Population size and yield of Baffin Bay beluga (*Delphinapterus leucas*) stocks

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[*] *This assessment was prepared by S. Innes for discussion at a meeting of the NAMMCO Scientific Committee in June 2000. After Stuart's death in May 2000, his manuscript was reviewed at that workshop. The paper presented here has been modified in response to comments at that meeting and by reviewers and includes more recent data, but is largely as Stuart left it. While it may not be as he would have finished it, we considered the approach worthy of publication and hope it will stimulate new explorations along the novel lines developed by Stuart. In this and many other things, Stuart is missed.*

ABSTRACT

A surplus production model within a Sampling, Importance Resampling (SIR) Bayesian analysis was used to estimate stock sizes and yields of Baffin Bay belugas. The catch of belugas in West Greenland increased in 1968 and has remained well above sustainable rates. SIR analysis indicated a decline of about 50% between 1981 and 1994, with a credibility interval that included a previous estimate of 62%. The estimated stock sizes of belugas wintering off West Greenland in 1998 and 1999 were approximately 5,100 and 4,100 respectively and were not significantly different than an estimate based on aerial surveys combined for both years. Projected to 1999 this stock can sustain median landings of 109 whales with a total kill of about 155, based on posterior estimates of struck and lost plus under-reporting. The declining stock size index series did not provide sufficient information to estimate the potential maximum rate of population growth, the number of whales struck and lost, or the shape of the production curve with precision. Estimating these parameters requires an index time series with a marked step change in catch or a series with increasing stock sizes. The stock size estimate for the belugas wintering in the North Water in 1999 was approximately 14,800 but there is no information about the population biology of these whales. The estimated maximum sustainable yield (landed) for the North Water stock was 317 belugas.

INTRODUCTION

Belugas or white whales (*Delphinapterus leucas*) occur throughout the Arctic and sub-arctic oceans, in the Gulf of St. Lawrence in Canada, and in Cook Inlet in the U.S.A. Within this range, most belugas migrate from wintering areas associated with pack ice to summering locations often associated with es- tuaries (Brodie 1989). In the North American Arctic, Inuit derive both food and cultural sig- nificance from beluga (Haller 1967, Heide- Jørgensen 1994, Stevenson *et al.* 1997), usually hunting them along migration paths or at sum- mering locations. In addition to subsistence hunting, nearly all beluga stocks have been commercially exploited at summering estuaries (Reeves and Mitchell 1987). Many stocks are

still depleted because of these historic catches in combination with continuing subsistence catches (Reeves and Mitchell 1989, Doidge and Finley 1993, Richard 1993, Lesage and Kingsley 1998).

Baffin Bay belugas migrate from wintering areas in pack-ice off West Greenland (Heide-Jørgensen *et al.* 1993, Heide-Jørgensen and Reeves 1996) and the North Water (Finley and Renauld 1980, Richard *et al.* 1998) into the Canadian archipelago via Lancaster Sound to estuaries on or near Somerset Island (Sergeant and Brodie 1975, Smith *et al.* 1985, Doidge and Finley 1993, Smith and Martin 1994). Whales from these wintering areas are different stocks within the Baffin Bay beluga group, as determined using contaminant signatures and genetic types (de March *et al.* 2002, Innes *et al.* 2002a). There may be further stock structure among the belugas that migrate to West Greenland; the contaminant signatures of belugas landed in Upernavik are different from those landed in Disko Bay (Innes *et al.* 2002a).

The Baffin Bay stocks were commercially hunted in the later 1800s (Reeves and Mitchell 1987) and have had average reported subsistence landings around 700 belugas per year from 1954 to 1999 (Heide-Jørgensen 1994, Heide-Jørgensen and Rosing-Asvid 2002, Fig. 1). The stocks of the Baffin Bay belugas wintering off West Greenland declined in number by 62% between 1981 and 1994 (Heide-Jørgensen *et al.* 1993, Heide-Jørgensen and Reeves 1996).

We conducted an assessment of these stocks by applying a Sampling, Importance Resampling (SIR) Bayes analysis to the index surveys and catch series. Specifically, the analysis used the series of stock index surveys conducted off the west coast of Greenland (1981 to 1994), one population estimate of the combined North Water–West Greenland stocks (Table 1), and a catch series from Canada and Greenland (1862–1999) to provide an estimate of yield and stock size for West Greenland and North Water beluga stocks. Bayesian methods allow population analysis without the use of strict assumptions by using non-informative priors (distributions) and a loss function.

