Fisheries and Oceans Canada — Pêches et Océans Canada

Science — Sciences

C S A S — S C C S

Canadian Science Advisory Secretariat — **Secrétariat canadien de consultation scientifique**

Research Document 2012/168 — **Document de recherche 2012/168**

Quebec Region — **Région du Québec**

Population modeling and harvest advice under the precautionary approach for eastern Hudson Bay beluga (*Delphinapterus leucas*)

Modélisation et avis sur la récolte en vertu du principe de précaution pour les bélugas (*Delphinapterus leucas*) de l'est de la baie d'Hudson

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

Maurice-Lamontagne Institute, Fisheries and Oceans Canada,
P.O. Box 1000, Mont Joli (QC) G5H 3Z4

ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)

Canada

Correct citation for this publication:

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.

ABSTRACT

Subsistence harvest of beluga whales by Nunavik communities is directed towards a mixture of several stocks, including the depleted Eastern Hudson Bay stock (EHB). The 2012 reported harvest consisted of 13 beluga taken in eastern Hudson Bay, 12 in Ungava Bay, 208 in Hudson Strait in the spring and 56 in the fall, 61 near Sanikiluaq (Nunavut), and 11 in the Long Island/James Bay area.

We incorporated recently updated information on stock structure and the results of the 2011 aerial surveys into a population model. Genetic variation at mtDNA loci was used to assess the contribution of each summering stock to the harvest and how these contributions vary spatially and seasonally. The model was fitted to survey estimates using Bayesian methods. The estimated stock size in 1985 was 3,799 animals with a 95% CI of 2,389–6,332. The lowest abundance point was estimated for the year 2001 at 3,016 individuals (95% CI 2,141–4,322), with a 2012 abundance of 3,229 individuals (95% CI 1,896–5,406). At current harvest levels, the stock abundance seems to have increased slightly over the last few years The model estimated struck-and-loss at 41% (95% CI 12–78%) and growth rate at 2.74% (95% CI -0.67 to +6.13%).

According to the model, removing 62 EHB animals per year for 10 years would have a 50% probability of causing a decline in the stock relative to its 2012 estimate. Limiting the harvest of EHB animals to 28 animals would reduce the probability of decline to 25%. Conversely, a harvest of 106 EHB beluga would have a 75% probability of leading to stock decline. In the absence of harvest, the probability of decline is 9%. A spring/summer harvest in Hudson Strait, with no harvest in the eastern Hudson Bay arc would have the lowest impact on the EHB stock, followed by a fall harvest in Hudson Strait only, again with no harvest allowed in the arc. If harvesting does occur in eastern Hudson Bay, then numbers taken in Hudson Strait must be reduced to obtain the same probability of increase, but the size of this reduction will depend on whether hunting occurs in the spring/summer or in the fall.

The model was used to estimate the probability of reaching a recovery target of 70% of the inferred maximum stock size under a precautionary approach framework. Projections over the next 25 and 50 years show that, at current harvest levels (~50 EHB beluga per year), there is a 33% probability of reaching a recovery target of 5,600 individuals after 25 years. After 50 years, this probability increases to 48%. In the absence of harvest, the probabilities of reaching the target are 58% after 25 years and 78% after 50 years. However, uncertainty about the historical stock size, current carrying capacity and density-dependent mechanisms place important limitations on our ability to make long-term predictions regarding the recovery of the EHB stock.

RÉSUMÉ

La chasse aux bélugas à des fins de subsistance par les communautés du Nunavik vise un mélange de plusieurs stocks, dont celui de l'est de la baie d'Hudson (EBH). En 2012, les prises rapportées étaient constituées de 61 bélugas tués près de Sanikiluaq (Nunavut), de 13 dans l'est de la baie d'Hudson, de 12 dans la baie d'Ungava, de 208 dans le détroit d'Hudson au printemps et de 56 à l'automne, ainsi que de 11 bélugas dans la baie James et la région de Long Island.

De récentes informations sur la structure des stocks ainsi que les résultats du relevé aérien de 2011 ont été incorporées dans un modèle de population. Des analyses génétiques de l'ADN mitochondrial ont permis d'évaluer les proportions de chaque stock parmi les animaux chassés, et la manière dont ces contributions varient selon l'endroit et la saison. Le modèle a été ajusté aux estimations d'abondance obtenues à partir des relevés aériens à l'aide de méthodes d'inférence bayésiennes. La taille du stock en 1985 a été estimée à 3 799 individus avec un intervalle de crédibilité (IC) de 95 % de 2 389 – 6 332. Le stock aurait atteint son plus bas niveau en 2001 avec un effectif de 3 016 individus (IC 95 % 2 141 – 4 322). La taille du stock en 2012 a été estimée à 3 229 individus (IC 95 % 1 896 – 5 406). Aux niveaux de capture actuels, la taille du stock semble avoir augmenté légèrement cours des dernières années. Le modèle a estimé la proportion de bélugas abattus mais perdus à 41 % (IC 95 % 12–78 %) et le taux d'accroissement à 2,74 % par an (IC 95 % de -0,67 % à +6,13 %).

D'après le modèle, un prélèvement annuel de 62 bélugas de l'EBH par an pendant 10 ans entrainerait un risque de 50 % de déclin du stock. Une diminution du prélèvement à 10 individus de l'EBH réduirait la probabilité de déclin à 25 %. Inversement, la prise de 106 individus de l'EBH aurait 75 % de chances d'entraîner un déclin. En l'absence totale de prélèvement de bélugas de l'EBH, la population aurait 9 % de chances de décliner. Une chasse de printemps/été dans le détroit d'Hudson, sans prélèvement dans l'est de la baie d'Hudson, constitue le scénario qui aurait le moins d'impact sur le stock de l'EBH, suivi de celui d'une chasse d'automne dans le détroit. Si des prélèvements ont lieu dans l'est de la baie d'Hudson, alors les prises dans le détroit doivent être réduites pour obtenir la même probabilité d'accroissement du stock, mais l'amplitude de cette réduction dépend de si la chasse a lieu au printemps/été ou à l'automne.

Le modèle a été utilisé pour estimer la probabilité d'atteindre une cible de rétablissement définie à 70 % de la taille maximale supposée du stock dans le cadre d'une approche de précaution. Les prédictions pour les 25 et 50 prochaines années montrent que, aux niveaux de prélèvement actuels (~50 bélugas de l'EBH) par année, il y a 33 % de chances d'atteindre une cible de rétablissement de 5 600 individus au bout de 25 ans. Après 50 ans, cette probabilité monte à 48 %. En l'absence totale de prélèvements, les probabilités d'atteindre cette cible se chiffrent à 58 % après 25 ans et 78 % après 50 ans. Cependant, les incertitudes qui caractérisent notre connaissance de la taille initiale du stock, de la capacité de charge du milieu et des mécanismes de densité-dépendance restreignent considérablement notre capacité à émettre des prédictions à long-terme concernant le rétablissement du stock de l'EBH.

INTRODUCTION

BELUGA SUBSISTENCE HUNT IN NUNAVIK

Nunavik communities have traditionally harvested beluga whales (*Delphinapterus leucas*) for subsistence. Recent genetic analyses have shown that most targeted beluga likely belong to a single breeding population (Turgeon et al. 2012). This population, however, divides into several stocks with distinct migratory routes and summering grounds (de March & Postma 2003; Richard 2010). The Nunavik harvest takes whales from the Ungava Bay, eastern Hudson Bay and James Bay summering grounds (Fig. 1), as well as migrating whales from a mixture of these stocks during spring and fall (COSEWIC 2004; Reeves and Mitchell 1989). Site fidelity of matrilineal herds to summering areas seems to prevent substantial exchange among stocks (Caron and Smith 1990; Smith et al 1994; Turgeon et al. 2012), thus making beluga vulnerable to local depletion. Therefore, the hunt has been managed on the basis of these summer stocks (Reeves and Mitchell 1987).

One of these management units, the eastern Hudson Bay stock (EHB), was depleted by intensive commercial hunting between the 1860’s and the early 1900’s and has decreased from an estimated pristine stock size of 12,500 to about 3,000 individuals in 2011 (Doniol-Valcroze et al. 2012a; Hammill et al. 2005; Reeves and Mitchell 1987). To promote its recovery, hunting has been managed through a combination of quotas and seasonal and regional closures (Lesage et al. 2009; Lesage & Doidge 2005; Lesage et al. 2001). Hammill et al. (2004) showed that the stock had continued to decline as late as 2001 despite these measures. In 2004, EHB beluga were designated "Endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004). In 2006, the signing of NILCA resulted in the establishment of the Nunavik Marine Region Wildlife Board (NMRWB), which shares responsibilities for the co-management of Nunavik beluga with DFO.

Managers and resource users aim at maintaining a sustainable harvest, while encouraging the recovery of individual stocks. However, monitoring changes in the EHB beluga stock is complicated by large uncertainty in abundance estimates (Gosselin et al. 2009). Moreover, genetic analyses of tissue samples obtained from hunters have shown that, while representing only about 5% of the overall number of beluga in Hudson Bay, the EHB stock comprises about 17% of the annual harvest (Turgeon et al. 2012). This proportion varies geographically and seasonally (de March & Postma 2003; Turgeon et al. 2012), which further complicates modelling efforts.

Bayesian statistics are well adapted to this situation because they allow the incorporation of prior existing knowledge of parameter values, including their associated uncertainty. A population model incorporating information on catch levels and stock composition was fitted to aerial survey estimates using Bayesian methods (Hammill et al. 2009). The 2011 update of the model indicated that the current stock size was likely stable but that a harvest exceeding 50 EHB animals would have a 50% probability of causing a decline in the stock (Doniol-Valcroze et al. 2012a).

THE PRECAUTIONARY APPROACH FRAMEWORK

Harvest advice in Nunavik has been based on the best available information on the status of the EHB stock. However, there is considerable uncertainty in survey estimates, population dynamics and harvest composition. In the past, failure to recognize the importance of this uncertainty in similar situations has led to severe harm to populations (Taylor et al. 2000). The Precautionary Approach (PA) strives to be more cautious when information is less certain, does not accept the absence of information as a reason for not implementing conservation measures, and defines, in advance, decision rules for stock management when the resource reaches clearly-stated reference points (Punt and Smith 2001).

These abundance levels are referred to as limit, precautionary, and target reference points (ICES 2001). The limit (or critical) reference point (N_{lim}) represents the estimated level at which continued removals would lead to serious harm to the population (Hammill and Stenson 2007). However, estimates of abundance are associated with considerable uncertainty and this uncertainty increases as the population is projected into the future. Managing a population close to the critical reference point could result in a high probability that the population declines below N_{lim}. Therefore, a Precautionary Reference Point (PRL) identifies a population range within which risk-adverse management control rules would apply to ensure that the population does not fall below the critical reference level. When a population is above the precautionary reference point, conservation is not the major consideration in setting quotas.

The current Nunavik beluga management plan is due for review in 2012-2013. Development and implementation of a new beluga management plan in the Nunavik Marine Region will be completed with the collaboration of the NMRWB and the Regional Nunavimmi Umajutvijiit Katajuaqatigininga. Canada has domestic and international commitments to implement the Precautionary approach into its decision-making framework for fisheries. NILCA also includes the creation of a wildlife co-management system for the Nunavik Marine Region that is “governed by and implements the principles of conservation” (Anonymous 2008). It is therefore important to recommend a recovery target under the precautionary approach.

In this context, our objectives were to:

1) revise the structure and priors of the model to reflect newly available information;

2) update the population model using survey estimates from 2011 and harvest data from 2012 to evaluate the abundance of EHB beluga;

3) determine the maximum number of belugas from the EHB population that can be harvested while maintaining a 25%, 50% and 75% chance of population increase

4) recommend recovery targets under the precautionary approach and provide scenarios which include the maximum number of EHB beluga whales that can be hunted each year and still provide for recovery within 25 and 50 years.

