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Research Document 2010/121

Document de recherche 2010/121

**Information on abundance and harvest
of eastern Hudson Bay beluga
(*Delphinapterus leucas*)**

**Information sur l'abondance et les
prélèvements de bélugas de l'est de la
Baie d'Hudson (*Delphinapterus leucas*)**

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This document is available on the Internet at:

<http://www.dfo-mpo.gc.ca/csas/>

Ce document est disponible sur l'Internet à:

ISSN 1499-3848 (Printed / Imprimé)

ISSN 1919-5044 (Online / En ligne)

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Canada

Correct citation for this publication:

La présente publication doit être citée comme suit :

Doniol-Valcroze, T, Hammill, M. O. and Lesage, V. 2011. Information on abundance and harvest of eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2010/121. iv + 13 p.

ABSTRACT

Subsistence harvest of beluga whales by Nunavik communities is directed towards a mixture of two populations: the Western Hudson Bay stock (WHB) and the depleted Eastern Hudson Bay stock (EHB). The 2010 harvest consisted of 45 beluga killed near Sanikiluaq (Belcher Islands), 16 in the eastern Hudson Bay area, 15 in Ungava Bay, 146 in Hudson Strait in the spring and 58 in the fall. Since 2009, it is assumed based on genetic data that all animals killed in EHB, 10% of those killed in the spring and summer in Hudson Strait, and 20% of those killed in Ungava Bay and during the fall in Hudson Strait are EHB beluga. It is also assumed that 12% of beluga killed by Sanikiluaq hunters belong to the EHB stock. Using these proportions, the 2010 harvest is equivalent to 51 EHB beluga.

A population model incorporating updated information on harvest statistics and stock composition was fitted to aerial survey estimates using Bayesian methods, and resulted in a 1985 population estimate of 4,118 animals with a 95% Credible Interval (CI) of 2,219–8765. The lowest abundance point was estimated at 2,977 (95% CI 1,970–4,674) for the year 2001. The model estimated a population in 2010 of 3,034 individuals (95% CI 1,390–6,181). At current harvest levels, the population has probably remained stable over the last few years. The model estimated struck-and-loss at 56% (95% CI 22–144%) and growth rate at 2.7% per year (95% CI -3.1–8.5%).

Removing 50 EHB animals in future harvests has a 50% probability of causing a decline in the population, while lower harvests would likely allow some recovery. Limiting the harvest of EHB animals to 10 individuals reduced the probability of decline to 25%. Conversely, a harvest of 100 EHB whales has a 75% probability of leading to population decline. No harvest scenario could produce a 5% probability of decline, since the probability of decline in absence of harvest was 18%. However, the number of animals that can be harvested without causing a decline in the EHB beluga population will depend on how catches are distributed between Eastern Hudson Bay, Ungava Bay and Hudson Strait, as well as the proportion of spring/summer vs. fall catches in Hudson Strait.

Analyses of the beluga harvest in Hudson Strait, combining age to probabilistic information on stock of origin determined from mitochondrial DNA, showed that the age structure of EHB beluga was strongly skewed towards younger individuals and contained less older individuals compared to the non-EHB whales. These results might indicate a disproportional catch of younger EHB animals, significant harvesting pressure on the EHB stock or both.

RÉSUMÉ

La chasse aux bélugas à des fins de subsistance par les communautés du Nunavik vise un mélange de deux populations: le stock de l'ouest de la baie d'Hudson (OBH) et celui de l'est de la baie d'Hudson (EBH). En 2010, les prises ont été constituées de 45 bélugas tués près de Sanikiluaq (îles Belcher), de 16 dans l'est de la baie d'Hudson, de 15 dans la baie d'Ungava, de 146 dans le détroit d'Hudson au printemps et de 58 à l'automne. Depuis 2009, il est présumé, sur la base des analyses génétiques, que tous les animaux tués dans l'est de la baie d'Hudson, 10 % des animaux tués au printemps et en été dans le détroit d'Hudson, et 20 % des animaux tués dans la baie d'Ungava et en automne dans le détroit d'Hudson sont des bélugas de l'EBH. Il est également présumé que 12% des bélugas tués par les chasseurs de Sanikiluaq appartiennent au stock de l'EBH. Selon ces proportions, la chasse de 2010 équivaut à 51 bélugas de l'EBH.

Un modèle de population intégrant les statistiques de chasse les plus à jour a été ajusté à l'aide de méthodes d'inférence bayésiennes aux estimations d'abondance obtenues à partir des relevés aériens, et a permis d'évaluer la population de 1985 à 4 118 individus avec un intervalle de crédibilité (IC) de 95 % de 2200–8765. La population aurait atteint son plus bas niveau en 2001 avec un effectif de 2 977 individus (IC 95% 1970–4674). La population de 2010 a été estimée à 3034 individus (IC 95% 1390–6181). Aux niveaux de capture actuels, la population semble être restée stable au cours des dernières années. D'après la modélisation, la proportion de bélugas abattus mais perdus est estimée à 56% (IC 95% 22–144%) et le taux d'accroissement à 2,7% par an (IC 95% -3,1–8,5%).