METHODS

A population model in a Bayesian inference framework was used to summarise the available information concerning the North Water (NW) and West Greenland (WG) stocks of belugas,
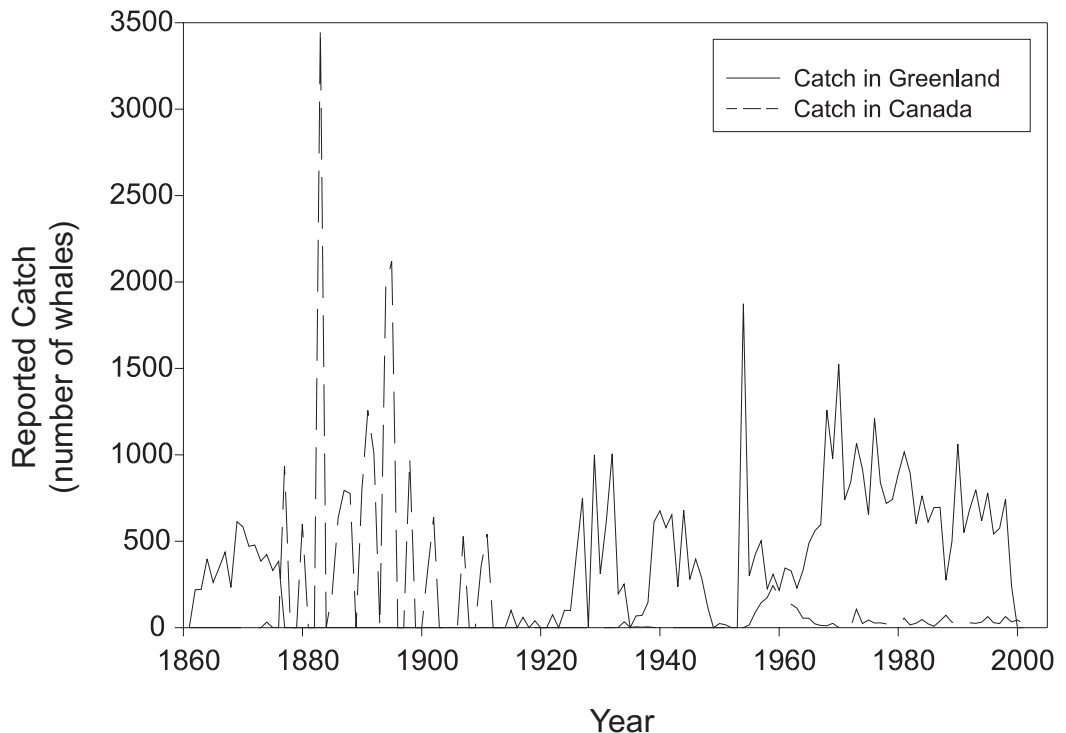

Fig. 1.
Reported landings of belugas in Canada and West Greenland from the Baffin Bay stocks from 1862 to 1998. See text for sources. Zeros represent a lack of reported catch from that year. No systematic survey of under-reporting is available for these catches.

Table 1. Population estimates used in likelihood calculations (1996), based on aerial surveys, adjusted for whales not at the surface and for whales at the surface but missed by observers and for comparison to SIR Bayes estimates.

Year$_{survey}$	N	S.E.	
1996 $_{(GL+NW)}$ 1998-99 $_{(GL)}$	21,213 7,941	5,359 3,256	Innes *et al.* 2002b Heide-Jørgensen and Acquarone 2002

and to estimate stock sizes, yields and other population and model parameters. The population model incorporated changes in recruitment (assumed to occur at age 0) with respect to the stock's size relative to its carrying capacity: $N_{WG, 1861}$ and $N_{NW, 1861}$ (*i.e.*, the population sizes the year before the first reported catch). We selected a general model based upon the discrete-time parametrisations of Pella and Tomlinson (1969). The population sizes for a future year (N_{t+1}) were:

$$N_{WG, t+1} = N_{WG, t} + N_{WG,t}(\lambda_{WG, max} - 1)$$
$$(1 - (N_{WG,t}/N_{WG,1861})^{\theta WG}) - b_{WG}C_{WG,t}$$
$$- b_{NW} C_{NW,t} (N_{WG,t}/(N_{WG,t}+N_{NW,t})) \qquad [1]$$

and

$$N_{NW, t+1} = N_{NW, t} + N_{NW,t} (\lambda_{NW, max} - 1)$$
$$(1 - (N_{NW, t}/N_{NW,1861})^{\theta NW})$$
$$- b_{NW}C_{NW,t}(N_{NW,t}/(N_{WG,t}+N_{NW,t})) \qquad [2]$$

for the West Greenland and North Water stock groupings, where $\lambda_{x,max}$ is the rate of increase at small population size when the density-dependent control of the population size is small; $N_{x,1861}$ is the carrying capacity of the population (one for West Greenland and one for the North Water); θ_x is a shaping parameter of the density-dependent response; and $C_{x,t}$ is the catch of belugas, by location and year, with the catch in Canada prorated on respective stock sizes. Parameter b_x was added to account for systematic biases for killed-but-lost and unreported whales for Canada and for West Greenland. Posterior distributions for parameters were computed numerically using a Sampling, Importance Resampling algorithm (Rubin 1987, McAllister *et al.* 1994, Gelman *et al.* 1995, Punt and Walker 1998). The algorithm followed these steps:

