Fisheries and Oceans Canada
Pêches et Océans Canada

Ecosystems and Oceans Science
Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2016/050

Quebec region

Modelling walrus population dynamics: A direction for future assessments

M.O. Hammill, T. Doniol-Valcroze, A. Mosnier, J.-F. Gosselin

Science Branch
Fisheries and Oceans Canada
Institute Maurice Lamontagne,
850 route de la mer
Mont-Joli, QC. G5H 3Z4

June 2016

Foreword

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Hammill, M.O., Doniol-Valcroze, T., Mosnier, A. and Gosselin, J.-F. 2016. Modelling walrus population dynamics: A direction for future assessments. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/050. v + 47 p.

TABLE OF CONTENTS

ABSTRACT

Walruses are harvested for subsistence in northern Canada. In this study a surplus production model was fitted to aerial survey data of abundance using Bayesian methods. The model was fitted to abundance data from two stocks: the Hudson Bay-Davis Strait stock and the Foxe Basin stock. The model estimated that walrus abundance in the northern Hudson Bay region of the Hudson Bay-Davis Strait stock declined from approximately 10,400 animals (rounded to the nearest 100) in 1954 to a minimum of 3,900 animals in 1986, but has increased since then to 7,000 walruses (95% Credibility Intervals =4,100–10,800). The model estimated a current population abundance in Foxe Basin of 12,500 (95% Credibility Intervals 8,600–18,500, rounded to the nearest 100). This population appears to have remained stable over the last 60 years. Walrus are considered Data Poor, consequently, Total Allowable Removals have been estimated using the Potential Biological Removal method. The population model can be used to provide inputs needed to estimate allowable removals. Given more data, the population model can be used to evaluate the probability that different harvest scenarios will meet management objectives.

Modélisation de la dynamique de population de morse : une voie pour les évaluations futures.

RÉSUMÉ

Les morses font l'objet d'une chasse de subsistance dans le nord du Canada. Dans la présente étude, un modèle de production excédentaire a été ajusté aux données du relevé aérien de l'abondance au moyen de méthodes bayésiennes. Le modèle a été ajusté en fonction des données sur l'abondance de deux stocks : le stock du détroit de Davis et de la baie d'Hudson, et le stock du bassin Foxe. Selon le modèle, on a estimé que l'abondance de morses du stock du détroit de Davis et de la baie d'Hudson dans la région du nord de la baie d'Hudson avait diminué, passant d'environ 10 400 animaux (arrondi à la centaine près) en 1954 à un minimum de 3 900 animaux en 1986, mais avait augmenté depuis pour remonter à 7 000 morses (intervalles de crédibilité de 95 % = 4 100 - 10 800). Le modèle a aussi permis d'estimer que l'abondance de la population actuelle dans le bassin de Foxe était de 12 500 animaux (intervalles de crédibilité de 95 %= 8 600 - 18 500 animaux, arrondis à la centaine près). La population semble être demeurée stable au cours des 60 dernières années. Le morse est considéré comme étant une espèce avec peu de données, en conséquence, le total autorisé des captures a été estimé à l'aide de la méthode du retrait biologique potentiel. Le modèle de population peut fournir les données nécessaires pour estimer les prélèvements autorisés. Avec plus de données, le modèle de population pourrait servir à évaluer la probabilité que divers scénarios de prélèvement atteignent les objectifs de gestion.

INTRODUCTION

The primary goal of a management model is to use data to make decisions that result in meeting management objectives that are usually defined by law, regulation or some management body (Taylor et al. 2000). The management of marine mammals in Canada is governed by the *Fisheries Act*, *Oceans Act* and *Species at Risk Act*. None of these pieces of legislation specify management objectives, consequently marine mammal harvesting in Canada is managed using a patchwork of approaches such as sustainable yield (Nunavik beluga, Doniol-Valcroze et al. 2013), a Precautionary Approach framework with precautionary and reference limit levels (Atlantic seal management, e.g., Hammill and Stenson 2007) and with harvests set using the Potential Biological Removal (PBR) formula (e.g., narwhal, bowhead, walrus, Doniol-Valcroze et al. 2015a, b, Stewart and Hamilton 2013).

PBR has found wide application in Canada in recent years because it requires only a single estimate of abundance (and standard error) to generate an allowable harvest that has a very low probability of causing significant harm to the stock. Unfortunately, in Canada, abundance data are limited for many marine mammal stocks (e.g., walrus), so PBR has fulfilled a need to provide harvest advice in such data-poor situations. However, the PBR was developed in tandem with the *Marine Mammal Protection Act* (MMPA) in the United States, which identified specific management objectives for this group of animals. In the United States, outside of Alaska, there is no directed harvesting of marine mammals. At the same time, it was realized that anthropogenic mortality of marine mammals would never fall to zero (e.g., incidental catches in fisheries). Therefore, some means was needed to identify an acceptable level of mortality that would allow industrial activities (e.g., fishing) to continue and would still fulfill the management objectives of the MMPA. The main management objective of the MMPA is to allow a stock to reach or maintain its ‘Optimum Sustainable Population’, which is defined as a population level between carrying capacity and the population level at maximum net productivity MNPL (Wade 1998), which can also be considered the population size that provides Maximum Sustainable Yield. An underlying philosophy behind PBR is that it does not address whether a population is increasing or not, or where it is situated with respect to MNPL. Instead, it addresses whether the level of removals could lead to a decline below MNPL (see Wade 1998 and references therein; Taylor et al. 2007). Simulation trials have shown that the method performs well with respect to the management objective under different types of bias and uncertainty (Wade 1998).

PBR is easy to estimate (see Wade 1998; Hammill et al. 2016a, b). Owing to its conservative properties, PBR can perform very well when there is considerable uncertainty associated with our understanding of the resource (Milner-Gulland et al. 2001; Wade 1998). There has been some debate on the strengths and weaknesses of PBR (e.g., Cooke et al. 2012; Lonergan 2011, 2012). The fact that PBR only requires a single population estimate (and standard error) is both a strength and a weakness. If only a single estimate is available, some advice on removals can be provided, but as more abundance information is accumulated, PBR levels will fluctuate with each new population estimate, often in ways that are not realistic for K-adapted species such as marine mammals, which adds to the difficulties for harvesters to plan harvesting activity and discourages buy-in into the management process. Moreover, PBR does not benefit from the information added by multiple survey estimates, meaning that additional data do not decrease uncertainty. Another problem is that the MMPA was designed to reduce takes to as close to zero as possible, therefore the PBR simulations did not consider the potential costs to harvesters of forgoing potential harvest. i.e., it only provides an estimate of removals that should allow a population to move towards or remain above MNPL. However, managers and harvesters are likely to make very different decisions concerning removals or takes that accept different levels of risk for populations that are abundant (e.g., harp seals> 7 million animals) compared to populations that are less abundant (e.g., St. Lawrence beluga <1200 individuals).

Surveys for marine mammals are often highly variable; insufficient to estimate vital rates and to understand mechanisms underlying population growth and decline. However, state-space models are a means of integrating data with population dynamics models and readily quantifying the various types of uncertainty, particularly when applied in a Bayesian framework. A state-space model consists of two components, a state process model and an observation model. The process model specifies the underlying dynamics of the population with the relevant population processes, such as the rate of increase, the density-dependent process, and carrying capacity (K), while the observation model relates the true population size to our observed information on abundance (Buckland et al. 2007; Mosnier et al. 2015; Wade 2000). This approach allows the simultaneous estimation of demographic parameters and the predicted trend of the population under different levels of harvest (Schaub and Abadi 2011; Mosnier et al. 2015; Doniol-Valcroze et al. 2013).

Abundance information for walrus populations in Canada is limited. However, time-series of counts are available for two of the four stocks of Atlantic walrus occurring in the central Arctic population (Fig. 1): nine surveys of walrus have been completed over the last 61 years in the Hudson Bay-Hudson Strait area and five surveys over the last 32 years in Foxe Basin. These surveys have differed in their methods, in area covered, and are characterized by large uncertainty. Bayesian statistics are well adapted to this situation because they allow the incorporation of prior existing knowledge of parameter values, including their associated uncertainty (Mosnier et al. 2015). In this paper, we have adapted a Bayesian model, that was initially developed for Eastern Hudson Bay beluga (Doniol-Valcroze et al. 2013), and applied it provide harvest advice for two stocks of Atlantic walrus in Canada. We have fitted the model to the Hudson Strait component of the Hudson Bay-Davis Strait and Foxe Basin stocks and used it to provide insights into the dynamics of each stock and provide recommendations for Total Allowable Removals. Since management objectives of walrus have not been stated clearly, we present the advice using two different management objectives: sustainable yield and PBR. Sustainable yield is the level of harvest that will allow the population to remain constant over a defined period of time. In this study, we define sustainable yield as harvest levels projected over a 10-year period that do not result in a decline of the population below 2014 levels. The objectives of PBR have been outlined in detail above, but here we estimate the PBR levels using outputs from the population model in order to benefit from all the available information rather than a single abundance estimate. We also discuss some of the implications of using these two approaches.

MATERIALS AND METHODS

SURVEYS

Hudson Bay-Davis Strait (HBDS) stock

A total of nine surveys have been flown to obtain estimates of abundance in the Hudson Bay-Hudson Strait area of this stock (Table 1). In August 1952, preliminary aerial surveys were flown at low altitude over Nottingham, Salisbury, Walrus and White islands using a RCAF Lancaster bomber, but no walrus were observed (Loughrey 1959). In July 1953, a flight with the US Fish and Wildlife Service over Coats and Walrus islands only detected 30 animals, but it was noted that animals began to scramble for the water when the aircraft was more than a ¼ mile away. The aircraft type was not specified. Further testing suggested that survey altitudes of 305 to 457 m minimized disturbance and in August 1954, two surveys were completed over seven haulout sites around Southampton-Walrus-Coats islands using a twin engine Anson 1954 (Loughrey 1959). This resulted in an average count of 2,900 animals, which the author felt to be within 15% of accuracy. We interpreted this as a coefficient of variation of 15%. A combination of boat and aerial surveys of the same area resulted in a count of 2,650 animals in 1961 (Mansfield 1962). Twelve flights in July–August 1976, and 10 flights were made in July and August 1977 around the Southampton-Walrus-Coast Island area flying at an altitude of 150 to 250 m. The surveys involved a combination of visual and photographic observations (Mansfield and St. Aubin 1991). We took the average of all 1976 flights to obtain a mean estimate for 1976. In 1977, only 26 animals were observed on one flight and six on a second flight. These counts were not included, leaving eight counts which were used to obtain a mean estimate for 1977 (range 138–2171) (Mansfield and St. Aubin 1991; Hammill et al. 2016a)(Table 1). Coastal surveys were completed around the same area, and included Nottingham and Salisbury islands as well during July–August in 1988, 1989 and 1990. Line transect surveys were flown using Twin Otter flying at 150 m in Hudson Strait from the eastern entrance of the Strait to as far west as about the northwestern point of Mansell Island during March–April 2012 (Elliot et al. 2013). Finally, a coastal survey covering Hudson Strait, Southampton, Walrus, Coats and Mansell islands was flown in September 2014. The survey altitude was 204–305 m. Visual and photographic data were collected (Hammill et al. 2016a). Since the Southampton/Coats Island and Nottingham/Salisbury Island complexes appear to account for the majority of walrus observations, these were considered as relatively complete surveys for looking at the northern Hudson Bay-Hudson Strait component of this stock.

The aerial surveys, with the exception of the March–April 2012 survey (Elliot et al. 2013) only report counts of animals hauled out. These counts must be corrected for the proportion of animals that are hauled out during the survey. Telemetry data are not available for these surveys, therefore we used a mean haulout proportion of 0.3 (SE=0.18) which was estimated from several published studies (Table 1 in Hammill et al. 2015). The line-transect survey of Hudson Strait already included corrections for perception and availability bias (Elliot et al. 2013).

Foxe Basin stock

A total of five different survey studies were completed to obtain information on walrus abundance in Foxe Basin (Table 2). The Foxe Basin abundance estimates were based on haulout counts from surveys flown in July–September 1983, 2010 and 2011, and systematic strip-transect surveys flown in July–August 1988 and 1989 (Orr et al 1986; Richard unpublished report; Stewart and Hamilton 2013; Stewart and Higdon unpublished report). As these data represent counts of animals hauled out, they need to be adjusted by the proportion of the population hauled out when the survey was flown.

On 19 and 20 August 1983, flights were flown, at an altitude of 61–457 m, with 150 m being the preferred altitude. A total of 2,722 walrus were counted (Orr et al. 1986).

During August 1988 and July 1989, east-west systematic strip transects were flown using a DeHavilland Twin Otter flying at an altitude of 457 m. Four hundred and forty-three walrus were counted in 1988, and 476 walrus were counted in 1989 (Higdon and Stewart unpublished report; Hammill et al. 2016b). This resulted in a hauled-out count of 5,128 (SE=4,390) in 1988 and 5,510 (SE=1,644) in 1989.

During August and September of 2010 and 2011 surveys were also flown in Foxe Basin using a de Havilland Canada DHC-6 Twin Otter at a target altitude of 300 m ASL and speed of 210 km/h flying approximately 1 km off the coastline (Stewart et al. 2013). Both visual and photographic data were collected. A time-distance criterion (45 km/24 h) was applied to reduce the probability of double-counting walrus at different haulouts, which meant that final counts were based on fewer haulout sites than were examined in total (Stewart et al. 2013). A total of

3,861 walrus were counted in 2010. Two haulout counts in 2011 resulted in 5,945 and 4,484 animals. Taking the average for the two, resulted in an average haulout counts of 5,214 (SE=1,033) walruses.

The Foxe Basin counts were not adjusted for animals in the water at the time the studies were completed. Satellite transmitters were deployed on animals in Foxe Basin during the 2010 and 2011 surveys and these were used to adjust the haulout counts of all surveys using a mean proportion of animals hauled out of 0.37 (SE=0.16) (Table 2).

HARVEST RECORDS

Harvest data are available from annual reports of landed catches (Table 3,4)(summarized in Hammill et al. 2016a, b). We assume that all walruses harvested by the communities in Hudson Strait, Ungava Bay, western Hudson Bay (Arviat, Chesterfield Inlet, Coral Harbour, Rankin Inlet, Naujjuat Whale Cove), eastern Hudson Bay (Akulivik, Puvirnituq) and the east Baffin Island communities of Iqaluit, Pangnirtung, Qikiqtarjuaq, and Clyde River are from the HBDS stock. We did not include harvests from Greenland. Similarly, it was assumed that animals harvested from the Foxe Basin stock were taken only by hunters from the communities of Igloolik and Hall Beach. The harvest records had several years where data were not reported. We substituted the average harvest of the most recent five years for the missing data (Tables 3, 4). Similarly, not all walrus that are killed are recovered and reported. Information on loss rates is limited. Loss rates of 20–30% have been reported for Greenland (Witting and Born 2005), and 30–60% for harvesting in Canada (Loughrey 1959). More recent estimates from the 1970s and 1980s range from 30–38% (Mansfield 1973, Orr et al. 1986, Freeman 1974/75 in Stewart et al. 2014). NAMMCO assumes a Struck and Loss of 30% unless there is more specific information available (DFO 2002; NAMMCO 2006). We incorporated this range of estimates in the prior formulation for the struck and loss factor (see below).

MODEL SPECIFICATION

A stochastic stock-production model, assuming density dependence acting on the population growth rate, was fitted by Bayesian methods. We sought to separate the observation error (associated with data collection and abundance estimation) from the process error (arising from natural variability in population dynamics). To this end, we developed a hierarchical state-space model that considers survey data to be the outcome of two distinct stochastic processes: a state process and an observation process (de Valpine and Hastings 2002).

The state process describes the underlying population dynamics and the evolution of the true stock size over time, using a discrete theta-logistic model, i.e., a re-parameterization of the Pella-Tomlinson model (Pella and Tomlinson 1969; Innes and Stewart 2002). Population size in each year N_t (from 1954 to 2014) is a multiple of the previous year's, with removals deducted:

$N_t = N_{t-1} + N_{t-1} \cdot (\lambda_{max} - 1) \cdot \left[1 - (N_{t-1}/K)^{\theta}\right] \cdot \varepsilon_{p_t} - R_t$, with $\varepsilon_{p_t} \sim logN\left(0, \tau_p\right)$

where r_{max} is the maximum growth rate, K is environmental carrying capacity and theta θ defines the shape of the density-dependent function. εp_t a stochastic term for the process error and R_t are the removals for that year. Removals were calculated as reported catches, C_t, corrected for the proportion of animals that were struck and lost, *SL*:

$R_t = C_t \cdot (1 + SL)$

The observation process describes the relationship between true population size and observed data. In our model, survey estimates S_t are linked to population size N_t by a multiplicative error term εs_t:

$S_t = N_t \cdot \varepsilon_{s_t}$, with $\varepsilon_{s_t} \sim logN(0, \tau_s)$

PRIORS

Existing information, traditional knowledge, and expert opinions were used to formulate prior distributions for the random variables included in the model (Table 5). We did not know what the starting population might be, but provided a wide range that encompassed the adjusted estimate of walrus from surveys completed in 1954 by Loughrey (1959). The initial population size (N_{1954}) was given a uniform prior between 500 and 30,000 individuals. In addition, we limited the initial population size, so that it could never be higher than K.

In previous assessments, the maximum annual rate of increase of walrus was set at λ_{max} =1.07 e.g., Stewart and Hamilton (2013), which agrees with some early work that estimated λ_{max} , by fitting an exponential curve to Soviet estimates of abundance from 1958 to 1975, when walrus were not considered to be food-limited (Sease and Chapman 1988). However, this estimate is likely to be conservative because it did not take into account the impacts of harvesting on population growth. More recent modeling suggests that the maximum rate of increase is 1.08, (Chivers 1999; Taylor and Udevitz 2015; Witting and Born 2014) and this is the default used in the United States in the most recent assessments of Pacific walrus. Consequently, in this assessment a λ_{max} of .08 was used.

We know little about carrying capacity and the theta density-dependence parameter for walrus in the Hudson Strait area of the Hudson Strait-Davis Strait stock. For K, we used a Uniform prior of 500 to 35,000, which encompassed the starting population size. Marine mammals are considered to reach maximum productivity between 50 and 85% of K (Taylor and DeMaster 1993), which results in theta lying roughly between 1 and 7. Trzcinski et al. (2006) used theta =2.4 to model the dynamics of grey seals (*Halichoerus grypus*), while recent work on walrus has used a range of values from 1 to 4 (Chivers 1999). Witting and Born (2005) modelled the dynamics of Greenland walrus populations and allowed the model to estimate theta. Their posterior values for theta were generally around 2.7 (95% credibility intervals 1.1–7.2). We assumed a Uniform Distribution for theta with a range of 1 to 7 (Table 5).

Reported harvests underestimate the number of walrus killed because of animals wounded or killed but not recovered, as well as an absence of harvest reports for some communities in different years. For communities with missing report data, we estimated the average number of walrus reported killed based on the most recent 5 years with harvest data. The loss rates in walrus hunts are not known exactly. We gave the struck-and-lost correction factor (*SL*) a moderately informative prior following a Beta (3, 4) distribution, with a median of 0.42 and quartile points at 0.29 and 0.55.