Un prélèvement de 50 individus de l'EBH dans le futur aurait un risque de 50% d'entraîner une diminution de la population. Une diminution du prélèvement à 10 individus de l'EBH réduirait la probabilité de déclin à 25%. Inversement, la prise de 100 individus de l'EBH aurait 75% de chances d'entraîner un déclin. Aucun scénario de chasse ne permettrait de réduire la probabilité de déclin à 5% car même en l'absence totale de prélèvement de bélugas de l'EBH, la population aurait quand même 18% de chances de décliner. Cependant, le nombre d'individus qui peuvent être capturés sans provoquer une diminution de la population de bélugas de l'EBH dépend de la répartition des prises entre l'est de la baie d'Hudson, la baie d'Ungava et le détroit d'Hudson de même que des proportions chassées au cours du printemps, de l'été, et de l'automne.

L'examen des échantillons prélevés sur les bélugas chassés dans le détroit d'Hudson, combinant l'âge des animaux et leur population d'origine déterminée à partir d'analyses génétiques, démontrent que la structure d'âge des bélugas provenant de l'EBH est fortement biaisée en faveur des animaux plus jeunes et contient peu d'individus plus âgés. Ces résultats pourraient indiquer une prise disproportionnée des jeunes bélugas de l'EBH, une pression de chasse trop intense sur le stock de l'EBH, ou les deux.

INTRODUCTION

Nunavik communities have traditionally harvested beluga whales (*Delphinapterus leucas*) along the shores of Hudson Bay, Hudson Strait and Ungava Bay. The targeted beluga belong mostly to two populations: the Western Hudson Bay stock (WHB), which numbers about 57,000 individuals (Richard 2005), and the Eastern Hudson Bay stock (EHB), which was depleted by intensive commercial hunting between the 1860's and the early 1900's and has decreased from an estimated pristine population size of 12,500 to about 3,000 individuals in 2009 (Hammill et al. 2009).

Current subsistence harvest is directed towards both resident populations during summer, and towards migrating whales from a mixture of populations during spring and fall. Aerial surveys flown in the mid-1980's to assess abundance (Smith and Hammill 1986) indicated that high subsistence harvests were limiting recovery of the eastern Hudson Bay beluga herd, which led to restrictions on harvesting through a combination of quotas and seasonal and regional closures (summarized in Lesage et al. 2001; 2009; Lesage and Doidge 2005) to allow for stock recovery (Reeves and Mitchell 1989). Concerns for beluga in the waters adjoining Nunavik also led to the designation of Ungava Bay and EHB beluga as "Endangered" (COSEWIC 2004).

Continued monitoring of changes in the EHB beluga population is made difficult by limited census data and large uncertainty in abundance estimates (Gosselin et al. 2009). Bayesian statistics are well adapted to data-poor situations 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). This model indicated that the current population size was likely stable but that a harvest exceeding 50 EHB animals would have a 50% probability of causing a decline in the population. However, the model comprises several sources of uncertainty, and in particular, there is a lack of data on vital rates, which limits opportunities to fully understand the dynamics of this population.

Changes in population dynamics of long-lived species in response to perturbation are usually slow and gradual, which presents a major challenge to their management (Dayton et al. 1995). In contrast, shifts in age structure often occur over shorter time frames and can reveal changes to underlying population parameters (e.g., fecundity, survival) that are difficult to detect from census data alone (Monson et al. 2000). Harvest statistics showed significant reductions in age of EHB beluga in recent years compared to beluga caught during the early 1980s (Lesage et al. 2009), but hunt closures in eastern Hudson Bay have limited our ability to monitor recent changes in the population age structure. Most current harvesting is taking place in the waters of Hudson Strait, a migration route for both EHB and WHB beluga populations. Thus, using genetic analysis to determine population identity, we can use harvest data from Hudson Strait to examine the age structure of EHB beluga and detect potential changes in population dynamics.

Here we update the population model using harvest data from 2010, and use information on age structure of harvested beluga to further inform management efforts.

MATERIALS AND METHODS

Population model

The model was built as a stochastic stock-production model. It was fitted by Bayesian methods, so existing information on, or guesses as to, the values of stock-dynamic parameters were included as prior distributions (for details, see Hammill et al. 2009). Parameter estimates are refined by updating the prior to a posterior distribution based on the data. Predictions are then based on the full multivariate posterior distribution of the parameter estimates.

Population size in each year was a constant multiple of the previous year's, with removals deducted:

$$N_t = N_{t-1} \cdot \exp(r) \cdot \varepsilon 1_t - R_t$$

The instantaneous rate of growth, r , was given a uniform prior in the range $-0.1 - +0.2$. The stochastic process error terms $\varepsilon 1$ were lognormally distributed with zero mean and uniform variance in log space. The sparse survey data tells us nothing about the process error, and an informative prior was assigned for the precision¹ parameter of the lognormal distribution with CV quartiles at 5.5% and 8.7%. A deterministic version of the model (i.e., without process error) was also run to assess if stochasticity influenced our predictions of future population trajectories.

Removals were calculated as catches corrected for animals that were struck and lost:

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

where struck-and-lost correction SL was given a moderately informative log-normal prior with quartile points at 0.43 and 0.85.

