

Age structure, growth, and mortality of eastern
Beaufort Sea beluga (*Delphinapterus leucas*): a
comparison among Canadian populations

Sebastián P. Luque and Steven H. Ferguson



CANADA/INUVIALUIT
FISHERIES JOINT MANAGEMENT COMMITTEE
TECHNICAL REPORT SERIES

**Age structure, growth, and mortality of eastern
Beaufort Sea beluga (*Delphinapterus leucas*): a
comparison among Canadian populations**

Sebastián P. Luque* and Steven H. Ferguson†

Canada/Inuvialuit Fisheries Joint Management Committee
#204 - 107 Mackenzie Road
P.O. Box 2120
Inuvik, NWT X0E 0T0
Canada

**Fisheries Joint Management Committee
Report 2006-1: v + 27p.**

*Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9,
Canada, email: sluque@mun.ca

†Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada,
email: fergusonsh@dfo-mpo.gc.ca

Copyright: The Fisheries Joint Management Committee, 2006
ISSN 1709-7738

Correct citation for this publication:

Luque, S.P. and S.H. Ferguson. 2006. Age structure, growth, and mortality of eastern Beaufort Sea beluga (*Delphinapterus leucas*): a comparison among Canadian populations. Canada/Inuvialuit Fisheries Joint Management Committee Report 2006-1: v + 27p.

Preface

This work has been done as part of contract No. F2402-050103.

The Canada Inuvialuit Fisheries Joint Management Committee (FJMC) Report Series was initiated in 1985 and reports were published sporadically in a variety of formats until 1998. Information on the earlier publications can be obtained directly from the FJMC office. The Series was re-initiated in 2003 and a common format established with concurrent publication on the FJMC website (<http://www.FJMC.ca>)

List of Figures

2.1	Location of communities sampled.	4
2.2	Age estimates from different readers.	6
3.1	Measures of central tendency in age of beluga.	9
3.2	Age distribution of catches per community.	10
3.3	Measures of central tendency in length of beluga.	12
3.4	Body length vs. age relationship.	13
3.5	Mortality ($Z \pm SE$) estimates for beluga populations.	14
4.1	History of catches from three beluga populations.	17
B.1	Catch curve regression r^2 with increasing class width.	26
B.2	Catch curves for beluga populations.	27

List of Tables

2.1	Sample sizes per population.	6
3.1	Estimated Gompertz growth parameters.	11
A.1	Sample sizes per community.	24

Abstract

The age structure, body length distribution, and mortality of eastern Beaufort Sea (EBS) belugas was studied and contrasted to four other populations in the eastern Arctic: Baffin Bay (BB), Cumberland Sound (CS), western (WHB) and eastern Hudson (EHB) Bay. Median age of EBS belugas was estimated at 29 and 31 yr for males and females, respectively. These values were significantly higher than those from CS and WHB. Age distributions also differed among populations in their shape. EBS belugas were significantly longer and their growth rate differed, relative to eastern Arctic populations, revealing a geographic gradient in a south, to north, northwest direction, so that EHB belugas were the smallest. Our results suggest that hunting pressure may have played a role in these responses. Mortality was highest among EBS belugas, but it was not significantly different from other Canadian Arctic populations.

Contents

1	Introduction	1
2	Materials and Methods	3
2.1	Database Preparation and Data Selection	3
2.2	Measurements and Analyses	5
3	Results	8
3.1	Age structure	8
3.2	Body Size and Growth	11
3.3	Mortality	14
4	Discussion	15
A	Classification of community catches into populations	24
B	Determination of age class width for catch curve analyses	25

1 Introduction

Belugas (*Delphinapterus leucas*) summering in the eastern Beaufort Sea (EBS hereafter) have been found to be relatively isolated from their conspecifics in the region (O’Corry-Crowe *et al.* 1997), so there is considerable interest in studying the changes in vital statistics of this group of animals for management purposes. Although EBS belugas remain in the Beaufort Sea during the summer, they are known to travel at least 1000 km away from the coast at that time, before migrating west and south to their Bering Sea wintering grounds (Richard *et al.* 2001). Therefore, obtaining information on abundance, structure and characteristics of individuals from this population remains a challenging task.

