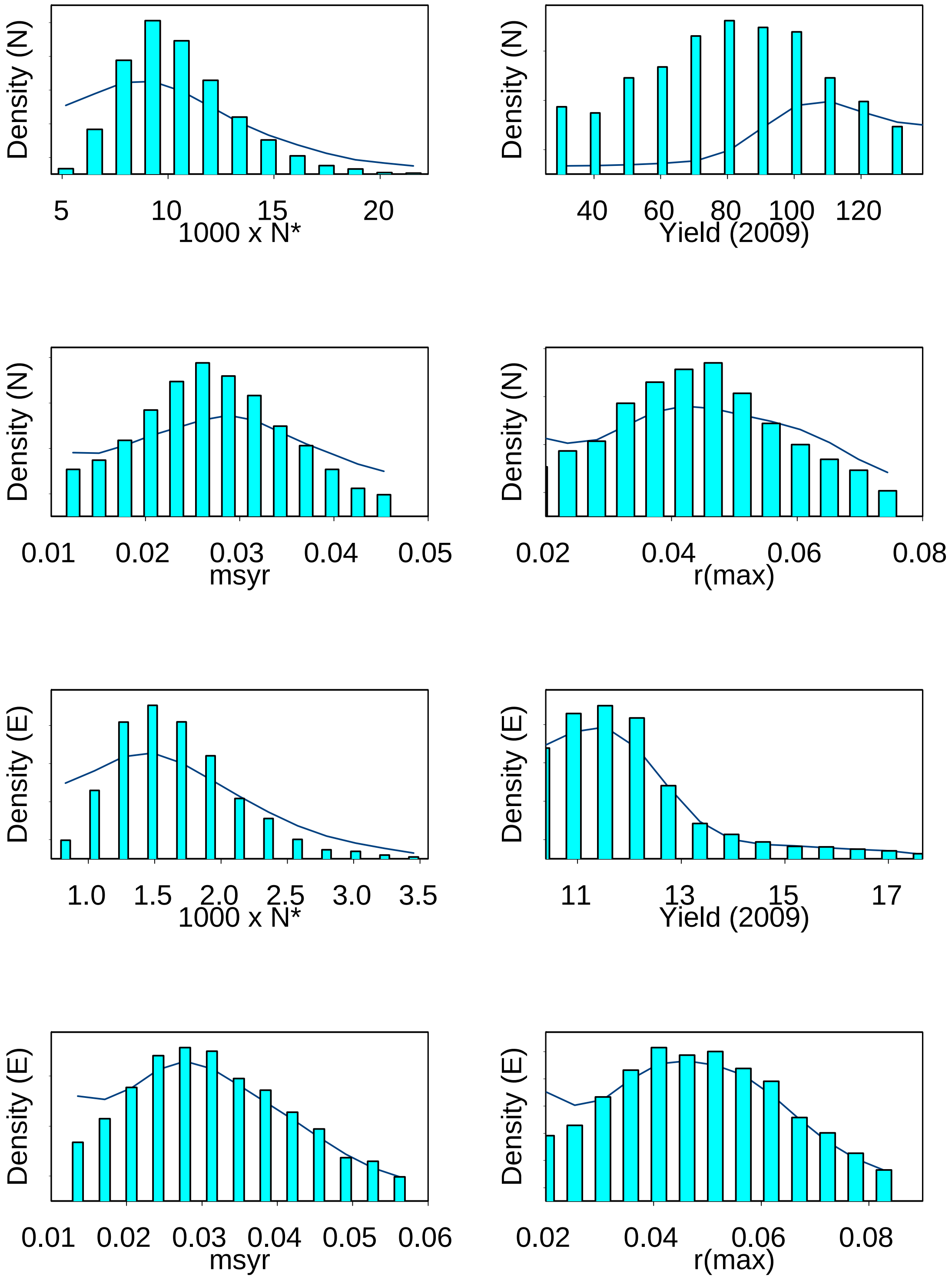

Figure 3: Selected posterior (bars) and realised prior (curve) distributions for Baffin Bay [upper four graphs (N), base case] and East Greenland [lower four graphs (E)] walruses. (Not updated)