Survey catchability was assumed to be 1, and survey estimates were linked to population size by a multiplicative error term:

$$\ln(S_t) = \ln(N_t) + \varepsilon 2_t$$

where the error terms ε were normally distributed with a mean of zero. The "precision" was given a moderately informative prior, $\text{gamma}(2.5, 0.4)$ with quartiles approximately equivalent to survey coefficients of variation (CV) of 35% and 55% or approximate symmetrical 95% CI on the CV 24%–99%.

The model was extended into the future for 10 years at 15 different catch levels (ranging from 0 to 200 whales) to produce predictions of stock trajectories expressed both as stock numbers and as the probability of stock decrease (from the estimated 2010 population size).

The model was run on the WinBUGS platform (Hammill et al. 2009). Typically, models of this kind produce highly correlated chains in MCMC sampling, so every 40th point was kept from

¹ The 'precision' parameter for a lognormal distribution is the reciprocal of the variance of the corresponding normal distribution in log space. In real space, it corresponds to the reciprocal of the square of the coefficient of variation.

chains of 10,000,000 iterations, for a total of 250,000 samples (every 200th point was kept in the case of the deterministic model). The model converged easily and took about 5 hours to run. We used median values of the posterior distribution of parameters, rather than the mean, because several distributions were skewed towards large values (King et al. 2010).

Survey data

Census data comprised five estimates from aerial surveys flown in 1985, 1993, 2001, 2004 and 2008 (Table 1). Survey counts were corrected for a decline in detection with distance from the survey platform using standard line-transect methods (Gosselin et al. 2009). Corrections were also applied for "unavailable" animals using: $N_t = N_{survey} / P_0 + N_{estuary}$, where the estimated proportion (P_0) of animals visible from an aerial survey platform is 0.478 (SE 0.0625) (Kingsley and Gauthier 2002). Beluga detected in estuaries ($N_{estuary}$) were assumed to represent total counts. 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 (see above).

Harvest composition and age structure

Harvest data came from annual reports of landed catches (summarized in Hammill et al. 2009, Lesage et al. 2009). The proportions of those landings that belonged to the EHB summer population were estimated from genetic analyses and the input catch series were revised accordingly (Table 2). Assessments prior to 2009 have used a proportion of EHB animals in the harvest of 21% for Hudson Strait and 13% for Ungava Bay (Hammill et al. 2004). In recent years, genetic analyses have shown changes in these proportions. Moreover, although data are lacking on the timing of the hunt for the years prior to 2004, there is a marked difference in the sampled proportion of EHB animals in the fall hunt compared to the spring hunt (Turgeon et al. 2009). Therefore, for this assessment and that of 2009, it was assumed that all animals killed in eastern Hudson Bay, 10% of those killed in the spring and summer in Hudson Strait, and 20% of those killed in Ungava Bay and during the fall in Hudson Strait are EHB beluga. It was also assumed that 12% of beluga killed by Sanikiluaq hunters belonged to the EHB stock.

Although the total allowable catch was reached in early November this year, 9 more beluga were taken in Hudson Strait after the hunt was officially closed. The final 2010 harvest consisted of: 45 beluga killed near Sanikiluaq (Belcher Islands, Hudson Bay), 16 in the eastern Hudson Bay area, 15 in Ungava Bay, as well as 146 in Hudson Strait in the spring and 58 in the fall. Using the proportions defined above, this harvest is equivalent to 51 EHB beluga.

To investigate the age structure of recent catch data, we combined age information from teeth, assuming the deposition of one growth layer group per year (Stewart et al. 2007), with probabilistic information on stock of origin determined from mitochondrial DNA analysis (De March and Postma 2003). We compared the age distribution of EHB beluga (n=90) vs. other stocks harvested in the Hudson Strait (n=402) over the years 2000-2009 and tested for statistical differences between the two groups using a two-sample Kolmogorov-Smirnov test. To account for the large difference in sample size between EHB and non-EHB beluga, we used random resampling to select a number of non-EHB beluga equal to the number of EHB beluga available in the dataset. We repeated this procedure 10,000 times and computed the number of times the mean age of EHB beluga was smaller than the mean age of non-EHB individuals.

RESULTS

The model incorporating removals and fitted to aerial survey estimates of abundance, resulted in a 1985 population estimate of 4,118 animals with a 95% Credible Interval (CI) of 2,219–8765). The lowest abundance point was estimated at 2,977 (95% CI 1,970–4,674) for the year 2001. The model estimated a population in 2010 of 3,034 individuals (95% CI 1,390–6,181). At current harvest levels, the population has probably remained stable over the last few years (Fig. 1).

The estimated rate of growth r of 2.7% (95% CI -3.1–8.5%) is within the range expected for other cetaceans with similar life histories. Its value was well updated from its prior distribution (median=5%, 95% CI -9.3–19.2%). Struck and loss was estimated at 56% (95% CI 22–144%), a minor update from its prior value of 61% (95% CI 23–161%). As detailed in Hammill et al. (2009), other priors were either not, or only slightly, updated (the pD index showed the model had only about 2½ ‘effective’ parameters). Notably, the informative prior for process error in the stochastic model was not updated. There were only minor changes to the posterior distribution of the survey error.