1. Select a prior distribution for each parameter;
2. Sample values for the model parameters from their assumed prior distributions;
3. Project the population trajectories from initial states;
4. Calculate the likelihood function for the projection based upon the index surveys of belugas off the West coast of Greenland (*i.e.*, $aN_{WG,t}$ Table 2) and the population estimate for the Canadian High Arctic (*i.e.*, $N_{x,t}$; Table 1). If any of the population sizes (*i.e.*, $N_{WG,t}$ or $N_{NW,t}$) reach zero then the likelihood is set to zero;
5. Repeat steps I to IV many times, in this case 200,000 repetitions;
6. Select 5,000 of these projections proportional to their likelihood with replacement (after Punt and Walker 1998).

Table 2. Index estimates of the number of beluga wintering off the west coast of Greenland (Heide-Jørgensen *et al*. 1993, Heide-Jørgensen and Reeves 1996, Heide-Jørgensen and Acquarone 2002) used in likelihood estimates.

Year	Estimate S.E.	
1981	3,302	958
1982	2,389	406
1990[1]	291	128
1991	1,471	382
1993	900	189
1994	1,078	194
1998	929	247
1999	735	205

[1] not used in analysis. It was thought that the beluga had started their migration prior to the survey.

Likelihood function

To determine the weight used in step 6, a squared loss function inverse weighted by variance was used to estimate likelihoods for each run (eq. 1 of Walters and Ludwig 1994). This is:

$$L = \exp(-(Y_i - U_i)^2 / 2V_i) \qquad [3]$$

where i is the survey year, Y_i is the estimated population size in Greenland or Greenland plus Canada depending on the survey year (Tables 1 and 2), U_i is the central estimator from the survey and V_i is the variance for that estimator. Parameter a was used to account for the bias in surveys associated with whales at the surface but not seen, whales not at the surface, and whales not in the survey areas. Unlike other Catch-per-Unit Effort data, the aerial survey indices and estimates do not violate most critical assumptions between survey estimate and density noted in Walters and Ludwig (1994). All calculations were done in the IML function of SAS (SAS Institute 1989). Descriptive statistics, such as medians, for the model output were calculated using Microsoft Excel spreadsheets.

Data and priors

Stocks of belugas

Members of a stock have similar demographic parameters, especially hunting and total mortality rates. There is strong evidence of complex stock structure with at least two stocks among the belugas that use the Baffin Bay, based on satellite-linked radio tags, genetics and trace contaminant signatures (Richard *et al*. 2001, de March *et al*. 2002, Innes *et al*. 2002a). There are belugas hunted by Canadian and North Greenland hunters (North Water stock), and by Canadian and West Greenland hunters (West Greenland stock). It is assumed that the North Water stock summer in the Canadian High Arctic and winter in the North Water. Similarly, it is assumed that the West Greenland stock summer in the Canadian High Arctic and winter off West Greenland.

Population size and trends

Population size has been assessed from survey data for the two stocks combined when they are in the Canadian High Arctic in 1996 (Innes *et al*. 2002b). The size of the West Greenland stock was estimated in 1998-99 (Heide-Jørgensen and Acquarone 2002, Table 1). Population size has been indexed for the West Greenland stock by visual surveys during March in the pack ice off West Greenland (Heide-Jørgensen *et al*. 1993, Heide-Jørgensen and Reeves 1996, Heide-Jørgensen and Acquarone 2002, Table 2). Based on empirical work during March surveys in the late 1990's, it was possible to use an informative prior for a = N(0.175, 0.04) from the estimate in Heide-Jørgensen and Acquarone (2002). For comparison, an analysis was completed also using a non-informative prior a = U(0,1).

Catches of belugas in Canada and Greenland

Catches (recorded landings) have been summarised by Heide-Jørgensen and Rosing-Asvid (2002). Slight differences in the Canadian catch statistics were corrected from original sources (Strong 1989, DFO 1991, 1992a,b, 1994a,b, 1995, 1996, 1997, 1999, K. Ditz, Department of Fisheries and Oceans, Iqaluit, NU, pers. comm.). Other historic catches made by whalers in the area of Lancaster Sound and summarised by Reeves and Mitchell (1987) were added (Fig. 1). Landings in Canada reflect reports from Clyde River, Pond Inlet, Arctic Bay, Resolute Bay, Grise Fiord, Pelly Bay, Spence Bay, and Gjoa Haven. Hunters from the three latter communities often travel to Creswell Bay to hunt belugas and occasionally pods from the Baffin Bay stocks are hunted nearer these communities. Records from Hall Beach and Igloolik that had been included previously (Heide-Jørgensen 1994) are now separated from this stock on the basis of genetic differences (Brown Gladden *et al*. 1997, 1999).