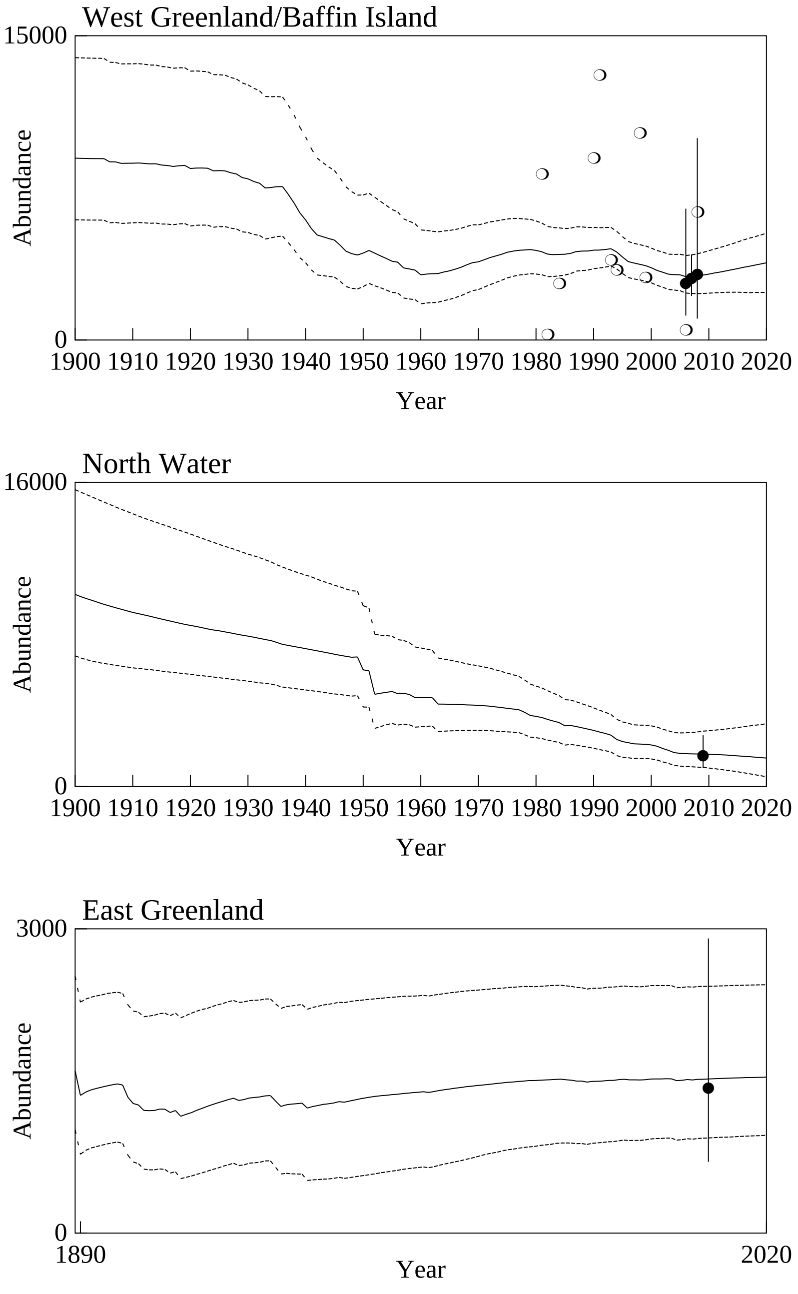

Figure 4: The projected median and 90% credibility intervals for the three populations, together with the fully corrected abundance estimates (filled circles) and the relative bias scales estimates (open circles) for West Greenland. (Not updated)