MATERIALS AND METHODS

AERIAL SURVEYS

Census data comprised six estimates from systematic visual aerial surveys flown in 1985, 1993, 2001, 2004, 2008 and 2011. All surveys were flown along similar parallel line designs (Fig. 1). Details on survey methods and analyses are available in Smith and Hammill (1986), Kingsley (2000), Hammill et al. (2004), Gosselin et al. (2009) and Gosselin et al. (2013).

The 1985 survey was flown as a strip transect survey whereas latter surveys were flown following line transect protocols (Buckland et al. 2001). Abundance estimates and their associated empirical variances were calculated using the Distance software for all line transect surveys (Thomas et al. 2006). The 1993 and 2001 survey data were also analyzed using strip transect analysis to estimate a line/strip transect correction factor, which was used to adjust the 1985 estimate (Hammill et al. 2004). Beluga detected in estuaries ($S_{estuary}$) were assumed to represent total counts and were added to survey estimates. Corrections were applied for animals "unavailable" for detection while underwater using:

$$S_t = S_{survey} / P_0 + S_{estuary},$$

where the proportion of beluga visible from an aerial survey platform is P_0 = 0.478 ± 0.0625 SE (Kingsley & Gauthier 2002). The resulting abundance estimates (SE) were 4,278 (557), 2,727 (1,092), 2,922 (1,404), 4,269 (1,581), 2,646 (1,244) and 3,351 (1,639), for 1985, 1993, 2001, 2004, 2008 and 2011, respectively.

HARVEST RECORDS AND GENETIC ANALYSES

Harvest data are available from annual reports of landed catches (summarized in Lesage et al. 2009). All beluga harvested directly in the eastern Hudson Bay arc during the summer are assumed to belong to the EHB summer stock. Harvest in other areas and during spring and fall, however, is directed towards migrating whales from a mixture of stocks (Fig. 2). Genetic variation at mtDNA loci has been used to assess the contribution of each summering stock to the harvest and how these contributions vary spatially and seasonally (Turgeon et al 2012).

Prior to 2009, no information was available as to the timing of the harvest and for some whales it was uncertain whether they were harvested in northeastern Hudson Bay, Hudson Strait, or Ungava Bay. For this reason, it has been assumed that 17% (SE 2.3%) of whales hunted by communities outside of the eastern Hudson Bay arc in 1985–2008 were from the EHB stock (Turgeon et al. 2012). Genetic analyses have shown differences in the proportion of EHB animals in fall samples compared to spring samples, and thus, since 2009, harvesting seasons have been separated into a spring-summer period and a fall period. Therefore, for 2009–2012, it was assumed that 13% (SE 5.2%) of animals killed in Hudson Strait and Ungava Bay in the spring and summer, and 21%(SE 5.1%) of those killed during the fall, were EHB beluga. It was assumed that 12% (SE 3.8%) of beluga killed by Sanikiluaq hunters in any year belonged to the EHB stock.

In previous assessments, these fixed proportions were used to revise the catch series, yielding a single number of EHB beluga takes for each year which was used as input to the model. There is, however, uncertainty associated with all these estimated proportions. To better reflect this uncertainty, these proportions are now incorporated in the model as statistical distributions (see below, priors). The raw catch data are now included in the model separately for each region (divided by season for 2009 and later). The resulting contribution of the EHB stock to the overall harvest is then estimated within the model.

In 2012, the Nunavik harvest was composed of 13 beluga taken in the eastern Hudson Bay, 10 in Ungava Bay in the spring and 2 in the fall, 208 in Hudson Strait in the spring and 56 in the fall, 61 near Sanikiluaq (P. Hall, pers. comm.), and 11 in the Long Island/James Bay area. The Long Island/James Bay harvest is not considered in the model because these beluga are believed to belong to a separate population (Postma et al. 2012). Of the 300 beluga landed, 12 were reported wounded but lost.

MODEL SPECIFICATION

A stochastic stock-production model 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 (Fig. 3) that considers survey data to be the outcome of two distinct stochastic processes: a state process and an observation process (De Valpine & Hastings 2002).

The state process describes the underlying population dynamics and the evolution of the true stock size over time, using an exponential-growth model. Population size in each year N_t (from 1985 to 2011) is a multiple of the previous year's, with removals deducted:

$$N_t = N_{t-1} \cdot e^r \cdot \varepsilon_{P_t} - R_t$$

where r is the instantaneous growth rate, εp_t is 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:

$$\ln(S_t) = \ln(N_t) + \varepsilon_{S_t}$$

PRIORS

Existing information, traditional knowledge and expert opinions were used to formulate prior distributions for the random variables included in the model (Table 1). The initial population size (N_{1985}) was given a uniform prior between 500 and 12,500 individuals. The lower bound reflects observations of at least a few hundred beluga in the EHB estuaries reported by local hunters in the mid-1980s (Reeves & Mitchell 1989) and during surveys (Smith and Hammill 1986), while the upper bound is based on a previous estimate of the pristine stock size for that stock (Hammill et al. 2005).

The rate of population increase has not been measured for beluga. Female beluga are known, however, to give birth to their first calf around 12 years of age (Stewart et al. 2006), and the minimum calving interval has been determined to be three years (Sergeant & Brodie 1975). Following Reilly and Barlow (1986), we solved the Euler-Lotka equation for different values of calf and adult survival to determine a range of plausible rates of population increase. The absolute maximum rate of population increase for beluga whales (assuming 100% survival rates, 60 years longevity and age-at-first-birth of 10 years) is 7.7%. We could not exclude the possibility of negative growth over the period considered, and therefore, we gave the instantaneous rate of growth, r, a prior following a Beta(2,3) distribution, rescaled to the range from -0.04 to +0.08. This is a narrower range than used in previous assessments, in which r had been given a uniform prior in the range -0.10 to +0.20 (Doniol-Valcroze et al. 2012a).

Reported harvests underestimate the number of beluga killed because of animals wounded or killed but not recovered, as well as under-reporting. The loss rates in Canadian hunts are not known exactly but are believed to range from around 20% for shallow water hunts up to 60% for deep-water hunting, e.g. along ice edges (Seaman & Burns 1981). Heide-Jørgensen and Rosing-Asvid (2002) calculated a struck-and-lost factor of 0.29 for Greenland, not including unreported catches. Innes and Stewart (2002) estimated a correction factor that accounted for struck-and-lost and whales not reported in Baffin Bay at 0.41 whales per whale landed. Actual loss rates could be higher due to some hunts resulting in several wounded animals that may eventually die from their wounds (Orr & Richard 1985). Therefore, 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. This is also a change from previous assessments, in which the struck-and-lost correction was given a log-normal prior with quartile points at 0.43 and 0.85 and a median value of 0.61, as there was little support in published reports for these high values (Doniol-Valcroze et al 2012a).

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 bounded gamma (1.5, 0.001) distribution. These parameters were chosen so that the resulting coefficients of variation (CV) would have quartiles of 5.5% and 8.7%, reflecting our belief that beluga stock dynamics are not highly variable.

Although estimates of uncertainty were available for each survey estimate, they were 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 actual CV for the survey abundance estimates.

The proportions of EHB beluga in the harvest given in Turgeon et al. (2012), together with their associated standard errors, originate from a Bayesian mixing model based on a multivariate Dirichlet distribution. Each univariate posterior distribution thus follows a Beta distribution, with known mean and standard error, but for which the α and β parameters are not available. We solved the system of equations for the mean and variance of a Beta distribution to determine the values of α and β that describe the observed distributions. These Beta distributions were then used as priors for the proportions of EHB animals in the hunt of Sanikiluaq, HS for all season (hunt prior to 2009) and HS for spring and fall (2009–2012).

PARAMETER ESTIMATION AND MODEL DIAGNOSTICS

Parameter estimates are refined by updating the prior to a posterior distribution based on the data. Parameter estimation was conducted using a Bayesian MCMC approach in WinBUGS 1.4.3 (Lunn et al. 2000). Posterior distributions were examined in the R programming language, using packages *R2WinBUGS* and *coda*. 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, every 40^{th} point was kept from 3 chains of 1,000,000 iterations, after a burn-in of 50,000 samples, for a total of 75,000 samples.

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 & Gelman 1998). The relative contributions of the parameters to the model were examined by estimating the pD statistic, which corresponds to the 'effective' number of parameters being fitted (Spiegelhalter et al. 2002).

We tested the sensitivity of the results to the values of two hyper-parameters: β_s used in the prior distribution of the precision of the survey error, and β_{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 (400,000 after a burn-in of 10,000, resulting in a thinned chain of 10,000 samples), but their point estimates were similar to those of the main model.

Sensitivity to changes in the prior distribution of the process error was investigated in details in Hammill et al. (2009, table 5) and was shown to have negligible impact on stock size estimates. Moreover, a model with deterministic dynamics (i.e., no process error) yielded results that were very similar to those of the model incorporating some stochasticity, suggesting that further investigation was unnecessary.

FUTURE PROJECTIONS AND HARVEST SCENARIOS UNDER THE PRECAUTIONNARY APPROACH

The model was extended into the future for 50 years to predict stock trajectory. These predictions were performed under 15 different harvest scenarios, with yearly catch levels ranging from 0 to 200 EHB beluga. To provide information in a useful format for risk-based management, we estimated the probability of stock decrease after 10 years for each of the scenarios, as was done in previous assessments, using the proportion of simulations in which the stock size in 2021 was below the estimated 2011 stock size.

We calculated the probability of recovery under the PA framework. The PRL, defined as 70% of the observed or inferred maximum population size, has been identified as a tentative recovery target for EHB beluga (Lawson et al. 2006). Pristine stock size (pre-1854) is unknown, but was estimated at 8,000 – 11,600, depending on assumptions of loss rates during commercial catches (Appendix 1). Therefore, two recovery targets were proposed to encompass this range: T1=5,600 and T2=8,000. These targets follow the framework that has been proposed for other marine mammals in Canada (Stenson et al. 2012). This framework also identifies a reference limit point N_{lim} at 30% of the maximum population size, i.e., about 2,400 beluga if using the lower estimate of maximum population size.

To estimate the probability of reaching these targets, we calculated the proportion of future population trajectories that reached T1 and T2 within 25 and 50 years for each of 15 harvest scenarios. We also calculated the risk of decreasing below N_{lim}.

RESULTS

MODEL CONVERGENCE

Each of the three chains showed rapid mixing and reached a stationary distribution (Geweke's diagnostic, all Z-scores < 1.96). Trace plots showed that the three chains with different initial values converged quickly to the same distribution (Fig. 4a). This was confirmed by the overall BGR statistic of R-hat=0.99921. When plotted over increasing numbers of iterations, R-hat stabilized within 0.01 of unity after about 2,000 iterations (Fig. 4b).

MODEL ESTIMATES AND UPDATE OF PRIORS

Posterior distributions of the model parameters are shown in Fig. 5, along with their prior distributions. The estimated rate of growth *r* was 2.74% (95% CI -0.67 to +6.13%). Its value was well updated from its prior distribution (median=3.37%, 95% CI -1.69 to +7.2%). With a median of 3,950 (95% CI 2,540 – 6,490), the initial (1985) stock size was also well updated from its prior value (median=6,270, 95% CI 795 – 11,700). The struck-and-lost factor was estimated at 41.3% (95% CI 12–77%), a minor update from its prior value of 42.2% (95% CI 12–78%). The posterior distribution of the survey error (median=0.35, 95% CI 0.23 – 0.60) was lower than its prior distribution (median=0.43, 95% CI 0.25 – 0.98). The informative prior for the process error was not updated.

The pD index showed the model had about 1.8 ‘effective’ parameters, hinting at some correlation between variables (Table 2). The largest correlation was between the initial population size and the growth rate (ρ = -0.78). The initial population size was also moderately correlated with the survey error (ρ = 0.13). The growth rate was moderately correlated with the struck-and-lost factor (ρ = 0.16).