The stochastic process error terms εp_t were given a log-normal distribution with a zero location parameter. The precision parameter for this lognormal distribution was assigned a moderately informative prior following a gamma (1.5, 0.001) distribution. These parameters were chosen so that the resulting error multiplier would have a median of 1 and quartiles of 0.98 and 1.02 reflecting our belief that walrus stock dynamics are not highly variable.

The uncertainty associated with each survey is poorly estimated. Therefore, this uncertainty was incorporated into the fitting process only by guiding the formulation of the prior distribution of the survey error. The survey error term εs_t followed a log-normal distribution with a zero location parameter. Its precision parameter was given a moderately informative prior following a gamma (2.5, 0.4) distribution. These parameters were chosen so that the resulting CV on the survey estimates would have quartiles of 35% and 55%, which are approximately equivalent to the range of what we consider to be plausible CV for the survey abundance estimates.

PARAMETER ESTIMATION AND MODEL DIAGNOSTICS

We obtained posterior estimates of all the parameters using a Gibbs sampler algorithm implemented in JAGS (Plummer 2003). Results were examined using packages *R2jags* and *coda* developed in the R programming language. With any MCMC simulation, it is important to check convergence of the sampled values to their stationary distribution (Brooks et al. 2004; King et al. 2010). Initial runs of the code were made to investigate convergence and mixing (i.e., the extent and spread with which the parameter space was explored by the chain), as well as autocorrelation. Following these initial runs, we kept one sample every 50 iterations from 5 chains of 45,000 iterations, after a burn-in of 50,000 samples, for a total of 4,500 samples. For the Foxe Basin models, one sample was kept every 30 iterations.

We tested for mixing of the chains using Geweke's test of similarity between different parts of each chain (Geweke 1996), and for convergence between chains using the Brooks-Gelman-Rubin (BRG) diagnostic, which compares the width of 80% Credible Interval (CI) of pooled chains with the mean of widths of the 80% CI of individual chains (Brooks and Gelman 1998).

We tested the sensitivity of the results for the HBDS runs, to the values of two hyper-parameters: α_s used in the prior distribution of the precision of the survey error, and α_{SL} used in the prior distribution of the struck-and-lost factor. To this end, we ran versions of the model with different values of each hyper-parameter and examined the influence of these parameters on the final population estimate as well as on the posterior distributions of the parameters themselves. These runs had fewer iterations (10,000 after a burn-in of 10,000, resulting in a thinned chain of 250 samples), but their point estimates were similar to those of the main model.

FUTURE PROJECTIONS AND HARVEST SCENARIOS UNDER THE PRECAUTIONNARY APPROACH

The model was extended into the future for up to ten years to predict stock trajectory. These predictions were performed under different harvest scenarios, with yearly catch levels ranging from 0 to 400 walrus. To provide information in a useful format for risk-based management, we estimated the probability of stock decrease after ten years for each of the scenarios, using the proportion of simulations in which the stock size in 2024 was below the estimated 2014 stock size i.e., the probability of a certain harvest level resulting in a population decline below 2014 levels after ten years.

RESULTS

MODEL CONVERGENCE

Each of the five chains showed rapid mixing and reached a stationary distribution (Geweke's diagnostic, all Z-scores < 1.96) for both models (Fig. 2a, b). The overall BGR statistics for both stocks were close to 1 (Tables 6, 7). There was some evidence of autocorrelation for K and to a lesser extent for the initial population and struck and loss in the HBDS stock model, but the number of effective iterations remained high (N>2600) (Fig. 3a). There was no evidence of autocorrelation in the Foxe Basin model (Fig. 3b).

HUDSON BAY-DAVIS STRAIT STOCK

Some additional sensitivity analyses were completed for this stock, as well as some additional runs. The model was first fitted to the entire survey time-series data (1954–2014) from the HBDS stock and included data from all communities that could be harvesting from this stock (Run 1). A second run included only surveys from 1988 and later to examine the impact of the early surveys on current estimates (Run 2). A third run assumed that only communities in

Hudson Strait, Ungava Bay and northern Hudson Bay were harvesting animals from the survey area i.e., harvests from communities along the east coast of Baffin Island (Iqaluit, Pangnirtung, Qikiqtarjuaq, and Clyde River) were excluded from the analysis (Run 3). This reduced the average annual harvest from 251 animals, if all villages are included, to 178 animals, if east Baffin Island communities are excluded, when the complete time series is used (1954–2014) or from an annual harvest of 85 to 63 animals, using the average harvest for the last five years.

SENSITIVITY TO PRIORS

The sensitivity of model outputs to the priors was only examined for Run 1. The median of the 2014 HBDS stock size estimate was little influenced by changes in the hyper-parameter α_{SL} used in the prior Beta(α_{SL}, β_{SL}) distribution of the struck and lost (Fig. 4). Using α_{SL} values of 2,3,6, and 10, shifted the median prior for Struck and Loss from 0.3 to 0.7. The posterior distribution for struck and loss was sensitive to changes in prior values, with median posterior values remaining within 0.1 of the median value for the prior. If the prior assumed a uniform distribution between 0.2 and 0.7, the prior median was 0.45, while the posterior value was 0.36 (95%CI=0.21-0.67). Changes in the hyper-parameters α_s and β_s used in the prior Gamma (α_s, β_s) distribution of the survey precision term had no perceptible influence on the 2014 point estimates of the stock size, but did have an impact on the associated uncertainty (Fig. 4).

In the HBDS model that used all harvest and all survey data (Run 1), the strongest correlation was observed between carrying capacity (K) and the estimated population size in 2014 (0.42), and between struck and lost and the initial population size (0.40, Fig. 5a). For the HBDS model that did not include surveys flown prior to 1988 (Run 2), cross-correlation was observed between Struck and Lost and K (0.33), and between Struck and Lost and the starting population size (0.53). For Run 3, which used all survey data but excluded harvests reported from east Baffin island communities, strong correlations were observed between K and the 2014 population size (0.42), between struck and lost and K (0.28), and between the 2014 population estimate and the starting population (0.4, Fig. 5c).

MODEL UPDATE OF PRIORS AND ABUNDANCE ESTIMATES

For the run that included all survey data (1954–2014) and all harvests from communities harvesting from this stock, there was significant updating of the priors for the starting population, K, theta, struck and loss, and to a lesser extent survey precision (Table 6a; Fig. 6a). Carrying capacity was updated from a mean of 17,764 to a mean of 12,901 (median=9,739, 95% Credibility Interval 7,021–32,417). The starting population was updated from a prior with a mean of 15,231 to a mean of 10,421 (median=9,461 95% CI=6,415–19,838). The theta parameter, which defines the shape of the density dependence relationship, was updated from a prior mean of 4 (Uniform distribution) to a posterior mean of 3.3 (median=3.0, 95% Credibility Intervals (1.1-6.7). The HBDS model also showed moderate updating from a prior mean of 0.43 for struck and lost to a posterior value 0.35 (Table 6a, Fig. 4a). For all runs, there was little difference between the priors and the posteriors for the process error.

The 1954, 1988, 1989, 1990, 2012 and 2014 survey estimates all lie within the 95% credibility intervals of the HBDS model (Fig. 7a, b). The point estimates from the 1976 and 1977 surveys lie below the 95% credibility interval (Fig. 7a, b). The model estimated a mean starting population in 1954 of 10,421 (before harvesting). The population declined, reaching a minimum of 3,600 animals (SE=900; 95% CI 2,600–6,100) in 1993, but has increased since then to a 2014 estimate (after harvesting) of 6,980 (SE=1641; 95%CI 4,137–10,753) (Fig. 7a, b). The posterior for theta had a median value of 3.0 (Table 6a), which means that maximum stock productivity would occur at 63% of carrying capacity. Accordingly, the finite rate of increase was at a minimum of 1.026 in 1954, increased to 1.075 in 1993 when the stock was at a minimum, then declined to 1.052 in 2014.

Excluding surveys prior to 1988 (Run 2) resulted in a model that was fitted to five surveys: a cluster of three surveys centred around 1988 and two surveys flown in 2012 and 2014, respectively. This resulted in a model that was essentially only fitted to two points, but had a long tail in which the dynamics were affected by the reported harvests (Table 6b, Fig. 6b, 7b). Excluding the aerial surveys allowed the model to drift more freely, relying on the reported harvests extending back to 1954, and the survey estimates from 1988 and onwards to fit the model. There was slightly less updating of priors using the reduced dataset than when using the complete dataset (Tables 6a, b; Fig. 6a, b). Compared to the results of Run 1, there was a slight reduction in K from 12,901 to 11,430, a slight change in the starting population from 10,421 to 9,458 and an increase in the estimated population in 2014 from 6,980 to 7,437.

Excluding harvests from east Baffin island villages (Run 3) resulted in significant updating of the priors for starting population, K, and theta, but no updating of the prior was observed for the struck and lost parameter (Tables 6a, b, c; Fig. 6a, b, c). The estimated 2014 population was slightly lower (Mean=6,356, SD=1,006; 95% Credibility intervals = 4,634–8,496) than in both other runs.

The probability that harvesting would lead to a decline in the population was only examined for Run 1. Reported annual harvests of 100, 150 and 267 animals from the HBDS stock over the next 10 years would result in probabilities of population decline below 2014 levels of 0.1, 0.2 and 0.5 respectively, and therefore would constitute sustainable yields (Fig. 8, 9). The PBR estimate for this stock using the 2014 model estimate of population size is 230, assuming a Recovery Factor of 1. For the runs when all surveys prior to 1988 are excluded, the PBR estimate is 249. The model run that excluded harvests from the east Baffin Island villages produced a PBR estimate of 223. All PBR estimates from the model were higher than the PBR of 218 estimated using the 2014 survey estimates only (Hammill et al. 2016a). The population model takes into account the uncertainty associated with struck and loss when estimating the probability of a decline under different harvest scenarios. However, the PBR calculation does not consider struck and lost. Instead, some assumptions must be made about the rate of struck and lost and the uncertainty associated with this estimate. The model provides a mean estimate of struck and lost of 0.35. Incorporating this into the PBR estimate, results in a revised PBR of 150 animals. Reported harvests from all villages have averaged 85 per year (SE=10.5) over the last five years for this stock and show a long term declining trend (Fig. 7). If the east Baffin Island communities are excluded, the average annual harvest over the last five years has been 63 animals per year. These harvests are below estimates of both sustainable yield and PBR.

FOXE BASIN

The Foxe Basin models exhibited strong correlation between the K parameter and the 2014 abundance estimate (Fig. 10). The mean, standard deviation, median and quantiles for prior and posterior parameters for the Foxe Basin stock model are shown in Table 7, Fig. 11. There was little difference between the priors and the posteriors for the process error, suggesting that there is not enough information in the model to inform this prior or that the difference between the observations and the “true” population size is already taken into account by the survey precision error. As a result, the time series of the median errors estimated by the model are evenly distributed around 1 with no obvious trend over time.

There was significant updating of the priors for the starting population, carrying capacity, theta and to a lesser extent survey precision. The K prior was updated from a mean of 20,234 to a mean of 13,583 (median=13,195, 95% Credibility Interval 9,466–20,030). The starting population was updated from a prior with mean of 20,242 to a mean of 11,862 (median=12,205, 95% CI=4,604–17,881). The theta prior introduced into the Foxe Basin model was based on the updated theta posterior from the HBDS model. We used a prior of (0.6+7*beta(2,3)). This prior had a mean of 3.4 (95% CI=1.1–6.3) compared to the Hudson Bay-Davis Strait posterior with mean of 3.3 (1.1–6.7). The prior was not updated (Table 6b, Fig. 4b). The prior for struck and lost introduced into the Foxe Basin model was also based on the updated struck and loss posterior from the HBDS model. Instead of using a beta distribution of beta (3,4), with a mean of 0.43 for the prior, we used a beta (2,4), with a mean of 0.35. This resulted in only minor changes for the Foxe Basin stock struck and lost parameter to a posterior mean of 0.33 (Table 7, Fig. 11).

In the Foxe Basin model, all five survey point estimates are either just on, or lie within the 95% credibility intervals (Fig. 12). The model estimated a mean starting 1954 population (before harvesting) of 11,682 (median=12,205, 95% CI=4,604–17,881)(Table 7). The model indicates that there has been little change in the population over the last 60+ years. The mean 2014 estimated (after harvesting) population is 12,489 (Median=12,158, 95% CI=8,574–18,489) (Fig. 12). The estimated theta had a median value of 3.4, which means that maximum productivity of the stock would occur at 65% of carrying capacity.

Sustainable yields are defined as harvests that result in less than a 50% probability of decline. The probability that reported harvests of 150, 163 and 172 animals from the Foxe Basin stock over the next 10 years would result in a population decline below 2014 levels was 10%, 50% and 80% respectively (Fig. 13, 14). The PBR estimate for this stock using the model estimate of population size in 2014 is 422, assuming a Recovery Factor of 1. This estimate is higher than the estimate of 385 from Hammill et al. (2016b).This figure does not take into account struck and lost. The mean struck and lost factor from the model was 0.33 (95% CI=0.05–0.71). Adjusting PBR to take into account struck and lost results in PBR estimates of 283 (95% CI= 122 to 400).

Reported harvests since 1954 in the villages of Igloolik and Hall Beach have been relatively stable, averaging 170 (SE=25) animals over the last five years (Fig. 10). At current harvest levels the model suggests that the population will decline below 2014 levels, but removals are below PBR levels after taking into account struck and lost in the PBR calculation.

DISCUSSION

Walruses are harvested for subsistence purposes throughout much of their range in Canada, Greenland and Alaska. Moreover, in some areas there is a small sports harvest. Once widely distributed in the eastern Canadian Arctic, Hudson and James bays, and down the Atlantic coast, to the Gulf of St Lawrence and Sable Island (e.g., Stewart et al. 2014), their current distribution appears to be restricted to northern Hudson Bay, and northwards, with only a few now seen south of Labrador and James Bay (Born et al 1995; Stewart et al 2014; Clark undated; in Loughrey 1959; COSEWIC 2006). Their gregarious nature makes walruses vulnerable to large local takes and, coupled with a narrow trophic niche and restricted seasonal distribution, makes them vulnerable to environmental changes (Born et al. 1995, COSEWIC 2006; Stewart et al 2014).

Unfortunately, survey activity of the individual stocks, and demographic information on walrus in Canada are limited. There have been some abundance surveys flown in Foxe Basin and northern Hudson Bay/Hudson Strait, which forms part of the HBDS stocks, but in the case of the latter stock, some of these surveys date back over 60 years and they appear to have covered only the major haulout sites.

State-space models particularly when applied in a Bayesian framework, are a means of integrating data with population dynamics models and readily quantifying the various types of uncertainty (Buckland et al. 2007), which makes this approach suited for application to walrus, where the data are limited and very uncertain. Using Bayesian methods, we fitted a surplus production model to these highly uncertain data, taking into account harvest information that extended back to the early 1950s, to obtain estimates of abundance, population trend and to identify the impact of future harvests on the population. Additional uncertainty is associated with several of the model parameters including, the estimated rate of increase of the stock, the correction factor for diving animals, estimates of struck-and-loss, and environmental carrying capacity. However, Bayesian methods allowed us to explicitly incorporate uncertainty around these parameters (Wade 2000), which are represented in the model by statistical distributions instead of single values. Bayesian fitting also ensured that uncertainty was propagated throughout the analysis, and that the correlations among parameters were preserved (Hoyle and Maunder 2004). The resulting stock trajectory is based on realistic population dynamics and offers more information than a simple trend analysis. It also allows for the explicit expression of the risk associated with different levels of harvest within the context of whether these harvests will respect management objectives.

We made certain assumptions about the prior distributions of the model parameters. Sensitivity analyses showed that these assumptions have a small impact on the final estimates of abundance, but can have a strong effect on the uncertainty around estimates, on future population trajectories, and on our interpretation of parameter values. For instance, point estimates of stock size were little influenced by changes in the hyper-parameter αs used in the prior distribution of the survey error. Their 95% CI, on the other hand, increased markedly with increasing values of α (which increase the CV of survey estimates). In other words, postulating higher uncertainty around aerial survey estimates also increased the uncertainty around model estimates. However, we note that the model was effective in reducing our uncertainty around our estimates of walrus abundance.

POPULATION MODELLING AND PARAMETER ESTIMATES

The estimated shape of the density-dependent parameter (θ) was well updated from its flat prior distribution in the HBDS model. The median value of 3.3 (HBDS model), was slightly higher than median values of 2.7 to 2.9 for walrus in Greenland, but were well within the 90% Credibility Intervals (Witting and Born 2005), resulting in Maximum Sustainable Yield levels at around 67% of K. On the other hand, theta values in the Foxe Basin model were not updated, indicating that there was insufficient information in the model to modify these values, which is not surprising, since the model shows a flat trajectory over the last 60 years There is some discussion concerning the maximum annual growth rate of walrus populations (see Materials and Methods), but 1.08 has been used as a default. We fixed this parameter, but realized growth rates were determined by both the shape parameter (θ) and the model estimates of population abundance in relation to K, with the result that the effective growth rate was normally much lower than the default. The model provided estimates of K, but we are unable to say how realistic these estimates might be. Recent efforts to reconstruct catch histories (Stewart et al. 2014) for some stocks may provide an opportunity to reconstruct pre-exploitation estimates of the population, which, although they may not be the same as current K, would still provide insights into possible carrying capacity levels.

The numbers of animals struck and lost are an important input into the models. Several estimates of Struck and Lost have been reported in the literature (see above), but these have been determined from different harvests in different areas and different time periods. The struck-and-lost factor was introduced into the model assuming a beta distribution, with a prior value of 42.2% (95% CI 12–78%), that we have used for Nunavik beluga. This is not to say that struck and lost rates for beluga and walrus are the same, but the beluga example provided suitable information that could be introduced into the model as a prior. When modelled for the

HBDS walrus stock, the prior was updated from a mean of 42% to a mean of 35% (95% CI=23 to 45%), which is comparable to a quasi-default value of 0.3 used by NAMMCO (2006). This posterior was subsequently used as prior in the Foxe Basin walrus models, but showed little modification from its prior values. This could suggest that the struck and lost distributions are similar between the two areas, and between studies, which is possible, but could also be explained by the fewer survey points flown in the Foxe Basin within a more restricted period, and a flat population that does not bring enough information to update the struck and lost parameters. One final consideration is that although defined as the proportion of animals that are struck and not recovered, this factor also include the effects of under-reporting (of which struck-and-lost is a subset).

In the HBDS model, K was moderately correlated with the struck and lost parameter, negatively correlated with the initial population size and had a small correlation with the abundance estimate for 2014. In the Foxe Basin models, a strong correlation was only observed between the carrying capacity parameter (K) and the 2014 estimate of population size. Overall, these correlations indicate that the historical population has remained close to carrying capacity, or because of a lack of a strong change, our modelling approach cannot provide credible information as to the actual values of these parameters. However, any independent estimation of the value of one or more of these parameters from a dedicated field program would increase our confidence in the estimation of the others as well as the accuracy of future projections.