There was little difference between the stochastic and deterministic models, except at low harvest levels. According to the stochastic model, removing 50 EHB animals per year in future harvests would have a 50% probability of causing a decline in the population (Fig. 2). Limiting the harvest of EHB animals to 10 reduced the probability of decline to 25%. Conversely, a harvest of 100 EHB whales would have a 75% probability of leading to population decline. No harvest scenario could produce a 5% probability of decline, since in the absence of harvest the probability of decline was 18%.

Examination of the harvest for the years 2000-2009 shows clear differences in age structure between EHB and WHB beluga. The mean age of EHB beluga was 4.5 years lower than that of non-EHB whales (EHB mean = 16.8, sd = 8.2; non-EHB mean = 21.3, sd = 9.6). The difference between the two age distributions was confirmed by both the Kolmogorov-Smirnov test ($p < 0.001$) and resampling tests (EHB mean age was lower than the mean age of random samples of non-EHB beluga 9,999 times out of 10,000). The age structure for EHB beluga was strongly skewed towards younger individuals and contained fewer older individuals compared to the non-EHB beluga harvested in Hudson Strait (Fig. 3). In particular, there was a reduced proportion of animals over 20 years of age and a paucity of animals over 30 years. The proportion of animals under 10 years of age was two times higher in the EHB catch (22%) than in the non-EHB catch (11%).

DISCUSSION

Population modelling

Modelling of this population is based on only five aerial survey estimates, all of them characterized by substantial uncertainty. Additional uncertainty is associated with the estimated maximum rate of increase of the population, correction factor for diving animals, and estimates of struck-and-loss. We had to make certain assumptions about the values and distributions of these parameters, which are represented in the model by statistical distribution instead of single values.

The model estimates a high level of struck-and-lost (> 55%). However, this term also includes the effects of under-reporting (of which struck-and-lost is a subset). Moreover, if we are under-estimating the proportion of EHB animals taken in the hunt, then this will be in part reflected in the value for the estimated struck-and-lost term. Nonetheless, a high struck-and-lost value indicates the need for further research, either to improve estimates of the declared harvest or to reduce the number of whales struck and lost. This would also result in an increase in numbers of whales available to communities, without increasing overall harvest rates. Or conversely, a reduction in struck-and-lost rates could reduce the harvest impact on this population, without having to lower quotas.

Age structure

The age structure of harvested animals belonging to the EHB herd was much younger than that from the WHB herd. Such differences may be due to differential migration timing between EHB and WHB beluga, coupled with potential segregation among age classes, making groups of younger EHB animals prone to disproportional catch. This phenomenon would be accentuated if females with calves and juveniles migrate closer to shore during travel (as observed in the Beaufort Sea, Loseto et al. 2006).

These differences could also indicate significant harvesting pressure on the EHB herd, indicating either a scarcity of adults in the population or a higher proportion of young animals. Intensive harvesting, particularly during the period 1970-2000, could have resulted in few adults surviving in the population. Similarly, high juvenile mortality would leave few survivors into adult age classes. Changes in life history traits (Skogland 1989) may also explain a higher proportion of juveniles, for instance by lowering age of first reproduction, reducing birth intervals and increasing pregnancy rate.

Though present data do not enable us to distinguish among these explanations, we note that these interpretations are all clear signs of stock depletion and emphasize the need for further research. These observations also hint at the potential long-term consequences of over-harvesting such as the possible consequences of a lack of mature females in a strongly social care-giving unit. Life-history changes experienced by species subject to intensive harvesting practices can bring forth evolutionary responses. Such compensation mechanisms (Sinclair and Pech 1996) could be beneficial for the recovery of the population if early maturation and higher fecundities can partially compensate reduced population size. However, these changes can also have detrimental effects on future population growth. For instance, female reproducing at a younger age could experience higher adult or calf mortality, especially if there are few experienced females left in their group. Such changes could create significant delays in recovery and have important management implications.

Management recommendations

Canada is a signatory of the United Nations *Agreement on Straddling and Highly Migratory Fish Stocks* (UNFA), which came into force in 2001, and commits Canada to use the Precautionary Approach in managing straddling stocks as well as, in effect, domestic stocks. In 2003, the Privy Council Office, on behalf of the Government of Canada published a framework applicable to all federal government departments that set out guiding principles for the application of precaution to decision making about risks of serious or irreversible harm where there is a lack of full scientific certainty. In 2009, management of beluga in Nunavik, fell under the responsibility of the Nunavik Marine Wildlife Management Board. As a result the Board is responsible for providing Total Allowable Take recommendations to DFO. The future approach to management

of beluga in Nunavik is not yet clear. Therefore it is important that the board develops a precautionary framework that will allow sustainable management of Nunavik beluga and recovery of this stock.