SENSITIVITY TO PRIORS

The median of the 2012 stock size was little influenced by changes in the hyper-parameter β_s used in the prior distribution of the survey error (Fig. 6a). The CI, however, increased markedly with increasing values of β_s (which increase the CV of survey estimates). Changes in the hyper-parameter β_{sl} used in the prior distribution of the struck-and-lost factor had no perceptible influence on the 2012 point estimates of the stock size or on its uncertainty, even when the informative prior was replaced with a flat Beta(1,1) distribution (Fig. 6b). However, the posterior distribution of *r* was sensitive to different priors of the struck-and-lost factor: the median value of *r* increased from 2.74% to 2.9% when the hyper-parameter β_{sl} was decreased from 4 (which resulted in a median *SL* factor of 0.43) to 2 (median *SL* of 0.61). The median posterior value of *r* was 2.38% when *SL* was given a uniform prior distribution.

POPULATION TRAJECTORY AND PROJECTIONS UNDER THE PRECAUTIONARY APPROACH

The model estimated a 1985 post-harvest stock size of 3,799 animals with a 95% CI of 2,389–6,332. The lowest abundance point was estimated for the year 2001 at 3,016 individuals (95% CI 2,141–4,322), with a 2012 abundance of 3,229 individuals (95% CI 1,896–5,406). At current harvest levels, the stock abundance seems to have increased slightly over the last few years (Fig. 7).

According to the model, removing 62 EHB animals per year for 10 years would have a 50% probability of causing a decline in the stock relative to its 2012 estimate (Fig. 8a). Limiting the harvest of EHB animals to 28 animals would reduce the probability of decline to 25%. Conversely, a harvest of 106 EHB beluga would have a 75% probability of leading to stock decline. In the absence of harvest, the probability of decline is 9%. A spring/summer harvest in Hudson Strait, with no harvest in the eastern Hudson Bay arc would have the lowest impact on the EHB stock, followed by a fall harvest in Hudson Strait only, again with no harvest allowed in the arc (Fig. 8b). If harvesting does occur in eastern Hudson Bay, then numbers taken in Hudson Strait must be reduced to obtain the same probability of increase, but the size of this reduction will depend on whether hunting occurs in the spring/summer or in the fall.

Projections over the next 25 and 50 years show that, at current harvest levels (~50 EHB beluga per year), there is a 33% probability of reaching the recovery target T1 of 5,600 individuals after 25 years (Table 3). After 50 years, this probability increases to 48%. In the absence of harvest, the probabilities of reaching T1 after 25 years is 58% and the probability of reaching T2 is 35%. When plotting the projected population trajectories (Fig. 9), we see that the median trajectory reaches T1 around 2032 in the absence of hunting but does not reach it within 50 years at current harvest levels. The trajectory corresponding to the lower 20% quantile never reaches the target, regardless of the harvest scenario (i.e., no scenario achieves an 80% probability of recovery). With an annual harvest of 50 EHB beluga, the probability of decreasing below N_{lim} is

30% after 25 years (Table 3). To maintain an 80% probability of remaining above N_{lim}, annual harvest levels should not exceed 30 EHB.

DISCUSSION

POPULATION MODELLING AND PARAMETER ESTIMATES

Modelling of this stock is based on six aerial survey estimates, all of them characterized by substantial uncertainty. Additional uncertainty is associated with the estimated rate of increase of the stock, the correction factor for diving animals, estimates of struck-and-loss, and the proportions of EHB whales in each regional harvest. Using 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 & Maunder 2004). The resulting stock trajectory is based on realistic population dynamics and offers more information than a simple trend analysis.

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 βs used in the prior distribution of the survey error. Their 95% CI, on the other hand, increased markedly with increasing values of βs (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 95% Credible Interval around the 2011 abundance estimate from the model is smaller than the 95% Confidence Interval around the 2011 aerial survey estimate, and should continue to decrease with additional data points (unlike the CI of separate survey estimates).

The estimated rate of growth *r* was well updated from its flat prior distribution. With a median value of 2.74%, it is within the range of 2 to 4% observed for other species with similar life histories, such as narwhals (Kingsley 1989), pilot whales (Kasuya et al. 1988) and spotted dolphins (Barlow & Boveng 1991). Considering that the stock is depleted, we would expect EHB beluga to exhibit a rate of increase close to their intrinsic maximum. The maximum natural growth rate of beluga populations is not well known but 4% is usually proposed as a default value for cetaceans (Wade 1998). However, other beluga populations that are small relative to their presumed carrying capacity have been shown to grow at lower rates. Kingsley (1998) estimated growth rate of the St Lawrence estuary population between 2 and 3% based on trend fitting of aerial survey estimates. Béland et al. (1988) also concluded that the potential for growth of the same population was 2 to 3% or less, using age-structured Leslie matrices based on stranding data.

Beluga whales are assumed to have a minimum 3 year calving interval (Sergeant & Brodie 1975), resulting in a maximum fecundity rate of 0.33. However, samples from harvested EHB beluga show that only 25.6% of caught females were pregnant (Doidge 1990), suggesting a lower average fecundity rate in the stock. Rates of increase for cetaceans with a fecundity of 0.25 do not exceed 3%, depending on calf and adult survival rates (Reilly and Barlow 1986), and are thus closer to our own estimates. It is not known whether intrinsic or external factors would be responsible for lower fecundity rates. It is possible that the high harvest of mature females has lowered the reproductive potential of the stock. Factors acting on *r* via mortality rates might also be involved.

The self-reported value for the struck-and-lost factor in 2012 was 4% (12 beluga were reported wounded but lost for 300 beluga landed). This value was included in the prior distribution of that parameter, but was not supported by the data; indeed, the struck-and-lost factor was estimated by the model at 41.3% (95% CI 12–77%). However, this is only a minor update from its prior value of 42.2% (95% CI 12–78%), suggesting that the data contain little information about this parameter. Changes in the hyper-parameter β_{SL} used in the prior distribution of the struck-and-lost factor had no perceptible influence on the 2012 point estimate and its uncertainty. On the other hand, the posterior distribution of *SL* was very sensitive to the choice of its own prior, which we chose based on a review of the literature. Therefore, it is difficult to draw any conclusions as to the true value of this parameter.

Choosing among plausible prior distributions for this parameter is complicated because, throughout Nunavik, different types of hunts are undertaken. In eastern Hudson Bay, the practice is to hunt animals in estuaries or close to shore, and the use of a harpoon to strike animals before killing is strongly encouraged. In parts of Hudson Strait, animals move into bays near villages, and the tides are quite large, so that animals are often shot close to shore, then recovered at low tide. Harvesting also occurs at the floe edge, which means that recovery depends on accessing dead animals before they sink. Furthermore, this term also includes the effects of under-reporting (of which struck-and-lost is a subset), as well as errors in reporting of the area where the animals were harvested (Hudson Bay vs. Hudson Strait).

The struck-and-lost factor was moderately correlated with the rate of growth r (ρ=0.16), suggesting that the model compensates for higher or lower struck-and-lost factors by adjusting the growth rate accordingly. Thus, our modelling approach cannot provide credible information as to the actual values of both *SL* and *r*. However, any independent estimation of the value of one of these two parameters from a dedicated field program would increase our confidence in the estimation of the other one as well as the accuracy of future projections.

The reliability of the model estimates depends on the accuracy of harvest data. Uncertainty in the proportions of EHB beluga in the harvest of regions other than eastern Hudson Bay (i.e., Belcher Islands, Hudson Strait, Ungava Bay) can have a strong impact on the model input term R_t, which in turn will influence the model outputs. In its previous form, the model did not include uncertainty around these proportions. In this assessment, the proportions of EHB beluga in each regional (and seasonal) harvest, derived from the latest genetic analyses (Turgeon et al. 2012), were entered as prior distributions. Although this change had a negligible impact on point estimates and CIs, we believe it constitutes a better representation of uncertainty. It should allow the model to separate the effects of uncertain struck-and-lost rates from stock assignment errors, and will make it easier to update with any new information on stock structure in the future.

POPULATION TRAJECTORY AND HARVEST LEVELS UNDER THE PRECAUTIONARY APPROACH

The population trajectory shows that the EHB stock continued to decline steadily even after quotas were enacted in the mid-1980s, because they failed to reduce catches in the eastern Hudson Bay arc. In 1995, seasonal closures of estuaries in eastern Hudson Bay forced several communities to shift their harvest to Hudson Strait, but only during certain months. Population modeling suggests that this management strategy did not slow the decline in stock abundance, perhaps because whales could be caught immediately before or after the seasonal closures. Only since the 2002 complete closure of the eastern Hudson Bay arc does there seem to have been a sustained reduction in EHB catches and some stabilization in the stock. In 2007, hunting resumed in eastern Hudson Bay arc, but its main estuaries (Nastapoka and Little Whale River) remained closed, and most villages had to continue taking their quotas from the Strait. This strategy appears to have been effective at maintaining EHB beluga catches at low levels. Recent management schemes separating the Hudson Strait harvest into spring and fall periods have allowed higher total catches without increasing the catch of EHB whales.

The model estimates that the 2012 harvest was equivalent to 60 EHB beluga. This increase from last year (55 EHB) is due for the most part to the increase of the Sanikiluaq harvest (61 vs. 32 in 2011). If 12% of these whales belonged to the EHB stock, this increase represents an additional 3 or 4 EHB beluga taken by Sanikiluaq. Although these whales are not included directly in the management plan (i.e., they are not subtracted from the Nunavik quota), they are included in the model and thus affect harvest advice for subsequent years. Currently, the harvest in Sanikiluaq is monitored but not controlled, except for a municipal motion prescribing that whales should be taken before July 15th or after September 30th. An earlier version of the municipal motion stopped hunting at the beginning of July, which was a good strategy to minimize the impact on the EHB stock because of the low proportions of EHB whales detected by haplotype analyses for the spring and fall (Turgeon et al. 2009). The recent changes in harvest dates may have made EHB animals more vulnerable to capture but there is still considerable uncertainty in our understanding of the seasonal movements of beluga whales around the Belcher Islands (Doniol-Valcroze et al. 2012b). If Sanikiluaq harvest levels continue to remain high or increase further, it might become necessary to decompose the harvest by season and to refine the analyses of the sampling programs to better determine the number of EHB beluga landed. In this case, it will be important to monitor the exact dates at which beluga are hunted around the Belcher Islands.

The model suggests that the EHB beluga stock has stopped its decline in recent years and even shows some indication of modest population growth. This conclusion is more optimistic than previous assessments and is due to the slightly higher 2011 survey estimate. Projections show that an annual removal of more than 62 animals from the EHB stock would have a 50% or higher risk of causing a stock decline (vs. 52 in the previous assessment). The effect of the 2011 survey is two-fold. First, there is a direct effect of the stock being about 200 beluga larger than what was predicted by the last assessment, which translates into more beluga being produced every year. Second, there is an indirect effect: the model has slightly increased the estimate of r and decreased the estimate of SL to better fit the last survey, which in turn results in additional beluga produced and “available” for harvest. Because the model relies on only six surveys, it is sensitive to the results of any one estimate (particularly the first and the last one).

Setting catches at levels that result in a 50% risk of decline in the resource is not deemed precautionary, and rebuilding the resource even to levels observed in the early 1980s is uncertain using this strategy. Developping a precautionary framework would facilitate sustainable management of Nunavik beluga and recovery of this stock. Lawson et al. (2006) proposed that the recovery target for EHB beluga should be equal to the PRL, i.e., 70% of the historical stock size. Since the historical stock size is unknown, we have calculated a range of plausible values to represent the inferred maximum stock size (Appendix 1). Based on these results, two recovery targets are proposed to encompass this range: T1=5,600 and T2=8,000. T1 in particular constitutes a more achievable target and is based on an inferred maximum stock size that may be easier for resource users to accept, as it is close to the number of beluga that were killed in a short period of intense commercial harvest.