Belugas have been traditionally hunted for food by people in native communities along the coasts of Alaska and northern Canada, including the Mackenzie river delta. This has provided a means to gather information on beluga populations that would otherwise be unavailable. Using catch data provided by hunters, Harwood *et al.* (2002) presented evidence that the EBS beluga population has been hunted sustainably between 1980 and 1999, based on the absence of any reduction in the availability of old and large individuals in such data. Harwood *et al.* (2002) also provided estimates of asymptotic length for males of this population and found no year effects on this statistic from 1988-1994. Despite the reduced spatial coverage of independent aerial surveys to assess EBS beluga abundance (Harwood *et al.* 1996), the currently available information suggests this beluga stock may be stable and close to the level the environment can sustain.

Comparable data from other beluga populations in Canada are available, but a systematic comparative analysis including EBS has not yet been carried out. However, some patterns have emerged by comparing growth of animals caught at various eastern Canadian Arctic communities. For instance, Doidge (1990) found that belugas from eastern Hudson Bay tend to be smaller than those from most other eastern Canadian Arctic locations. Stewart (1994) corroborated this finding using samples from additional locations, concluding that belugas from western Hudson Bay were smaller than those from the High Arctic and Southeast Baffin, but were as large as those from eastern Hudson Bay. Interestingly, significant size and growth differences were found between populations that were under heavy hunting pressure; namely animals from Cumberland Sound and eastern Hudson Bay. The asymptotic lengths presented by Harwood *et al.* (2002) are similar to those from Cumberland Sound and Alaska (Doidge 1990). Habitat differences between presumed populations may account for these size patterns.

There is also considerable variation in the composition of the catch, in terms of the age and sex of animals caught among Canadian beluga populations. For example, median age of animals caught in the Mackenzie river delta during the early 90's was approximately 24 for both males and females, while males were about twice as numerous as females in the catch (Harwood *et al.* 2002). In contrast, the median age of belugas caught in eastern Hudson Bay was reported at 8.5 yr during approximately the same time period, although significant reductions in age were observed in the entire Nunavik region, compared to animals caught in the 80's (Lesage and Doidge 2005). Compared to EBS belugas, eastern Hudson Bay beluga abundance may have been negatively affected by hunting pressure. This has led to quota restrictions in eastern Hudson Bay, which have not yet resulted in any reversal in the age composition of the catches, relative to years prior to the peak harvests.

Such contrasts in the response of beluga to hunting pressure and changes in relative abundance prompted the present study to compare the age and sex structure, as well as mortality of beluga populations across Canada, based on the most complete and updated morphometric and age data available, to set baseline demographic and growth information on this population. Our objectives for this project were, therefore, to determine the age structure of EBS beluga, model the growth, and provide an estimate of mortality for animals of this population using this updated database. In an effort to address the issue of uncertainties in the selectivity of hunters with respect to the available population, we compared these aspects among different putative beluga populations in Canada. Assuming that hunter selectivity is the same across populations, the spatial and temporal coverage of this analysis can help identify common mechanisms controlling the response of beluga to differences in the environmental and anthropogenic influences.

2 Materials and Methods

2.1 Database Preparation and Data Selection

The first task in preparation for our analyses was to complete and reorganize EBS beluga data which has been maintained by Fisheries Joint Management Committee (FJMC) and the Department of Fisheries and Oceans (DFO) over almost three decades, in collaboration with hunters and members of local communities. This involved the inclusion of age data from a large number of individuals available from DFO, but not correctly matched with morphometric data from FJMC and viceversa. Several conflicts in the identity and sex of individuals between both data sets were also identified and resolved by a careful re-examination of original records and inclusion of additional genetically determined sex information (available from DFO). Data from the eastern Canadian Arctic were also similarly re-examined for accuracy in the identity and sex of individuals, which resulted in an increase in the sample size available for most populations. Thus, 983 EBS belugas, and 1752 belugas for all populations combined¹ can now be correctly identified and attributed an estimate of age (dentine growth layer group count). The corrected and complete database is now available as a Microsoft Access database with appropriate relationships defined between tables.