In 2006, DFO developed its own Precautionary Approach framework. This identifies three zones of risk: a healthy zone, cautious zone and a critical zone, depending on the status of the resource. When a population is in the healthy zone, then socioeconomic concerns are considered to be the most important when setting harvest levels. However, if the population declines into what is identified as the cautionary zone, then conservation is to assume an increasingly important role in the decision making process. If the population declines further and falls into the critical zone, then conservation is to become a priority and harvest levels should be reduced to minimum levels or stopped to allow the population to recover. There is some flexibility in establishing the threshold separating the three zones. One possibility would be to borrow from the approach used to manage Atlantic seals and to set the precautionary level separating the healthy zone from the cautious zone at 70% of the estimated pristine population size, i.e. 8,800 animals if the pristine population size was 12,500 (DFO 2005). The limit reference level which separates the cautious zone from the critical zone would be set at about 2,800 animals for EHB beluga using the framework developed for fish, or at about 3,750 animals using the framework developed for seals. At a current population size of about 3,050 animals, the EHB population would fall into the lower end of the cautious zone or in the critical zone, depending on where the limit reference level is set in a Precautionary Framework (Fig. 4).

Under recent management plans, overall harvest rates have declined and the model suggests that the rate of decline in the Nunavik beluga population has also slowed or stopped. However, there is no indication of substantial population growth. The model indicates that a removal of more than 50 animals from the EHB population, i.e., a harvest similar to what has been allowed over the last 4 years, would have a 50% or higher risk of causing a decline in the population. There is currently no stated objective for managing the Nunavik beluga harvest. Setting catches at levels of around 50 EHB whales per year is not precautionary and rebuilding the resource even to levels observed in the early 1980s is unlikely using this management strategy.

Different approaches could be used to reduce the impact of the harvest on the EHB population, while ensuring access to animals in Hudson Strait. A spring/summer harvest in Hudson Strait, with no harvest in EHB would have the lowest impact on the EHB population, followed by a fall harvest in Hudson Strait only, again with no harvest allowed in EHB. If harvesting does occur in EHB, then numbers taken in Hudson Strait must be reduced, but the size of this reduction will depend on whether hunting occurs in the spring/summer or in the fall.

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).

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Table 1. Aerial survey estimates of beluga populations in eastern Hudson Bay. The 1985 survey data were adjusted to account for differences between strip-transect and line-transect methods (Hammill et al. 2004). Aerial survey estimates have been corrected for diving animals (Kingsley and Gauthier 2002) and corrected for estuary animals by adding in estuary counts in EHB of 474, 18, 39, 5 and 0, for 1985, 1993, 2001, 2004 and 2008, respectively (Hammill et al. 2009).

Year	Distance line-transect (\pm SE)	Estimate corrected for diving animals (\pm SE)
1985	2,294	4279 (\pm 620)
1993	1,314 (\pm 489)	2727 (\pm 1,012)
2001	1,418 (\pm 635)	2922 (\pm 1,368)
2004	2045 (\pm 698)	4269 (\pm 1,499)
2008	1,265 (\pm 570)	2646 (\pm 1,959)

Table 2. Number of eastern Hudson Bay animals removed from the population. For the 1985-2008 period, assumed herd composition was: Hudson Bay (100%), Sanikiluaq (12.6%), Hudson Strait (21%), and Ungava Bay (12.6%), regardless of season. For 2009 and 2010, it is assumed that 10% of animals killed in the spring and summer in Hudson Strait, and 20% of those killed in Ungava Bay and during the fall in Hudson Strait are EHB beluga

Year	Harvest of EHB whales
1985	84
1986	69
1987	81
1988	76
1989	144
1990	77
1991	144
1992	99
1993	105
1994	128
1995	103
1996	101
1997	98
1998	102
1999	106
2000	104
2001	129
2002	49
2003	54
2004	43
2005	41
2006	29
2007	59
2008	53
2009	38
2010	51