POPULATION TRAJECTORY AND HARVEST LEVELS UNDER THE PRECAUTIONARY APPROACH

The HBDS model Run 1 assumed that animals that were surveyed in Hudson Strait in March–April 2012, and during the surveys flown during July–September in other years were available to harvesters living in Nunavik communities north of Inukjuak, the northwestern and northeastern Hudson Bay communities, Coral Harbour, Nunavut communities in Hudson Strait, and along the east coast of Baffin island. Walrus counts and harvests from Greenland, with which this stock is shared were not included. There is some movement between areas, but the level of exchange is not well understood. The surveys of the northern Hudson Bay-Hudson Strait area resulted in a population estimate of 7,000 (95% CI 4,100–10,800, rounded to the nearest 100). A 2007 survey of the east Baffin component of the HBDS stock resulted in an estimate of 2,500 (95% CI=1,800–3,500) for that region. It is not possible at the current time to add the two estimates together because of the seven year difference in timing of the surveys and because of uncertainty in the extent of movement between Greenland, east Baffin Island and Hudson Strait. If the late summer-early autumn surveys of Hudson Strait-Hudson Bay represent the population harvested by hunters in this area, then perhaps modeling east Baffin and Greenland haulouts separately, as has been done to date is adequate (e.g., Witting and Born 2005, 2014).

Additional runs of the HBDS model excluded surveys flown prior to 1988. Excluding surveys from the 1970s, 60s and 50s essentially resulted in the model fitting to only two points, with a slightly higher estimate of the population in 2014 than was obtained using the more complete dataset. This also resulted in a higher estimate for PBR due to the higher estimate of population size as well as a slightly lower level of uncertainty associated with the population estimate. The earlier surveys did not cover as large an area as the surveys flown after 1988, but they did survey the main haulout sites and provided the model with useful information to improve fitting and updating of model priors such as K, theta, the starting population and struck and lost. Including these surveys indicated that the population was probably greater than it is today, and had probably declined after the 1950s, which is more in line with our understanding of the status of walrus in this area (e.g., see Loughrey 1959, Mansfield 1962).

The model did not fit well to the 1976 and 1977 data. Unlike the other surveys which were based on only one or two counts of important haulout sites, the July–August, 1976–1977 estimates were mean counts from multiple surveys carried out over a 2 month period in the Southampton-Coats Island area. These counts were highly variable (Mansfield and St. Aubin 1991), reflecting the considerable variability in walrus haulout behaviour which we likely have not captured very well in our analysis of walrus counts (Doniol-Valcroze et al. 2016). Nonetheless, they provide useful information to the model. The model shows that the HBDS stock declined from the 1950s, reaching a minimum in the early 1990s, and is likely to be increasing under current reported harvests, while the Foxe Basin model suggest that there has been little change in stock size over the last 60 years. The HBDS benefitted from having more estimates of abundance that stretched out over many years. The Foxe Basin model had difficulties in reconciling the starting population size and environmental carrying capacity and there was a strong correlation between K and the model estimate of the 2014 population size. This may be linked to the fact that the first aerial survey of Foxe Basin was flown in 1982, but we incorporated into the model, harvest data that extended back to 1954, which may have provided the model with too much flexibility prior to the onset of the survey time series. We will continue to explore possible factors that might be affecting this model, but with no strong trend in harvests over the last 60 years, no clear trend in abundance, limited survey effort that is more constrained in time (compared to the HBDS model), there may not be enough information to inform the Foxe Basin model further. Thus this model believes that the current population is near stock carrying capacity, with little change occurring over the last 60 years.

In signing the United Nations Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, Canada has committed to managing fisheries resources to maintain or restore stocks to levels capable of producing maximum sustainable yield and to apply the precautionary approach with stock specific reference points. A precautionary approach framework was developed and implemented for Atlantic seals in 2003 (e.g., Hammill and Stenson 2003, 2007, 2013), while departmental guidelines were developed in 2006 (DFO 2006), and some additional discussions on the precautionary approach in Canada and in other jurisdictions has occurred within the marine mammal peer review group (e.g., Hammill and Stenson 2013; Doniol-Valcroze et al. 2013, Stenson et al. 2012). The DFO guidelines suggest that a precautionary reference level be set at 80% of the population size at Maximum Sustainable Yield (MSY), and a critical reference limit be set at 40% of the population size at MSY, which divides the management space into three zones, a healthy, cautious and critical zone. Where a stock lies with respect to the precautionary and critical reference limits, determines in which zone it lies. Within northern communities, harvesting is also governed by the different land-claim agreements, which tend to reflect two objectives:

i) subsistence harvesting can only be limited if there is conservation concern;
ii) harvesting is governed by the Principles of Conservation, which includes:
    a. the maintenance of the natural balance of ecological systems;
    b. the protection of wildlife habitat; the maintenance of vital, healthy, wildlife populations capable of sustaining harvesting needs as defined, and
    c. the restoration and revitalization of depleted populations of wildlife and wildlife habitat.

In the absence of a Precautionary Approach framework for walruses, we used two approaches to illustrate the risk of different harvest levels not respecting the management objectives we identified. We specifically tested the risk of a range of harvest levels not respecting a management objective of sustainable yield, where sustainable yield was defined as the number of animals that can be removed, in this case over a ten-year period, without resulting in the population declining below 2014 levels. In a second approach we assumed that the management objective was to maintain the population above the level that results in MSY. We estimated acceptable levels of removals using population model outputs as data inputs for the PBR formula and compared these with PBR estimates from the most recent survey (Hammill et al. 2016a, b) We also incorporated the Struck and Lost posterior mean into the PBR estimate to provide a range of PBR values. Looking at the Hudson Bay Davis Strait stock, both the sustainable yield and PBR methods indicated that current harvests are likely to respect both of the identified management objectives here. The PBR indicated that hunters could remove up to 190 animals after taking into account struck and lost. Unlike what is normally done, using model outputs to calculate the PBR means that, this calculation benefits from the information contained in the full survey series and catch records. The model estimate of PBR is higher than the PBR estimate from the aerial survey, which including struck and lost had a PBR of 126, for F_R of 1. The difference results from the lower CV associated with the population model estimate of the 2014 walrus population. For example the CV associated with the survey estimate of the population size is 0.58. The CV associated with the estimate of population size that is obtained from the population model is 0.23. In other words, the higher precision of the model estimate, which benefits from additional information compared to traditional PBR calculations, could result in a larger allowable harvest while still adhering to the same precautionary principles.

For the Foxe Basin stock, there were major differences in allowable harvests between the sustainable yield harvest estimates and those obtained from PBR. These differences arise from the underling differences in management objectives between the two approaches and where the two stocks lie with respect to estimated environmental carrying capacity. The Foxe Basin stock appears to be close to K. Owing to density-dependent factors affecting the dynamics of the stock, this means that the effective rate of increase of the population was less than 2%. To maintain a constant population, only about 2% of the resource was potentially available to harvesters if the management objective was that of sustainable yield. However, the management objective for PBR is to maintain a population above MSY. For walrus, PBR assumes that the rate of increase is fixed at ½ of the maximum rate of increase, which for walrus we defined as 4% (50% of 0.08), resulting in a PBR estimate of 290 animals. The comparable estimates of PBR from the aerial surveys with F_R=1 (i.e., after taking into account struck and lost) were 206 using the 2010 survey and 269 using the 2011 survey estimate. The difference is due to the lower CV in the 2014 estimate from the model (CV=0.20), than from the surveys alone (CV=0.43).

An alternative to PBR is to estimate removals directly using the population model and to provide an estimate of the probability or ‘risk’ that different harvest levels will respect the management objective. Assuming the PBR default that MSY occurs at 0.5K, then the model indicates that yearly harvests of 233 walruses from the HBDS stock would have a 95% probability of remaining above MSY after 10 years. Using the same approach to estimate harvests in Foxe Basin, then harvests of 418 would have a 95% probability of the population remaining above MSY, if MSY is set at 0.5 of K. Thus, one of the values of the population model approach is that the probability of respecting the management objectives can be presented and discussed in a more explicit manner than is possible using the PBR formula only.

In this study, a population model was fitted to very uncertain survey data, collected over the last 60 years, using Bayesian methods, to provide inference into the impacts of harvesting and insights into current abundance. The model has been developed to include the possibility that some communities may be harvesting from different stocks. However, for the simulations presented here, we assumed a single stock composition of the harvest in each model i.e., Igloolik and Hall Beach only harvested from the Foxe Basin stock, and communities in Ungava Bay, Hudson Strait, northeastern Nunavik, and northern Hudson Bay only harvested from the northern Hudson Bay component of the Hudson Bay-Hudson Strait stock, because the amount of exchange between the different stocks is not known. As more information becomes available, this feature can easily be ‘switched’ on.

The model can also be used to provide a risk evaluation approach in evaluating whether different harvest or other removal scenarios (e.g., mortality due to ship strikes) will respect management objectives. Compared to the simplistic approach of PBR, the integrated population model improves our understanding of the dynamics of the population and helps to identify underlying uncertainties in the assessment that require additional work.

An important factor in any assessment is recent data on abundance. The HBDS stock was surveyed in 2014, but the Foxe Basin stock was last surveyed in 2011. Model uncertainty increases with increasing time since the last survey, which affects our ability to evaluate the impact of harvesting on the population. Thus new surveys will not only reduce current uncertainty, they will also, over time, reduce our reliance on the ‘historical’ surveys as new data are incorporated into the model.

In this study, we assumed that the proportion of animals hauled out was fixed and that the error around its estimate could be described using a binomial distribution. However, others have shown that haulout behaviour is more complex and variable than can be represented using a binomial distribution (Udevitz et al. 2009; Lydersen et al. 2008; Doniol-Valcroze et al. 2016). Trying to incorporate this uncertainty directly into the fitting process is one direction to try to improve the model. Struck and lost is an important source of uncertainty in marine mammal hunts. Improving information on struck and lost will not only improve model inference, related to this parameter, but may also reduce uncertainty in other model parameters as well. We did not examine the impacts of non-reporting. From the perspective of the model, non-reporting comprises an important subset of the struck and lost parameter, but in any harvest management, an understanding of actual removals is crucial. The impact of non-reporting is to increase uncertainty associated with struck and loss levels, which will result in more conservative estimates of acceptable take levels. Finally, we modelled Foxe Basin and HBDS walrus separately, assuming that they form two discrete stocks and that community harvests were assigned to the appropriate stock. Within the model, it is easy to include uncertainty related to stock identity of community harvests, but currently data are not available for this parameter.

LITERATURE CITED

Born, E.W., Gjertz, I. and Reeves, R.R. 1995. Population assessment of Atlantic walrus. Norsk Polarinst. Medd. 138: 100 p.

Brooks, S. P. and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. J. Comput. Graph. Stat. 7:434–455.

Brooks, S., King, R. and Morgan, B. 2004. A Bayesian approach to combining animal abundance and demographic data. Anim. Biodivers. Conserv. 27: 515–529.

Buckland, S.T., Newman, K. B., Fernandez, C., Thomas, L. and Harwood, J. 2007. Embedding population dynamics models in inference. Statist. Sci. 22: 44–58.

Chivers, S.J. 1999. Biological indices for monitoring population status of walrus evaluated with an individual-based model. *In* Marine mammal survey and assessment methods. Edited by G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald, and D.G. Robertson. A.A. Balkema, Rotterdam, Holland. 287 p.

Cooke J., Leaper, R., Wade, P., Lavigne, D. and Taylor, B. 2012. Management rules for marine mammal populations: A response to Lonergan. Mar. Policy 36, 389–92.

COSEWIC. 2006. COSEWIC assessment and update status report on the Atlantic walrus *Odobenus Rosmarus rosmarus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ix+65 pp.

de Valpine, P., and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. Ecol. Monogr. 72: 57–76.

DFO. 2002. Atlantic Walrus. DFO Sci. Stock Status Rep. E5-17, 18, 19, 20.

DFO. 2006. A Harvest Strategy Compliant with the Precautionary Approach. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2006/023

Doniol-Valcroze, T., Gosselin, J.-F., and Hammill, M.O. 2013. Population modeling and harvest advice under the precautionary approach for eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2012/168. iii + 31 p.

Doniol-Valcroze, T., Gosselin, J.F., Pike, D., Lawson, J., Asselin, N., Hedges, K., and Ferguson, S. 2015a. Abundance estimates of narwhal stocks in the Canadian High Arctic in 2013. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/060. v + 36 p.

Doniol-Valcroze, T., Gosselin, J.-F., Pike, D., Lawson, J., Asselin, N., Hedges, K., and Ferguson, S. 2015b. Abundance estimate of the Eastern Canada – West Greenland bowhead whale population based on the 2013 High Arctic Cetacean Survey. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/058. v + 27 p.

Doniol-Valcroze, T., Mosnier, A., and Hammill, M.O. 2016. Testing estimators of walrus abundance: insights from simulations of haul-out behaviour. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/040. v + 18 p.

Elliot, R.E, Moulton, V.D., Raborn, S.W. and Davis, R. A. 2013. Hudson Strait marine mammal aerial surveys, 10 March to 2 April. Report prepared by LGL Ltd for Baffinland Iron Mines Corp. 107 p. (LGL Report No. TA8129-2. Prepared by LGL Limited, King City, ON for Baffinland Iron Mines Corporation, Toronto, ON. 87 p.)

Geweke, J. 1996. Evaluating the Accuracy of Sampling-based Approaches to the Calculation of Posterior Moments, *In* Bayesian Statistics 4 Edited by Bernardo, J.M., Berger, J.M., Dawid, A.P., and Smith, A.F.M. Oxford University Press:169–193.

Hammill,M.O. and Stenson, G.B. 2003. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals: A Discussion Paper. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/067.

Hammill, M.O. and Stenson, G.B. 2007. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals. ICES J. Mar. Sci. 64: 702–706.

Hammill, M.O. and Stenson, G.B. 2013. A Discussion of the Precautionary Approach and its Application to Atlantic Seals. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/030. v + 25 p.

Hammill. M.O., Mosnier, A., Gosselin, J.-F., Higdon, J.W., Stewart, D.B., Doniol-Valcroze, T., Ferguson, S.H., and Dunn, B. 2016a. Estimating abundance and total allowable removals for walrus in the Hudson Bay-Davis Strait and south and east Hudson Bay stocks. DFO Can. Sci. Advis. Sec.Res. Doc. 2016/036. v + 37 p.

Hammill, M.O., Blanchfield, P., Higdon, J.W., Stewart, D.B., and Ferguson, S.H. 2016b. Estimating abundance and total allowable removals for walrus in Foxe Basin. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/014. iv + 20 p.

Hoyle, S. and Maunder, M. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. Anim. Biodivers. Conserv. **27**: 247–266.

Innes, S. and Stewart, R.E.A. 2002. Population size and yield of Baffin Bay beluga (*Delphinapterus leucas*) stocks. NAMMCO Sci. Publ. 4: 225–238.

King, R., Gimenez, O., Morgan, B., and Brooks, S. 2010. Bayesian Analysis for Population Ecology. Chapman & Hall / CRC Press. 442 p.

Lonergan, M. 2011. Potential biological removal and other currently used management rules for marine mammal populations: A comparison. Mar. Policy. 35: 584–589.

Lonergan, M. 2012. The targets of management rules for marine mammal populations require justification: A reply to Cooke et al. Mar. Policy. 36: 1188-1190. doi:10.1016/j.marpol.2012.02.010

Loughrey A.G. 1959. Preliminary investigation of the Atlantic walrus *Odobenus rosmarus rosmarus* (Linnaeus). Can. Wildl. Serv. Bull. (Ott.) (Series 1) 14: 123 p.

Lydersen C, Aars, J., and Kovacs, K.M. 2008. Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. Arctic, 61: 119–128.

Mansfield, A.W. 1962. Present status of the walrus population at Southampton and Coats islands, pp. 41-52 (No. 16). In H.D. Fisher (In Charge), Fisheries Research Board of Canada, Arctic Unit (Montreal, Quebec), Annual Report and Investigator's Summaries, April 1, 1961 to March 31, 1962. [Available online from Fisheries and Oceans Canada libraries]

Mansfield A.W. 1973. The Atlantic walrus *Odobenus rosmarus* in Canada and Greenland. IUCN (Intl Union Conserv. Nat. Nat. Resour.) Publ. New Ser. Suppl. Pap. 39: 69–79.

Mansfield, A.W., and St. Aubin, D.J. 1991. Distribution and abundance of the Atlantic walrus *Odobenus rosmarus rosmarus,* in the Southampton Island-Coats Island region of northern Hudson Bay. Can. Field-Nat. 105: 95–100.

Milner-Gulland, E.J., Shea, K., Possington, H., Coulson, T., and Wilcox, C. 2001. Competing harvesting strategies in a simulated population under uncertainty. Anim. Conserv. 4: 157–167.

Mosnier, A, Doniol-Valcroze, T., Gosselin, J.-F., Lesage, V., Measures, L.N., and Hammill, M.O. 2015. Insights into processes of population decline using an integrated population model: the case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). Ecol. Model. 314: 15–31.

NAMMCO. 2006. NAMMCO (North Atlantic Marine Mammal Commission) Scientific Committee Working Group on the stock status of walruses in the North Atlantic and adjacent seas, Final Report. Copenhagen, 11-14 January 2005. 27 p.

Orr J.R., Renooy, B., and Dahlke, L. 1986. Information from hunts and surveys of walrus (*Odobenus rosmarus*) in northern Foxe Basin, Northwest Territories, 1982–1984. Can. Manuscr. Rep. Fish. Aquat. Sci. 1899: iv + 29 p.

Pella, J.J., and Thomlinson, P.K. 1969. A generalized stock production model. Bull. Inter-Amer. Tropical Tuna Comm. 13: 420–496.

Plummer, M. 2003. A program for analysis of Bayesian graphical models using Gibbs sampling, in: Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Vienna, Austria.

Schaub, M., and Abadi, F. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152: 1–11.

Sease, J.L., and Chapman, D.G. 1988. Pacific walrus *Odobenus rosmarus divergens*. *In* Selected marine mammals of Alaska Species account with research and management recommendations. Edited by J. W. Lentfer. Marine Mammal Commission, Washington, D.C. 275 p.

Stenson, G.B., Hammill, M.O., Ferguson, S., Stewart, R.E.A., and Doniol-Valcroze, T. 2012. Applying the precautionary approach to marine mammals in Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/107. ii + 15 p.

Stewart, R.E.A., and Hamilton, J.W. 2013. Estimating total allowable removals for walrus (*Odobenus rosmarus rosmarus*) in Nunavut using the potential biological removal approach. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/031. iv + 13 p.

Stewart, R.E.A., Hamilton, J.W., and Dunn, J.B. 2013. Results of Foxe Basin walrus (*Odobenus rosmarus rosmarus*) surveys: 2010-2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/017. iv + 12 p.