A second step was to define the putative populations on which to base our comparisons. Enough evidence has accumulated to ascertain that EBS belugas are relatively isolated from individuals in the eastern Canadian Arctic (O’Corry-Crowe *et al.* 1997, Brown Gladden *et al.* 1999), so they were considered as a single homogenous population in this study. Information on the population structure of eastern Canadian Arctic belugas is still debatable (Koski *et al.* 2002, Richard *et al.* 1990, Stewart 1994, O’Corry-Crowe *et al.* 1997, Innes *et al.* 2002), but allows the definition of 4 relatively discrete areas that represent different groups of belugas forming separate management units, or stocks (Figure 2.1): 1. eastern Beaufort Sea (EBS), 2. Baffin Bay (BB), 3. Cumberland Sound (CS), 4. Western Hudson Bay (WHB), and 5. Eastern Hudson Bay (EHB). This grouping of communities’ catches is consistent with available information of spatiotemporal movements of belugas in these regions (Koski *et al.* 2002, Smith 2004, Cosens and Dueck 1991, Suydam *et al.* 2001).

¹These figures include all individuals aged and not the final sample size used in the present study (see below for details on further subsetting of the data)

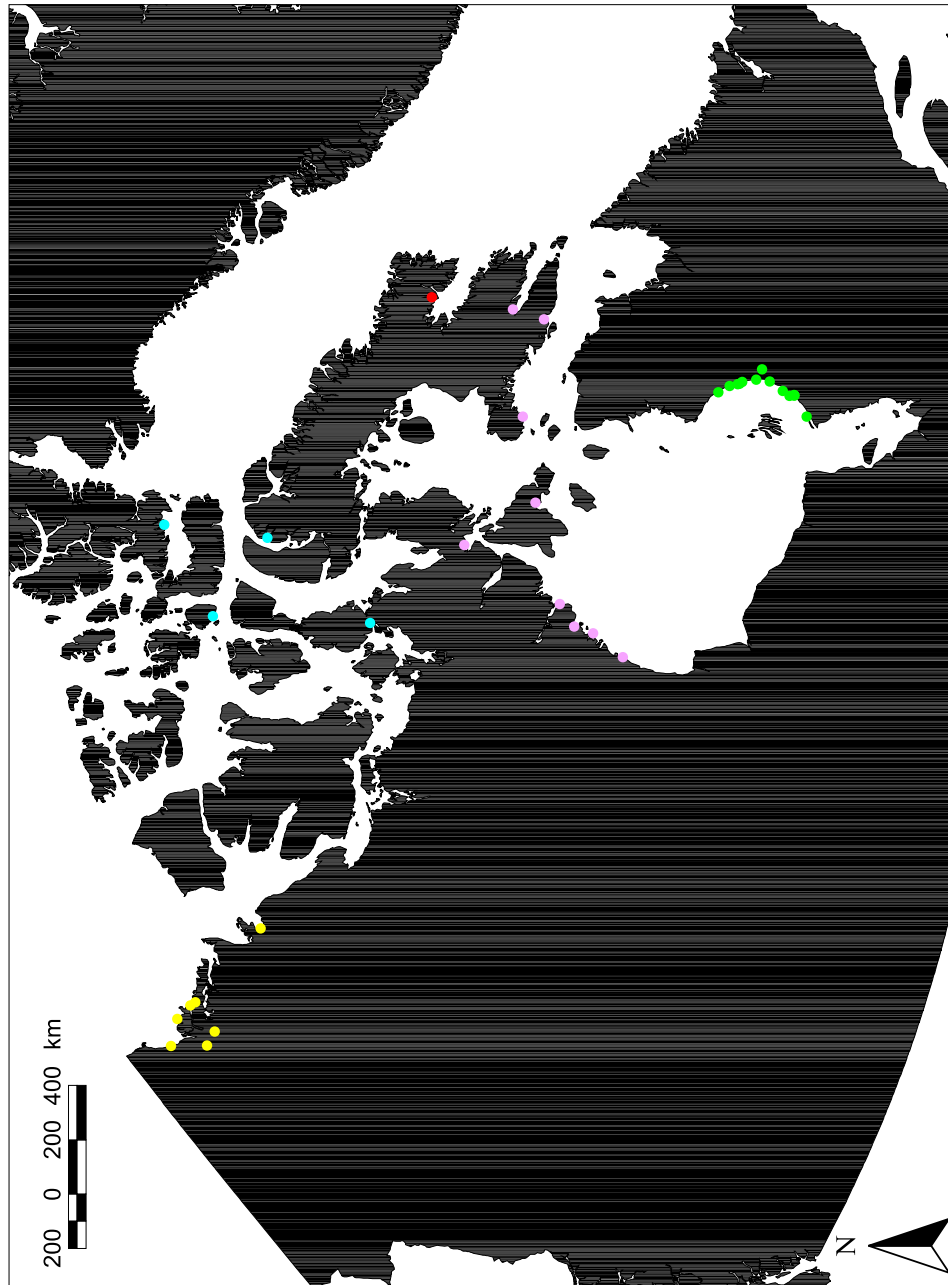


Figure 2.1. Location of communities representing different beluga stocks in the eastern Canadian Arctic from where morphometric and age data were collected. Five putative beluga populations were defined, grouping catches from various communities: a) eastern Beaufort Sea (yellow), b) Baffin Bay (light blue), c) Cumberland Sound (red), d) Western Hudson Bay (purple), and e) Eastern Hudson Bay (green). Communities where samples came from are listed in Appendix A.

2.2 Measurements and Analyses

Morphometric measurements including body mass, standard length and girth were obtained from the animals' carcasses according to procedures described elsewhere (Stewart 1994, Sergeant and Brodie 1969, Brodie 1971, Doidge 1990). Because body mass may change dramatically depending on the nutritional status of the individual (Peters *et al.* 1983, LaBarbera 1989), we used standard length as an index of body size for belugas in this study.