Reported catches underestimate the number of belugas killed by hunters due to 2 negative biases. Some whales were killed but not landed and some belugas were landed but not included in the catch statistics. Limited information is available on the number of whales struck and killed, but not landed, for hunts in these stocks.

Reported catches include recorded landings and estimated landings based on sales of beluga skin as food (Heide-Jørgensen 1994, Heide-Jørgensen and Rosing-Asvid 2002). In Greenland, most belugas were taken as part of

drive hunts with little loss (Heide-Jørgensen 1994) until drive hunts were banned in late 1995 (JCNB 1997). The ban is still in effect. The killed-but-lost rates for Canadian and Greenlandic open water hunts are likely between one and two whales killed for each whale landed (IWC 1980, 1992, Finley and Miller 1982, Orr and Richard 1985, Strong 1989). For West Greenland 1.25 whales killed per whale landed was suggested as appropriate (IWC 1992). Heide-Jørgensen and Rosing-Asvid (2002) calculated a correction factor of 1.29 for killed and lost plus unreported catches. The negative bias in the catch statistics was investigated by incorporating a specific parameter, *b* for this bias using a uniform prior between 1 and 3 (U(1,3)) to span all the estimates.

$N_{x, 1861}$ or carrying capacity

The year 1861 was chosen to represent carrying capacity. There may have been a few hundred whales killed in West Greenland annually between 1850 and 1861 (Reeves and Mitchell 1987) but recorded harvest statistics begin in 1862. The impact of previous harvests on the model's results are expected to be small because that level of catch was small relative to the population size at the time. The stocks were virtually unexploited by Thule cultures (Savelle 1994) and were not pursued by commercial whalers in Canada at that time (Reeves and Mitchell 1987). Moreover, the bounds for the prior distribution on K are wide enough to capture such a small variation and the small harvests may have included other stocks. Initial population size for all Baffin Bay belugas was separated into carrying capacity for the North Water stock and carrying capacity for the West Greenland stock. $N_{total, 1861}$ is the sum of belugas in the North Water stock, $N_{NW, 1861}$, and the West Greenland stock, $N_{GL, 1861}$. Based on initial trials and to bracket possible initial population sizes, $N_{x,1861}$ was given a uniform population distribution between 0 and 80,000. While initial population size is not a key population parameter of interest in this study it is necessary to the dynamic model selected and provides information about the level of depletion in the stocks.

λ_{max} or rate of population increase

The rate of population increase, λ_{max} has not been measured for belugas (Doidge 1990).

However the upper boundary for the prior on λ_{max} can be determined by setting the adult and neonatal survival to 1 and using available fecundity information. Female belugas first ovulate between 4 and 8 years of age (Brodie 1969, 1971, Sergeant and Brodie 1975, Burns and Seaman 1985, Heide-Jørgensen and Teilmann 1994, Stewart 1994), and give birth to their first calf between 5 and 9 years of age (Brodie 1969, Heide-Jørgensen and Teilmann 1994). A three year inter-calf interval can be derived from the observed pregnancy and lactation periods (Sergeant and Brodie 1975), or observed adult female fertility rate of approximately 0.33 (Burns and Seaman 1985; Heide-Jørgensen and Teilmann 1994, Stewart 1994). Given this information, the extreme upper limit to λ_{max} for beluga is 1.087 (Euler-Lotka equation solved for P=1, fecundity at ages $\geq$ 6 years = m_{6+}=0.165, see Brodie 1971, 1989, Reilly and Barlow 1985). The lower limit for the prior on population growth is λ_{max} = 1.

Béland *et al*. (1988), using stranded belugas (d_x), estimated age-specific annual survivals of S_{0-2} = 0.935 and S_{3-20} = 0.97 ($\pm$0.029, *n* = 18) for a beluga population that is depleted but no longer hunted. Using these age-specific survival rates and age specific fecundity rates yields a λ_{max} = 1.049 (95% CI 1.038 to 1.061) for the expected rate of increase of a beluga population that is small relative to its carrying capacity. Based on the above estimates, the prior distribution of λ_{max} was described by a uniform distribution between 0 and 10% growth per year (U(1, 1.10)), broad enough to span all these estimates.

θ

Theta (θ) shapes the production curves and determines where the maximum net productivity level (MNPL) occurs. For most marine mammals, it has been proposed that MNPL lies between 50 and 80 per cent of carrying capacity as θ increases from 1 to 7.5 (Taylor and DeMaster 1993). A uniform distribution between 1 and 7.5 was selected as the non-informative prior.