Stewart, D.B., Higdon, J.W., Reeves, R.R., and Stewart, R.E.A. 2014. A catch history for Atlantic walruses (*Odobenus rosmarus rosmarus*) in the eastern Canadian Arctic. NAMMCO Sci. Publ. 9: 219–314.

Taylor B.L., De Master, D.P. 1993. Implications of non-linear density dependence. Mar. Mamm. Sci. 9: 360–371.

Taylor, R.L., and Udevitz, M.S. 2015. Demography of the Pacific walrus (*Odobenus rosmarus divergens*): 1974–2006 Mar. Mamm. Sci. 31: 231–254.

Taylor, B.L., Wade, P.R., De Master, D.P., and Barlow, J. 2000. Incorporating uncertainty into management models for marine mammals. Biol. Cons. 14: 1243–1252.

Taylor, B.L., Martinez, M., Geordette, T., Barlow, J., and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. Mar. Mamm. Sci. 23: 157–175.

Trzcinski, M.K., Mohn, R., and Bowen, W.D. 2006. Continued Decline Of An Atlantic Cod Population: How Important Is Gray Seal Predation? Ecol. Appl. 16(6): 2276–2292.

Udevitz, M.S., Jay, C.V., Fischbach, A.S., and Garlich-Miller, J.L. 2009. Modeling haul-out behaviour of walruses in Bering Sea ice. Can. J. Zool. 87(12): 1111–1128.

Wade, P. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar. Mamm. Sci. 14: 1–37.

Wade, P. R. 2000. Bayesian Methods in Conservation Biology. Conserv. Biol. 14: 1308–1316.

Witting, L., and Born, E.W. 2005. An assessment of Greenland walrus populations. ICES J. Mar. Sci. 62: 266–284.

Witting, L., and Born, E.W. 2014. Population dynamics of walruses in Greenland. NAMMCO Sci. Publ. 9: 191–218.

TABLES

Table 1. Abundance observations from Nottingham/Fraser/Salisbury island complex and the Walrus – Coats island complex. The SE of the adjusted number was calculated by combining the variance of the abundance estimates with the variance of proportion hauled out using the Delta method, i.e, $SE_{adj} = N_{adj}\sqrt{\frac{SE_N{}^2}{N^2} + \frac{SE_P{}^2}{P^2}}$

Location / Survey type	Date	Number (SE)	Proportion hauled out (SE)	Adjusted number (SE)	Source
Hudson Strait to Southampton Island	Sept 2014	2144	0.30 (0.173)	7147 (4122)	Hammill et al. 2015
Hudson Strait	Mar-Apr 2012	55		5254 (1591)	Elliot et al. 2013
Walrus-Coats Island-Southampton Island					
Aerial surveys	August 1954	2900 (435)	0.30 (0.173)	9667 (5760)	Loughrey 1959
Aerial/boat surveys	Aug 1961	2650	0.30 (0.173)	8833 (5094)	Mansfield 1962
Aerial surveys	July-Aug. 1976	254-1491 (Mean=820 SE=442)	0.30 (0.173)	2733 (2156)	Mansfield and St Aubin 1991
Aerial surveys	July –Aug 1977	6-2171 (Mean=65, SE=670)	0.30 (0.173)	2707 (2692)	Mansfield and St Aubin 1991
Aerial surveys	Aug 1988	757+92	0.30 (0.173)	2830 (1632)	[1]Richard 1993
Aerial surveys	July 1989	1231+97	0.30 (0.173)	4427 (2553)	[1]Richard 1993
Aerial surveys	Aug 1990	1373+461	0.30 (0.173)	6113 (3526)	[1]Richard 1993

[1] Richard, P.R. 1993. Summer distribution and abundance of walrus in northern Hudson Bay, western Hudson Strait and Foxe Basin :1988-1990. AFSAC meeting 17-18 February 1993. Background report. 21 p.

Table 2. Survey year, count/estimate, proportion of animals hauled out, and adjusted counts for walrus in Foxe Basin. Source where the original count data can be found, but counts were adjusted as outlined by Hammill et al. 2016b. The SE of the adjusted number was calculated by combining the variance of the abundance estimates with the variance of proportion hauled out using the Delta method, i.e., $SE_{adj} = N_{adj}\sqrt{\frac{SE_N{}^2}{N^2} + \frac{SE_P{}^2}{P^2}}$

Year	Number (N)	SE (N)	Proportion hauled out	SE (P)	Adjusted Number	SE	Source
1983	2,722		0.37	0.16	7,357	3,182	Orr et al. 1986
1988	5,128	4,390	0.37	0.16	13,859	13,293	[1]Richard 1993
1989	5,510	1,644	0.37	0.16	14,892	7,824	[1]Richard 1993
2010	3,861		0.37	0.16	10,435	4,513	Stewart et al. 2013
2011	5,945		0.37	0.16	16,068	6,949	Stewart et al. 2013
2011	4,484		0.37	0.16	12,119	5,241	Stewart et al. 2013
2011	(4,484+5,945)/2	1033	0.37	0.16	14,093	6,704	2011 data combined

[1] Richard, P.R. 1993. Summer distribution and abundance of walrus in northern Hudson Bay, western Hudson Strait and Foxe Basin :1988-1990. AFSAC meeting 17-18 February 1993. Background report. 21 p.

Table 3. Adjusted harvest statistics for communities harvesting walrus from the Hudson Bay-Davis Strait for the period 1954–2014. In years where there were no reports, the five year average harvest was used to replace the blank cell. Data from communities in Ungava Bay, and Hudson Strait, plus Akulivik, Coral Harbour, Repulse Bay, Chesterfield Inlet, Rankin Inlet and Arviat.

Year	Harvest	Year	Harvest	Year	Harvest
1954	603	1969	284	1995	193
1955	528	1970	307	1996	187
1956	462	1971	328	1997	120
1957	448	1972	310	1998	97,8
1958	543	1973	367	1999	66
1959	391	1974	377	2000	97
1960	426	1975	454	2001	81
1961	400	1976	244	2002	139
1962	300	1977	279	2003	90
1963	311	1978	198	2004	95
1964	324	1979	277	2005	111
1965	288	1980	339	2006	155
1966	338	1981	306	2007	118
1967	384	1982	352	2008	93
1968	311	1983	323	2009	93
1969	284	1984	233	2010	94
1970	307	1985	211	2011	88
1971	328	1986	273	2012	114
1972	310	1987	175	2013	59
1973	367	1988	243	2014	72
1974	377	1989	168		
1975	454	1990	211		
1976	244	1991	229		
1977	279	1992	187		
1978	198	1993	220		
1979	277	1994	194		

Table 4. Adjusted harvest statistics for Igloolik and Hall Beach which are assumed to be the only communities harvesting from the Foxe Basin stock for the period 1954–2014. In years where there were no reports, the five year average harvest was substituted.

Year	Harvest	Year	Harvest	Year	Harvest
1954	425	1978	138	2002	120
1955	154	1979	325	2003	199
1956	198	1980	187	2004	178
1957	79	1981	310	2005	190
1958	267	1982	300	2006	290
1959	195	1983	300	2007	89
1960	31	1984	210	2008	107
1961	58	1985	210	2009	159
1962	700	1986	151	2010	216
1963	202	1987	168	2011	136
1964	104	1988	185	2012	219
1965	550	1989	137	2013	175
1966	100	1990	178	2014	103
1967	108	1991	178		
1968	150	1992	295		
1969	200	1993	225		
1970	60	1994	201		
1971	62	1995	111		
1972	69	1996	146		
1973	103	1997	193		
1974	120	1998	213		
1975	50	1999	178		
1976	130	2000	262		
1977	218	2001	92		

Table 5. Prior distributions, parameters and hyper-parameters used in Hudson Bay-Davis Strait walrus population model "dist." denotes a hyper-parameter with its own prior distribution. The same parameters were used for the Foxe Basin Model except for the Struck and Loss parameter. In Foxe Basin, this parameter followed a Beta (2,4).

Parameters	Notation	Prior distribution	Hyper parameters	Values
Survey error (t)	εs_t	Log-normal	μ_s τ_s	0 dist.
Precision (survey)	τ_s	*Gamma*	α_s β_s	2.5 0.4
Process error (t)	εp_t	Log-normal	μ_p τ_p	0 dist.
Precision (Process)	τ_p	Gamma	α_p β_p	1.5 0.001
Density dependence Shape fusion	θ	Uniform	N_{upp} N_{low}	7 1
Struck-and-lost	SL	Beta	α_{SL} β_{SL}	3 4
Initial population	N_{1954}	Uniform	N_{upp} N_{low}	40,000 500
Carrying capacity	K	Uniform	N_{upp} N_{low}	40,000 500
Maximum annual growth rate	λ_{max}			1.08

Table 6a. Model outputs for the Hudson Bay-Davis Strait stock using all aerial survey and harvest data (Run 1). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	R-hat	N.eff
K	12901	6990	7021	8382	9739	14517	32417	1.002	2600
K.prior	17764	9964	1352	9137	17759	26402	34143	1.001	120000
Theta	3.3	1.6	1.1	2.0	3.0	4.5	6.7	1.001	19000
Theta.prior	4.0	1.7	1.1	2.5	4.0	5.5	6.8	1.001	120000
Deviance	162.6	2.5	159.3	160.9	162.1	163.8	169.0	1.001	120000
Prec.process	1502.9	1228	106.4	606.7	1185.8	2058.5	4654.3	1.001	35000
Prec.process.prior	1503.7	1226	107.2	607.3	1187.2	2058.9	4677.4	1.001	120000
Prec.surv	6.4	2.6	2.3	4.5	6.0	7.9	12.5	1.001	120000
Prec.surv.prior	6.2	3.9	1.0	3.3	5.4	8.3	16.0	1.001	120000
Startpop	10421	3513	6415	7931	9461	11919	19838	1.001	5900
Startpop.prior	15231	8505	1236	7852	15209	22573	29260	1.001	67000
Struck.and.lost	0.35	0.15	0.09	0.23	0.33	0.45	0.68	1.001	120000
Struck.and.lost.prior	0.43	0.17	0.12	0.30	0.42	0.55	0.78	1.001	120000
N2014	6980	1641	4137	5968	6879	7794	10753	1.001	50000

Table 6b. Model outputs for the Hudson Bay-Davis Strait stock excluding surveys flown before 1988 (Run 2). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
K	11430	5006	7038	8573	9954	12038	28899	1.0	3700.0
K.prior	17816	9934	1373	9259	17877	26421	34121	1.0	30000.0
Theta	3.4	1.8	1.1	1.8	3.1	4.9	6.8	1.0	22000.0
Theta.prior	4.0	1.7	1.2	2.5	4.0	5.5	6.9	1.0	50000.0
Deviance	88.9	2.4	86.1	87.2	88.3	89.9	95.3	1.0	39000.0
Prec.process	1506	1231	109	612	1190	2055	4724	1.0	50000.0
Prec.process.prior	1510	1238	109	606	1184	2065	4717	1.0	50000.0
Prec.surv	7.4	3.6	2.0	4.7	6.8	9.4	15.8	1.0	50000.0
Prec.surv.prior	6.2	4.0	1.1	3.3	5.4	8.3	16.0	1.0	50000.0
Startpop	9458	1832	6710	8082	9171	10585	13611	1.0	35000.0
Startpop.prior	15336	8517	1265	7993	15383	22712	29306	1.0	50000.0
Struck.and.lost	0.38	0.17	0.09	0.25	0.37	0.5	0.74	1.0	50000.0
Struck.and.lost.prior	0.43	0.17	0.12	0.3	0.42	0.55	0.78	1.0	50000.0
N2014	7437	1576	4579	6524	7387	8240	10737	1.0	33000.0

Table 6c. Model outputs for the Hudson Bay-Davis Strait stock including all surveys but harvests from east Baffin Island are excluded (Run 3). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

			Quantiles						
	Mean	SD	0.025	0.25	0.5	0.75	0.975	Rhat	n.eff
K	8076.6	2918.5	5676.4	6756.3	7529.8	8509.2	14934.3	1.001	16000
K.prior	17735.5	9969.1	1366.8	9085.7	17720.2	26359.8	34136.4	1.001	220000
Theta	3.2	1.6	1.1	1.8	2.8	4.3	6.7	1.001	67000
Theta.prior	4.0	1.7	1.1	2.5	4.0	5.5	6.9	1.001	220000
deviance	162.1	2.3	159.3	160.4	161.5	163.2	167.9	1.001	220000
prec.process	1499.7	1225.7	109.6	606.1	1184.0	2052.1	4654.9	1.001	210000
prec.process.prior	1501.4	1228.7	106.0	605.2	1181.7	2058.1	4677.0	1.001	220000
prec.surv	6.6	2.7	2.5	4.7	6.3	8.2	12.8	1.001	220000
prec.surv.prior	6.3	4.0	1.0	3.3	5.4	8.3	16.1	1.001	120000
Startpop	7446.3	1156.8	5510.9	6598.2	7328.1	8191.1	9959.0	1.001	220000
Startpop.prior	17739.9	9962.7	1361.5	9115.8	17739.0	26381	34136.1	1.001	220000
struck.and.lost	0.43	0.17	0.13	0.30	0.42	0.54	0.76	1.001	220000
struck.and.lost.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	220000
N2014	6356	1006	4634	5784	6288	6821	8496	1.001	190000

Table 7. Model outputs for the Foxe Basin stock. Mean, Standard deviation (SD), median, 25th and 75 th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation.

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	R-hat	N.eff
K	13583	2770	9466	11812	13195	14853	20030	1.00	120000
K.prior	20234	11383	1502	10384	20202	30115	38980	1.00	120000
Theta	3.4	1.4	1.1	2.4	3.4	4.4	6.3	1.01	120000
Theta.prior	3.4	1.4	1.1	2.4	3.4	4.4	6.3	1.01	40000
Deviance	96.88	2.03	94.53	95.41	96.39	97.81	102.11	1.00	100000
Prec.process	1497	1222	106	606	1182	2050	4663	1.00	10000
Prec.process.prior	1506	1225	109	611	1189	2064	4678	1.00	120000
Prec.surv	7.87	3.71	2.36	5.16	7.30	9.97	16.66	1.00	120000
Prec.surv.prior	6.24	3.95	1.03	3.34	5.42	8.27	16.05	1.00	120000
Startpop	11862	3297	4604	10229	12205	13905	17881	1.001	120000
Startpop.prior	20242	11402	1499	10345	20226	30168	39032	1.001	32000
Struck.and.lost	0.330	0.178	0.051	0.190	0.309	0.450	0.711	1.001	120000
Struck.and.lost.prior	0.334	0.178	0.052	0.194	0.315	0.455	0.717	1.001	120000
N2014	12489	2537	8574	10853	12158	13701	18489	1.00	120000

FIGURES

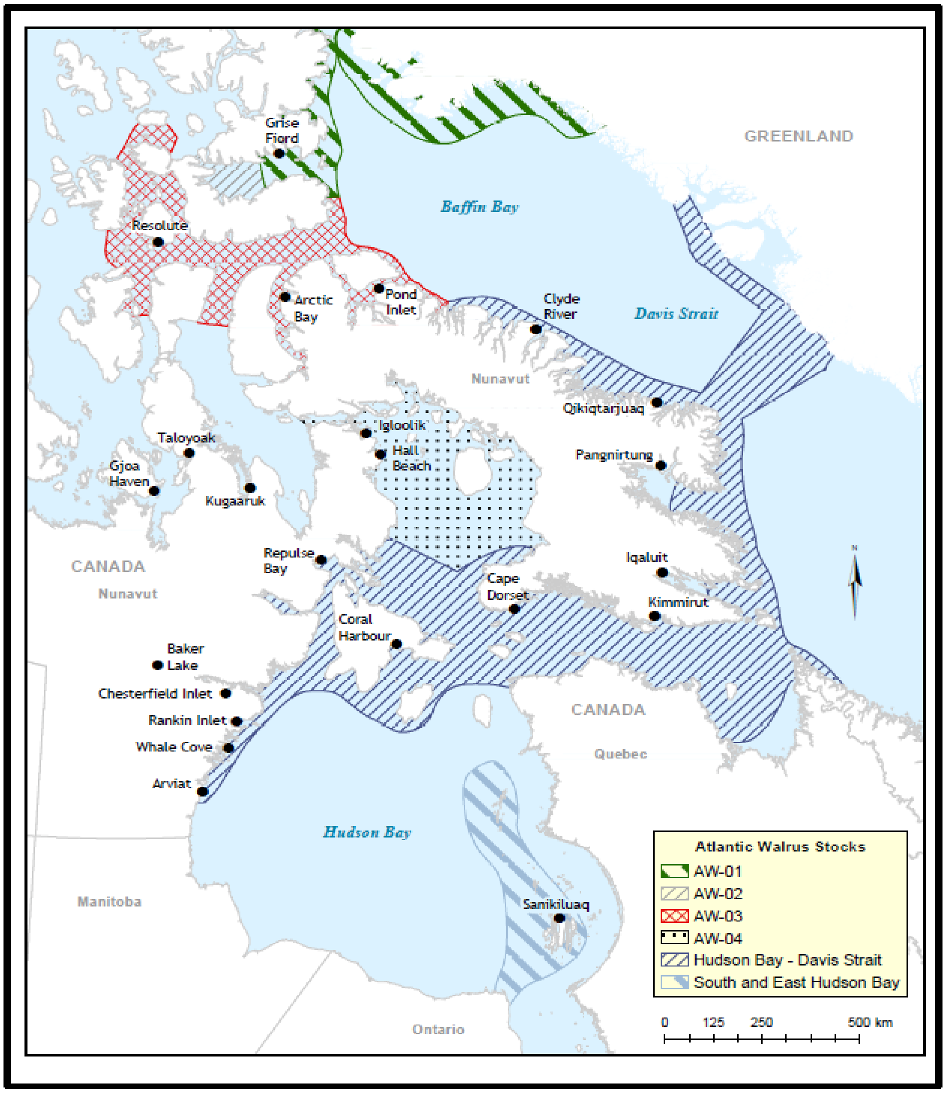

Figure 1. Location of Atlantic walrus stocks as identified by management units in the eastern Canadian Arctic. The stocks are Baffin Bay (AW-01). West Jones Sound (AW-02). Penny Strait-Lancaster Sound (AW-03). North and Central Foxe Basin stocks (AW-04). Hudson Bay-Davis Strait and South and East Hudson Bay stocks.