Details of the process of age determination for the samples analyzed here have been previously described (e.g. Sergeant 1959, Lesage and Doidge 2005, Stewart 1994). Briefly, a tooth from the lower mandible was extracted by boiling the jaw, and later cast in resin for longitudinal sectioning and counting of growth layer groups. Calibration of the method to obtain an estimate of age remains a controversial issue, which we have reviewed and submitted as a manuscript for a peer-reviewed publication². However, aquarium-raised individuals, a reanalysis of previous published evidence, and an allometric relationship lend support to the hypothesis of one dentinal growth layer group (GLG) being deposited annually in beluga, rather than the commonly used value of two GLG per annum. This assessment is consistent with analyses recently carried using carbon isotopic methods applied to beluga teeth³. Therefore, ages were assigned to animals in the present study using one GLG per annum (i.e. age equals the GLG count for any given individual).

All dentine counts were performed by one reader for samples collected after 1993, except for a few individuals, but by a different reader for samples collected previously. Therefore, the possibility for any reader effects in the age estimates was examined before proceeding with further analyses. Considerable differences in the distribution of ages in relation to the reader was found, indicating that individuals aged by these readers were not comparable (Figure 2.2). Therefore, only samples collected by the single known reader were used in all subsequent analyses, so that sample sizes were reduced to 628 EBS belugas and 1397 belugas for all populations combined (Table 2.1). Specific details on the communities from where data were available and assignment of catches to particular populations are provided in Appendix A.

²Luque S.P., Higdon J.W., Ferguson, S.H. (submitted) Dentine deposition rates in beluga (*Delphinapterus leucas*): an analysis of the evidence

³Personal communication. R.E.A. Stewart, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada, stewartr@dfo-mpo.gc.ca