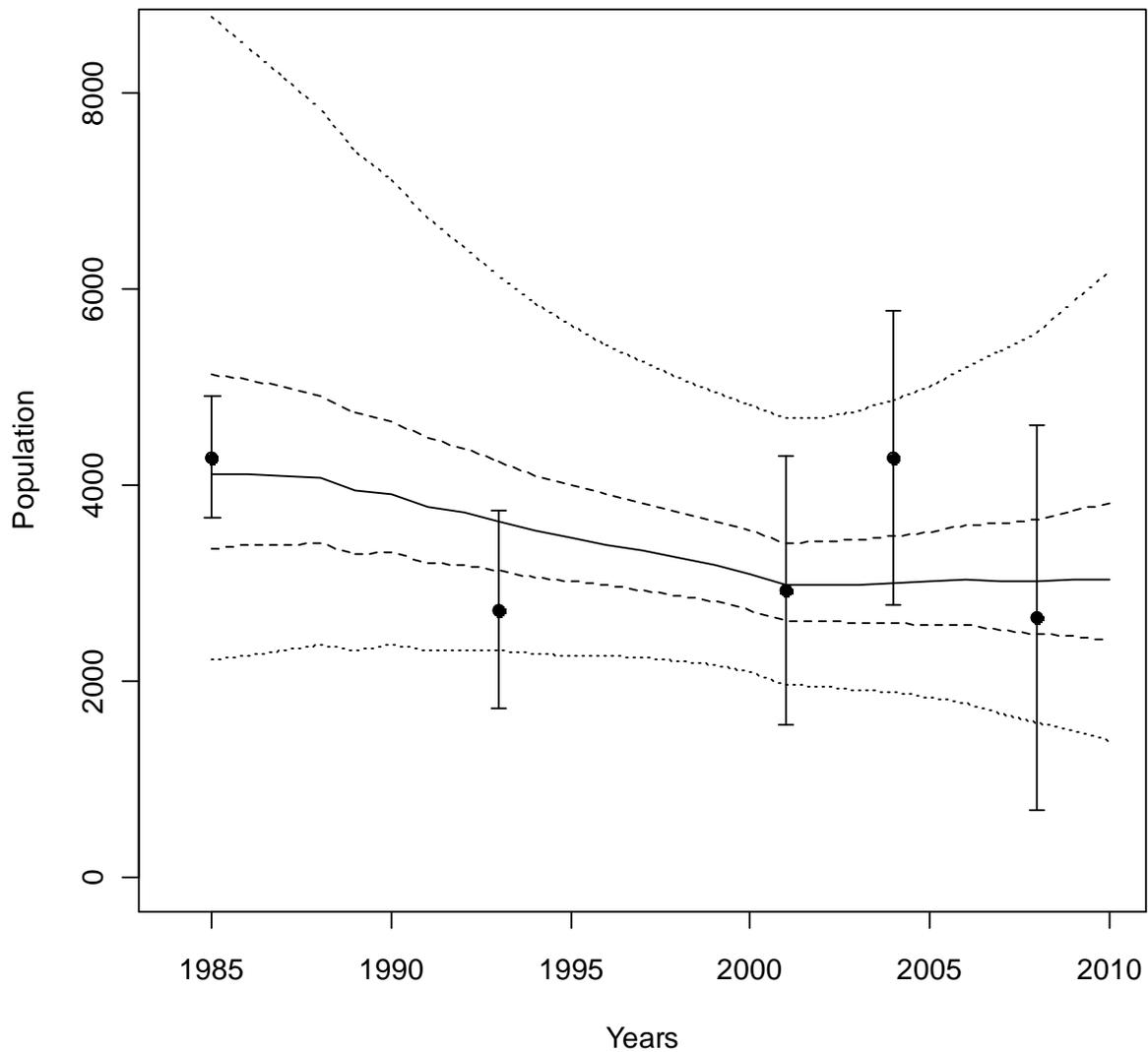


Figure 1. Model estimates of Eastern Hudson Bay beluga abundance. Solid line: median estimates. Dashed lines: 25% and 75% quartiles. Dotted lines: 2.5% and 97.5% quartiles (= Bayesian Credible Interval). The model was fitted to aerial survey estimates corrected for animals at the surface (closed circles, \pm SE).

