

# Bayesian assessment of Kangerlussuaq Muskoxen based on density regulated dynamics

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## Abstract

Historical catches from 1965 to 2004, 12 minimum count estimates of the total abundance, 13 aerial survey estimates of the total abundance, and five estimates of the calf abundance, age-class zero abundance, were used in an age- and sex-structured model for a Bayesian assessment of the Kangerlussuaq Muskox (*Ovibos moschatus*). The model assumes density regulated dynamics, a non-equilibrium population in 1965, and it projects the population from 1965 to 2010 under the influence of the historical catches. Given the data, the model estimates the probability by which the defined management objective for the population is met for future catches between 500 and 2500 individuals per year. During the simulated period the yearly production varied from 7 (CI:6-10) individuals in 1965 to 1330 (CI:1170-1650) in 2003, with the production in 2005 being 1300 (CI:1130-1620). The equilibrium abundance  $N^*$  was estimated to 8450 (CI:5470-20000) individuals, and the maximum sustainable yield level to 0.61 (CI:0.52-0.73). The minimum depletion ratio was 0.00 (CI:0.00-0.01) in 1965, while the abundance in 2005 is close to the equilibrium, with an estimated depletion ratio of 0.88 (CI:0.38-1.08).

## 1 Introduction

The management of a harvested population is faced with a trade-off that reflects our incomplete knowledge on the dynamics and status of the stock. If knowledge was complete we could exactly calculate the implications of a given harvest, and it would be easy to set the harvest to a level where the objectives for the future status of the population would be met. In real life, however, the uncertainty trade-off implies that a given harvest at best can be associated with a certain probability that the objectives for the population will be met.

In this paper we use an age- and sex-structured population model *i*) to reconstruct the population dynamics of the Kangerlussuaq Muskox (*Ovibos moschatus*) starting from 1965, *ii*) to assess the current status of the population, and *iii*) to estimate the uncertainty trade-off between the management objectives for the population and a future harvest from it. The method that is applied is a Bayesian assessment based on the assumption of density regulated

Year	$N^i$	$cv$	Year	$N^i$	$cv$
1965	27	0.00	1988	1286	0.00
1977	150	0.00	1990	2120	0.00
1979	230	0.00	2000	4235	0.00
1981	400	0.00	2001	4721	0.00
1985	967	0.00	2002	4186	0.00
1987	1261	0.00	2004	4236	0.00

Year	$N^{ii}$	$cv$	Year	$N^{ii}$	$cv$
1982	550	0.22	1990	2544	0.22
1983	700	0.22	1990	4039	0.22
1985	1150	0.22	1993	2524	0.22
1987	1500	0.22	1994	3053	0.22
1987	2379	0.22	1995	3258	0.22
1988	1543	0.22	1996	3159	0.14
1988	2383	0.22	-	-	-

Year	$N_0^{iii}$	$cv$	Year	$N_0^{iii}$	$cv$
1991	600	0.00	2001	894	0.00
1999	1106	0.00	2003	760	0.00
2000	1164	0.00	-	-	-

Table I: **Abundance estimates** and their  $cv$  (error coefficient of variance) for the Kangerlussuaq Muskoxis used for model fitting. There are three time series of estimates, denoted by superscripts  $i$ ,  $ii$  and  $iii$ . The total abundance estimates  $\mathbf{N}^i$ , the total abundance estimates  $\mathbf{N}^{ii}$ , and the age-class zero abundance estimates  $\mathbf{N}_0^{iii}$ .

population growth. The data that are used are the catch history from 1965 to 2004 as given by 12 minimum counts of the total abundance, 13 aerial survey estimates of the total abundance, and five minimum calf counts of the age-class zero abundance.

We propose the management objective for the Kangerlussuaq Muskox be set as follows. For stocks below the maximum sustainable yield level (msyl) a harvest shall be permitted so long as the harvest allows the population to increase toward that msyl, and for populations at or above the msyl a harvest shall be permitted so long as the total removals do not exceed 90 per cent of the maximum sustainable yield (msy). Given a model of density regulated dynamics, in this paper we calculate the probability that this objective be met for yearly catches between 500 and 2500 individuals in the period from 2005 to 2010.

## 2 Method

### 2.1 Data

The data for the modelling are abundance estimates and estimates of the historical catches. Three time series ( $\mathbf{N}^i$ ,  $\mathbf{N}^{ii}$ , &  $\mathbf{N}_0^{iii}$ ) of abundance estimates are used; the first  $\mathbf{N}^i$  containing 12 minimum counts of the total abundance, the second  $\mathbf{N}^{ii}$  containing 13 aerial survey estimates of

the total abundance, and the third  $\mathbf{N}_0^{iii}$  containing five minimum counts of the calf abundance, age-class zero abundance. The abundance estimates are given in Table I, and the historical catches are given in Table VI in the Appendix.

### 2.1.1 Additional variance

Following Butterworth *et al.* (1993) and Wade (2002), an additional variance term is added to the total abundance  $\mathbf{N}^i$  and the age-class zero abundance  $\mathbf{N}_0^{iii}$  in order to estimate variance between the abundance estimates that are not accounted for by the variance estimates of the abundance estimates. The cause for the additional variance is unknown, and no attempt is made to model the processes that might generate additional variance.

The additional variance is parameterised as a coefficient of variation that is considered to be 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  $x \in \{i, iii\}$ , can be given as

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

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.