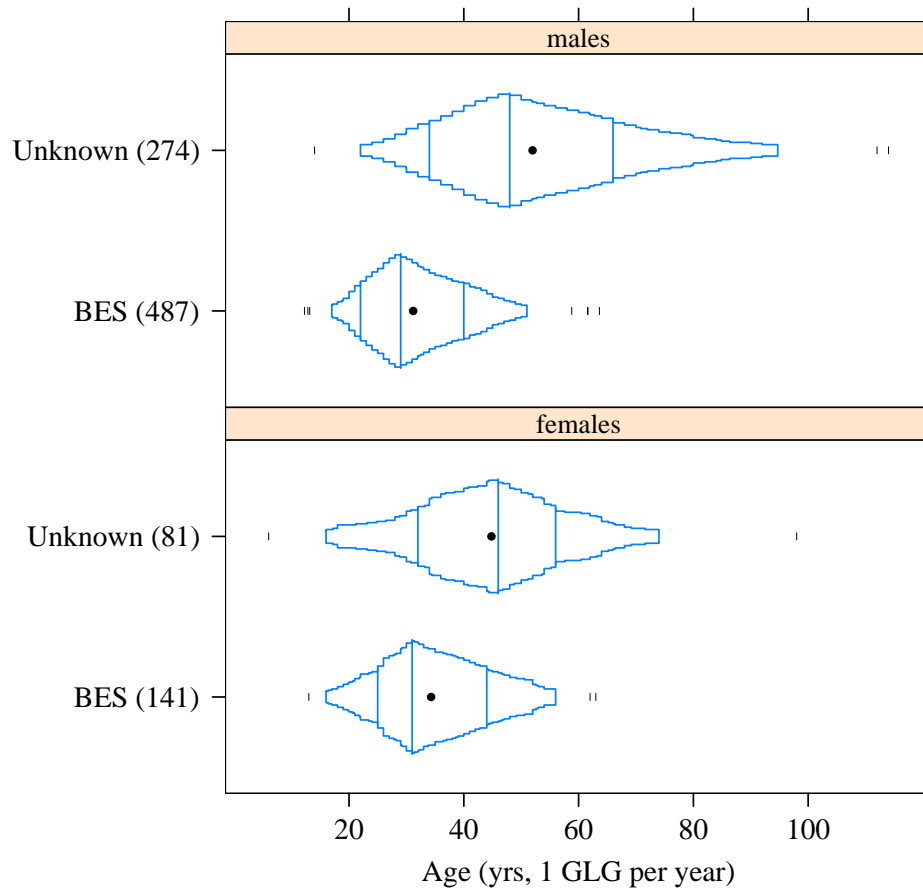


Figure 2.2. Comparison of estimated age by different readers of male and female belugas collected from the Mackenzie river delta. BES: known reader.

Table 2.1. Number of known age belugas for which GLG counts were available from the same reader (yearly mean catches in parenthesis).

Putative population	Female	Male
EBS	141 (12.8)	487 (44.3)
BB	23 (3.8)	15 (3.0)
CS	58 (8.3)	86 (12.3)
W Hudson	171 (17.1)	203 (20.3)
E Hudson	109 (7.8)	104 (7.4)
All	502 (22.8)	895 (40.7)

Age distributions were first visualized by smoothing them using a gaussian kernel density estimator, whereby bandwidth was optimally chosen from the standard deviation and the interquartile range (Scott 1992). The purpose of using this initial approach was to overcome limitations associated with a particular choice of age class width that often tend to obscure the underlying distribution, including small number of frequency classes. To test for differences between the smoothed distributions, a non-parametric bootstrap procedure was used (Bowman and Azzalini 1997), which tested the null hypothesis that the age distribution was the same among all beluga populations. This test was performed for each sex separately.

To compare growth of individuals across populations, a Gompertz model was fit to each combination of population and sex:

$$length_t = A \cdot e^{-b \cdot e^{-k \cdot age}} \quad (2.1)$$

where $length_t$ represents length at age t , A represents asymptotic length; k represents the rate of exponential growth decay, and b is a constant describing initial growth (Windsor 1932, Winship *et al.* 2001). A von Bertalanffy model and a linear model on the semi-log transformed relationship revealed undistinguishable fits for the Gompertz and von Bertalanffy models, whereas the semi-log relationship did not accurately describe the growth data, as linearity assumptions were violated (Zar 1996). Therefore, the Gompertz model was chosen to describe growth for each combination of population and sex. The standard error for each model estimate of asymptotic length and growth coefficient were compared to determine differences in body size and growth rate among populations. Probabilities for pairwise comparisons were adjusted for their multiplicity, following recommendations in Bretz *et al.* (2001).