RESULTS

West Greenland wintering stock

There were 1,515 of 200,000 simulations that
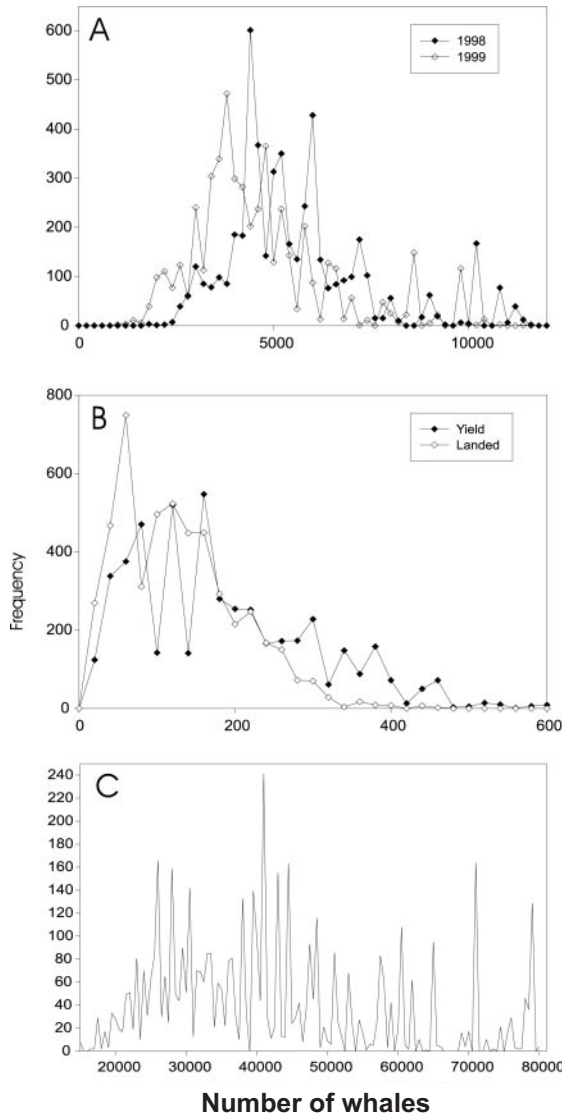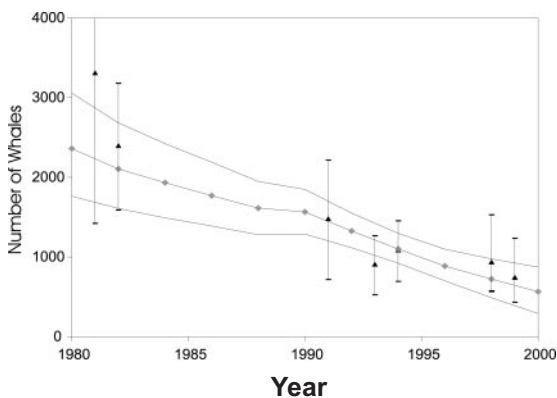
had non-zero likelihoods, and these were sampled (~50,000 iterations) with replacement proportional to their likelihoods. The median population size estimate based on the posterior distribution for belugas wintering off West Greenland in March 1998 ($N_{WG,1998}$) was 5,100 (2,806-10,727) (median estimates are presented with a 95% credibility interval unless stated otherwise) and for 1999 was 4,132 (1,916-9,629). The posterior distributions of $N_{WG,1998}$ and $N_{WG,1999}$ were positively skewed (Fig. 2A). The trajectories discounted the 1981 survey West Greenland result as being too high to be consistent with the model (Fig. 3).

The median estimate of potential yield between March 1999 and February 2000 was 156 whales killed (21-527) or 109 whales landed (16-284). The posterior distribution of this parameter was also right skewed (Fig 2B).

The median of the posterior density estimate of population size in 1861 was approximately 40,000 (Table 3). The posterior distribution of $N_{WG,1861}$ was nearly symmetrical (Fig. 2C). The population size in 2000 (3,977, 1,668-9,426) was 10.8% (0.3-24.0%) of carrying capacity.

The posterior distribution of the adjustment factor (*a*) to convert population size to the index for the surveys off West Greenland had a median of 0.142 (0.075-0.204) less than the median and mean of 0.175 of the prior. Without an informative prior, the posterior distribution for the adjustment factor for the surveys was also bell-shaped (Fig. 4A). Minor variations in parameter *a* could cause the posterior projection to under-estimate the Greenland survey indices, but all projections were within the 95% confidence interval of the index surveys (Fig. 3).

The median estimate of the maximum rate of population increase (λ_{max}) was 1.037 (1.01-1.09) (Fig. 4B). There was a slight positive skew (mean: 1.041).

The posterior distribution for θ was uniform with a median estimate of 2.99 (1.17-7.14), less than the mean (3.40) indicating some positive skew (Fig. 4C). The 95% credibility interval spanned virtually the whole prior distribution (1 to 7.5).