## 2.2 Population dynamic model

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

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

where  $N_{t,a}^{m/f}$  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 age distribution of catches being sex specific and proportional to the age-structured abundance, except that no catches are taken from age-class zero.

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

$$s_a = \begin{cases} s_{juv}s_{ad} & \text{if } a = 0 \\ s_{juv} & \text{if } 1 \leq a \leq a_{ad} \\ s_{ad} & \text{if } a > a_{ad} \end{cases} \quad (3)$$

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  $a_{ad} = 1$  and  $x = 7$ .

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

$$B_t = \sum_{a=a_m}^x B_{t,a} \quad (4)$$

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

$$B_{t,a} = b_t M_{t,a}^f \quad (5)$$

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

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

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

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

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

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

where  $b^*$  is the birth rate at population dynamic equilibrium  $N^*$ ,  $b_{max}$  is the maximal birth rate, and  $z$  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  $z$ . Disregarding the influence that the difference in the stable age-structure over the depletion ration  $d = N/N^*$  may have on the shape of the production function, the msyl was estimated from

$$\begin{aligned} b &= b^* + \mu(1 - \tilde{d}^z) \\ 0 &= \rho b \tilde{d} - \text{syr} \end{aligned} \quad (9)$$

where  $\tilde{d}$  is the depletion ratio relative to the mature  $\tilde{N}$  component of the population,  $\rho$  is a constant,  $\mu = b_{max} - b^*$ , and syr is the sustainable yield rate of the mature component. The msyl is then given by the depletion ratio  $\tilde{d}$  at  $dsyr/dD = 0$  where

$$\text{msyl} = \left( \frac{b_{max}}{\mu[z + 1]} \right)^{1/z} \quad (10)$$

and the msyr is calculated as the syr at the msyl.

### 2.3 Statistical methods

The population dynamic model was fitted to the abundance estimates by projecting the population from 1965 under the influence of the historical catches, assuming that the age-structure was stable in 1965, given the fecundity and catch of that year. 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.

<i>Par</i>	$s_{ad}$	$s_{juv}$	$b_{max}$	$a_m$	$\vartheta$	$N^*$	$N^{1965}$	msyl	$\beta^i$	$\beta^{ii}$	$\beta^{iii}$	$cv_{ad}^i$	$cv_{ad}^{iii}$
<i>Pd</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>i</i>	<i>p</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>u</i>	<i>u</i>
<i>X</i>	0.85	0.60	0.50	2	0.50	2000	27	0.50	0.40	0.50	0.20	0.10	0.10
<i>Y</i>	0.99	0.99	2.00	4.00	-	30000	56	0.80	1.00	1.20	1.00	0.45	0.90

Table II: **Prior distributions.** *Par* is 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,  $N^*$  the equilibrium abundance,  $N^{1965}$  the abundance in 1965, msyl the maximum sustainable yield level,  $\beta^i$  the bias of abundance estimates  $\mathbf{N}^i$ ,  $\beta^{ii}$  the bias of abundance estimates  $\mathbf{N}^{ii}$ ,  $\beta^{iii}$  the bias of abundance estimates  $\mathbf{N}_0^{iii}$ ,  $cv_{ad}^i$  the additional variance of abundance estimates  $\mathbf{N}^i$ , and  $cv_{ad}^{iii}$  the additional variance of abundance estimates  $\mathbf{N}_0^{iii}$ . *Pd* is the type of probability distribution; *u*=uniform, *i*=discrete uniform, and *p* a parameter with fixed value. *X* is the min value if  $pd = u$  or  $pd = i$ , and a fixed parameter value if  $pd = p$ . And *Y* is the max value if  $pd = u$  or  $pd = i$ .

The 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 1965 until 2004. For each draw an importance weight, or ratio, was then calculated

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)} \quad (11)$$

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

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_1} w(\theta_j)} \quad (12)$$

This generates a random sample of the posterior distribution of size  $n_2$ . The resample of the posterior distribution was set to  $n_2 = 5000$ , and the sample from the joint prior distribution was set to  $n_1 = 240,000,000$ .

The method of de la Mare (1986) is used to calculate the likelihood  $L$  under the assumption that observation errors are 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 one ( $\mathbf{N}^i$ ), the abundance of time series two ( $\mathbf{N}^{ii}$ ) and the abundance of time series three ( $\mathbf{N}_0^{iii}$ ) the likelihood function is

$$L = \prod_t \exp\left(-\frac{[\ln(N_t^i/\beta^i N_t)]^2}{2cv_t^2}\right) / cv_t \quad (13)$$

$$\prod_t \exp\left(-\frac{[\ln(N_t^{ii}/\beta^{ii}N_t)]^2}{2cv_t^2}\right) / cv_t$$

$$\prod_t \exp\left(-\frac{[\ln(N_{0,t}^{iii}/\beta^{iii}N_{0,t})]^2}{2cv_t^2}\right) / cv_t$$

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

Independent of the  $n_1$  number of samples in the sampling-importance-resampling routine, there is always a small probability that a parameter set with very high likelihood has not been sampled. Convergence towards a global optimum is therefore not guaranteed, however, if  $n_1$  is sufficiently large and the corresponding frequency distribution of likelihood is sufficiently smooth around the maximum, approximate convergence toward the true posterior can generally be assumed.