Mortality was estimated using the methods outlined by Chapman and Robson (1960), Robson and Chapman (1961), assuming that survival/mortality, both natural and hunting, and that year class strength have remained constant during the ages covered in the sample (Haddon 2001). The method involves fitting a regression line through the descending limb of log transformed frequency of age classes, as this represents the ages at which the animals have been fully recruited to the sampled population. A search for the minimum age class width at which all classes were represented was performed by increasing class width from 1 to 10 yr and plotting the frequency against the corresponding age classes. Based on this analysis, a class width of 5 yr was deemed optimal for estimating the catch curve (Appendix B). Analysis of covariance (ANCOVA) was used to test for parallelism of regression lines among populations (Zar 1996).

3 Results

3.1 Age structure

Comparison of measures of central tendency of ages indicated differences between populations were relatively small (Figure 3.1), particularly among males. Male Median age ranged from 15 for BB to 29 yr for EBS animals, while it ranged from 17 for Cumberland Sound to 31 yr for EBS females. Maximum ages were found in the W Hudson Bay samples with values of 77 yr for males, and 74 yr for females. There were not any age differences between males and females. Despite the extensive overlap in the distributions, there were significant differences in median ages between populations (Kruskal-Wallis test $\chi_3^2 = 75.53; 67.74, P < 0.01$ both), but they were all due to EBS animals being significantly older than those from CS and W Hudson Bay (Behrens-Fisher test, $P < 0.01$ males and females).

The kernel smoothed age distributions showed that their shapes were not homogeneous among beluga populations (bootstrap test for equality of density distributions $P < 0.001$). Most populations displayed a first “peak” in the distribution which was similar for all males at 20-23 yr of age (Figure 3.2), except for BB males whose most abundant age frequency was 10 yr. A second, much weaker, “peak” was observed for EBS males, which probably explains their significantly older median age, at about 45 yr of age. Males from other populations also displayed this second increase in frequencies, but they were much more tenuous and occurring at ages ranging from 37 to 40 yr. Compared to males, variability among distribution shapes was considerably larger among females, with the most abundant ages being clearly higher for EBS females. Differences among females from other populations were not as large, with maximum age frequencies occurring between 11 yr (Cumberland Sound), to 18 yr (EHB). Females also showed a secondary increase in age frequencies, which spread over a much wider range than that observed in males; from a minimum of 35 yr (E Hudson), to a maximum of 54 yr (EBS).