Table 3. Yield estimates from SIR simulations for the West Greenland and North Water stocks of beluga. 200,000 simulations, 1,515 non-zero likelihoods. N = estimated population size, N_{1861} estimated carrying capacity, MSY = maximum sustainable yield.

	Lower 2.5%ile	Median, 50%ile	Upper 97.5%ile
West Greenland Stock			
N_{1861}	19,812	39,790	78,588
N_{1998}	2,806	5,100	10,727
N_{1999}	1,916	4,132	9,629
Yield, Killed$_{1999}$	21	156	527
Yield, Landed$_{1999}$	16	109	284
North Water Stock			
N_{1861}	5,053	15,966	30,748
N_{1996}	4,985	14,839	25,544
N_{1999}	4,966	14,810	25,521
Yield, Killed$_{1999}$	15	48	99
Yield, Landed$_{1999}$	8	27	43
MSY$_{NW-landed}$	25	317	1,107

The median of the posterior distribution for the parameter b_{WG} that accounted for struck, killed and lost, or not reported whales was 1.41 (1.02-2.42) or 1.4 whales killed for each whale landed and recorded. There was a greater density nearer to 1 than 3 (Fig. 4D).

North Water stock

The median population estimates for the North Water stock of belugas in 1996 and 1999 were both approximately 15,000 (Table 3), 1,100 to 1,200 animals less than the median estimate of the stock's carrying capacity (Table 3). The me-
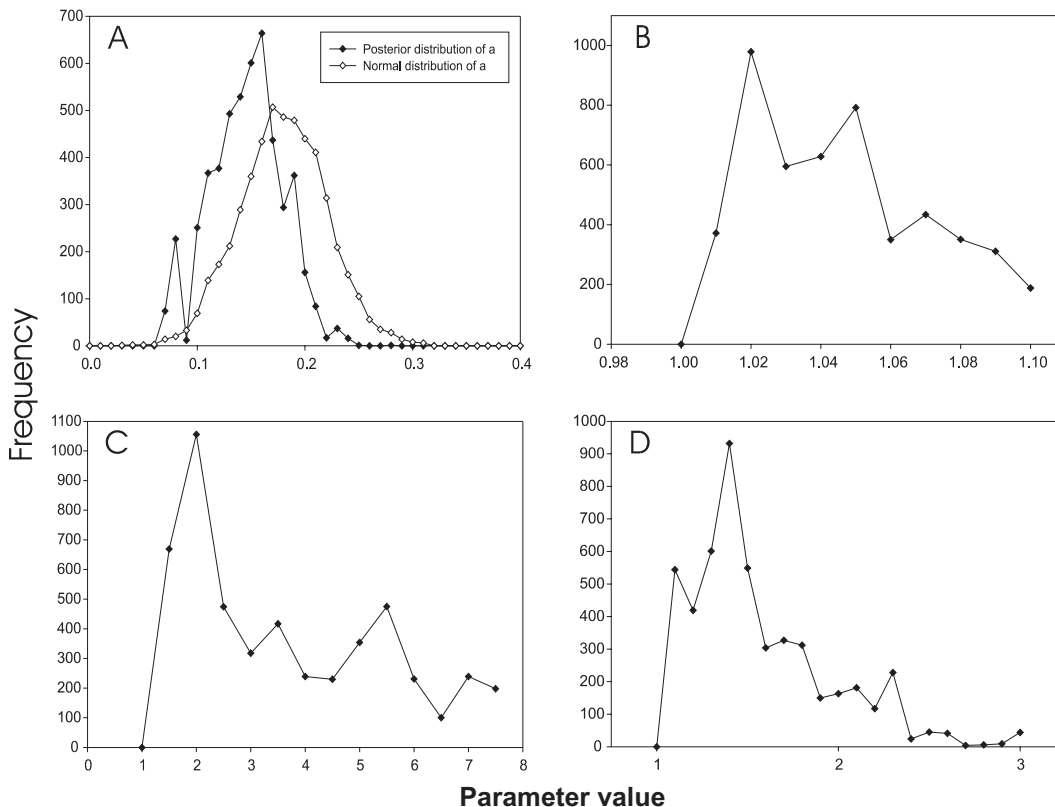

Fig. 4.
Posterior distributions, West Greenland stock, for (A) the parameter a that scaled the population size to the numbers seen during index surveys using an informative prior (♦) and without the informative prior (◊), (B) the maximum rate of population growth ($\lambda_{WG, max}$), (C) the shape parameter of the production curve (θ), and (D) parameter b that scaled catch to the number of whales killed.

dian estimate of population size for 1996 was 17,328 (5,750-27,996). The median estimated maximum sustainable yield (landed whales) was 317 (25-1107) with a 20th percentile (see Wade 1998) of 103 whales landed. The posterior distributions of the population parameters λ_{max}, θ, and the b_{NW} were all uniformly distributed as were their priors.