To illustrate whether convergence has occurred we calculated the maximum importance weight of a parameter set relative to total summed importance weight over all  $n_1$  draws. McAllister *et al.* (2001), e.g., suggest that the maximum importance weight need 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.

### 2.3.1 Probability of meeting the objective

In this paper, the proposed management objective for the Kangerlussuaq Muskox permits a harvest on a population below the msyl so long as the total take allows the population to increase toward the msyl, and for a population at or above the msyl harvest is permitted so long as the total take does not exceed 90% of the msy.

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

$$p(ob) = \sum_{i=1}^{n_2} g(\theta_i, c) / n_2 \quad (14)$$

$$g(\theta_i, c) = \begin{cases} 1 & \text{if objective met} \\ 0 & \text{if objective not met} \end{cases}$$

over the complete random sample of the posterior distribution.

### 2.3.2 Prior distributions

The parameters that are treated as priors (i.e., with a defined plausible range to the parameter, Table II) are adult survival ( $s_{ad}$ ), juvenile survival ( $s_{juv}$ ), the maximal birth rate ( $b_{max}$ ), the age of reproductive maturity ( $a_m$ ), the equilibrium abundance ( $N^*$ ), the abundance in 1965 ( $N^{1965}$ ),

Par.	$s_{ad}$	$s_{juv}$	$b_{max}$	$a_m$	$N^*$	$N^{1965}$	$z$	msyr	msyl	$\beta^i$	$\beta^{ii}$	$\beta^{iii}$	$cv_{ad}^i$	$cv_{ad}^{iii}$
Avg.	0.93	0.83	1.33	3	9580	38	3.02	0.28	0.62	0.61	0.84	0.57	0.19	0.35
Median	0.93	0.86	1.32	3	8450	38	2.60	0.28	0.61	0.61	0.83	0.55	0.18	0.30
5.0th	0.87	0.64	0.72	2	5470	28	1.23	0.19	0.52	0.45	0.58	0.38	0.13	0.16
95.0th	0.99	0.94	1.93	4	20000	52	6.08	0.40	0.73	0.77	1.09	0.85	0.28	0.68

Table III: **Parameter estimates** and their 90% credibility intervals.

the maximum sustainable yield level (msyl), the bias of abundance estimates  $\mathbf{N}^i$  ( $\beta^i$ ), the bias of abundance estimates  $\mathbf{N}^{ii}$  ( $\beta^{ii}$ ), the bias of abundance estimates  $\mathbf{N}_0^{iii}$  ( $\beta^{iii}$ ), the additional variance of abundance estimates  $\mathbf{N}^i$  ( $cv_{ad}^i$ ), and the additional variance of abundance estimates  $\mathbf{N}_0^{iii}$  ( $cv_{ad}^{iii}$ ). And the fraction of females at birth ( $\vartheta$ ) is treated as fixed parameters across all model iterations.

All the priors uniform are drawn from uniform continuous distributions, except for age of reproductive maturity that is treated as a uniform discrete integer variable. The minimum and maximum values of the prior distributions are given in Table II, together with the fixed value of the fraction of females at birth ( $\vartheta$ ).

Apart from the distributions given in Table II, 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 not an explicit parameter of the model the msyl was treated as a prior, by calculating the corresponding compensation parameter  $z$  for each randomly selected msyl.

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.

## 3 Results

### 3.1 Posterior distributions

The maximum importance weight relative to the total sum of importance weights for the 240,000,000 parameter sets that were sampled was 0.2%. The number of unique parameter sets in the resample of 5000 parameter sets was 3543, and the maximum occurrences of a unique parameter set in the resample was 16.

The posterior estimates of the priors and their 90 % credibility intervals are given in Table III, and the correlation matrix for the parameters of the posterior distribution is given in Table IV. The complete distributions of the posteriors and the realised priors are shown in Figures 1 and 2, with the realised priors being estimated from a random sample of 5000 parameterisations from the joint prior. The posterior distributions represent the parameter estimates that are the most likely (have the highest probability) given the data and the model, i.e., when the current model is used to explain the data.

Par.	$s_{ad}$	$s_{juv}$	$b_{max}$	$a_m$	$N^*$	$N^{1965}$	$z$	msyr	msyl	$\beta^i$	$\beta^{ii}$	$\beta^{iii}$	$cv_{ad}^i$	$cv_{ad}^{iii}$
$s_{ad}$	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
$s_{juv}$	-0.13	1.00	-	-	-	-	-	-	-	-	-	-	-	-
$b_{max}$	-0.45	-0.54	1.00	-	-	-	-	-	-	-	-	-	-	-
$a_m$	0.25	0.20	0.30	1.00	-	-	-	-	-	-	-	-	-	-
$N^*$	-0.02	-0.07	0.03	-0.03	1.00	-	-	-	-	-	-	-	-	-
$N^{1965}$	-0.08	0.03	-0.06	0.00	0.19	1.00	-	-	-	-	-	-	-	-
$z$	0.01	-0.06	0.02	0.03	-0.34	-0.12	1.00	-	-	-	-	-	-	-
msyr	0.00	-0.34	0.65	0.58	-0.30	-0.20	0.56	1.00	-	-	-	-	-	-
msyl	0.02	-0.05	0.00	0.04	-0.41	-0.14	0.97	0.59	1.00	-	-	-	-	-
$\beta^i$	0.02	-0.13	0.11	0.00	-0.12	-0.78	0.27	0.27	0.30	1.00	-	-	-	-
$\beta^{ii}$	0.03	-0.12	0.08	0.04	0.06	-0.66	0.30	0.23	0.31	0.85	1.00	-	-	-
$\beta^{iii}$	0.36	0.43	-0.43	0.22	-0.21	-0.35	0.08	-0.05	0.11	0.33	0.25	1.00	-	-
$cv_{ad}^i$	0.11	-0.03	0.03	0.09	0.12	-0.01	-0.10	-0.00	-0.11	0.04	0.02	0.05	1.00	-
$cv_{ad}^{iii}$	0.13	-0.14	0.05	0.05	0.25	-0.13	0.04	0.07	0.03	0.17	0.25	0.08	0.07	1.00