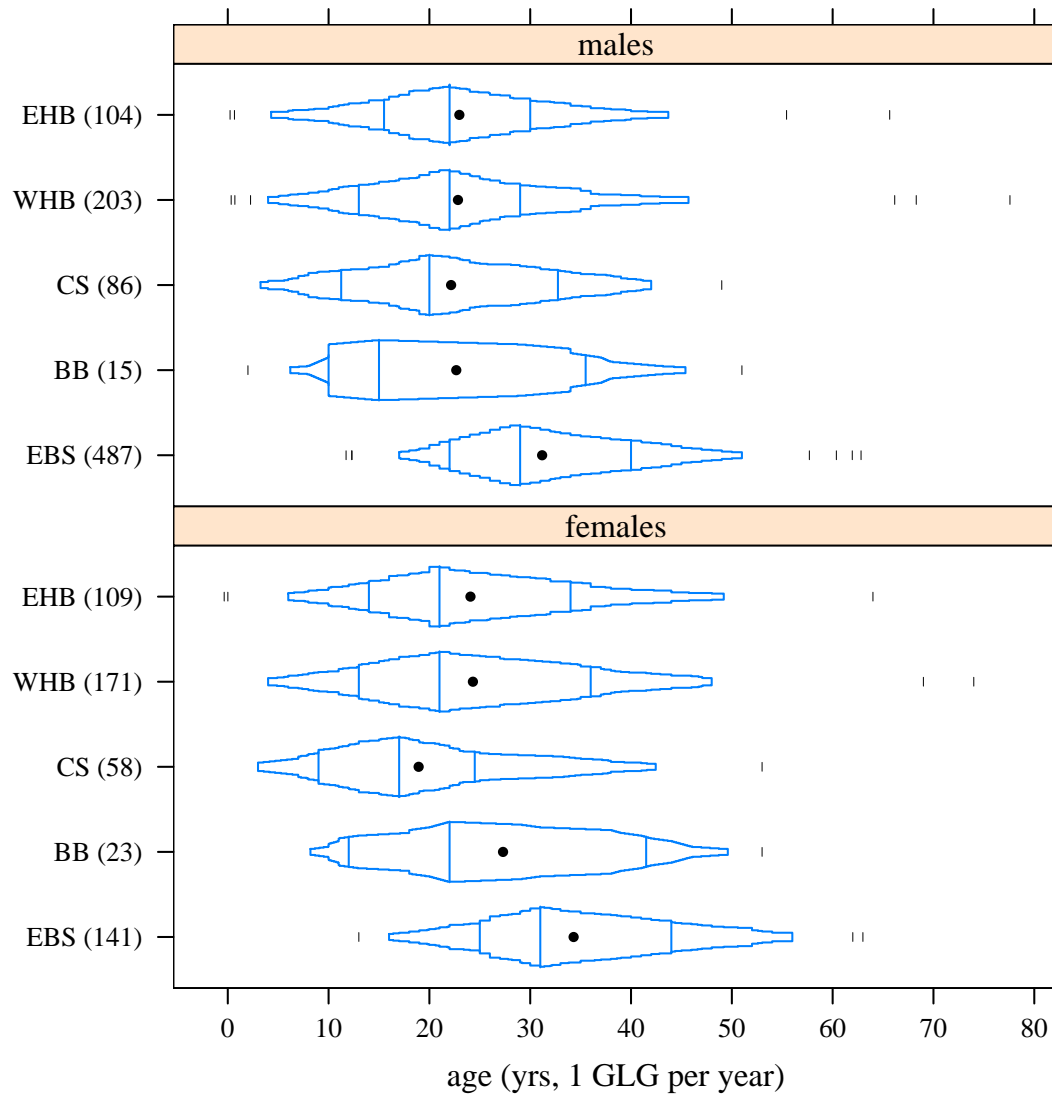


Figure 3.1. Age distribution of male and female beluga collected from five populations across the Canadian Arctic. Samples were collected between 1993 and 2004, except for CS and WHB, where collection started in 1991 and 1989, respectively. All quantiles from 5th through 95th, mean (dot), median, and 25 and 75th quantiles (reference lines) of the distributions. Sample sizes in parentheses after the population name.