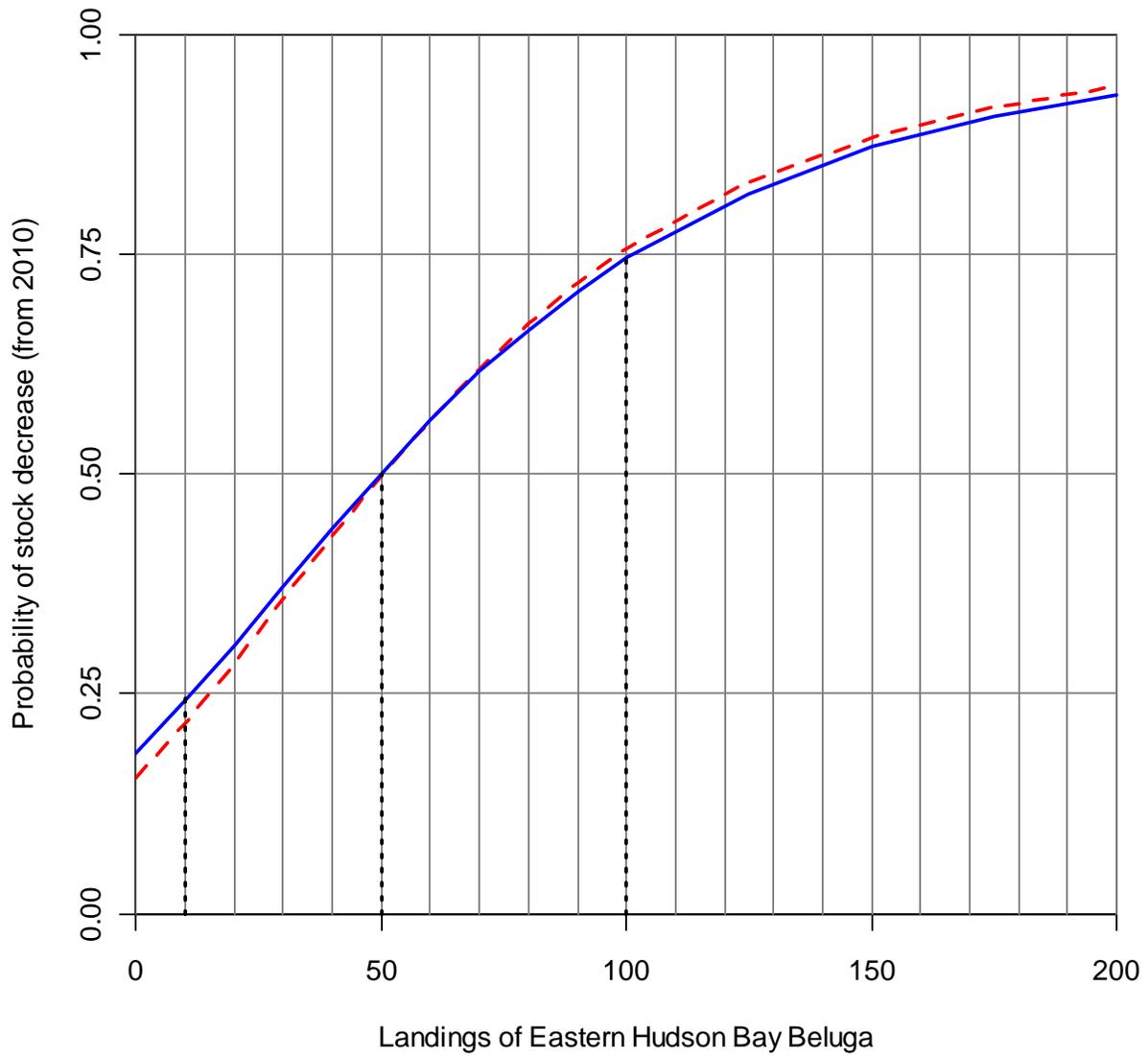


Figure 2: Eastern Hudson Bay beluga. Probability of stock decrease (from the 2010 population estimate) estimated by Bayesian stock-production models assuming stochastic (solid blue line) and deterministic (dashed red line) stock dynamics. Dotted lines indicate levels of harvest corresponding to 25%, 50% and 75% probability of decline.

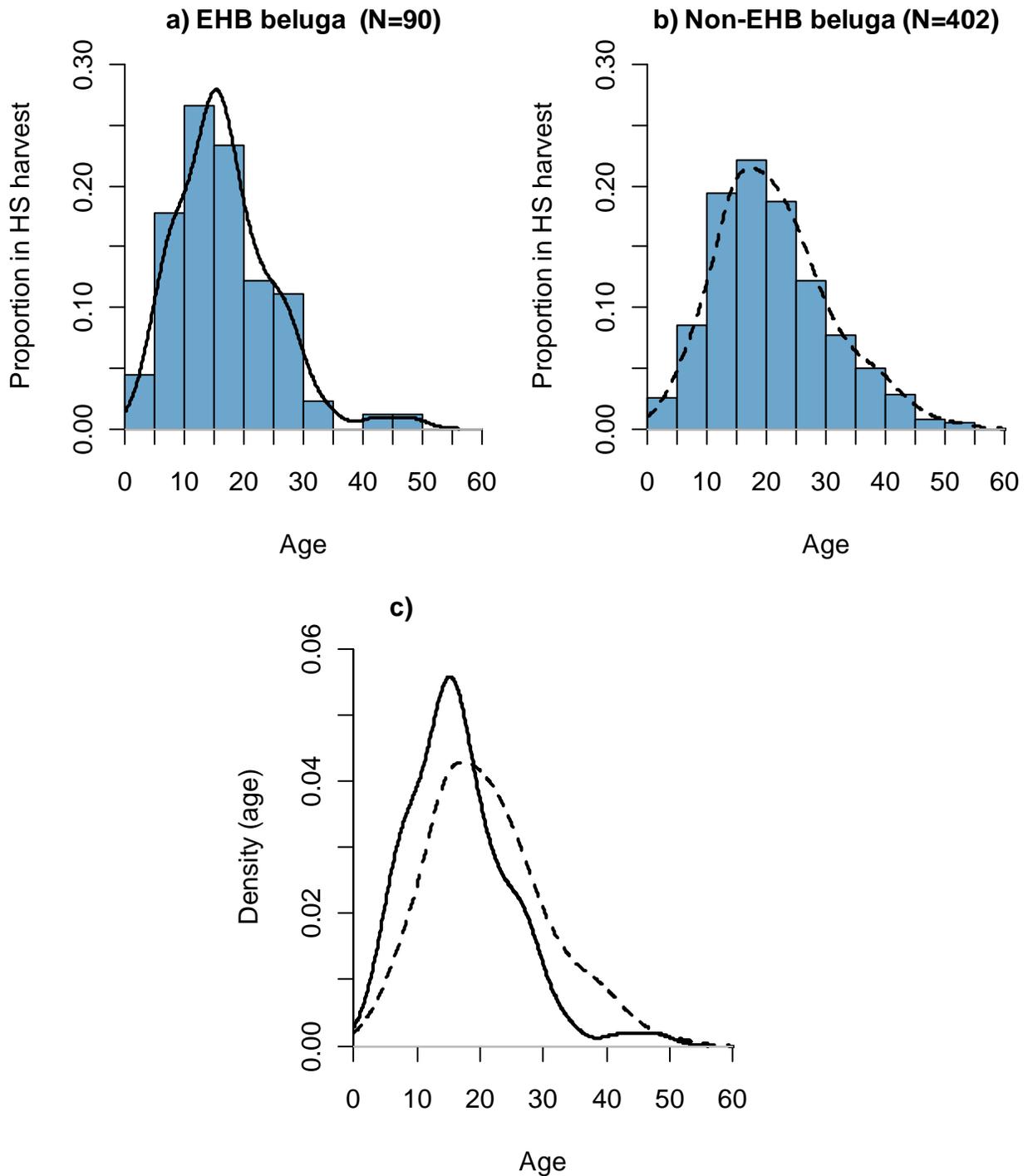


Figure 3. Age structure of beluga harvested in Hudson Strait. Histograms indicate proportion of each 5-year age class in harvest. Lines show smoothed density estimates. Stock identity was assessed from probabilistic analyses based on mtDNA data: a) EHB stock; b) non-EHB stock; c) comparison of density distributions (solid line: EHB, dashed line: non-EHB).