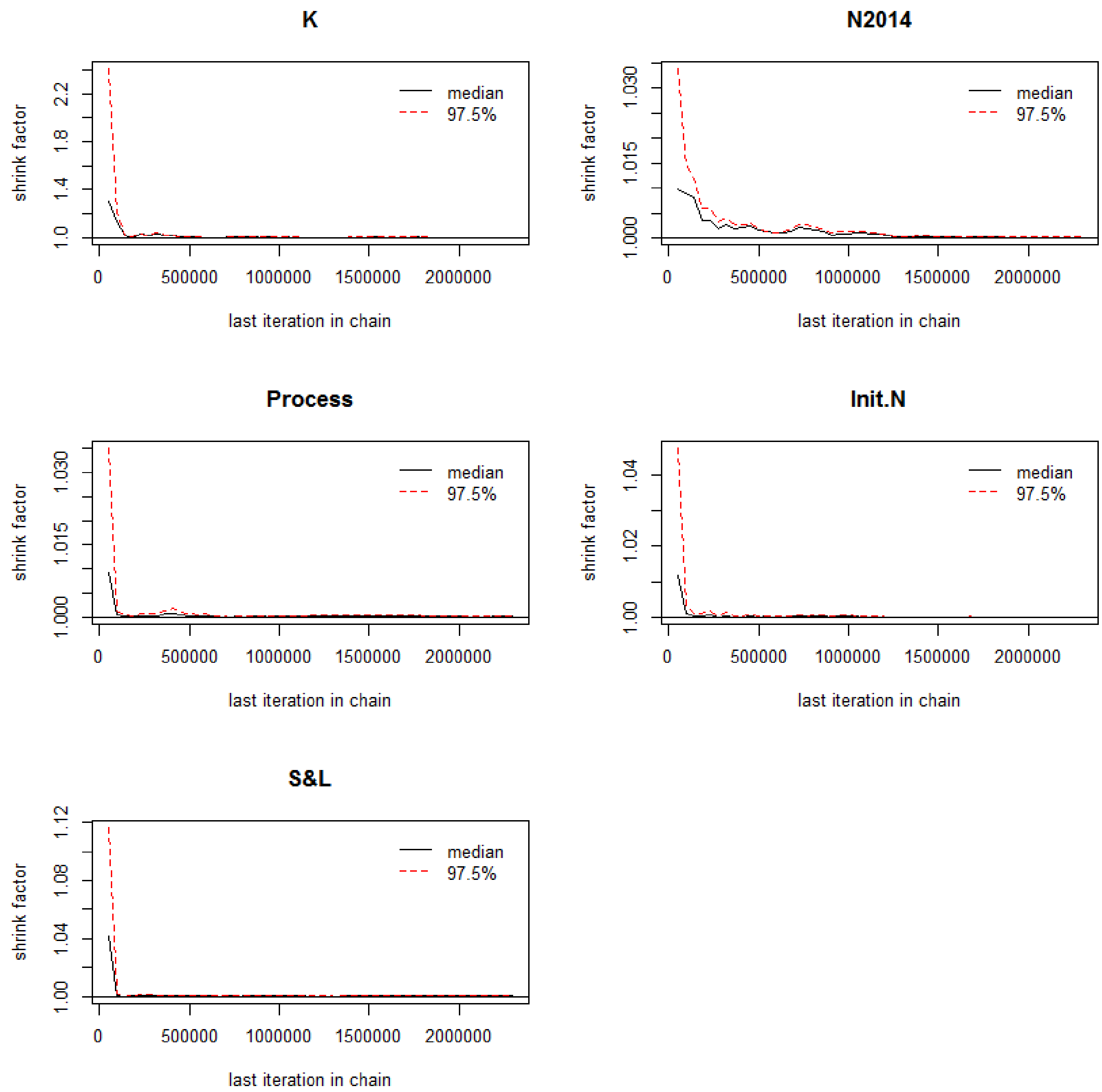

Figure 2a. BGR convergence diagnostic for carrying capacity (K), population size in 2014 (N2014), Process error, initial population (init.N) and Struck and Lost (S&L) for the five chains plotted for increasing numbers of iterations (up to 1.000.000). Values close to 1 indicate good convergence for the Hudson Bay-Davis Strait stock.

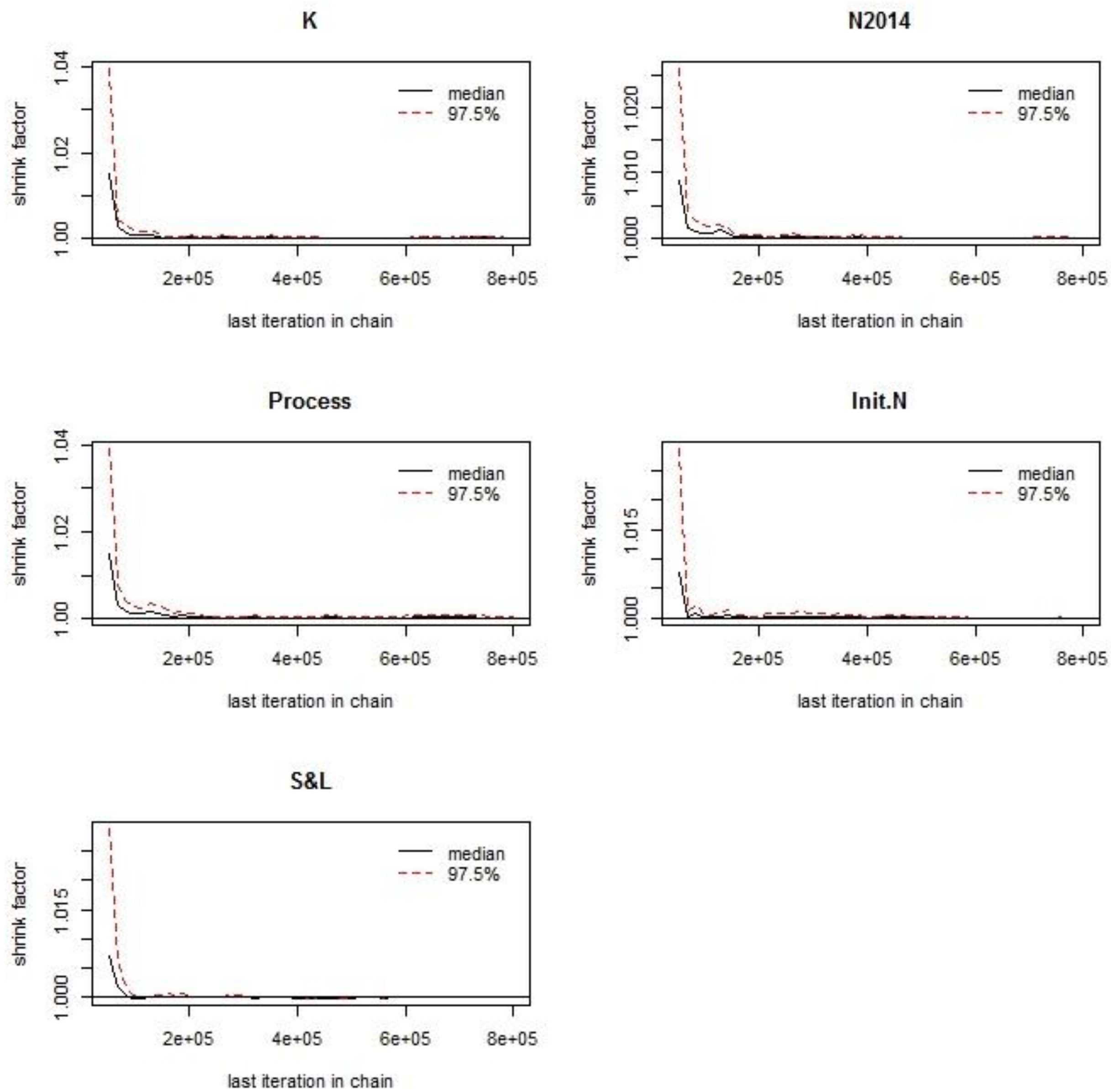

Figure 2b. BGR convergence diagnostic for the Foxe Basin stock with haulouts adjusted using a haulout proportion of 0.37. Variables shown include carrying capacity (K), population size in 2014 (N2014), process error, initial population (init.N) and Struck and Lost (S&L) for the five chains plotted for increasing numbers of iterations (up to 1.000.000). Values close to 1 indicate good convergence.

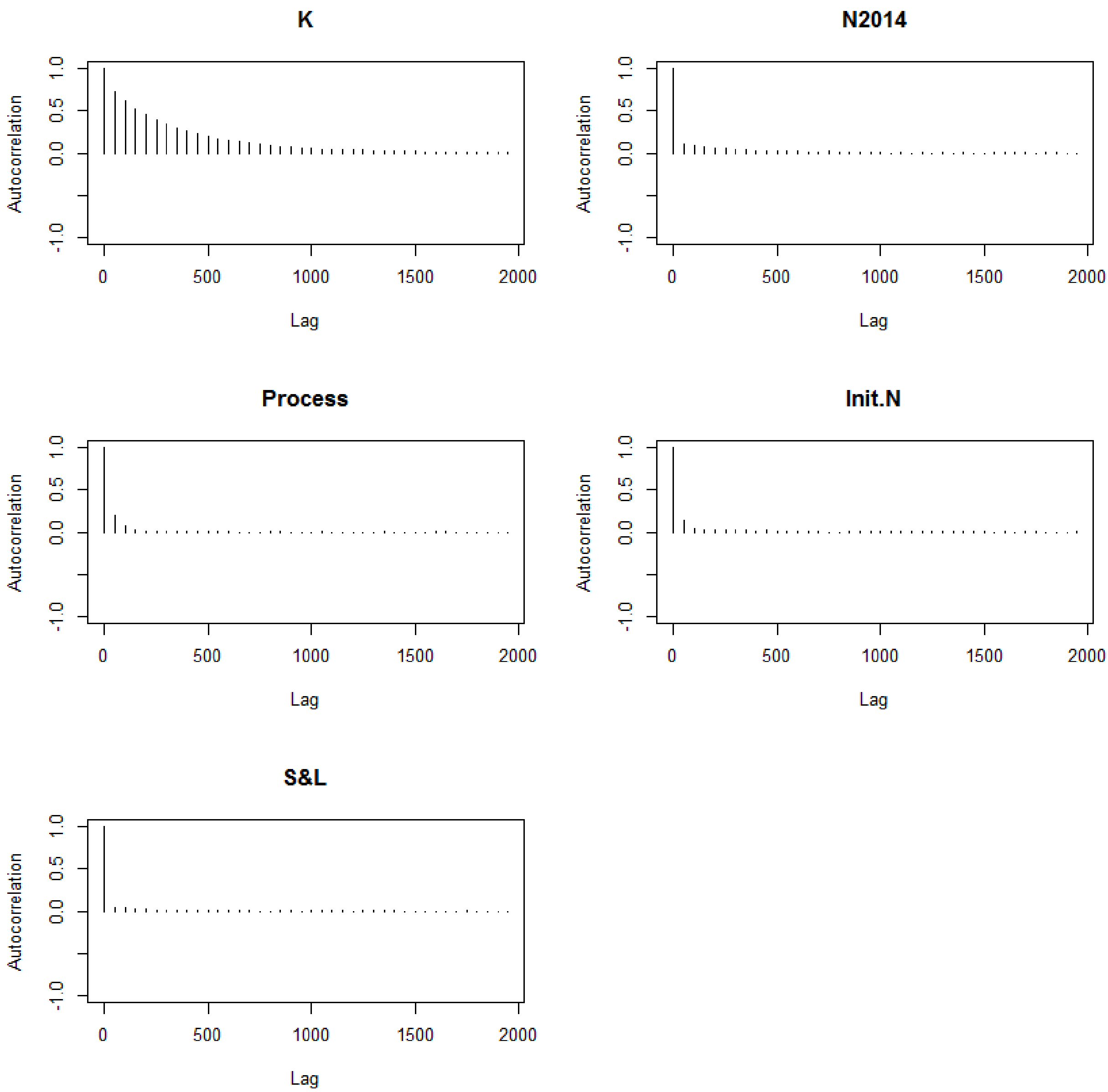

Figure 3a. Plots showing evidence for auto-correlation within each chain for variables carrying capacity (K), 2014 population estimate (N2014), process error, initial population size (init.N) and struck and lost (S&L) for the Hudson Bay-Davis Strait stock.

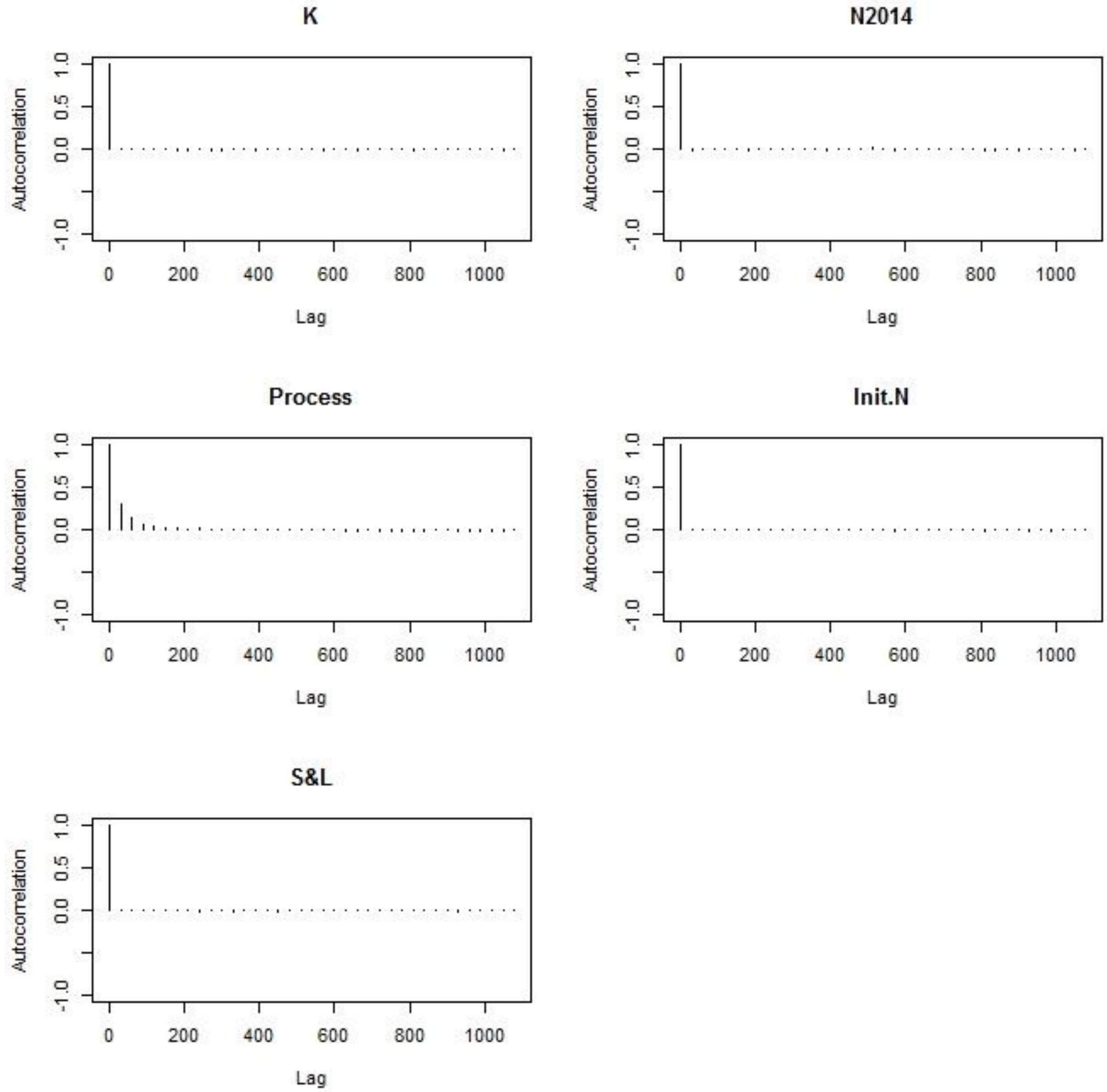

Figure 3b. Plots showing evidence for auto-correlation within each chain for variables carrying capacity (K), 2014 population estimate (N2014), process error, initial population size (init.N) and struck and lost (S&L) for Foxe Basin stock after adjusting counts using a haulout proportion of 0.37.

a) b)

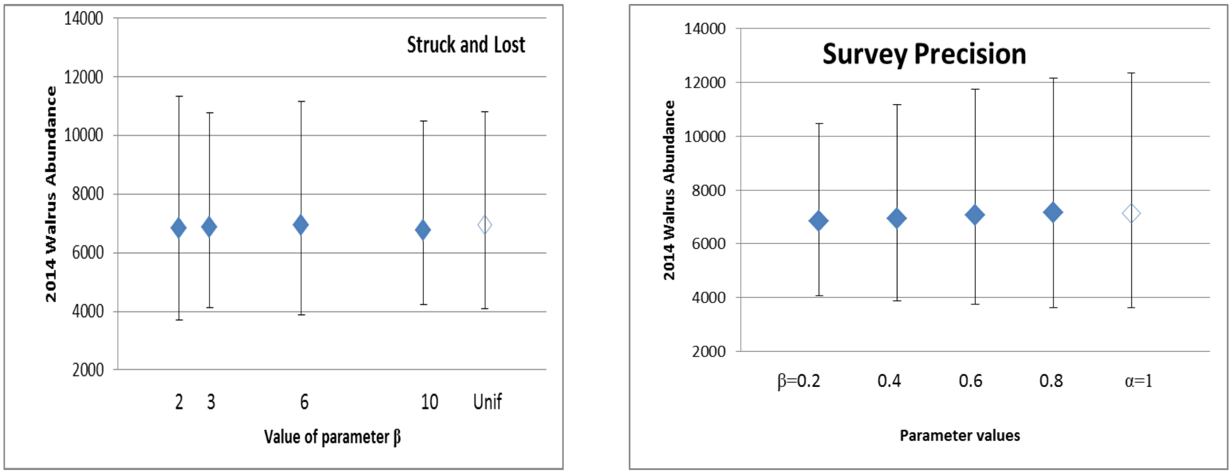

Figure 4. Sensitivity of median population estimates (diamonds) and 95% CI (bars) to the hyper-parameters used in prior distributions for Struck and Lost and Survey precision. a) Struck-and-lost factor (beta distribution (α. β). Closed diamonds: αsl = varies from 2 to 10. βsl was fixed at 4. Open diamond: Uniform distribution (0.2 to 0.7). b) Survey precision (Gamma (α. β). Closed diamonds: α s =2.5. β s =0.2 to 0.8. open circle: α s =1. β s =0.4. for the Hudson Bay-Davis Strait stock.