Table IV: **Parameter correlation matrix.**  $s_{ad}$  is adult survival,  $s_{juv}$  juvenile survival,  $b_{max}$  the maximal birth rate,  $a_m$  the age of reproductive maturity,  $N^*$  the equilibrium abundance,  $N^{1965}$  the abundance in 1965,  $z$  the compensation parameter, msyr the maximum sustainable yield rate, msyl the maximum sustainable yield level,  $\beta^i$  the bias of abundance estimates  $\mathbf{N}^i$ ,  $\beta^{ii}$  the bias of abundance estimates  $\mathbf{N}^{ii}$ ,  $\beta^{iii}$  the bias of abundance estimates  $\mathbf{N}_0^{iii}$ ,  $cv_{ad}^i$  the additional variance of abundance estimates  $\mathbf{N}^i$ , and  $cv_{ad}^{iii}$  the additional variance of abundance estimates  $\mathbf{N}_0^{iii}$ .

The parameters are estimated by the posterior distributions (which represents the most likely parameter estimates given the data and the model) and the smaller the overlap  $0 \leq \rho \leq 1$  between the uninformative priors and the posterior distributions the higher the signal in the data for the estimate of a specific parameter. For the present study there were no parameters that were estimated with a high precision where  $\rho \leq 0.40$ . The parameters that were estimated with medium precision  $0.40 < \rho \leq 0.80$  were the equilibrium abundance ( $\rho = 0.53$ ), the bias of abundance estimates  $\mathbf{N}^i$  ( $\rho = 0.75$ ), the bias of abundance estimates  $\mathbf{N}_0^{iii}$  ( $\rho = 0.71$ ), the additional variance of abundance estimates  $\mathbf{N}^i$  ( $\rho = 0.41$ ), the additional variance of abundance estimates  $\mathbf{N}_0^{iii}$  ( $\rho = 0.55$ ), the depletion ratio in 2005 ( $\rho = 0.60$ ), and the replacement yield in 2005 ( $\rho = 0.60$ ). The parameters that were estimated with low precision  $0.80 < \rho$  were adult survival ( $\rho = 0.91$ ), juvenile survival ( $\rho = 0.85$ ), the maximal birth rate ( $\rho = 0.87$ ), the age of reproductive maturity ( $\rho = 0.95$ ), the abundance in 1965 ( $\rho = 0.81$ ), the compensation parameter ( $\rho = 0.83$ ), the maximum sustainable yield rate ( $\rho = 0.86$ ), the maximum sustainable yield level ( $\rho = 0.81$ ), and the bias of abundance estimates  $\mathbf{N}^{ii}$  ( $\rho = 0.84$ ).

One dimension of the overlap is the degree to which the posterior is contained within the limits of the prior. It is only when this is the case that we have explored the complete parameter space that may explain the data. While the posterior should preferably be contained within the prior for data rich cases, there might be good reasons to limit the posteriors by the priors in data poor cases, where the prior information on the parameters might have a higher degree of confidence than the parameter estimates provided by a non-limited model.

For the analysis in this paper there are two posterior distributions that are contained com-



pletely within the limits of the priors. They are the 2005 depletion ratio (estimated 2005 abundance divided by equilibrium abundance  $N^*$ , which is also known as the carrying capacity), and the 2005 replacement yield (the change in abundance between two years if no harvest, e.g., recruitment if increasing). There are no posterior distributions that extend beyond the prior only in the upper end of the distribution. There are two posterior distributions – adult survival, and the maximum sustainable yield level – with upper limits that are contained within the priors, while the lower limits extend beyond the priors. And there are 12 posterior distributions that extend beyond both the upper and the lower limits of the prior. They are juvenile survival, the maximal birth rate, the age of reproductive maturity, the equilibrium abundance, the abundance in 1965, the compensation parameter, the maximum sustainable yield rate, the bias of abundance estimates  $\mathbf{N}^i$ , the bias of abundance estimates  $\mathbf{N}^{ii}$ , the bias of abundance estimates  $\mathbf{N}_0^{iii}$ , the additional variance of abundance estimates  $\mathbf{N}^i$ , and the additional variance of abundance estimates  $\mathbf{N}_0^{iii}$ .

The relatively large estimate of the additional variance [0.18 (CI:0.13-0.28)], and a 5.0<sup>th</sup> percentile that is larger than zero, could indicate that the abundance estimates either underestimate the variance in the abundance estimates, or that the population dynamic model is unable to deal with the inter annual variation in the abundance. The former occurs if some of the uncertainty in the corrections factors for the abundance estimate is excluded from the abundance estimate. The latter results if the dynamics in the abundance of the Kangerlussuaq Muskox is influenced by stochastic processes, or if only a fraction of the population is covered by the abundance count and this fraction varies between years.