DISCUSSION

The catches of belugas from West Greenland have been higher than the estimated upper 97.5% credibility level of the maximum net productivity (MNP) and yield since about 1968 when catches, or at least reports of catches, increased by an order of magnitude (Fig. 1). This harvest has reduced the West Greenland stock to about 11% of stock size estimated in 1861. The median stock sizes estimated from the posterior distributions (Table 3) were smaller than the aerial survey population estimate for offshore West Greenland, combined for March 1998 and 1999 (Table 1), corrected for whales missed by observers and for whales not at the surface (Heide-Jørgensen and Acquarone 2002). Both projections fell within the 95% confidence interval (3,650-17,278) of the combined survey estimate but the estimate and projections are not independent. Two index estimates (1998 and 1999) that were subsumed in the combined population estimate (Heide-Jørgensen and Acquarone 2002) were used in the model projections (Table 2). In model runs without these two indices, the 1998-99 population estimate was approximately equal to the upper 97.5 percentile of the model. The model projections discounted the 1981 survey data as being too high given the other information (Fig. 3). Previous analyses had also discounted this survey (Heide-Jørgensen and Reeves 1996).

The SIR Bayesian analysis suggested a median decline of 50% (36% to 62%) between 1981 and 1994, compared to 62% based on all the surveys (Heide-Jørgensen and Reeves 1996). These estimates are not statistically different.

The replacement yield estimates for the West Greenland group (killed or landed) in 1999 are the key parameters of the analysis. These estimates are also the most robust of the estimates

since it is the productivity of the modelled population that allows the projection to pass near the index surveys.

The SIR analysis indicates that the sustainable yield in 1994 was 285 (42-801) belugas killed or 205 (34-392) landed. Since 1994, the number of West Greenland belugas has declined and the median yield estimate for 1999 was 156 whales killed, equal to 109 whales landed (Table 3). Estimated catches for 1999 range from 239 to 311 belugas (Heide-Jørgensen and Rosing-Asvid 2002).

The Bayesian analysis also estimated two parameters that have been difficult to determine directly. These are the adjustment factor for the survey index estimates to stock size (*a*) and the number of whales that are killed but not recorded in the catch statistics (*b*). In early surveys, it had been assumed that all whales at the surface would be seen by an observer during aerial surveys (Davis and Evans 1982). However, this is not the case and it is now accepted that observers usually miss a proportion of the animals that are visible. In addition, aerial surveys of marine mammals are negatively biased because not all the whales are at the surface (*e.g.* Norton and Harwood 1985, Harwood *et al*. 1996). For these stocks, about 30-40% of belugas in open water are within 2 m of the surface based on data collected from time-depth satellite linked radio tags (Heide-Jørgensen and Acquarone 2002, Innes *et al*. 2002b). For the belugas surveyed off West Greenland the adjustment factor determined during the survey was 5.7 (0.175^{-1}) times the estimate (Heide-Jørgensen and Acquarone 2002), which included adjustments for whales on the surface missed by observers and whales that were under water and not visible to the observers. The Bayesian analysis suggested that an even smaller proportion were observed ($a = 0.142$, correction = $0.142^{-1} = 7.0$). This estimate appears to be robust since a similar estimate was obtained when a non-informative prior was used (Fig. 4). Moreover, the 95% credibility interval (0.08-0.20) encompasses the previous estimate.

The estimate for the parameter (*b*) for struck and lost whales and underreporting suggests that a considerable adjustment is necessary to

move from the catch statistics to the number of belugas killed. Before 1996, most of the catch in West Greenland was from drive fisheries which had low losses (Heide-Jørgensen 1994). Thus, either the rest of the harvest had high struck and lost rates, or a large number of whales were landed but were not reported in the catch statistics. Either is possible because catch statistics were never truly complete, the methods of reporting catch changed during the catch series, and their reliability has varied (Heide-Jørgensen 1994, Heide-Jørgensen and Rosing-Asvid 2002).

Parameter b includes both unreported whales as well as struck-and-lost whales in the West Greenland hunts. Combining these factors, the posterior distribution estimate of 1.4 was similar to a recent analysis of killed and lost plus under-reporting (Heide-Jørgensen and Rosing-Asvid 2002) that estimated $b = 1.3$. Actual struck-and-lost rates would be less, when unreported catches are removed from this parameter. It has been suggested that losses range from 1.1 to 1.25 whales killed per whale landed (Heide-Jørgensen 1994, IWC 1992). The difference between these values and the adjustment factor (b) implies that there was a significant proportion of landings which were not reported and can not be estimated from ancillary evidence. The estimated yield from this stock should not be affected by a change in bias since it has remained relatively constant during most of the period covered by the West Greenland indexing surveys.