The key element within PA is the avoidance of serious harm to the resource. Consequently, uncertainty associated with population estimates is considered when identifying the probability of reaching the recovery target. Under the proposed framework for marine mammals, the lower 20th percentile of the estimate is used to determine if the population is below the PRL. In other words, there must be an 80% probability that the population will be above the PRL in order to consider that a population has recovered. Our long-term projections indicate that none of the harvest scenarios (even zero harvest) can meet this requirement over a 50 year timeframe, even when using the lower PRL level (T1). A scenario with no harvest has a 78% and a 66% probability of reaching T1 and T2, respectively, in 50 years (Table 3). The median estimate, however, reaches these targets by 2032 (T1) and 2045 (T2).

Another element of the PA framework to avoid serious harm is the identification of a reference limit point at 30% of the maximum population size (Hammill and Stenson 2007). The closer a population is to this N_{lim}, the more conservative and risk-averse harvesting strategies must be. Under this framework, N_{lim} would be set at ~2,400 beluga if the lower estimate of maximum population size is used. At a current stock size of about 3,200 animals, the EHB summer stock thus falls into the lower end of the cautious zone (the zone between N_{lim} and the PRL). With an annual harvest of 50 EHB beluga, the probability of decreasing below N_{lim} is 30% after 25 years. To maintain an 80% probability of remaining above N_{lim}, annual harvest levels should not exceed 30 EHB.

T1 and T2 are not the only possible recovery targets. Alternative targets could be based on the minimum stock size required to yield an acceptable sustainable harvest defined by resource-users. Another possibilty would be to reach a stock size for which an acceptable harvest maintains an 80% probability of staying above $N_{lim.}$ It should be noted that the 1985 stock size of 4,000 is not a plausible estimate of maximum stock size because the stock had to be higher to sustain the recorded commercial harvest levels. Therefore, it should not be used to propose a recovery target under the Precautionary Approach framework.

There are several sources of uncertainty in this PA analysis. First, the recovery target depends on our estimate of the inferred maximum stock size. Our estimates of the stock size in 1854 was based on 10 years of commercial harvest reports and assumptions regarding population dynamics and the number of beluga remaining after 1864. There is considerable uncertainty regarding these estimates. Moreover, ecological conditions present in the 1800's may no longer apply to current environmental conditions. Eastern Hudson Bay has undergone several changes (geostatic rebound, reduction in ice cover, changes in fish abundance and composition) that may have had an effect on carrying capacity. The impacts of climate change and environmental variability on this stock are not well understood and it is possible that our recovery target is not realistic. At this point, however, we consider that we are using the best estimate of historical stock size (which is used as a proxy for carrying capacity), and the data available do not allow us to provide a more reliable estimate of current carrying capacity. Also, even if carrying capacity has changed, it is important to emphasize that any attempt to increase number of whales in the EHB stock will at some point result in a higher sustainable harvest.

Another source of uncertainty is that the current model does not include a mechanism for density-dependence, and therefore might not provide an accurate representation of population dynamics in the vicinity of the carrying capacity. In many models, density dependent factors begin to reduce population growth rates at about 70% of the pristine population size. This would lower the rate at which the recovery target is reached (i.e., our predictions would be too optimistic). However, we note that the currently estimated r (2.74%) is already much lower than the theoretical maximum value for beluga whales (4%). At this point, it is not clear how density-dependent mechanisms would act upon the EHB beluga as the stock size increases. Nevertheless, future efforts within the PA framework might benefit from a new model formulation that incorporates density-dependent effects.

It should also be noted that uncertainty increases when projecting further into the future. If surveys are conducted at regular intervals, the level of uncertainty should decrease (i.e., the CI around the 2037 stock size will be smaller when calculated in 2025 than it is with the actual projections).

ACKNOWLEDGEMENTS

We thank the Nunavik hunters and Uumajuit wardens for providing skin and teeth samples and reports on catches. We thank the Nunavik Hunting, Fishing and Trapping Association for assistance with the sampling program. We also thank Lianne Postma and Denise Tenkula for DNA analyses, Samuel Turgeon for database management, Peter May for beluga aging data, and the Makivik Corporation and D.W. Doidge from the Nunavik Research Center for coordinating this program. This work was supported by Species at Risk funding to the Department of Fisheries and Oceans, the Interdepartmental Recovery Fund (Environment Canada) and the Centre of Expertise for Marine Mammalogy (CEMAM).

LITERATURE CITED

Anonymous. 2008. Nunavik Inuit Land Claims Agreement. Pages 22-53. Ottawa, Canada.

Barlow, J. and Boveng, P.1991. Modeling age-specific mortality for marine mammal populations. Marine Mammal Science 7:50-65.

Béland, P., Vézina, A. and Martineau, D. 1988. Potential for growth of the St. Lawrence (Québec, Canada) beluga whale (*Delphinapterus leucas*) population based on modelling. ICES Journal of Marine Science 45:22-32.

Brooks, S., King, R. and Morgan, B. 2004. A Bayesian approach to combining animal abundance and demographic data. Animal Biodiversity and Conservation 27:515-529.

Brooks, S. P. and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. Journal Of Computational And Graphical Statistics 7:434-455.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. 2001. Introduction to Distance Sampling. Oxford University Press.

Caron, L.M.J. and Smith, T.G. 1990. Philopatry and site tenacity of belugas, *Delphinapterus leucas*, hunted by the inuit at the Nastapoka estuary, eastern Hudson Bay. In Smith, T.G., D.J. St.Aubin, and J.R. Geraci (ed.). Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224: 69-79.

COSEWIC. 2004. COSEWIC assessment and update status report on the beluga whale *Delphinapterus leucas* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 70 pp.

de March, B. G. E. and Postma, L. D. 2003. Molecular genetic stock discrimination of belugas

(*Delphinapterus leucas*) hunted in Eastern Hudson Bay, Northern Quebec, Hudson Strait, and Sanikiluaq (Belcher Islands), Canada, and comparisons to adjacent populations. Arctic 56:111-124.

de Valpine, P., and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. Ecological Monographs 72:57-76

Doidge, D. 1990. Age and stage based analysis of the population dynamics of beluga whales, *Delphinapterus leucas*, with particular reference to the northern Quebec population, Ph.D. thesis, McGill University, Montreal

Doniol-Valcroze, T., Hammill, M.O. and Lesage, V. 2012a. Information on abundance and harvest of eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2011/119. iv + 17 p.

Doniol-Valcroze, T. and Hammill, M. O. 2012b. Harvest advice for beluga in the Belcher, King George, and Sleeper Islands in relation to the eastern Hudson Bay stock. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/125. iv + 8 p.

Geweke, J. 1996. Evaluating the Accuracy of Sampling-based Approaches to the Calculation of Posterior Moments, in: Bernardo, J.M., Berger, J.M., Dawid, A.P., and Smith, A.F.M. (eds.): Bayesian Statistics 4. Oxford University Press:169-193.

Gosselin, J-F. Lesage, V. and Hammill, M.O. 2009. Abundance indices of beluga in James Bay, eastern Hudson Bay and Ungava Bay in 2008. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/006. iv + 25 p.

Gosselin, J.-F., Doniol-Valcroze, T. and Hammill, M.O. 2013. Abundance estimate of eastern Hudson Bay beluga and James Bay, summer 2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/016. vii + 20 p.

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., Lesage, V., Gosselin, J.-F., Bourdages, H., de March, B. G.E. and Kingsley, M.C.S. 2004. Changes in abundance of northern Quebec (Nunavik) beluga. Arctic 57:183-195.

Hammill, M.O., Lesage, V. and Gosselin, J.-F. 2005. Abundance of Eastern Hudson Bay belugas. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/010. iv + 17 p.

Hammill, M.O., Kingsley, M.C.S., Lesage, V. and Gosselin, J.-F. 2009. Abundance of Eastern Hudson Bay belugas. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/009

Heide-Jørgensen, M. and Rosing-Asvid, A. 2002. Catch statistics for beluga in West Greenland 1862-1999. NAMMCO Scientific Publications 4:127-142.

Hoyle, S. and Maunder, M. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. Animal Biodiversity and Conservation 27:247-266.

Innes, S. and Stewart, R. 2002. Population size and yield of Baffin Bay beluga (*Delphinapterus leucas*) stocks. NAMMCO Scientific Publications 4:225-238.

International Council for the Exploration of the Sea (ICES). 2001. Report of the study group on further developments of the precautionary approach to fishery management. ICES CM 2001/ACFM:11

Kasuya, T., Sergeant, D. and Tanaka, K. 1988. Re-examination of life history parameters of the long-finned pilot whale in Newfoundland waters. Scientific Reports of the Whales Research Institute 39:103-119.

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

Kingsley, M. 1989. Population dynamics of the narwhal *Monodon monoceros*: an initial assessement (Odontoceti: Monodontidae). Journal of Zoology 42:676-208.

Kingsley, M. 1998. Population index estimates for the St Lawrence belugas, 1973-1995. Marine Mammal Science 14:508-530.

Kingsley, M. 2000. Numbers and distribution of Beluga whales *Delphinapterus leucas*, in James Bay, eastern Hudson Bay, and Ungava Bay in Canada during the summer of 1993. Fishery Bulletin 98:736-47

Kingsley, M.C.S. and Gauthier, I. 2002. Visibility of St Lawrence belugas to aerial photography, estimated by direct observation. NAMMCO Scientific Publications Vol. 4: 259-270.

Lawson, J., Hammill, M.O. and Stenson, G.B. 2006. Characteristics for Recovery: Beluga Whale. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/075. iv + 16 p.

Lesage, V. and Doidge, DW. 2005. Harvest statistics for beluga in Nunavik, 1974–2004. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/012. iv + 25 p.

Lesage, V., Doidge, D.W. and Fibich, R. 2001. Harvest statistics for beluga whales in Nunavik, 1974–2000. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/022. 35 pp.

Lesage, V. Baillargeon, D., Turgeon, S. and Doidge, DW. 2009. Harvest statistics for beluga in Nunavik, 2005–2008. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/007. iv + 25 p.

Lunn, D. J., Thomas, A. Best, N. and Spiegelhalter, D. 2000. WinBUGS -- A Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325-337.

Orr, J. and Richard, P.1985. Information collected from beluga whale (*Delphinapterus leucas*) hunts in Cumberland Sound, Baffin Island, Northwest Territories, 1982-1984. Canadian Data Report of Fisheries and Aquatic Sciences 490: iv + 32 p.

Postma, L.D., Petersen, S.D., Turgeon, J., Hammill, M.O., Lesage, V., and Doniol-Valcroze, T. 2012. Beluga whales in James Bay: a separate entity from eastern Hudson Bay belugas? DFO Can. Sci. Advis. Sec. Res. Doc. 2012/074. iii + 23 p.

Punt, A. E. and Smith D.M. 2001. The gospel of maximum sustainable yield in fisheries management: birth, crucifixion and reincarnation. In Conservation of exploited species, pp. 41-66. Ed. by J. D. Reynolds, G. M. Mace, K. H. Redford and J. G. Robinson. Cambridge University Press, Cambridge, UK.

Reeves, R.R. and Mitchell, E.D. 1987. History of white whale (*Delphinapterus leucas*) exploitation in eastern Hudson Bay and James Bay. Canadian Special Publications on Fisheries and Aquatic Sciences 95. 45p.

Reeves, R.R. and Mitchell, E. 1989. Status of white whales, *Delphinapterus leucas*, in Ungava Bay and eastern Hudson Bay. Can. Field-Nat. 103: 220-239.

Reilly, S. and Barlow, J. 1986. Rates of increase in dolphin population size. Fishery Bulletin 84:527-533.

Richard, P.R. 2010. Stock definition of belugas and narwhals in Nunavut. DFO Can. Sci. Advis.Sec Res. Doc. 2010/022. iv + 14p.

Seaman, G. and Burns, J. 1981. Preliminary results of recent studies of belukhas in Alaskan waters. Report of the International Whaling Commission 31:567-574.