### 3.2 Population dynamics

Figure 3 shows the median and the 90% credibility intervals for the projections of the total abundance and the total abundance, together with the corresponding points estimates that are bias corrected for time series  $\mathbf{N}^i$  and  $\mathbf{N}^{ii}$ . And Figure 4 shows the corresponding projections of the yearly replacement yield and birth rate.

The equilibrium abundance, or carrying capacity herd size, was estimated to 8450 (CI:5470-20000), and the population dynamics was initiated at an estimated abundance of 38 (CI:28-52) individuals in 1965 and projected to an estimated abundance of 6140 (CI:3110-10400) individuals in 2010. The population was most severely depleted in 1965 where the depletion ratio was 0.00 (CI:0.00-0.01). And the abundance in 2005 is close to the equilibrium, with an estimated depletion ratio of 0.88 (CI:0.38-1.08).

During the projection, the yearly replacement yield, or recruitment, varied from 7 (CI:6-10) individuals in 1965 to 1330 (CI:1170-1650) individuals in 2003, with the yield in 2005 being 1300 (CI:1130-1620) individuals. The maximum sustainable yield rate was estimated to 0.28 (CI:0.19-0.40), and the maximum sustainable yield level to 0.61 (CI:0.52-0.73).

### 3.3 Meeting objectives

Assuming that the fraction of females in the future catches is 0.28, based on past harvests (Appendix A), we calculated the probabilities of meeting the population dynamic objectives

Catch	$p(ob)$	Catch	$p(ob)$	Catch	$p(ob)$	Catch	$p(ob)$	Catch	$p(ob)$
500	1.00	1000	0.82	1500	0.32	2000	0.09	2500	0.02
600	1.00	1100	0.66	1600	0.23	2100	0.06	0	0.00
700	1.00	1200	0.57	1700	0.18	2200	0.05	0	0.00
800	0.99	1300	0.50	1800	0.15	2300	0.03	0	0.00
900	0.93	1400	0.40	1900	0.11	2400	0.02	0	0.00

Table V: **Catch objective trade-off.** The trade-off between the yearly catch from 2005 to 2010 and the probability  $p(ob)$  of meeting the population objective.

given the data and the model of density regulated dynamics. This was done for yearly catches of 500 to 2500 individuals in the period from 2005 to 2010 (Table V).

## References

- Berger, J. O. 1985. “Statistical decision theory and Bayesian analysis”, second ed., Springer-Verlag, New York.
- Buckland, S. T. 1992. Proposal for standard presentation of abundance estimates, *Rep. int. Whal. Commn.* **42**, 235.
- Butterworth, D. S., De Oliveira, J. A. A., and Cochrane, K. L. 1993. Current initiatives in refining the management procedure for the South African anchovy resource, in “Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations” (G. Kruse, D. M. Eggers, R. J. Marasco, C. Pautzke, and T. J. Quinn, Eds.), Alaska Sea Grant College program Report No. 93-02, University of Alaska, Fairbanks.
- De la Mare, W. K. 1986. Fitting population models to time series of abundance data, *Rep. int. Whal. Commn.* **36**, 399–418.
- McAllister, M. K., Pikitch, E. K., and Babcock, E. A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding, *Can. J. Fish. Aquat. Sci.* **58**, 1871–1890.
- Oh, M. S. and Berger, J. O. 1992. Adaptive importance sampling in Monte Carlo integration., *J. Stat. Comp. Sim.* **41**, 143–168.
- Press, S. J. 1989. “Bayesian statistics: principles, models, and applications”, John Wiley, New York.
- Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions, in “Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, 1–5 June 1987” (J. M. Bernardo, M. H. DeGroot, D. V. Lindley, and A. M. Smith, Eds.), pp. 395–402, Clarendon Press, Oxford.
- Wade, P. R. 2002. A Bayesian stock assessment of the Eastern pacific gray whale using abundance and harvest data from 1967–1996, *J. Cetacean Res. Manage.* **4**, 85–98.

## A Appendix

Year	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$	Year	$m$	$f$
1965	0	0	1973	0	0	1981	0	0	1989	213	87	1997	372	72
1966	0	0	1974	0	0	1982	0	0	1990	249	101	1998	387	70
1967	0	0	1975	0	0	1983	0	0	1991	285	116	1999	603	185
1968	0	0	1976	0	0	1984	0	0	1992	317	129	2000	484	236
1969	0	0	1977	0	0	1985	0	0	1993	413	168	2001	501	167
1970	0	0	1978	0	0	1986	0	0	1994	512	208	2002	709	373
1971	0	0	1979	0	0	1987	0	0	1995	373	116	2003	810	682
1972	0	0	1980	0	0	1988	142	58	1996	292	78	2004	810	682

Table VI: **Yearly catch** of male ( $m$ ) and female ( $f$ ) Kangerlussuaq Muskoxen. Data from Cuyler (unpublished).