Parameter b was constrained to be greater than 1 (Fig. 4). Although available data and previous analyses indicate this was a reasonable constraint, future trajectories could allow b to be less than one.

There was a feasibility boundary between carrying capacity and $\lambda_{WG,max}$ (Fig. 5). Combinations to the left of and below this boundary did not produce

enough recruits to sustain the population to 2000 and thus had zero likelihoods assigned. Although these data were strongly clustered in an ellipse above this boundary, there was some evidence that the results were truncated for $\lambda_{max} > 1.1$. Future applications of this model could expand the range of λ_{max} to explore these effects.

A simplified model was necessary because the age and sex distribution of the catch has not been determined. Estimates of survivorship could be used to examine age distribution. There are data for the St. Lawrence stock of belugas (Béland *et al*. 1988), a stock that is small relative to carrying capacity and is expected to have low natural mortality. However these values are based on beach-cast carcasses and may be biased. The mean age of the catch in Upernavik (1989-90) based on Heide-Jørgensen (1994) was 4.4 years with some of the older animals having worn away the neonatal line in their teeth. The role of hunter selectivity, for which there are no data, in this low average age is unknown. Moreover, adding the age distribution of the catch to the model would only be useful if the recruitment age or the distribution of catch was different from the age structure of the stock. There are no data on sex distribution in the catch.

Another way of estimating an appropriate catch level for this stock is to apply the Potential Biological Removal (PBR) method (Wade 1998) used in the U.S.A. Under this method the
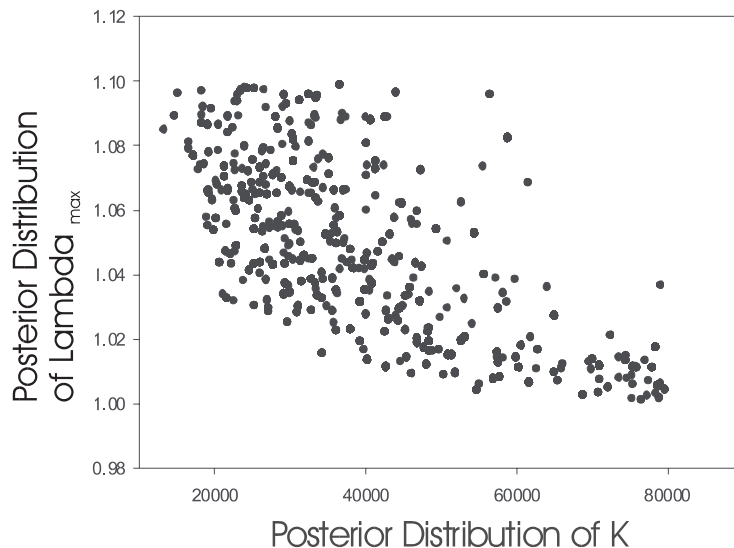

Fig. 5.
The posterior distribution of N_{1861} for the West Greenland stocks in relation to the $\lambda_{WG, max}$ in the simulations. There is a feasibility boundary along the left and lower sides.

PBR for a stock which is below its MNPL but not endangered is $0.5 \cdot \lambda_{max} \cdot$ the 20th percentile from the distribution of N. Using λ_{max} of 3.7% from the posterior distribution and the 1998-99 aerial survey estimate (7,941, cv = 0.41, Heide-Jørgensen and Acquarone 2002) yields a PBR of 108 whales killed. The distribution of population estimates from the SIR analysis were positively skewed and the 20th percentile was calculated from the estimates rather than by following Wade (1998) which would produce slightly higher values. This calculation estimated PBR in 1998 as 79 and in 1999 as 62 whales killed.

The estimate of stock size in Canada in 1996 was 21,093 (NW: 14,839, WG: 6,254), not significantly different than the estimate derived from an aerial survey that year (Table 1). The SIR Bayes analysis suggested that the North Water stock is not greatly depleted from K and as a consequence, yield estimates for 1999 were low (Table 3). Recent harvests have been below MSY.

In the sense of Walters *et al*. (1988) the decline of beluga in West Greenland could be regarded as part of an ecological experiment on these stocks. While such declines can yield important information, the complete "experiment" requires at least two widely different hunting mortalities. A fishing mortality that allows the stock to increase will allow a better determination of the maximal rate of population increase.

The application of SIR Bayesian analysis frees the calculation of the population trajectories from constraining assumptions. By allowing uninformed priors, the model can not only select feasible trajectories, but, by generating posterior distributions, suggest informed priors for future analysis. Moreover, the model is amenable to testing a variety of options for priors, such as widely different calving rates or changes in struck-and-loss rates. Also, because it iterates on an annual basis, the model should be responsive to any future increases in stock size.

ACKNOWLEDGMENTS

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