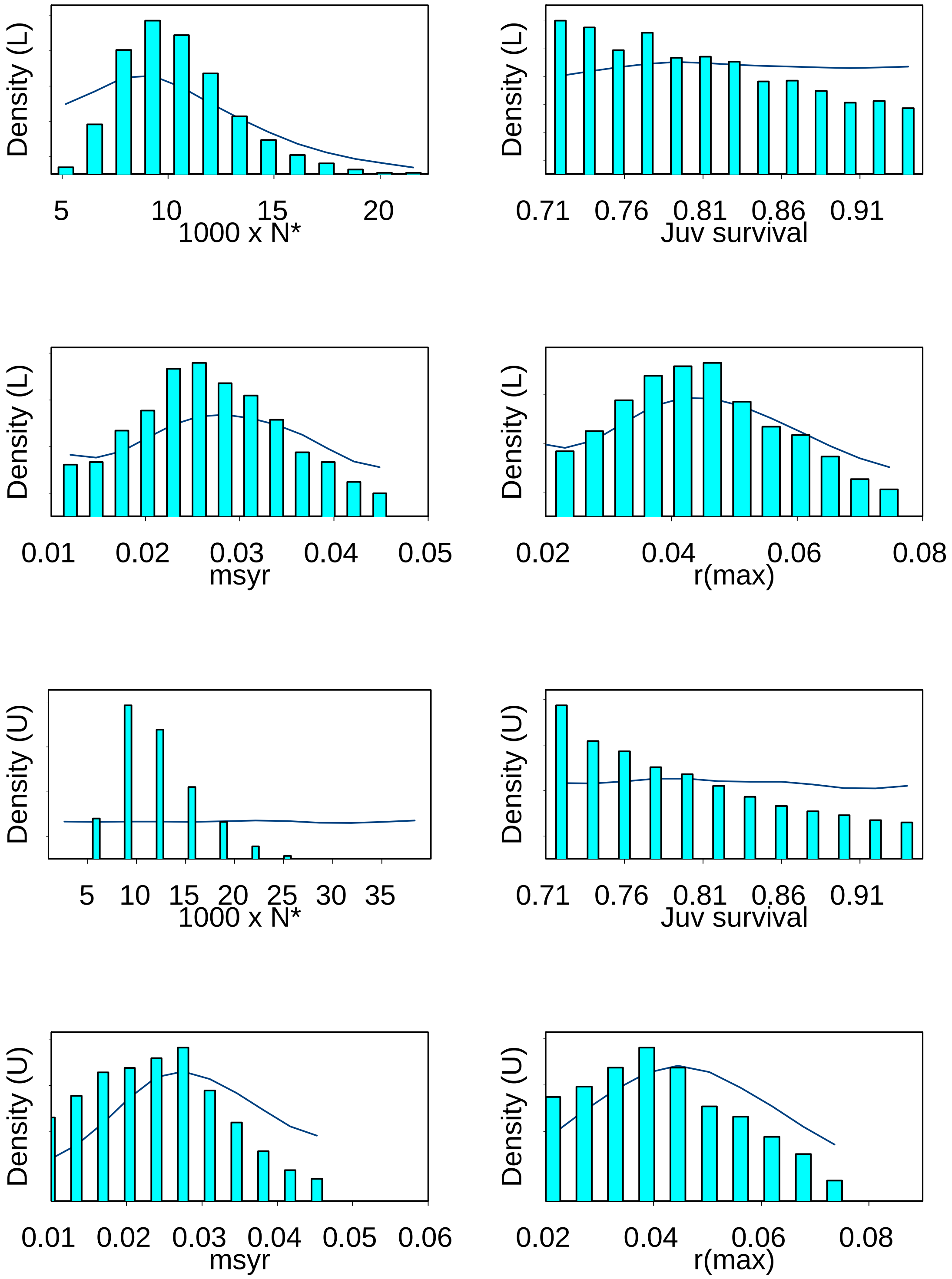

Figure 5: Selected posterior (bars) and realised prior (curve) distributions for base case Baffin Bay walruses with a log normal [upper four graphs (L)] and Uniform [lower four graphs (U)] abundance prior. (Not updated)