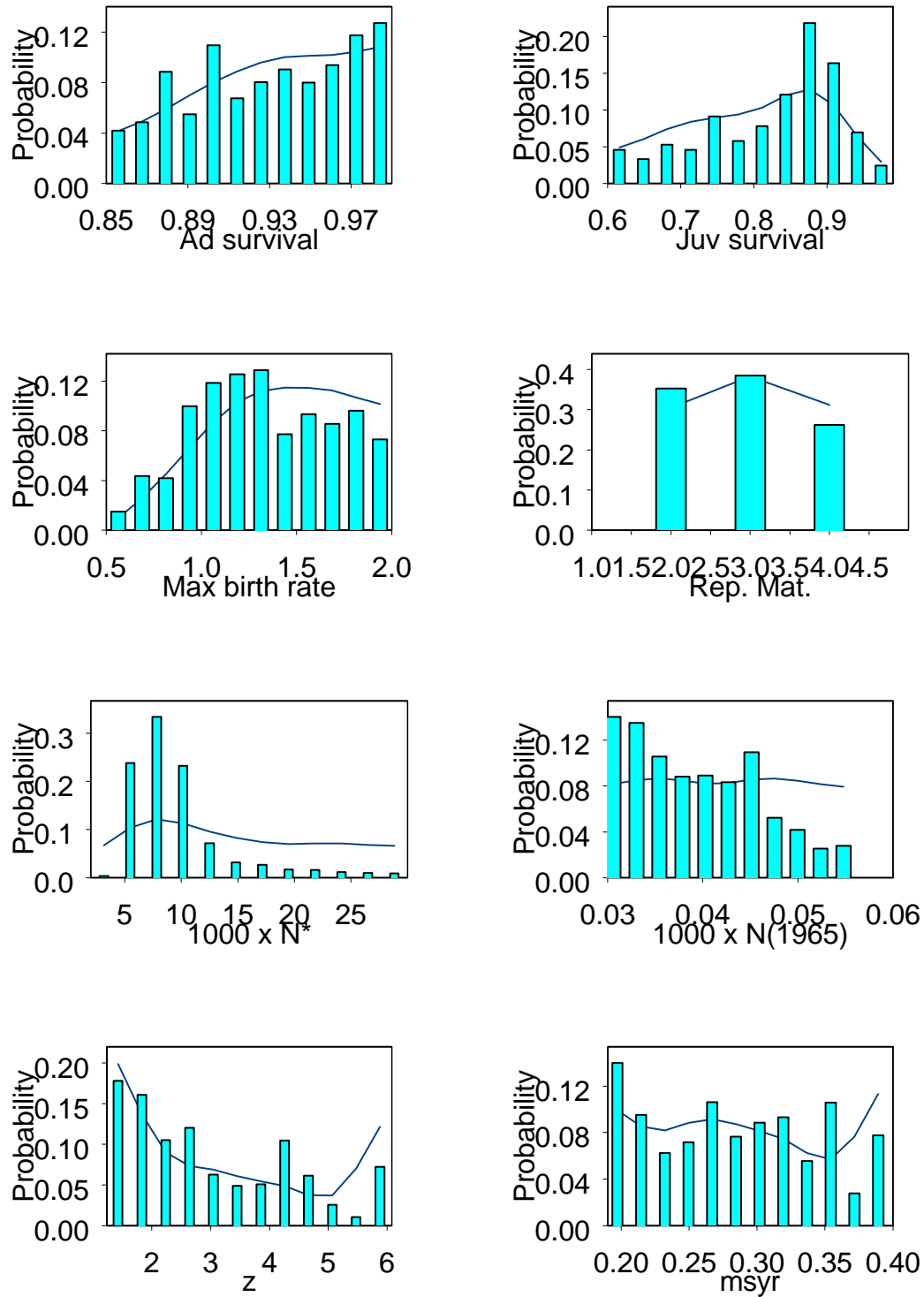


Figure 1: Posterior distributions (bars) and realised priors (curve) for the Kangerlussuaq Muskox.