Sergeant, D. and Brodie, P. 1975. Identity, abundance, and present status of populations of white whales, *Delphinapterus leucas*, in North America. Journal of the Fisheries Research Board of Canada 32:1047-1054.

Smith, T.G. and Hammill, M.O. 1986. Population estimates of white whale, *Delphinapterus leucas*, in James Bay, Eastern Hudson Bay and Ungava Bay. Can. J. Fish. Aquat. Sci. 43: 1982-1987.

Smith, T.G., Hammill, M.O. and Martin, A.R. 1994. Herd composition and behaviour of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries. Meddellelser om Grønland, Bioscience 39:175-184.

Spiegelhalter, D. J., Best, N. G. Carlin, B. P. and Van Der Linde, A. 2002. Bayesian measures of model complexity and fit (with discussion). Journal of the Royal Statistical Society - Series B: Statistical Methodology 64:583-639.

Stenson, G.B., Hammill, M. Ferguson, S. Stewart, R. and Doniol-Valcroze, T. 2012. Applying the Precautionary Approach to Marine Mammal Harvests in Canada DFO Can. Sci. Advis. Sec. Res. Doc. 2012/XX.

Stewart, R. E. A., Campana, S. E., Jones, C. M. and Stewart, B. E. 2006. Bomb radiocarbon dating calibrates beluga (Delphinapterus leucas) age estimates. Canadian Journal of Zoology 84:1840-1852.

Taylor, B. L., Wade, P. R., De Master, D. P. and Barlow, J. 2000. Incorporating Uncertainty into Management Models for Marine Mammals. Conservation Biology 14:1243-1252.

Thomas L., Laake, J.L., Strinberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St Andrews, UK

Turgeon, J., Duchesne, P., Postma, L. D. and Hammill, M. O. 2009. Spatiotemporal distribution of beluga stocks (*Delphinapterus leucas*) in and around Hudson Bay: Genetic mixture analysis based on mtDNA haplotypes. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/011. iv + 14 p.

Turgeon, J., Duchesne, P., Colbeck, G., Postma, L. D. and Hammill. M. 2012. Spatiotemporal segregation among summer stocks of beluga (*Delphinapterus leucas*) despite nuclear gene flow: implication for the endangered belugas in eastern Hudson Bay (Canada). Conservation Genetics 13:419-433.

Wade, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14:1-37.

Wade, P. R. 2000. Bayesian Methods in Conservation Biology. Conservation Biology 14:1308-1316.

Table 1. Prior distributions, parameters and hyper-parameters used in Nunavik beluga population model. "est." denotes a parameter that follows a distribution and which value is estimated by the model.

Parameters	Notation	Prior distribution	Hyper-parameters	Values
Survey error (t)	εs_t	Log-normal	μ_S τ_S	0 *est.*
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 *est.*
Precision (process)	τ_p	Gamma	α_p β_p	1.5 0.001
Growth rate	r	Beta*	α_r β_r	2 3
Struck-and-lost	SL	Beta	α_{SL} β_{SL}	3 4
Initial population	N_{1985}	Uniform	N_{upp} N_{low}	12,500 500
Proportion EHB *(HS, all seasons)*	P_{HS}	Beta	α_{HS} β_{HS}	45 216
Proportion EHB *(Sanikiluaq)*	P_{SAN}	Beta	α_{SAN} β_{SAN}	8.3 60
Proportion EHB *(HS, spring)*	P_{SPRING}	Beta	α_{SPRING} β_{SPRING}	5.5 38
Proportion EHB *(HS, fall)*	P_{FALL}	Beta	α_{FALL} β_{FALL}	13.5 50

* was rescaled to the range -0.04 to +0.08

Table 2. Cross-correlation matrix among posterior distributions of main model variables. Symbols are defined in table 1. Correlations <0.01 are not shown.

	Survey σ	r	N_{1985}	SL	Process σ
Survey σ	1				
r	-0.05	1			
N_{1985}	0.13	-0.78	1		
SL	-	0.16	0.08	1	
Process σ	-	0.02	0.04	-	1

Table 3. Probability of reaching the recovery targets T1 and T2 after 25 or 50 years, and risk of decreasing under N_{lim}, under different annual harvest levels of EHB beluga.

harvest	T1 = 5,600		T2 = 8,000		N_{lim} = 2,400	
	25 yrs	**50 yrs**	**25 yrs**	**50 yrs**	**25 yrs**	**50 yrs**
0	58%	78%	35%	66%	6%	6%
10	53%	72%	31%	61%	10%	10%
20	48%	66%	28%	55%	14%	15%
30	42%	60%	25%	50%	18%	20%
40	38%	54%	22%	44%	24%	28%
50	33%	48%	19%	39%	30%	35%
60	29%	42%	16%	34%	37%	44%
70	25%	36%	14%	29%	44%	51%
80	22%	31%	12%	25%	50%	58%
90	19%	26%	10%	22%	56%	65%
100	16%	22%	9%	18%	62%	70%
125	11%	14%	6%	12%	74%	81%
150	7%	9%	4%	7%	83%	89%
175	4%	5%	2%	4%	89%	93%
200	3%	3%	2%	3%	93%	96%

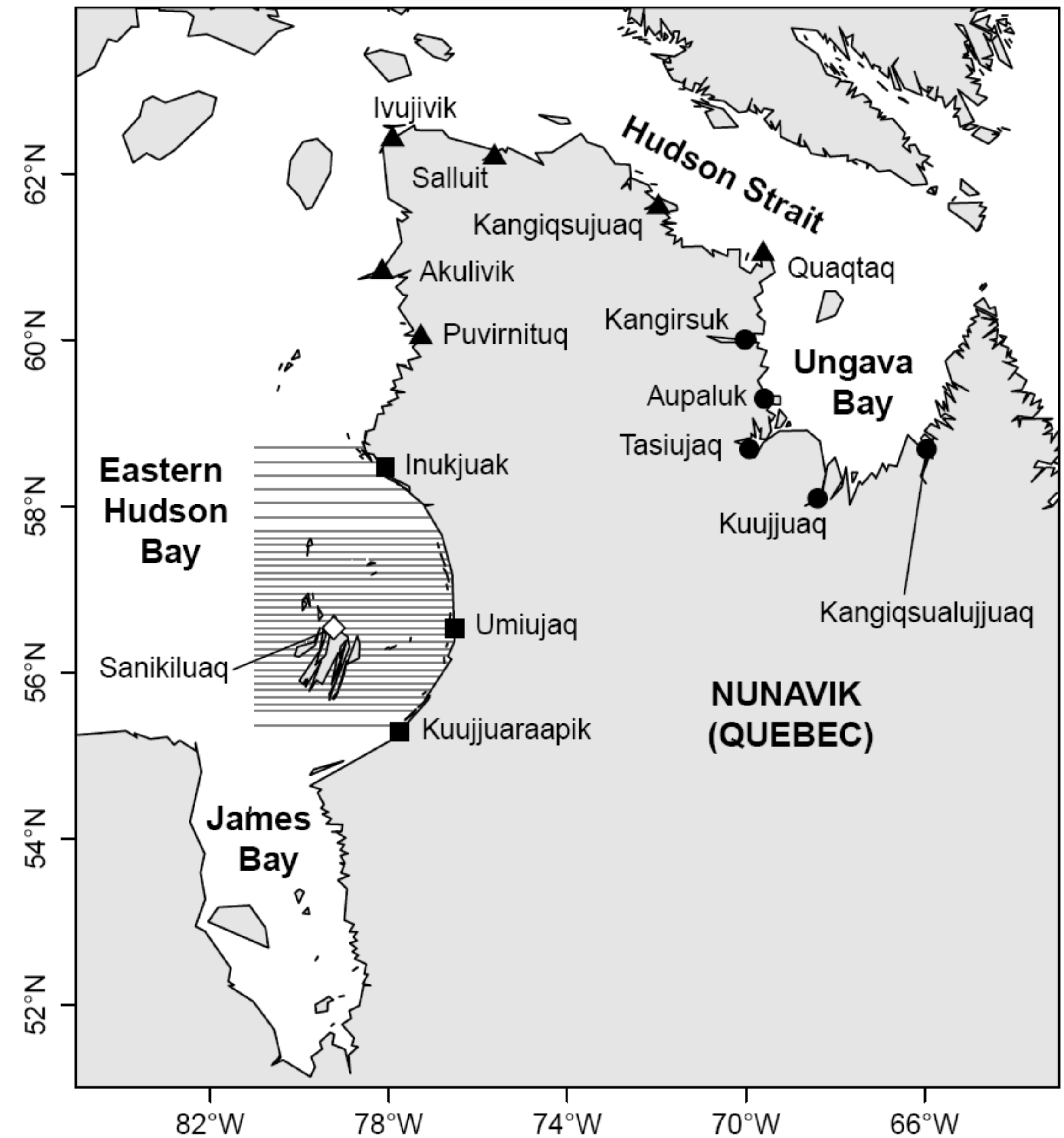


Figure 1. Map of Nunavik communities and aerial survey lines in the eastern Hudson Bay arc used to estimate abundance of the EHB beluga stock during summer. Squares: eastern Hudson Bay arc communities. Triangles: Hudson Strait and north-eastern Hudson Bay communities. Circles: Ungava Bay communities. White lozenge: Sanikiluaq (Belcher Islands, Nunavut).