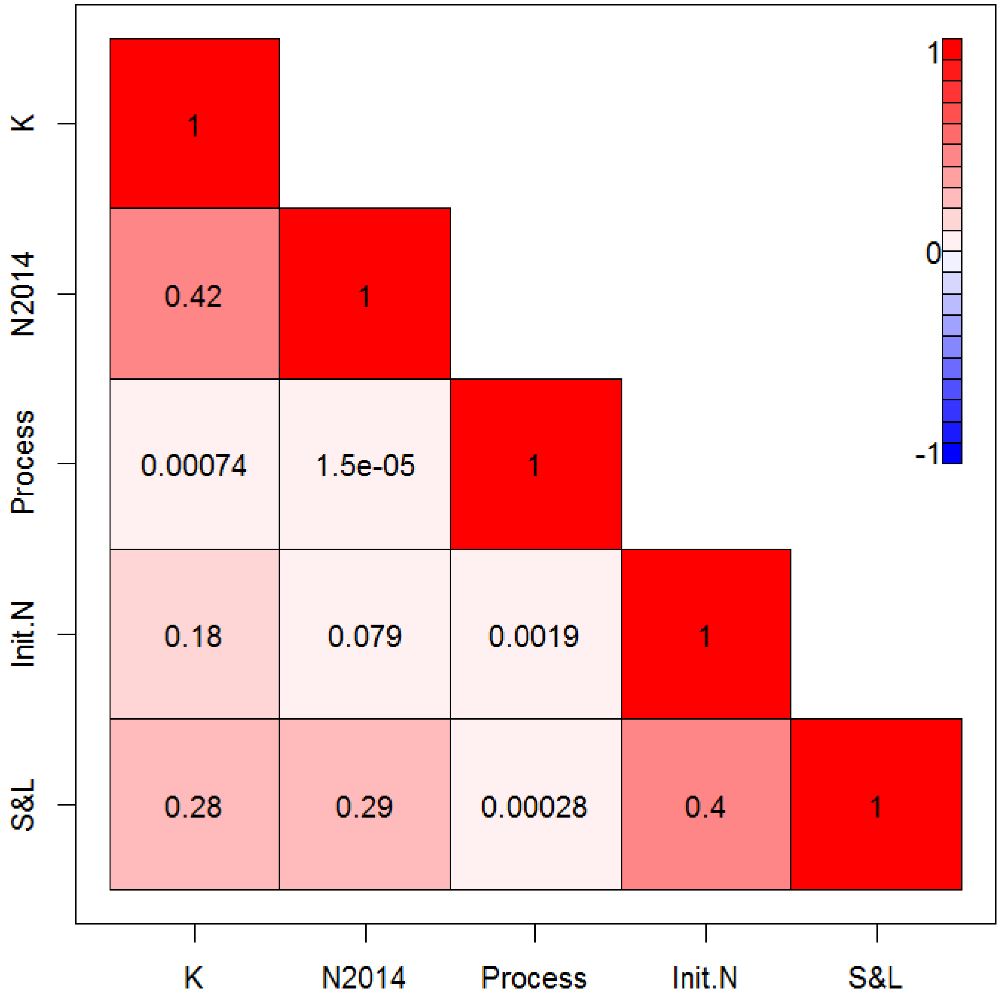

Figure 5a. Hudson Bay-Davis Strait stock model runs that included all survey data and reported harvests from all communities. Correlations are shown between model parameters carrying capacity (K), the 2014 population estimate (N2014), process error (Process), initial population size (Init.N), and struck and lost (S&L).

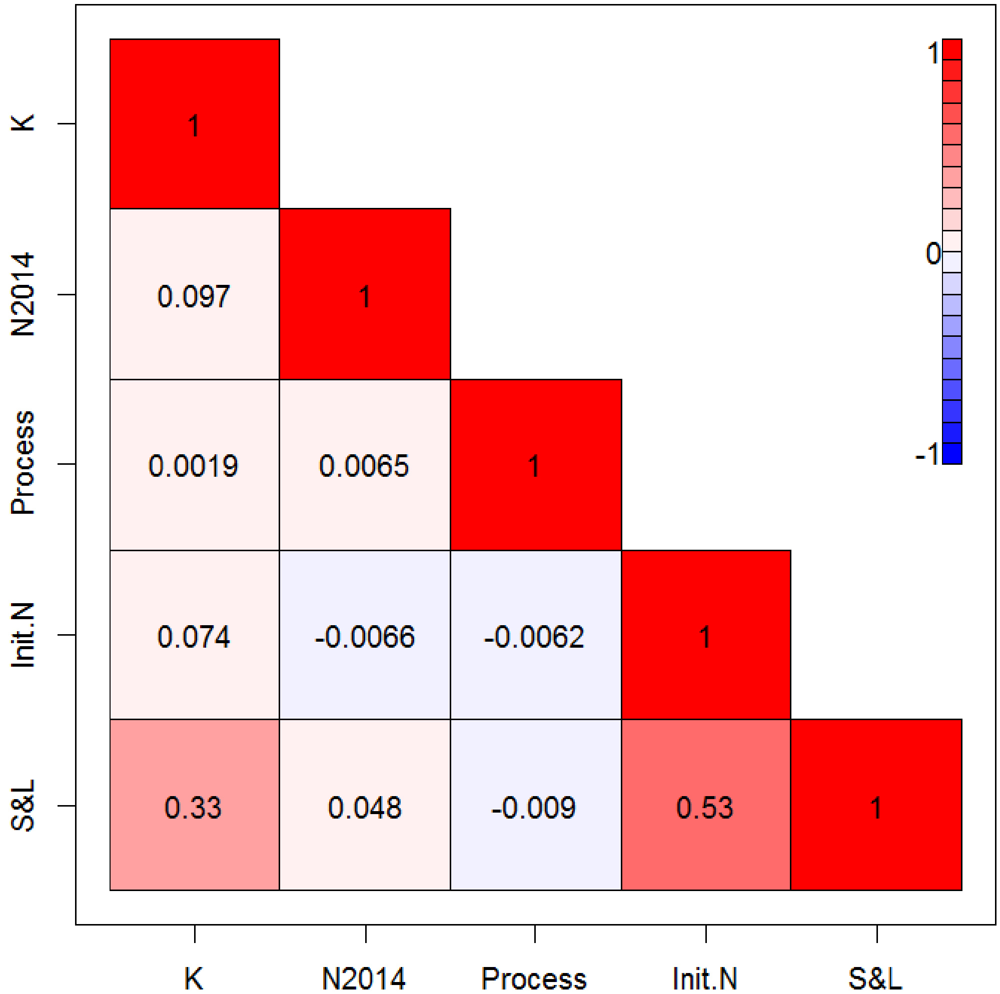

Figure 5b. Hudson Bay-Davis Strait stock model run with surveys flown before 1988 excluded. Correlations are shown between model parameters for variables carrying capacity (K), 2014 population estimate (N2014), process error (Process), initial population size (init.N) and struck and lost (S&L).

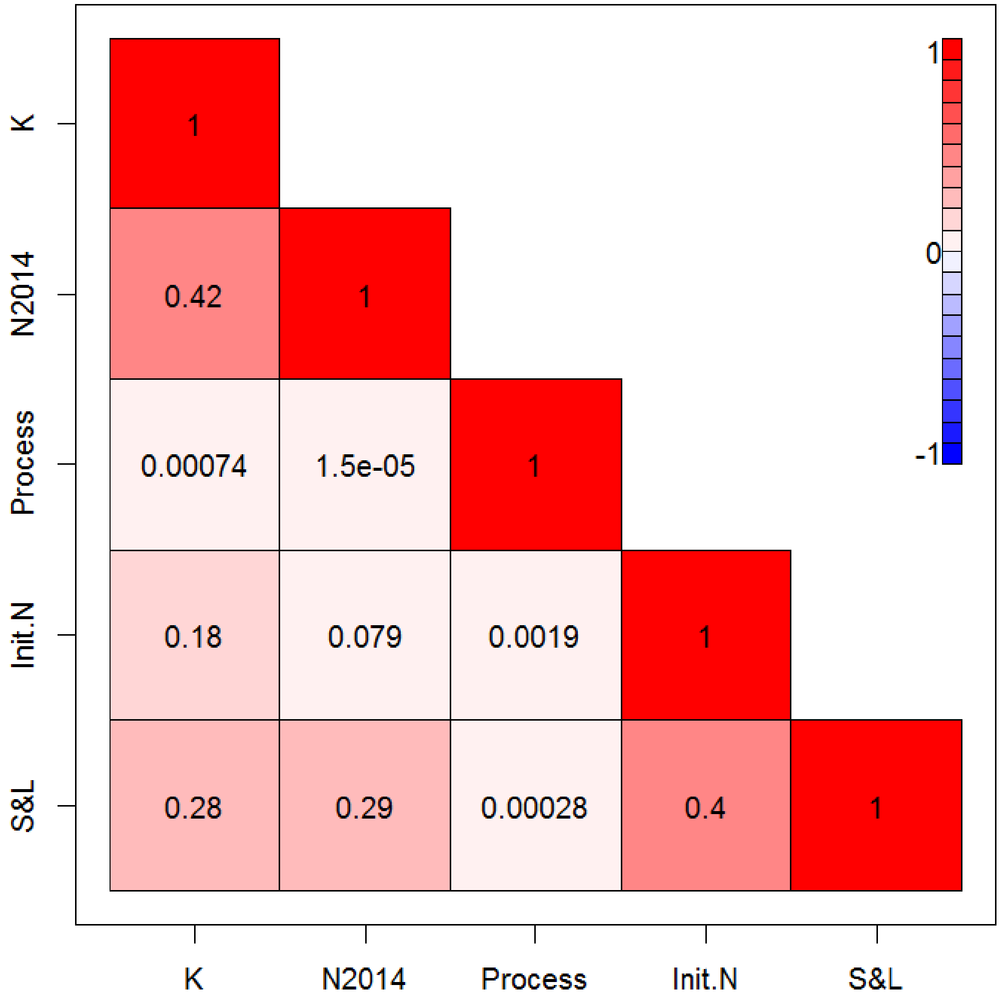

Figure 5c.Hudson Bay-Davis Strait model run with harvests from east Baffin excluded. Correlations are shown between model parameters for variables carrying capacity (K), 2014 population estimate (N2014), process error (Process), initial population size (init.N) and struck and lost (S&L).

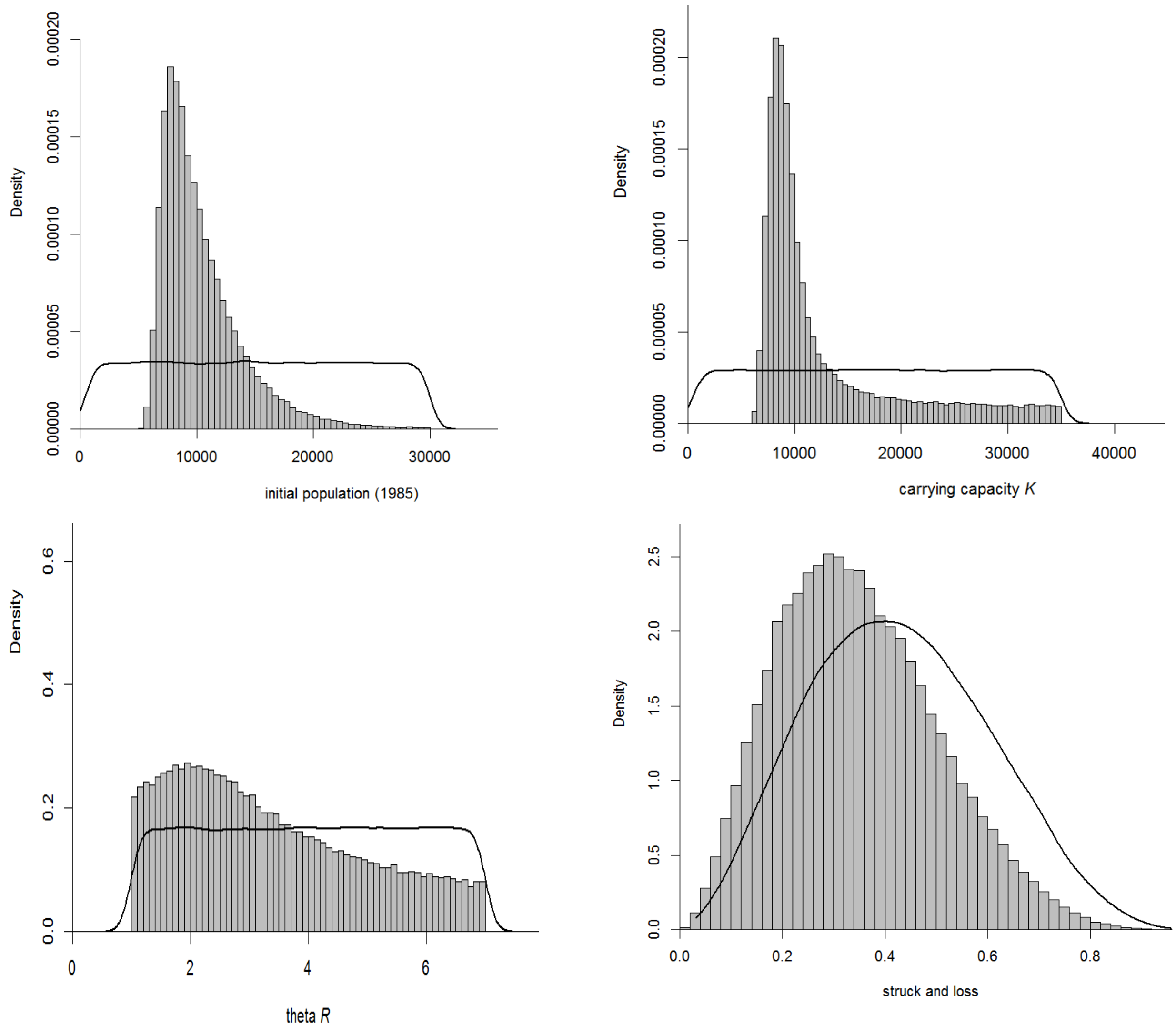

Figure 6a. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock model run that included all surveys and harvests from all communities. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6a.

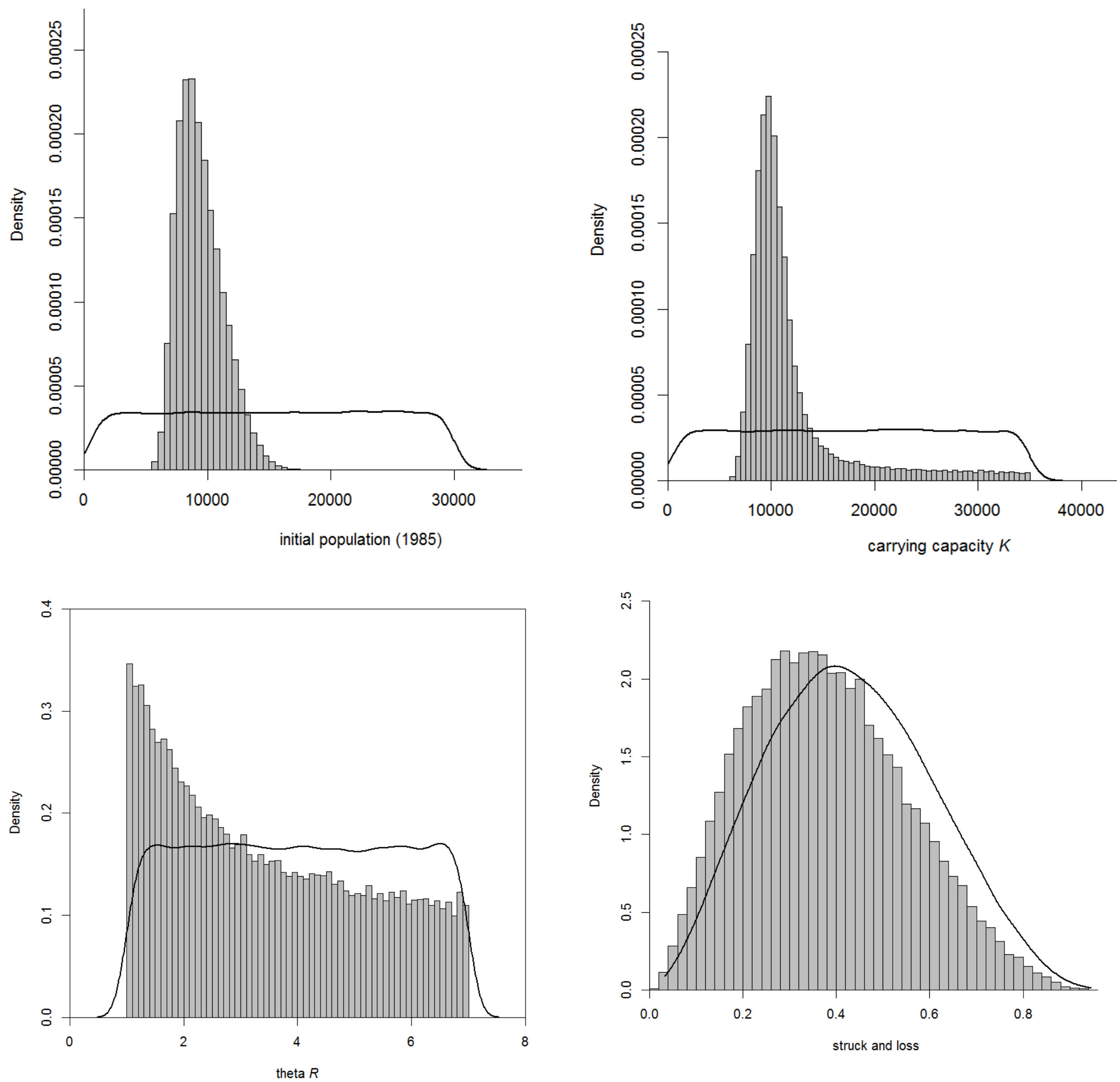

Figure 6b. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock for the run that did not include surveys flown before 1988. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6b.