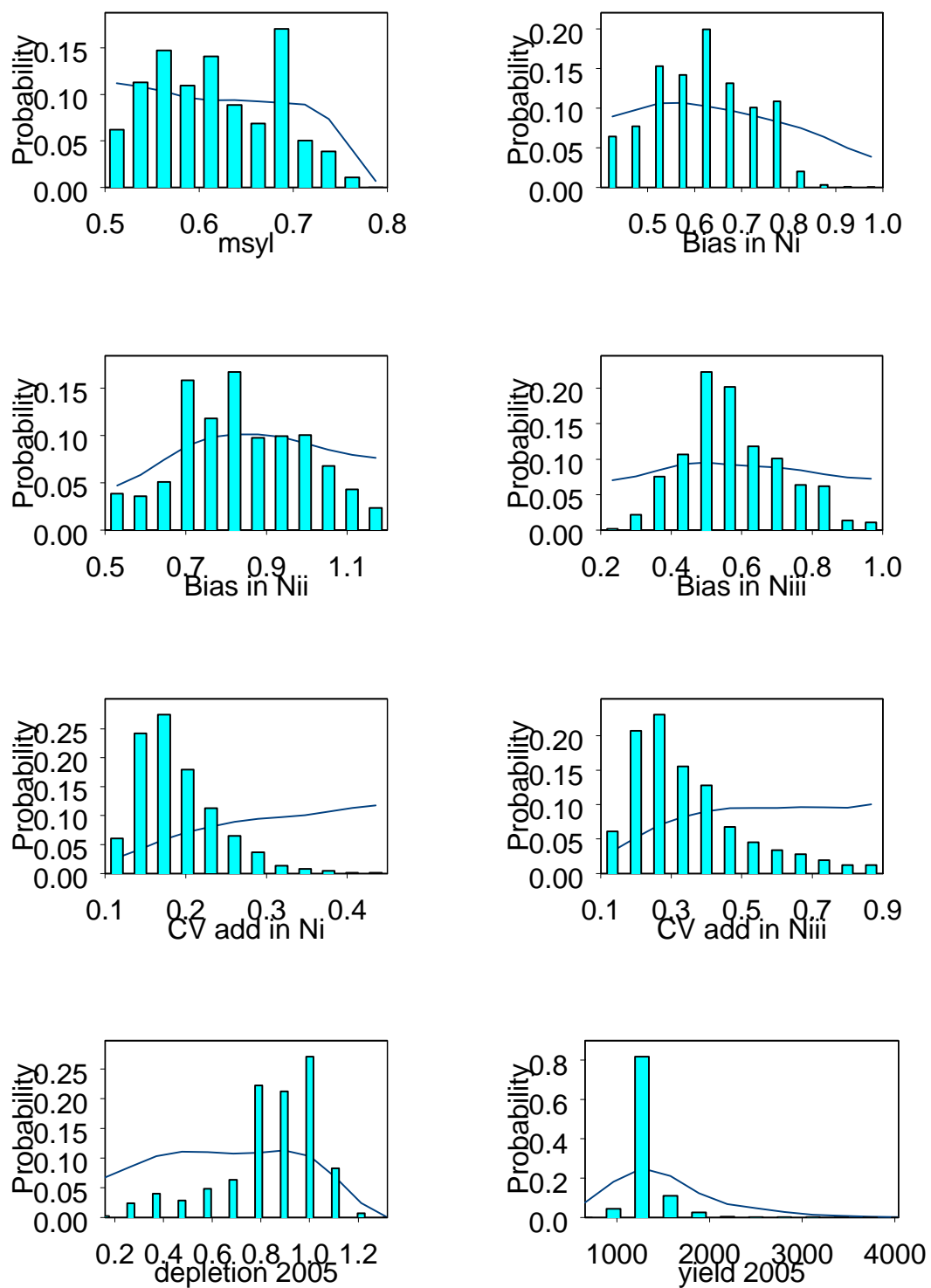


Figure 2: Posterior distributions (bars) and realised priors (curve) for the Kangerlussuaq Muskox.