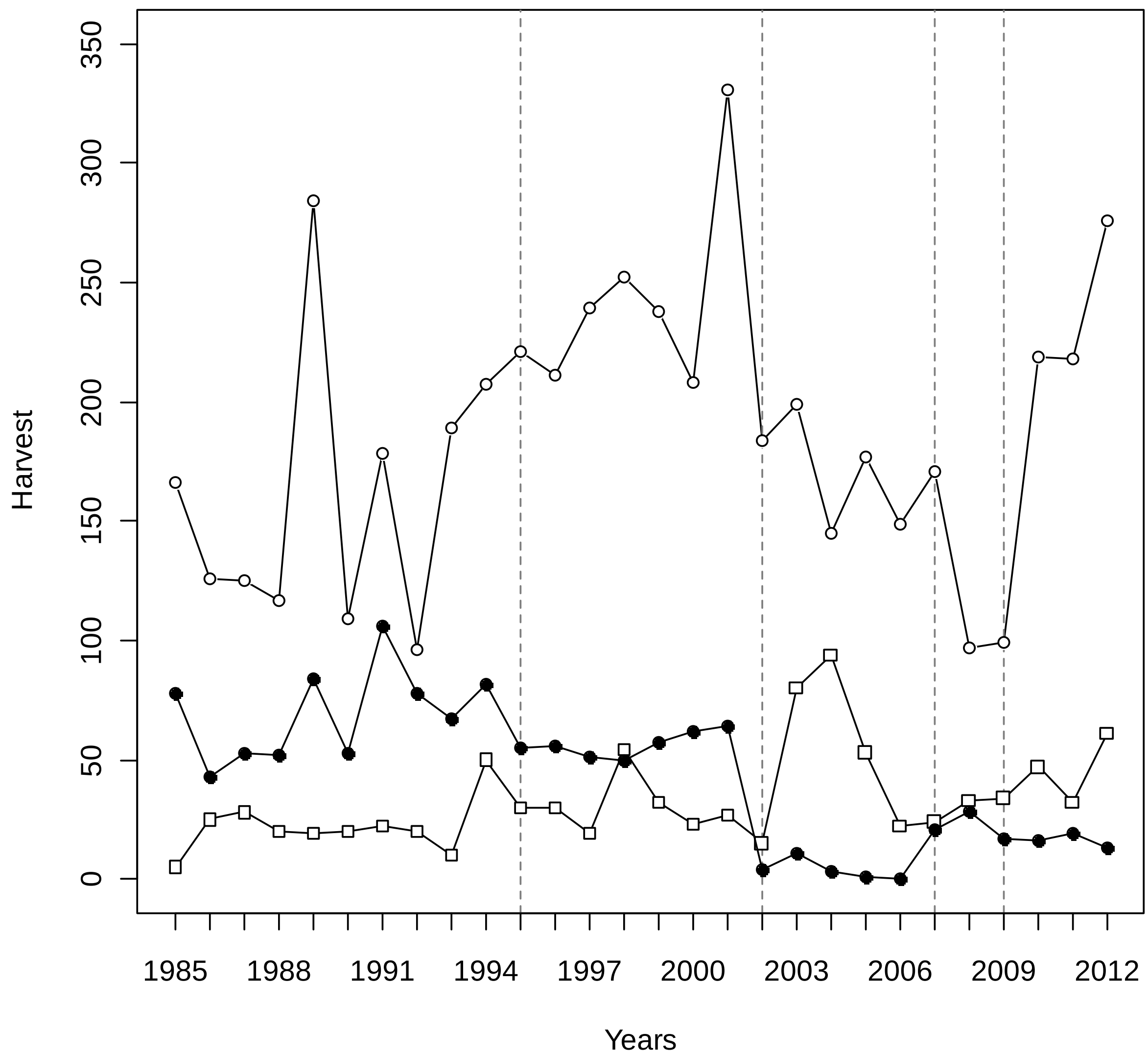


Figure 2. Beluga harvest in Nunavik for the period 1985 – 2012, broken down by region. Open circles: Hudson Strait and Ungava Bay. Closed circles: eastern Hudson Bay arc. Squares: Sanikiluaq (Belcher Islands, Nunavut). Vertical dashed lines indicate main management periods. 1985: Introduction of quotas; 1995: Seasonal closures of estuaries in eastern Hudson Bay. Puvirnituq shifts harvest from Nastapoka river to Hudson Strait; 2002: Complete closure of eastern Hudson Bay arc and Ungava Bay; 2007: Hunting resumes in eastern Hudson Bay arc and Ungava Bay, but Nastapoka, Little Whale and Mucalic river estuaries remain closed. Sanikiluaq starts restricting summer catches; 2009: Separation of Hudson Strait harvest into spring and fall periods, allowing higher total catches.

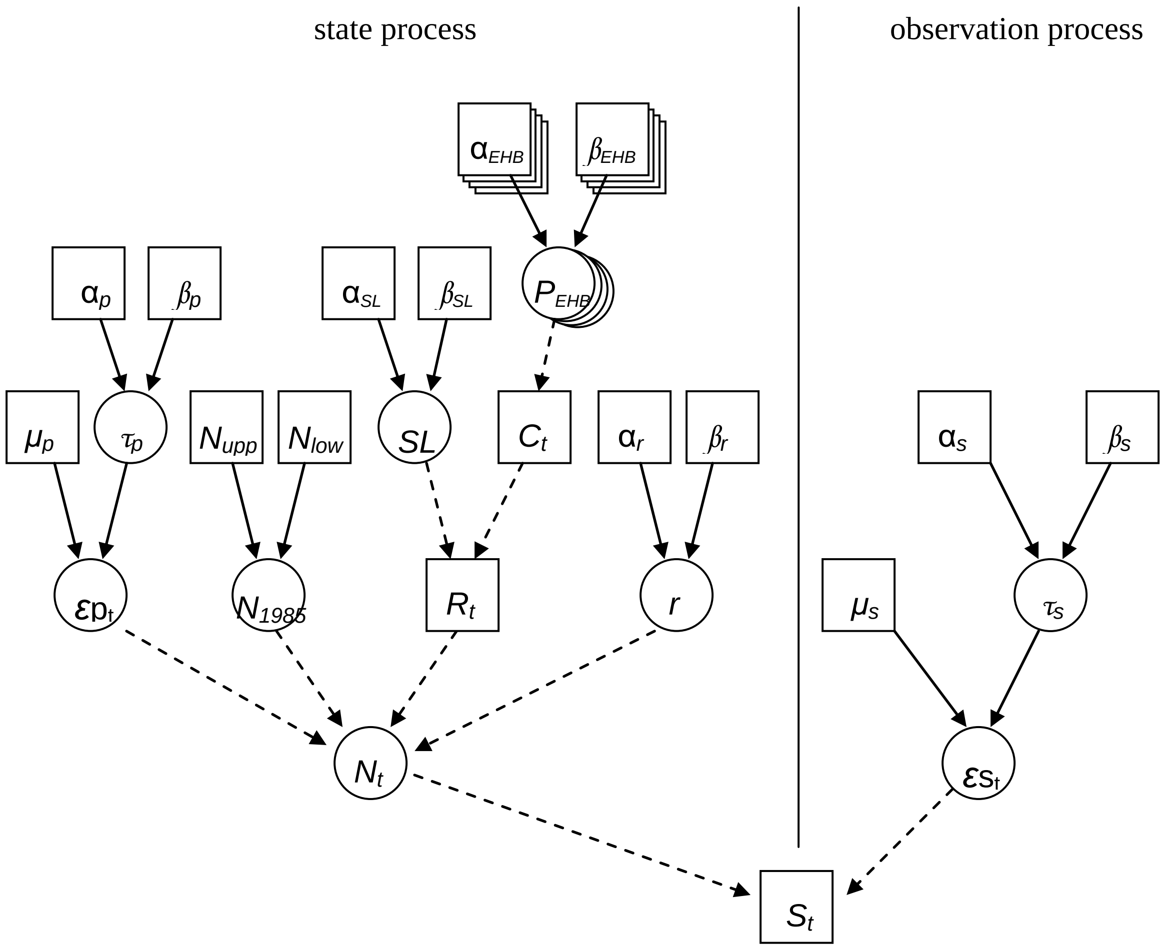


Figure 3. Directed acyclic graph for the beluga population model. Square nodes represent fixed values (observed data or prior parameter values). Circular nodes represent parameters to be estimated (cf. Table 1). Edges represent relationships between variables, with broken lines representing deterministic relationships and solid lines representing stochastic relationships. t subscript represents variables that take a different value for each year. St: Survey estimate at time t. Nt: Abundance estimate at time t. Rt: Total removals for year t (including struck-and-lost, SL). Ct: Catches of EHB beluga based on harvest in all Nunavik regions. PEHB: Proportions of EHB beluga in regions other than the EHB arc (Sanikiluaq, Hudson Strait for all seasons, in spring and in the fall). Other symbols and values are defined in table 1.

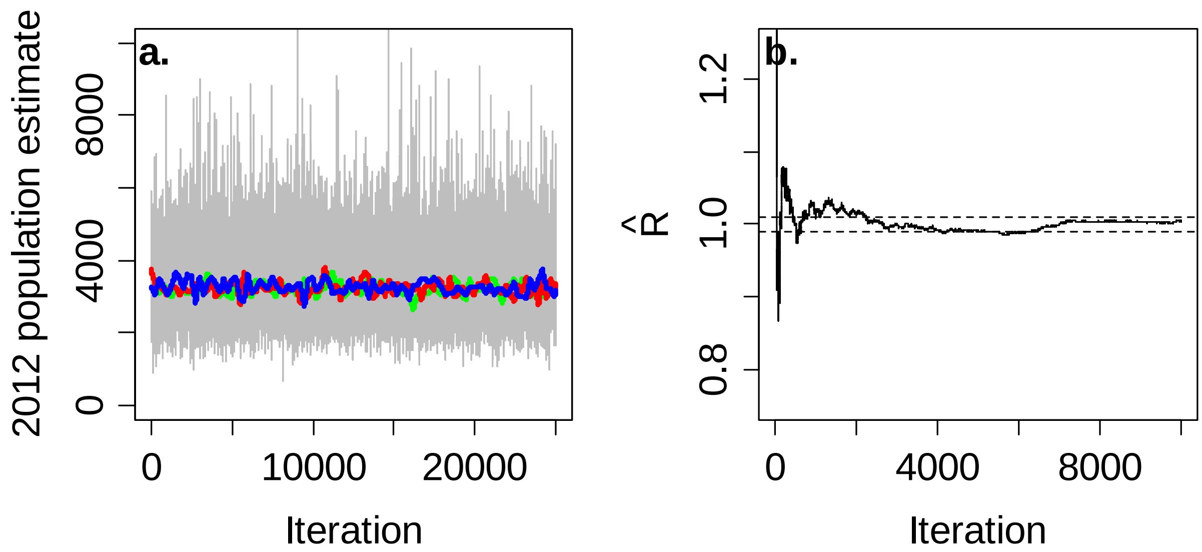


Figure 4. a) Trace plot of the 25,000 iterations of the three MCMC chains (gray lines) for the final population estimate. The smoothed traces of the three chains (blue, green and red bold lines) show good mixing and convergence. b) BGR convergence diagnostic of the three chains, plotted for increasing numbers of iterations (up to 10,000). Dashed lines indicate the 0.99 – 1.01 range. Values close to 1 indicate good convergence.

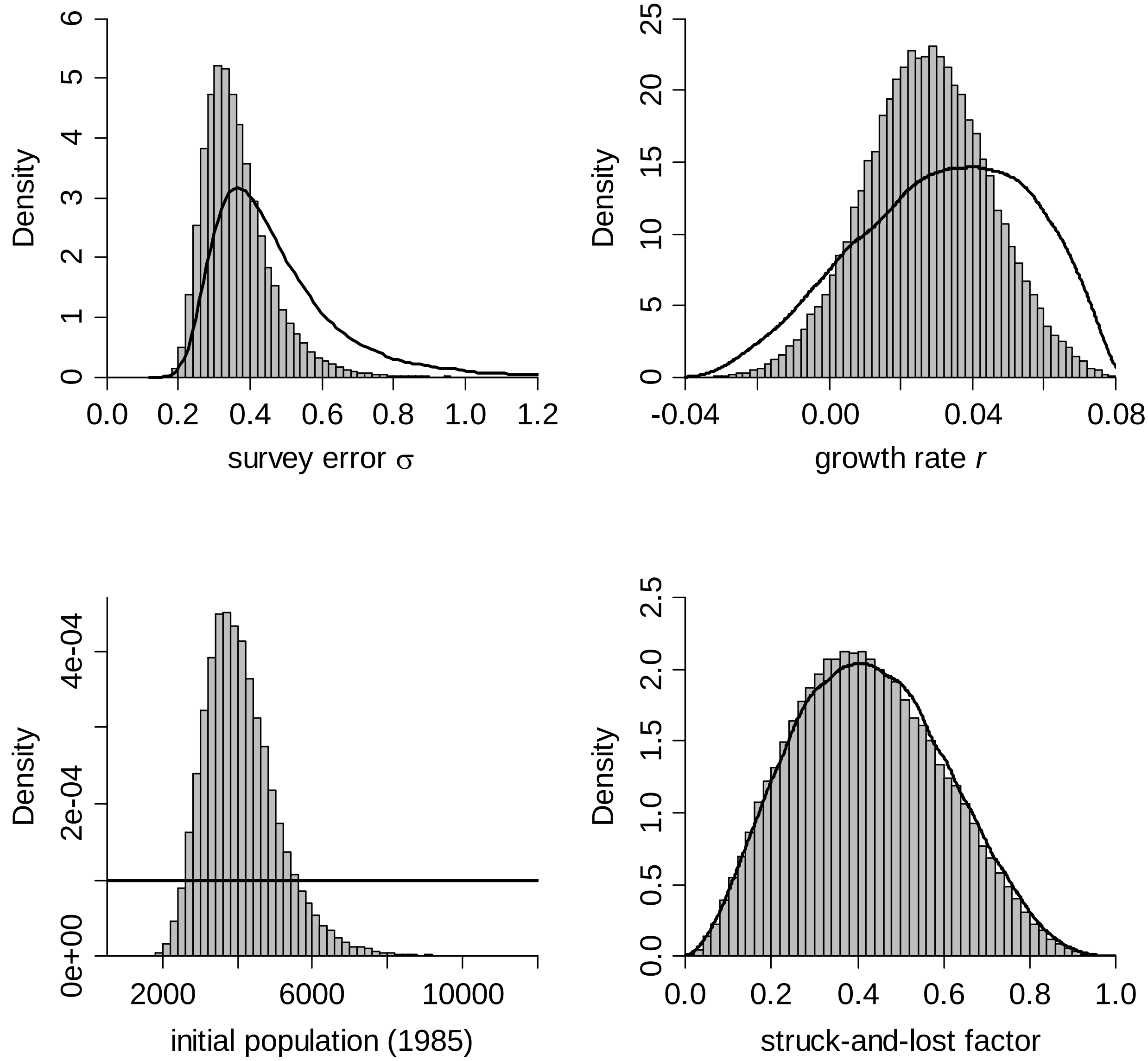


Figure 5. Prior (lines) and posterior (bars) distributions of four parameters estimated by the beluga population model. The prior for the process error was not updated and is not shown.