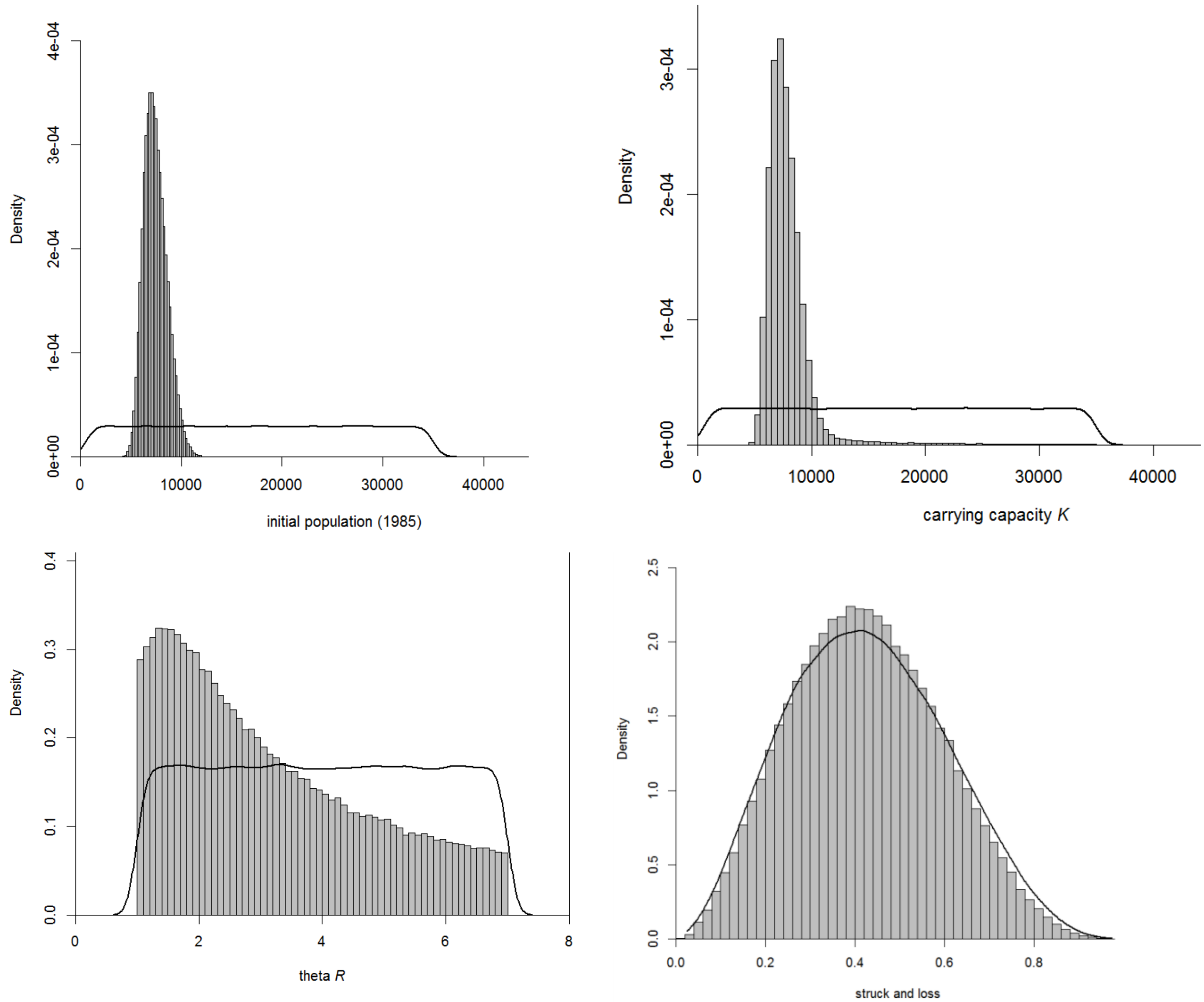

Figure 6c. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock for the run that did not include harvests from east Baffin Island. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6c.

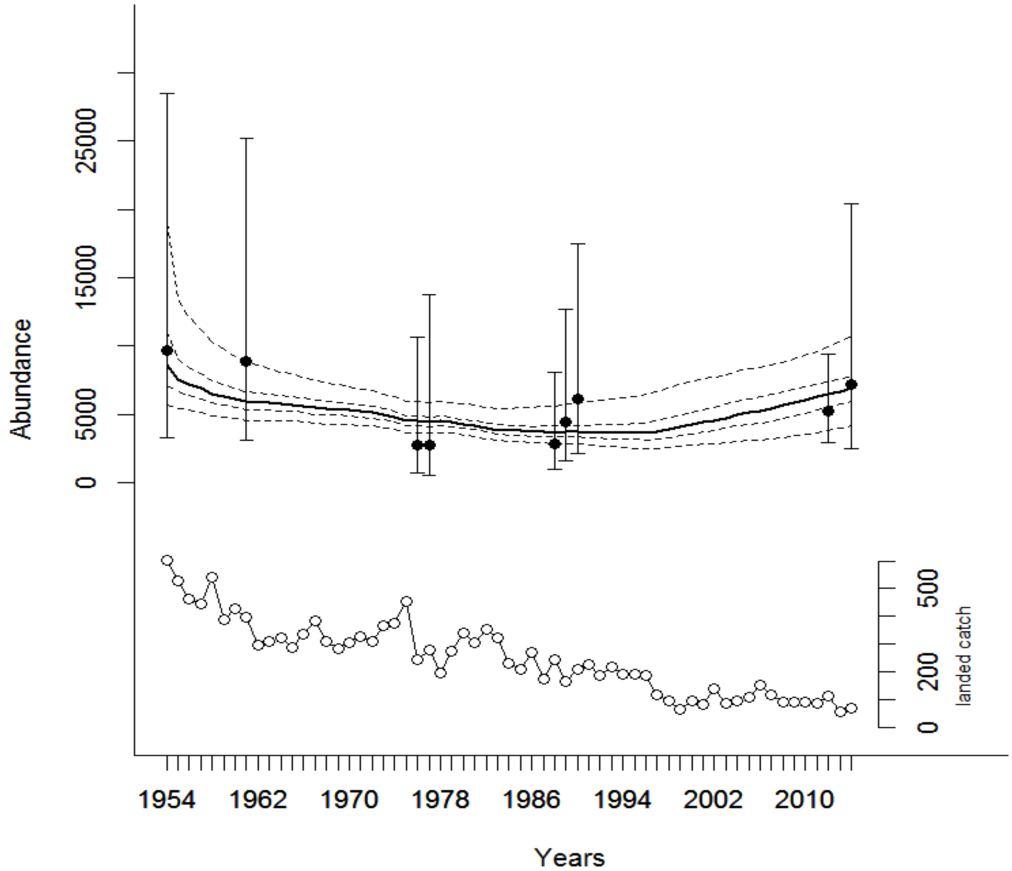

Figure 7a. Estimates of Hudson Bay-Davis Strait walrus abundance obtained by fitting the model to all aerial survey estimates. Solid line: median estimates. Inner dashed lines: 25% and 75% quantiles. Outer dashed lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). The model was fitted to aerial survey estimates corrected for animals at the surface (closed circles. ± 95% confidence intervals). Right y-axis: Reported catch of walrus from Ungava Bay, Hudson Strait, northeastern Hudson Bay, Southampton Island and northwestern Hudson Bay communities (open circles). For communities with missing data, the average of the most recent five years of catches was substituted.

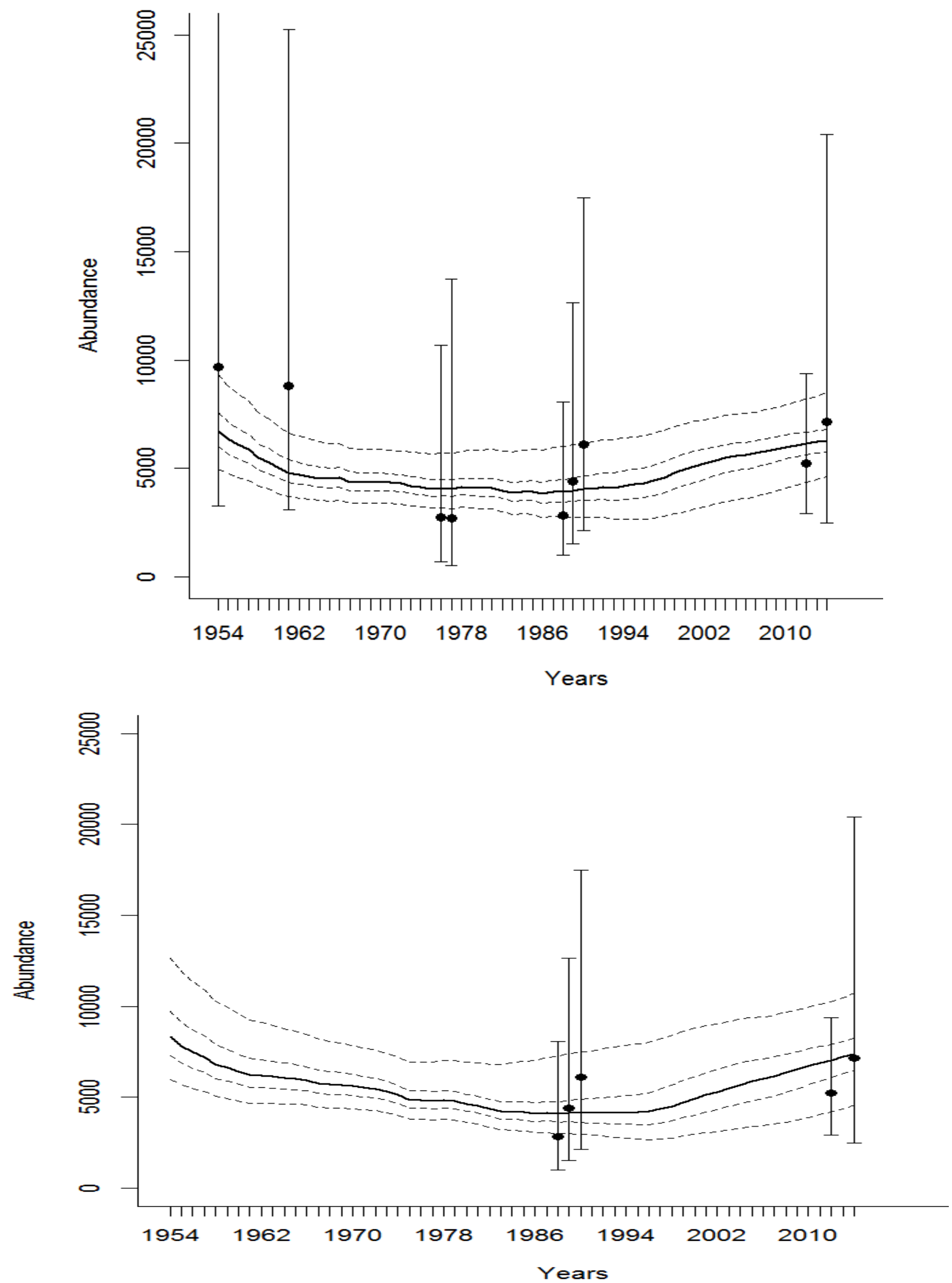

Figure 7b. Model estimates of Hudson Bay-Davis Strait walrus abundance taking into account all harvests and all aerial surveys (top) or if surveys prior to 1988 are excluded from the model (bottom). Solid line: median estimates. Inner dashed lines: 25% and 75% quantiles. Outer dashed lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). Aerial survey estimates are corrected for animals at the surface (closed circles, ± 95% CL).

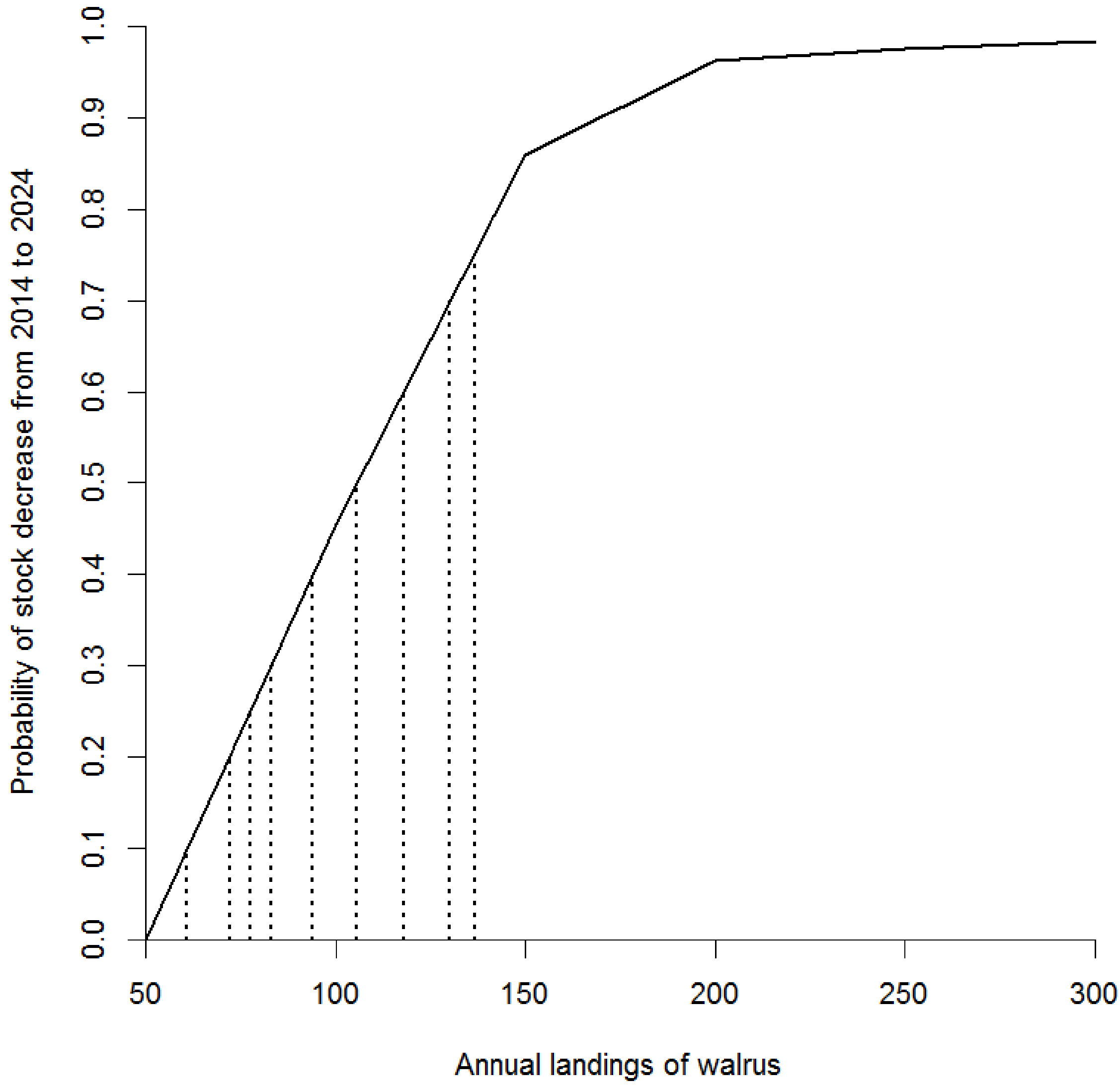

Figure 8. Probability of Hudson Bay-Davis Strait walrus stock decrease from the 2014 abundance estimate after ten years of harvest estimated by a stochastic Bayesian stock-production model; as a function of the number of reported walruses removed from the stock every year. Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of decline (y-axis).

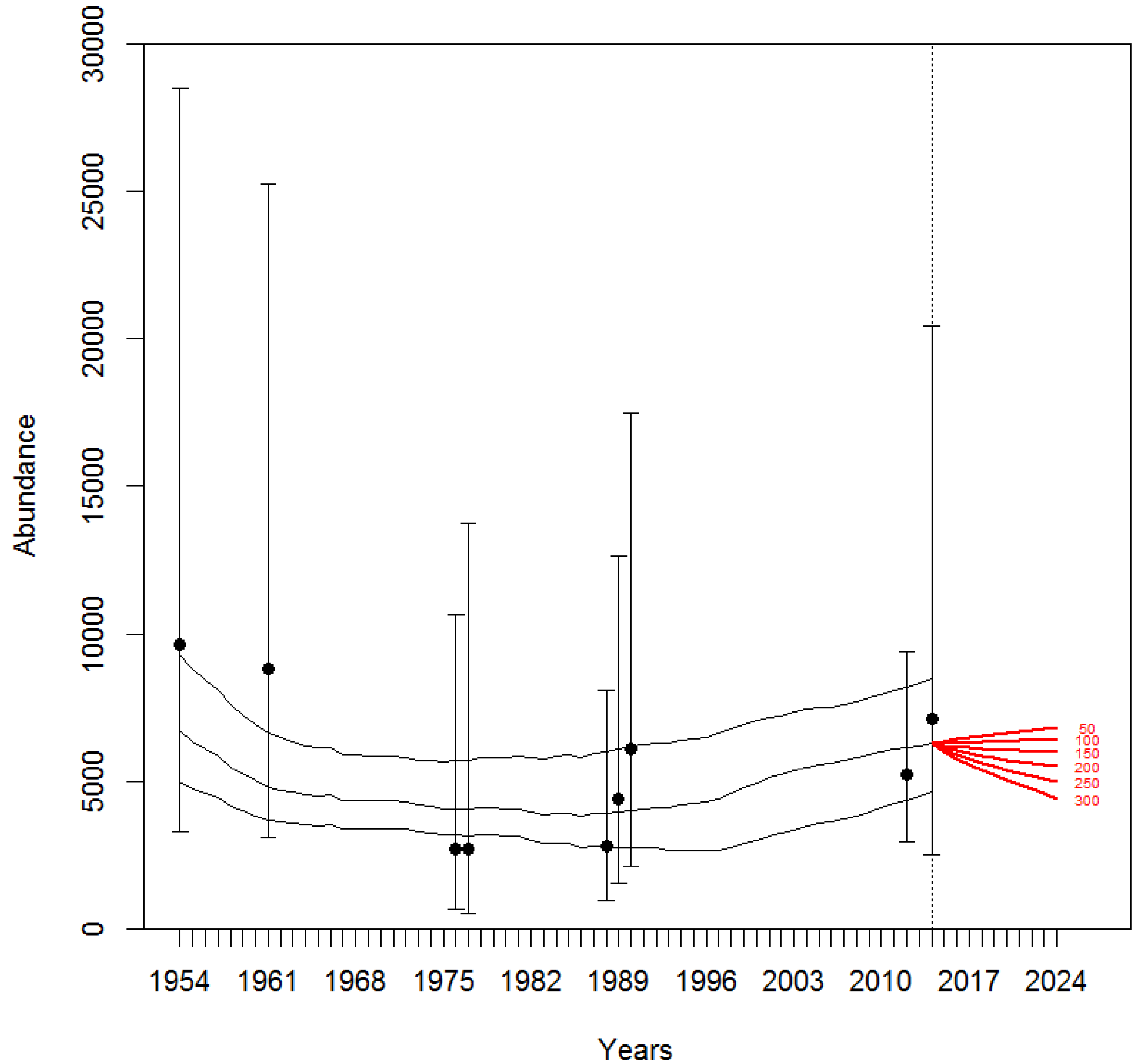

Figure 9. Model estimates of the Hudson Bay-Davis Strait walrus stock abundance and predicted trends in median population size if the same reported harvest (0, 50,100,150, 200, 250 or 300 animals) is removed annually over the next 10 years. Middle line is the median estimate. The outer black lines represent the 95% Credibility intervals. Aerial survey estimates are corrected for animals at the surface (closed circles, ± 95% CL).