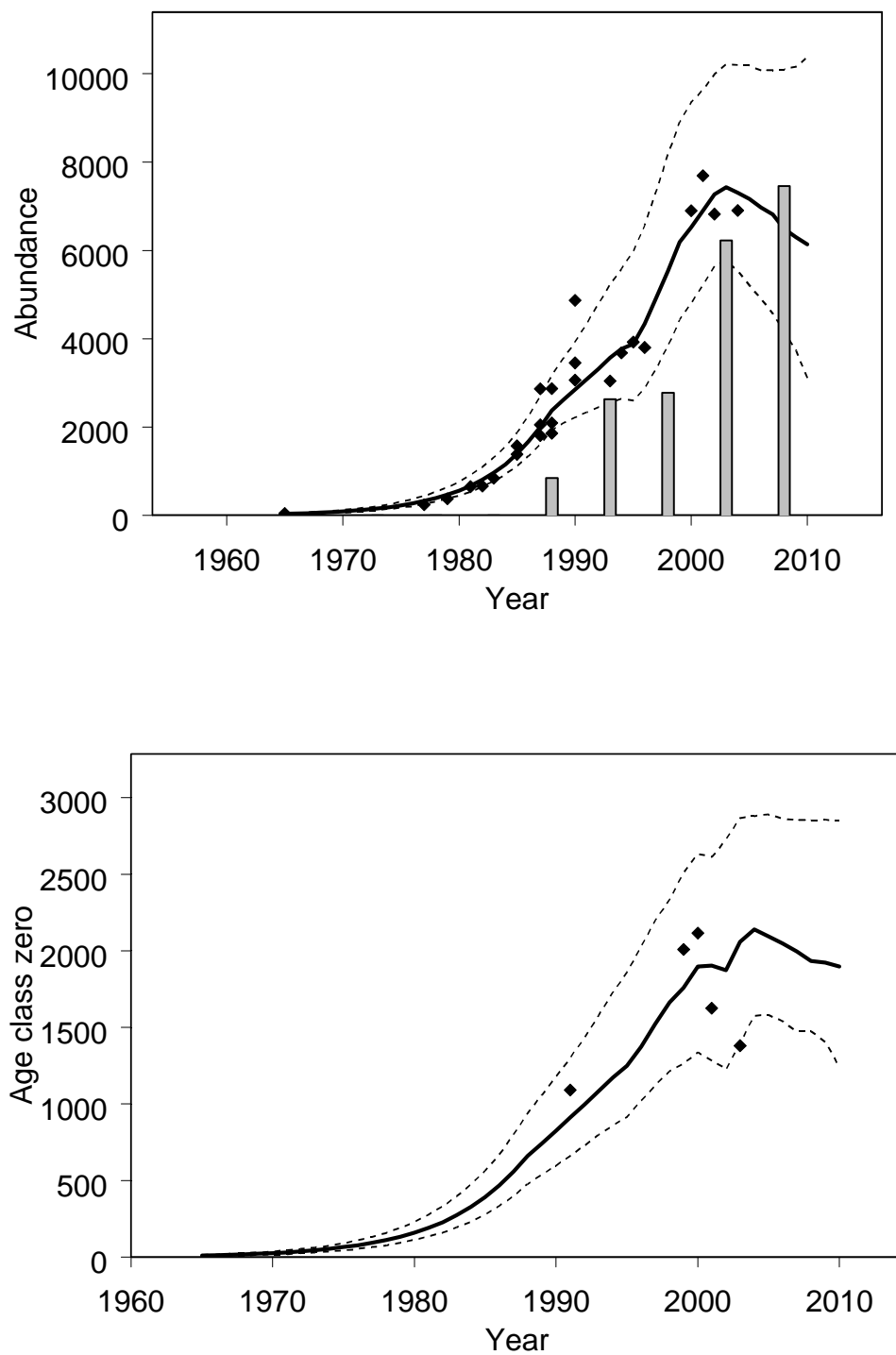


Figure 3: Projections of the median and the 90% credibility intervals of the total abundance and the total abundance for Kangerlussuaq Muskoxs. The bars show the catches summed over five year intervals, with the catches after 2004 being set to the catches in 2004.

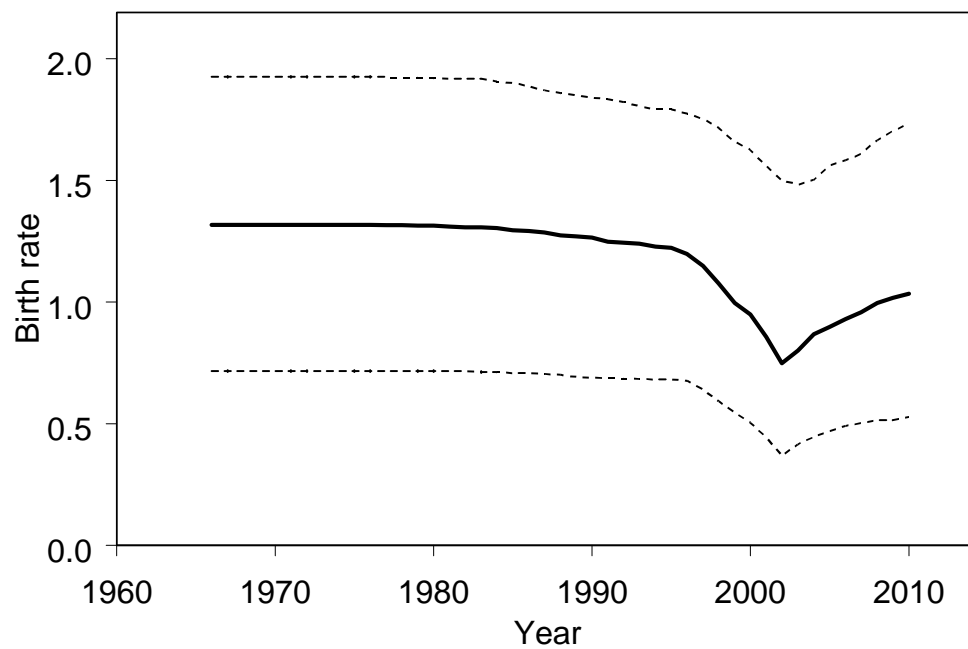
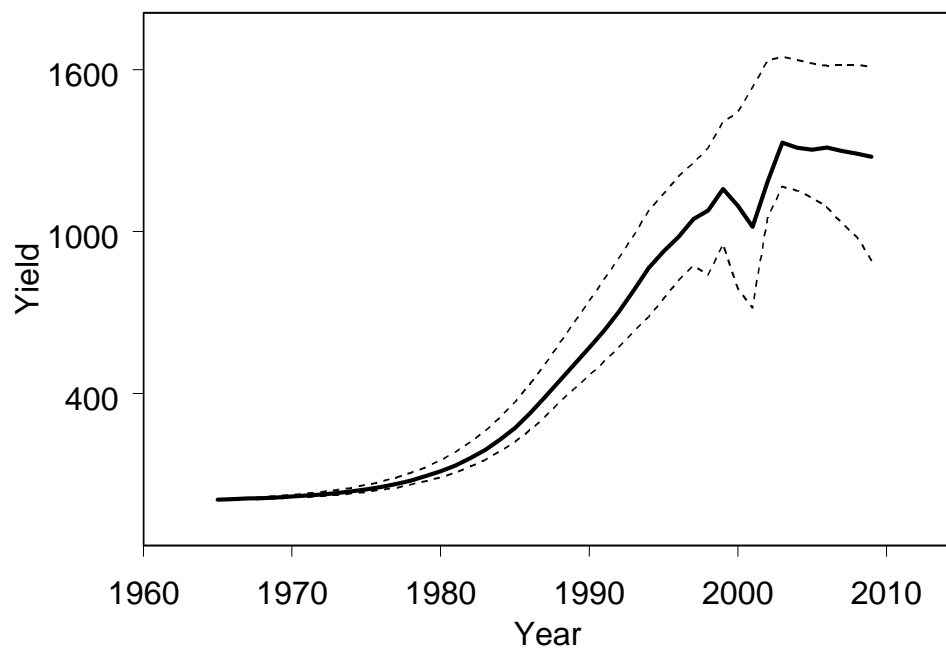


Figure 4: Projections of the median and the 90% credibility intervals of the replacement yield and the birth rate for Kangerlussuaq Muskoxs. The yearly catches after 2004 are set to the catches in 2004.