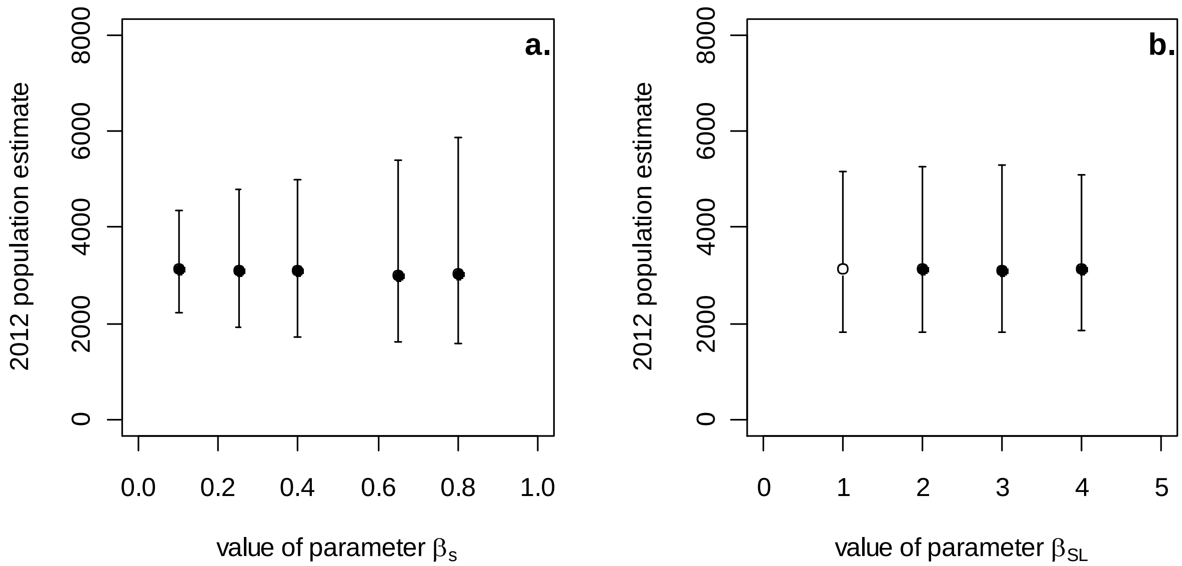


Figure 6. Sensitivity of median population estimates (circles) and 95% CI (bars) to the hyper-parameters used in prior distributions. a) Survey precision. b) Struck-and-lost factor. Closed circles: αsl = 3, βsl varies from 2 to 4. Open circle: αsl = 1, βsl = 1 (i.e., uniform distribution).

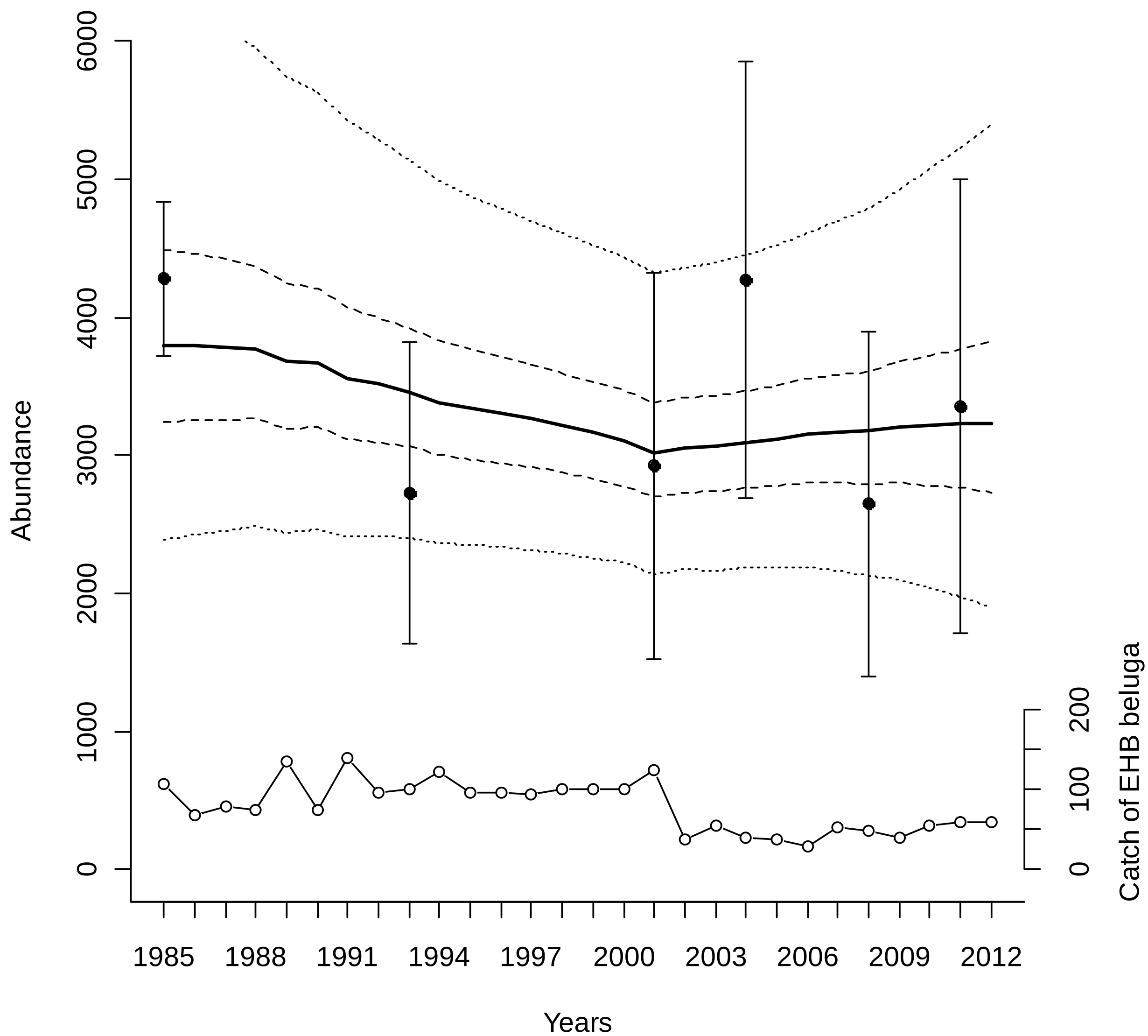


Figure 7. Model estimates of eastern Hudson Bay (EHB) beluga abundance. Solid line: median estimates. Dashed lines: 25% and 75% quantiles. Dotted lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). The model was fitted to aerial survey estimates corrected for animals at the surface (closed circles, ±SE). Right y-axis: Catch of EHB beluga based on the catch series of different regions in Nunavik multiplied by the estimated proportions of EHB whales in each harvest (open circles).

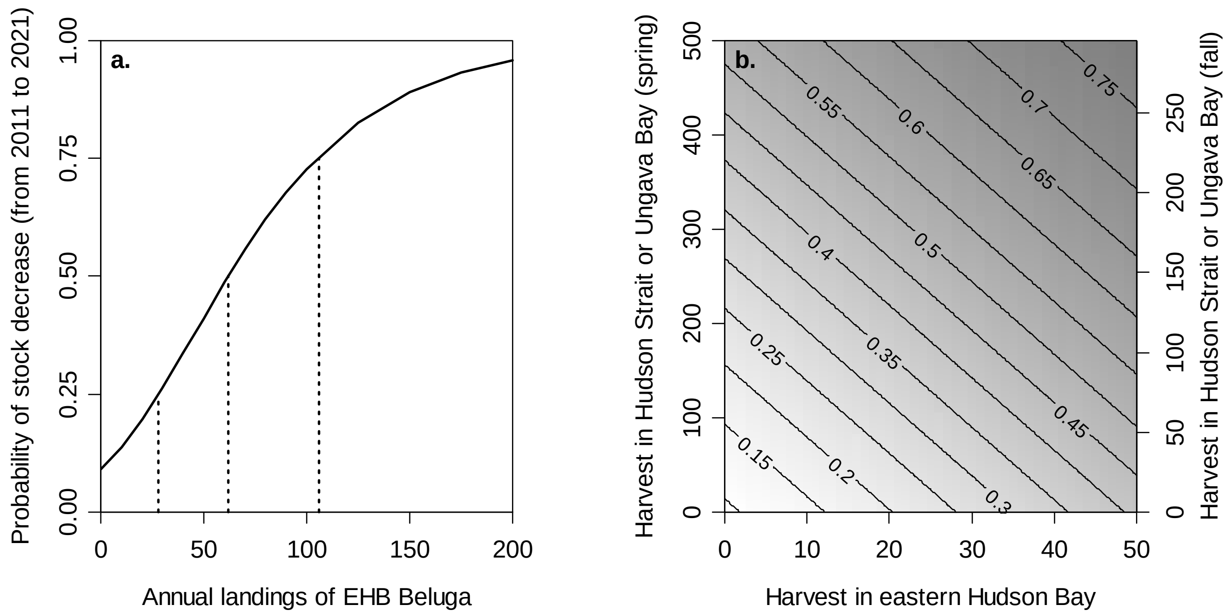
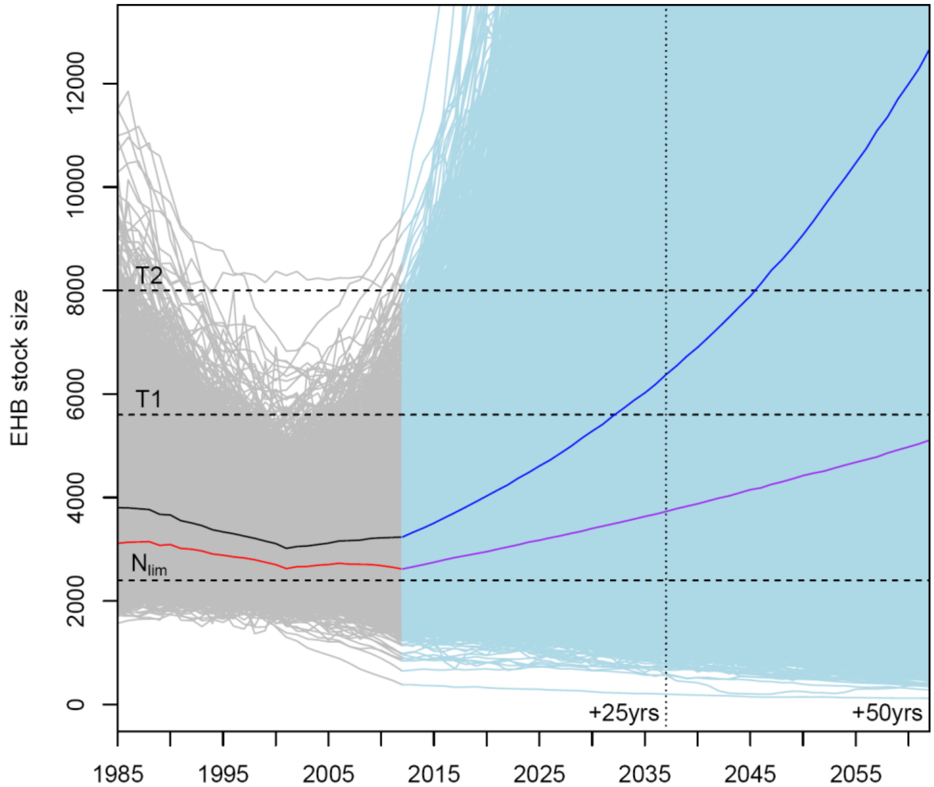


Figure 8. Probability of EHB beluga stock decrease from the 2012 abundance estimate after 10 years of harvest, estimated by a stochastic Bayesian stock-production model. a.) As a function of the number of EHB beluga removed from the stock every year. Dotted lines indicate levels of harvest corresponding to 25%, 50% and 75% probability of decline. b.) As a function of the sum of harvest in the EHB arc (x-axis) and harvest in Hudson Strait or Ungava Bay in the spring (left y-axis), or in the fall (right y-axis). For example a 20% probability of a population decline, would occur if 20 animals were taken from EHB only, 165 taken from Hudson Strait only during the spring, or 96 animals were removed from Hudson Strait only in the fall. More complex combinations would be possible by balancing the number of animals harvested in the different areas or seasons: removing 200 beluga from Hudson Strait in the spring plus 10 beluga from eastern Hudson Bay would result in a 30% probability of decline.