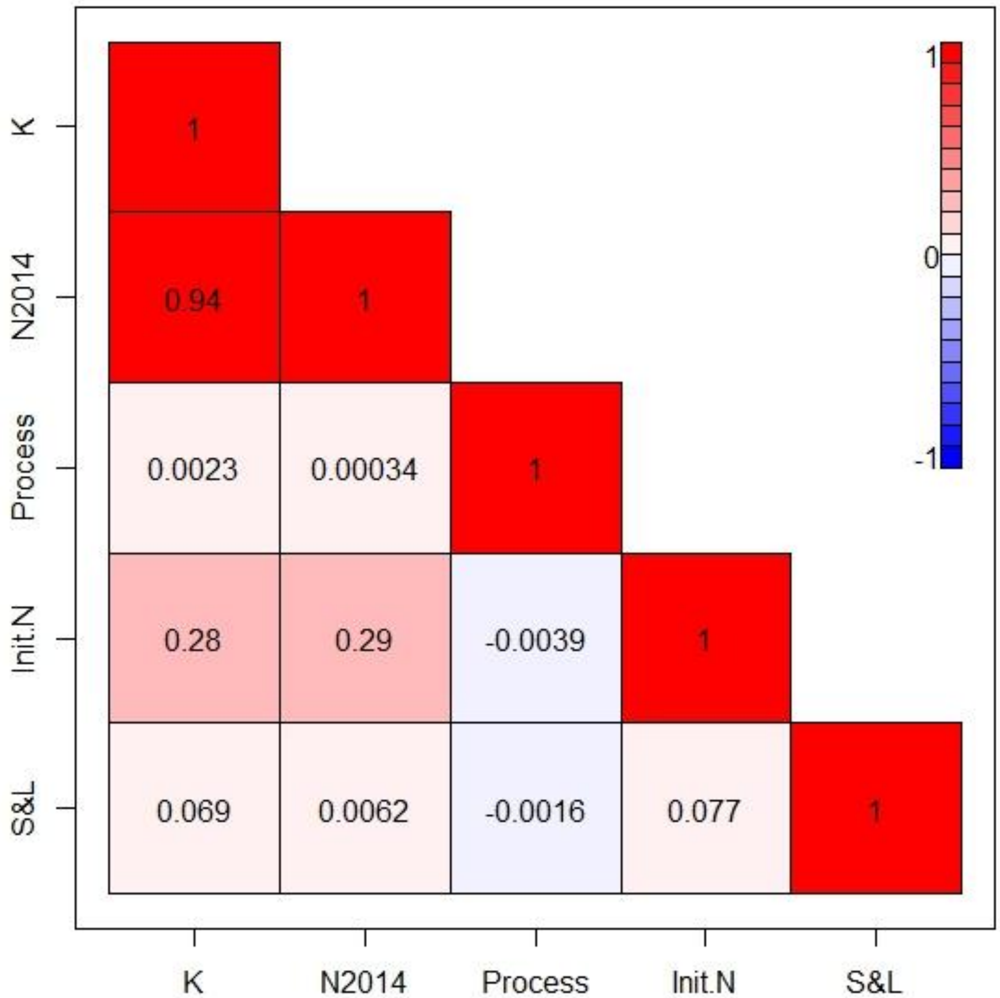

Figure 10. Foxe Basin stock model runs that included all survey data and reported harvests from all communities. Correlations are shown between model parameters carrying capacity (K), the 2014 population estimate (N2014), process error (Process), initial population size (Init.N) and struck and lost (S&L). Haulout counts were adjusted assuming a proportion of 0.37 of the population was hauled out.

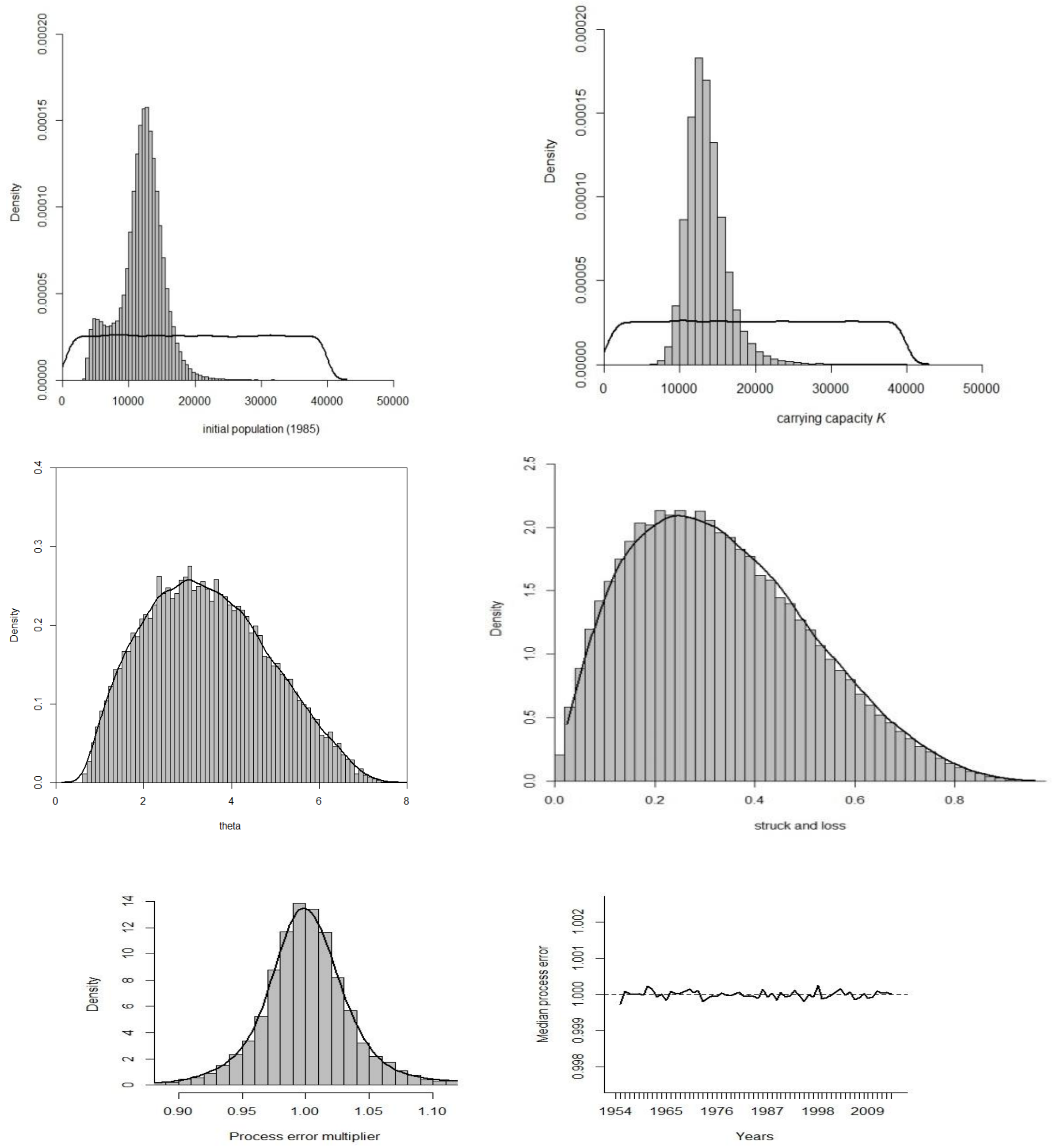

Figure 11. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Foxe Basin. The prior for the process error was not updated and is not shown. The Foxe Basin haulout counts were adjusted assuming a proportion of 0.37 of the population was hauled out. Prior and posterior means, Quantiles and 95% Credibility Intervals are shown in table 7.

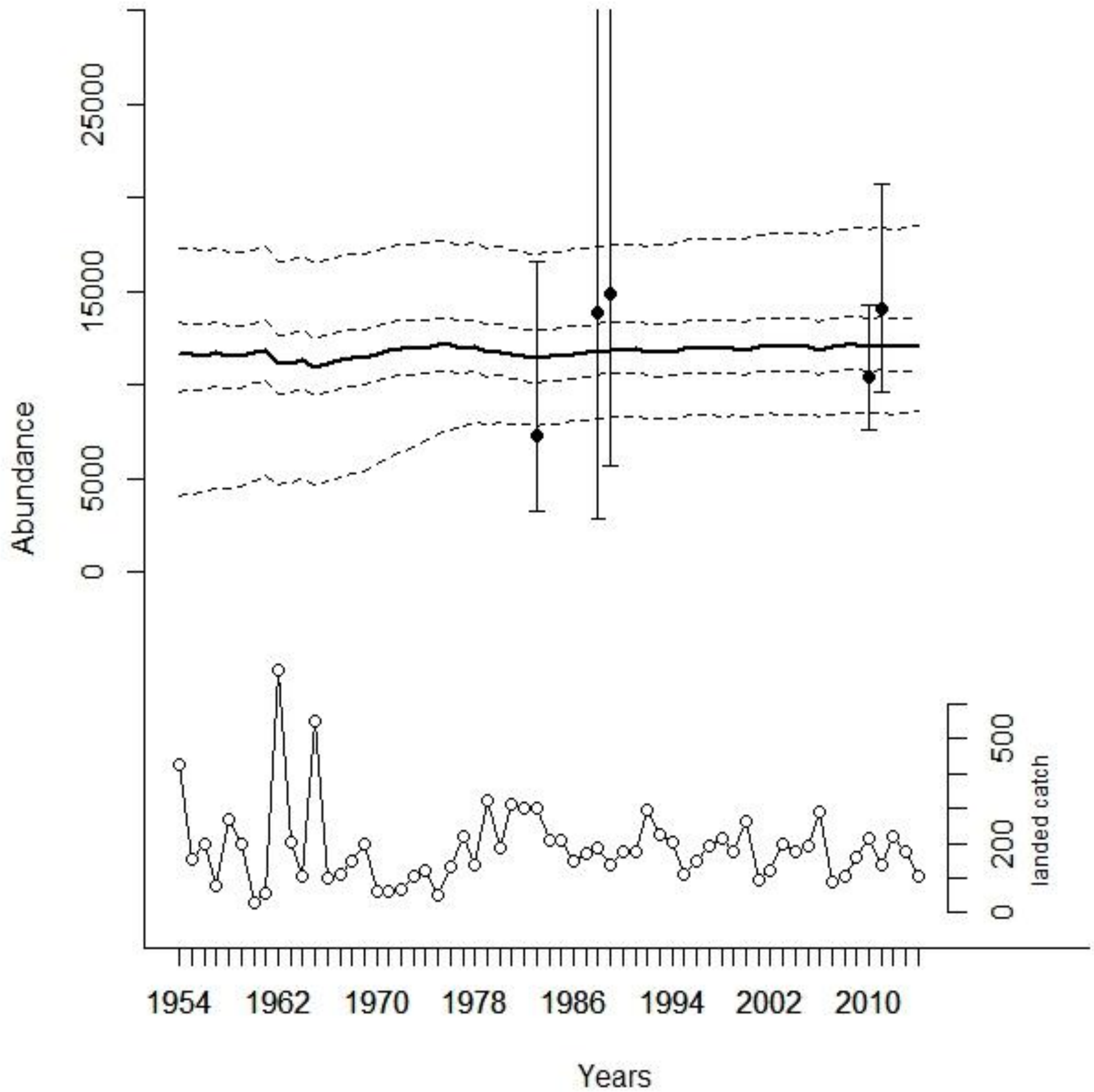

Figure 12. Model estimates of Foxe Basin walrus abundance (adjusted assuming that the proportion of the population hauled out was 0.37). Solid line: median estimates. Inner dashed lines: 25% and 75% quantiles. Outer dashed lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). The model was fitted to aerial survey estimates corrected for animals at the surface (closed circles. ±95% CL). Right y-axis: Reported catch of walrus from Igloolik and Hall Beach (open circles). For missing data. the average of the most recent five years of catches were substituted, except for catches prior to 1957 when Hall Beach did not exist as a community.

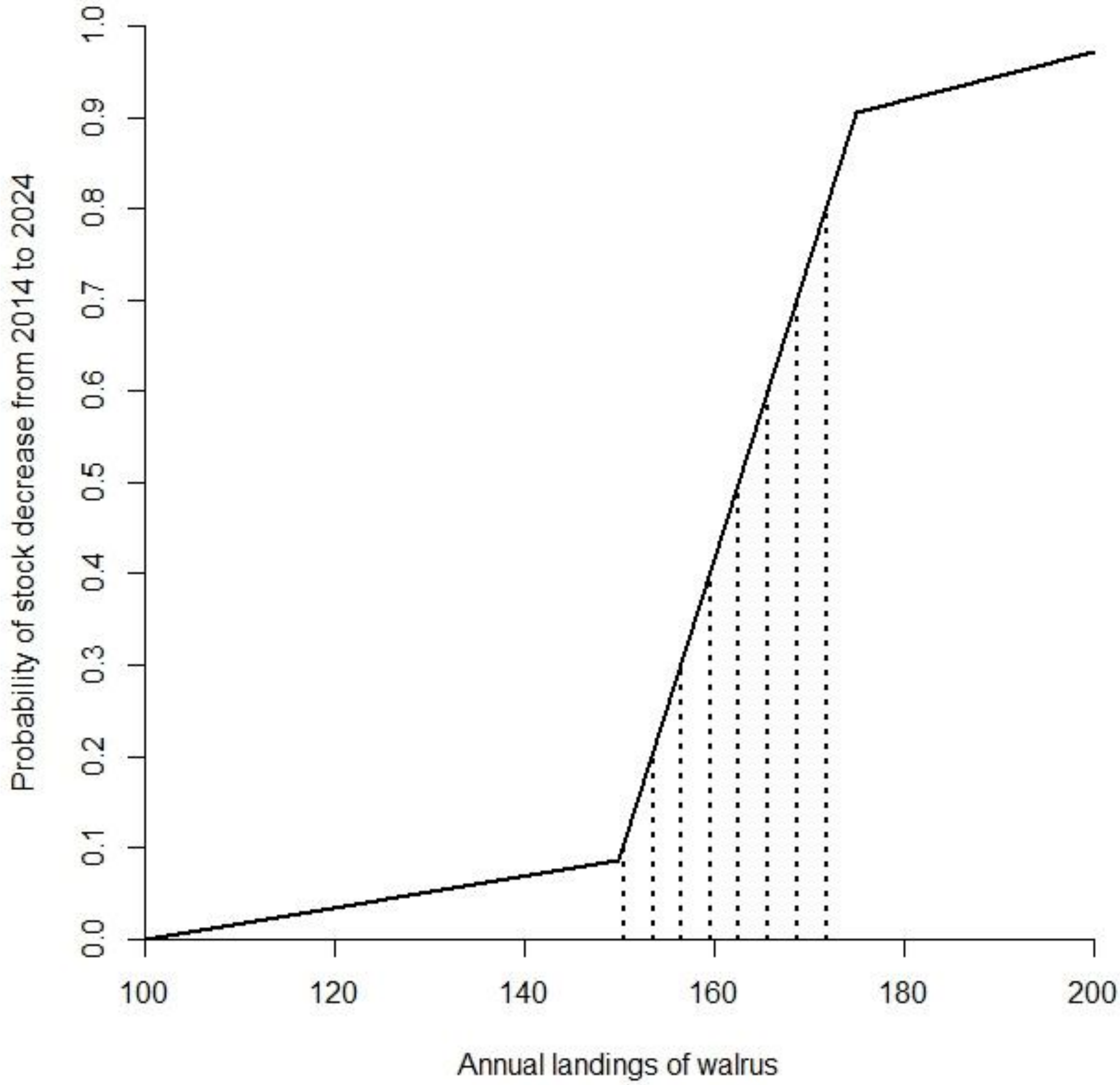

Figure 13. Probability of Foxe Basin walrus stock decrease from the 2014 abundance estimate (adjusted assuming that the proportion of the population hauled out was 0.37) after ten years of harvest estimated by a stochastic Bayesian stock-production model; as a function of the number of walrus removed from the stock every year. Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of decline (y-axis).

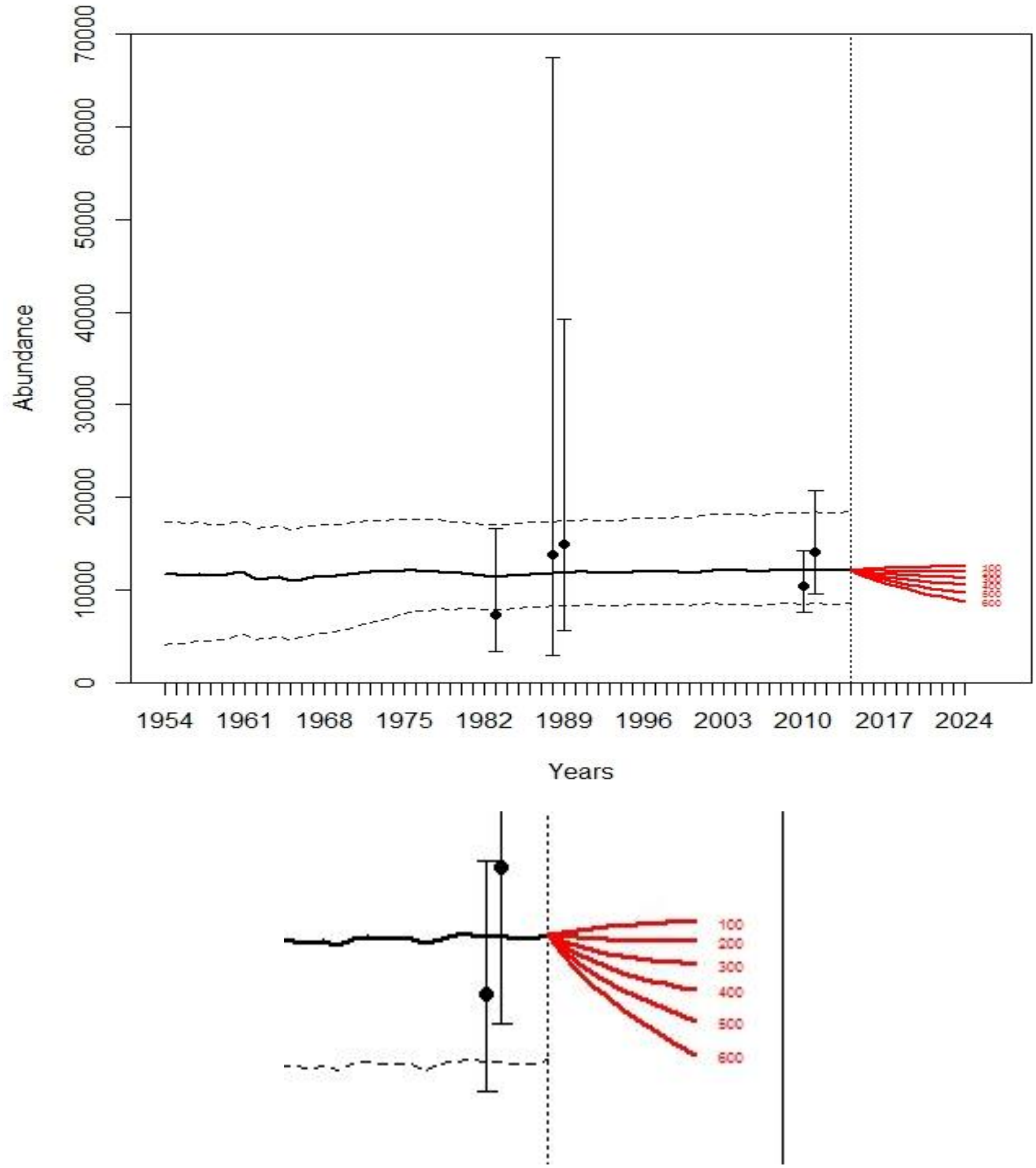

Figure 14. Model estimates of the Foxe Basin walrus population (adjusted assuming that the proportion of the population hauled out was 0.37) and predicted trends in median population size if the same reported harvest (100, 200, 300, 400, 500 or 600 animals) is removed annually over the next 10 years.