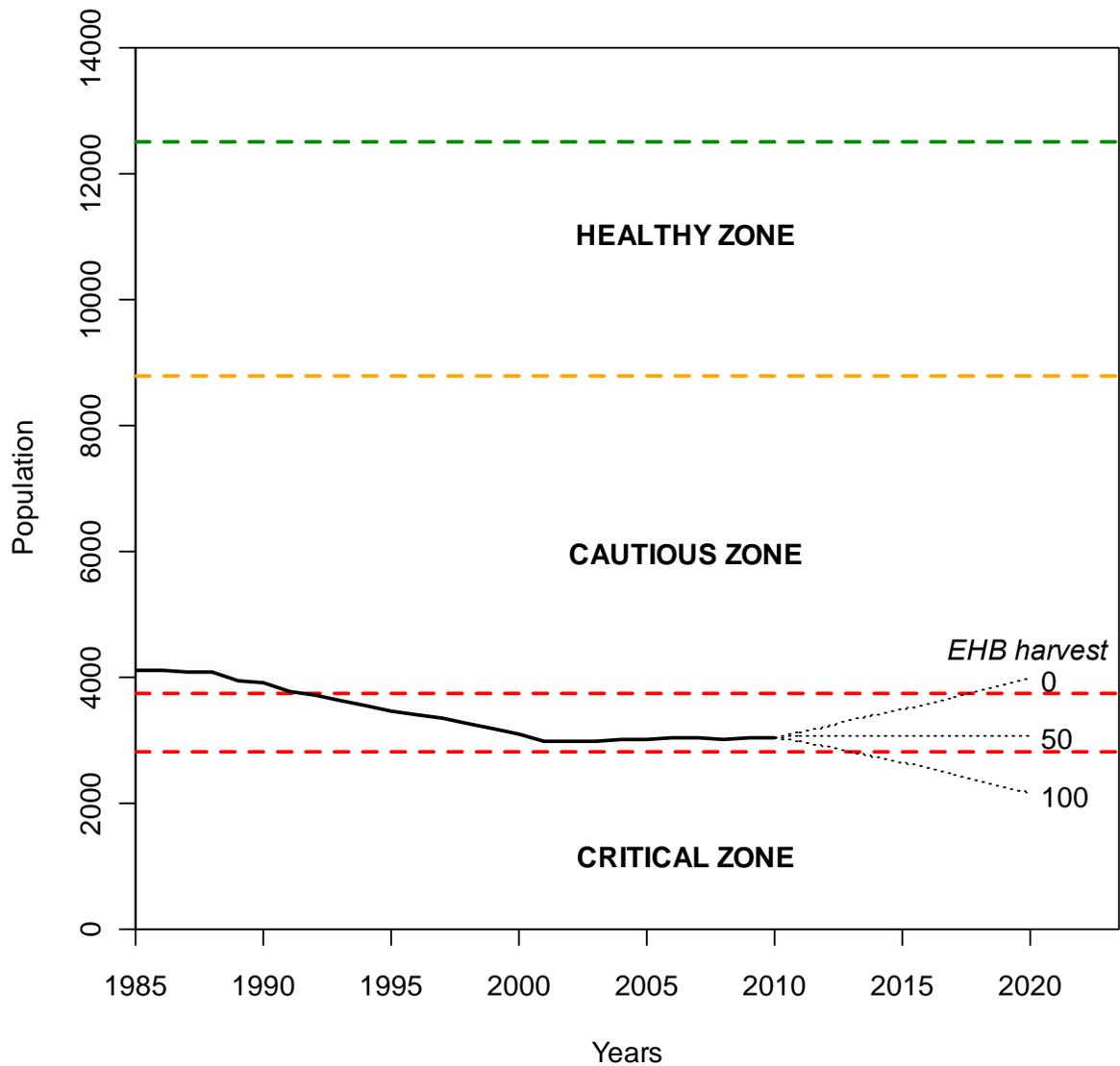


Figure 4. Current estimates of the EHB population size (solid line) within the context of a possible Precautionary Approach framework (for illustrative purposes). The dotted lines represent future modeled population trajectories at three harvest levels. The upper dashed line represents the estimate of pristine population size during the 1850s. The middle dashed line represents a precautionary level that separates a healthy zone from a cautious zone where conservation should assume a greater role when establishing harvest levels. The two lower dashed lines represent two possible reference limit thresholds that separate the cautious zone from the critical zone. For a population in the critical zone, conservation should be a priority and harvesting should be reduced to allow population recovery.