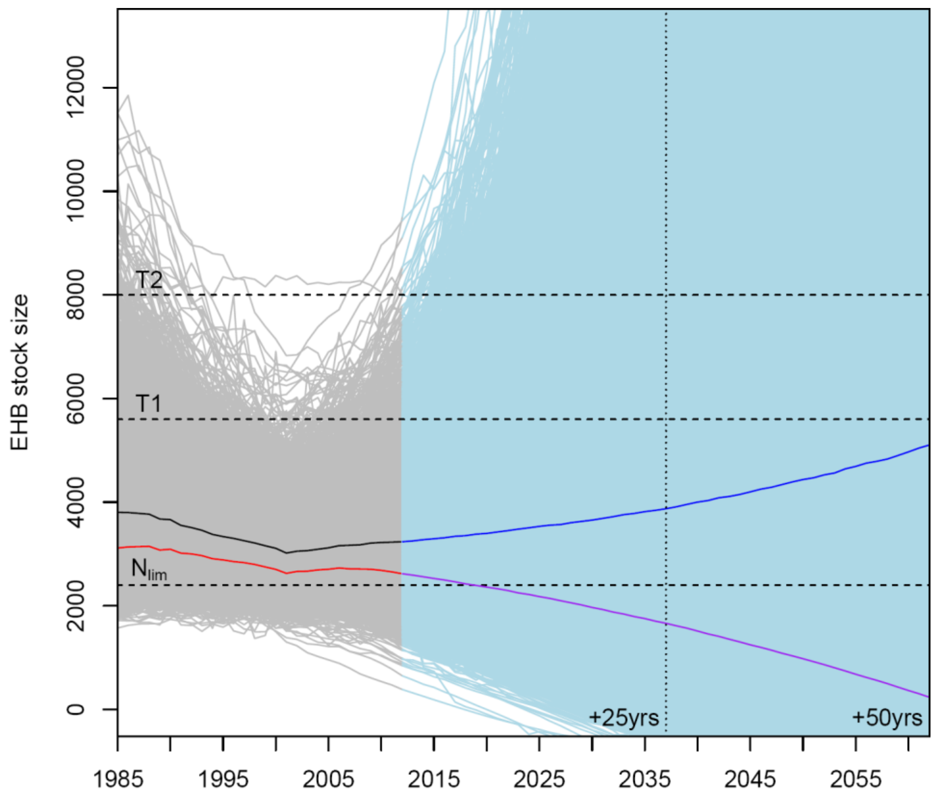


*Figure 9. Current estimates of the EHB stock size within the context of a Precautionary Approach framework. Grey lines represent modeled past stock trajectories and blue lines represent future trajectories. Black and blue lines: median estimates. Red and purple lines: 20% quantile.*top: no harvest scenario; bottom: annual harvest of 50 EHB beluga per year.

APPENDIX 1

ESTIMATING INFERRED MAXIMUM SIZE OF THE EHB STOCK

RATIONALE

Pristine stock size, N_{1854} (i.e., estimated abundance in year 1854, prior to the main period of commercial exploitation) was estimated by Hammill et al. (2005) at 12,500 (with a range of 8,447–17,117). However, they assumed loss rates that could range from 0 to 100%. These loss rates may not be appropriate for commercial harvest techniques that used nets to block entrances of river estuaries and presumably resulted in most of the trapped beluga being landed. Consequently, this previous estimate of N_{1854} may be biased and may result in unrealistic recovery targets. Moreover, there are now better techniques to simultaneously incorporate the uncertainty around each of the model parameters (e.g., growth rate, shape of the density-dependent response). Therefore, our objective was to re-estimate N_{1854} with the same dataset using a Bayesian model to fully integrate the uncertainty in population dynamics.

METHODS

A modified Pella-Tomlinson model (Pella and Tomlinson 1969) was fitted using Bayesian methods in WinBugs to estimate stock trajectory during a period of high commercial catches (1854–1863). Population dynamics were modelled using:

$$N_t = N_{t-1} \cdot e^{r \cdot (1 - \frac{N_{t-1}}{K})^{\theta}} - R_t$$

where N_t is stock size at year t, K is carrying capacity, r is the intrinsic rate of population growth, θ is the shape of the density-dependant relationship, and R_t is the reported harvest for year t (Table A1).

We followed Hammill et al. (2005) in assuming that approximately 1,000 beluga had to survive at the end of the commercial hunt for the stock to persist. We added an error term around the final stock size, which followed a normal distribution with zero mean and an SD of 100, i.e., $N_{1863} \sim 1000 + N(0,100)$. We also assumed that the EHB stock had been near its carrying capacity before 1854 (i.e., $N_{1854} = K$)

The growth rate r was given a uniform distribution between 1 and 7%. The initial stock size N_{1854} was given a uniform distribution between 5,000 and 20,000. The shape of the density-dependent relationship, θ, followed a gamma distribution with parameters shape α=2 and rate β=2, censored to the interval 1 – 7 (resulting in a median of 3.3).

There is uncertainty regarding the loss rates during commercial harvest. It is likely that drive hunts had little loss (Heide-Jørgensen 1994) but some unreported catches cannot be excluded. Therefore, it seems likely that the loss rate was between 0 and 0.5 whales per whales landed. Consequently, we performed two model runs, one with the raw catch data and the other with harvest levels multiplied by 1.5.

Each model run consisted of a single MCMC chain of 55,000 iterations after a burn-in of 5,000, with a thinning factor of 50, resulting in a final sample of 1,000. A high level of thinning was necessary due to the high level of autocorrelation in the MCMC chain.

RESULTS & DISCUSSION

Assuming no losses during harvest, the median of the posterior distribution of N_{1854} was 8,012 (95%CI 7,216 – 8,673, Fig. A1). The prior of r was only slightly updated and had a median of 3.9%. The posterior distribution of the θ showed a small update from its prior distribution and had a median of 3. When run with a loss factor of 1.5, the median of the posterior distribution of N_{1854} was 11,630 (95%CI 10,430 – 12,480, Fig. A1).

Most parameters were not updated from their prior distribution (because the data did not contain information about r or θ). However, our aim was not to infer population dynamic parameters but rather to integrate our uncertainty about their values.

The estimate of the 1854 stock size of ~8,000 beluga (assuming no losses) is close to the total number of catches over the 10 year period (7,875), which was expected considering that the stock had little time to respond to the rapid depletion with compensatory mechanisms. The estimate assuming a high loss rate (1.5) was ~11,600. It is likely that a subsistence hunt took place in addition to the commercial catches. Compared to the commercial hunt, however, its impact would have been relatively small. The actual pristine stock size is likely in the range between the two estimates. We suggest that for the purpose of establishing recovery targets, both values can be considered plausible estimates of inferred maximum stock size.

LITERATURE CITED

Hammill, M.O., Lesage, V. and Gosselin, J.-F. 2005. Abundance of Eastern Hudson Bay belugas. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/010. iv + 17 p.

Heide-Jørgensen, M.P. 1994. Distribution, exploitation and population status of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in West Greenland. Meddr. Grønland. Biosci. 39:135-149.

Pella, J.J. and Tomlinson, P.K. 1969. A generalized stock-production model. Bulletin of the Inter-American Tropical Tuna Commission 13:421-58.

Reeves ,R.R. and Mitchell, E.D. 1987. History of white whale (*Delphinapterus leucas)* exploitation in eastern Hudson Bay and James Bay. Canadian Special Publications on Fisheries and Aquatic Sciences 95. 45 p.

Table A1. Commercial catches of EHB beluga in the Little Whale and Great Whale rivers during the period 1854 – 1863 (Reeves and Mitchell 1987).

Year	Harvest
1854	423
1855	707
1856	747
1857	1366
1858	1023
1859	1043
1860	1511
1861	30
1862	229
1863	796

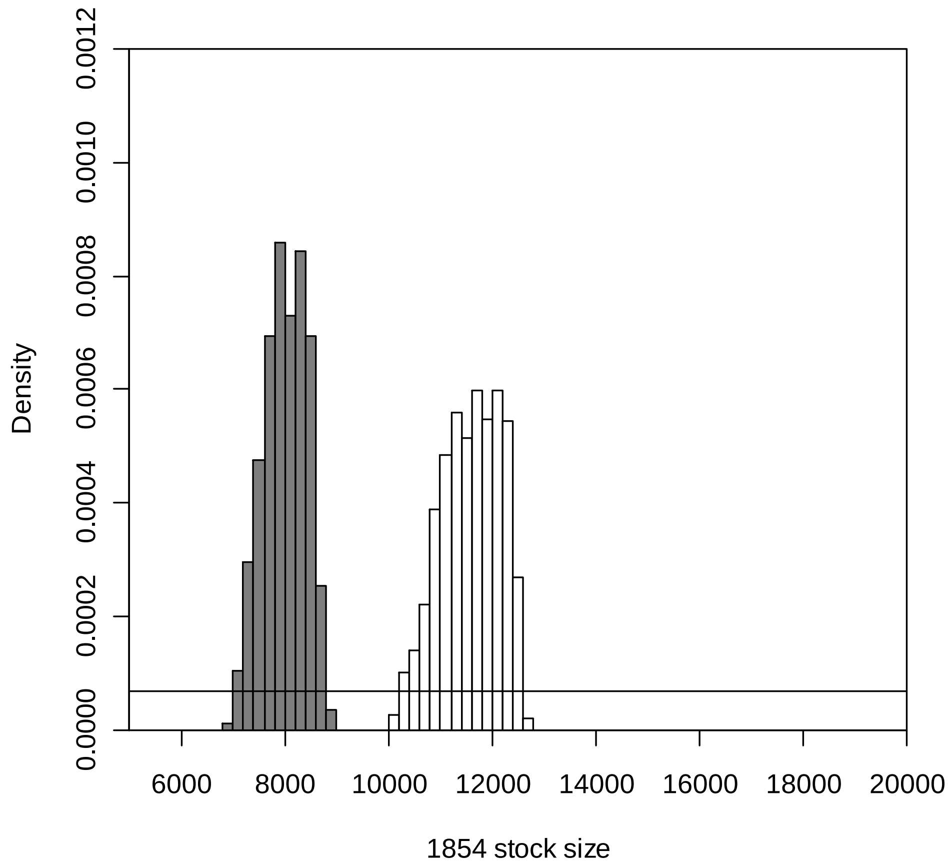


Figure A1. Posterior distributions of the 1854 stock size. Grey bars: assuming no harvest losses. White bars: assuming a loss factor of 1.5. Horizontal line: prior distribution.