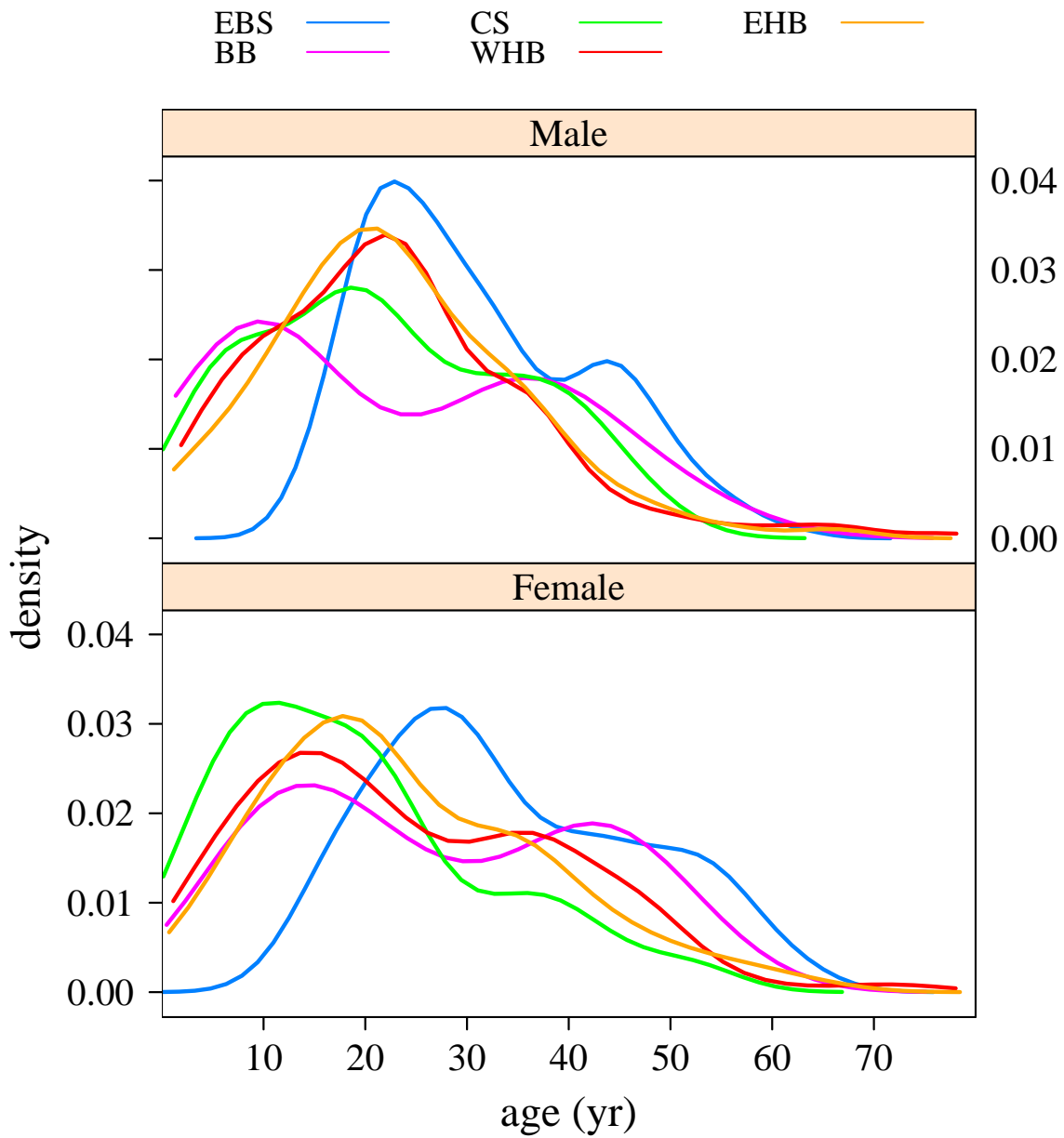


Figure 3.2. Smoothed age distributions for five beluga populations from across the Canadian Arctic between 1993 and 2004 (except for CS and WHB, where collection started in 1991 and 1989, respectively).

3.2 Body Size and Growth

Variation in the body length of belugas showed a significant interaction between population and sex ($F_{4,1100} = 4.94$, $P < 0.001$), so it was interpreted separately for each sex. However, both sexes showed the same general pattern, such that the smallest animals were those from EHB, followed, in increasing size order, by those from WHB, CS, BB, with EBS belugas being the largest animals caught (Figure 3.3). Multiple comparisons among populations indicated that all differences were significant ($P < 0.001$), except for those between EBS and BB, and between CS and BB, which were indistinguishable ($P > 0.1$). Differences among females were not significant, and more gradual, so that a clear pattern could not be elucidated.

Baffin Bay was excluded from growth analyses due to small sample size for length at age data, which was insufficient to fit the Gompertz model (2.1). The relationship between body length and age showed that growth varied considerably among populations, with asymptotic lengths ranging from 389.7 (E Hudson) to 448.2 cm (CS) among males. Asymptotic length of females varied from 338.1 (E Hudson) to 385.7 cm (CS) (Table 3.1).

Table 3.1. Estimated parameters of the Gompertz growth model ($length_t = A \cdot e^{-b \cdot e^{-k \cdot age}}$) for each beluga population and sex. *SE* for each parameter is shown in parentheses.

Putative population	Sex	N	<i>A</i>	<i>b</i>
EBS	Male	370	432.3 (2.44)	1.2 (0.49)
	Female	105	381.5 (3.54)	7.6 (16.18)
CS	Male	84	448.2 (13.22)	0.6 (0.07)
	Female	55	385.7 (9.24)	0.5 (0.08)
W Hudson	Male	183	411.5 (8.90)	0.6 (0.05)
	Female	151	360.5 (5.25)	0.5 (0.07)
E Hudson	Male	68	389.7 (14.32)	0.7 (0.07)
	Female	69	338.1 (6.30)	0.5 (0.13)

Animals from EBS had higher coefficients of growth decay, consistent with their relatively older ages, which meant that a greater proportion of individuals have attained physical maturity or were close to reaching the age of maximum length (Figure 3.4). Although CS male belugas displayed the highest asymptotic lengths, standard error of parameter estimates indicated relatively large uncertainties in these comparisons.

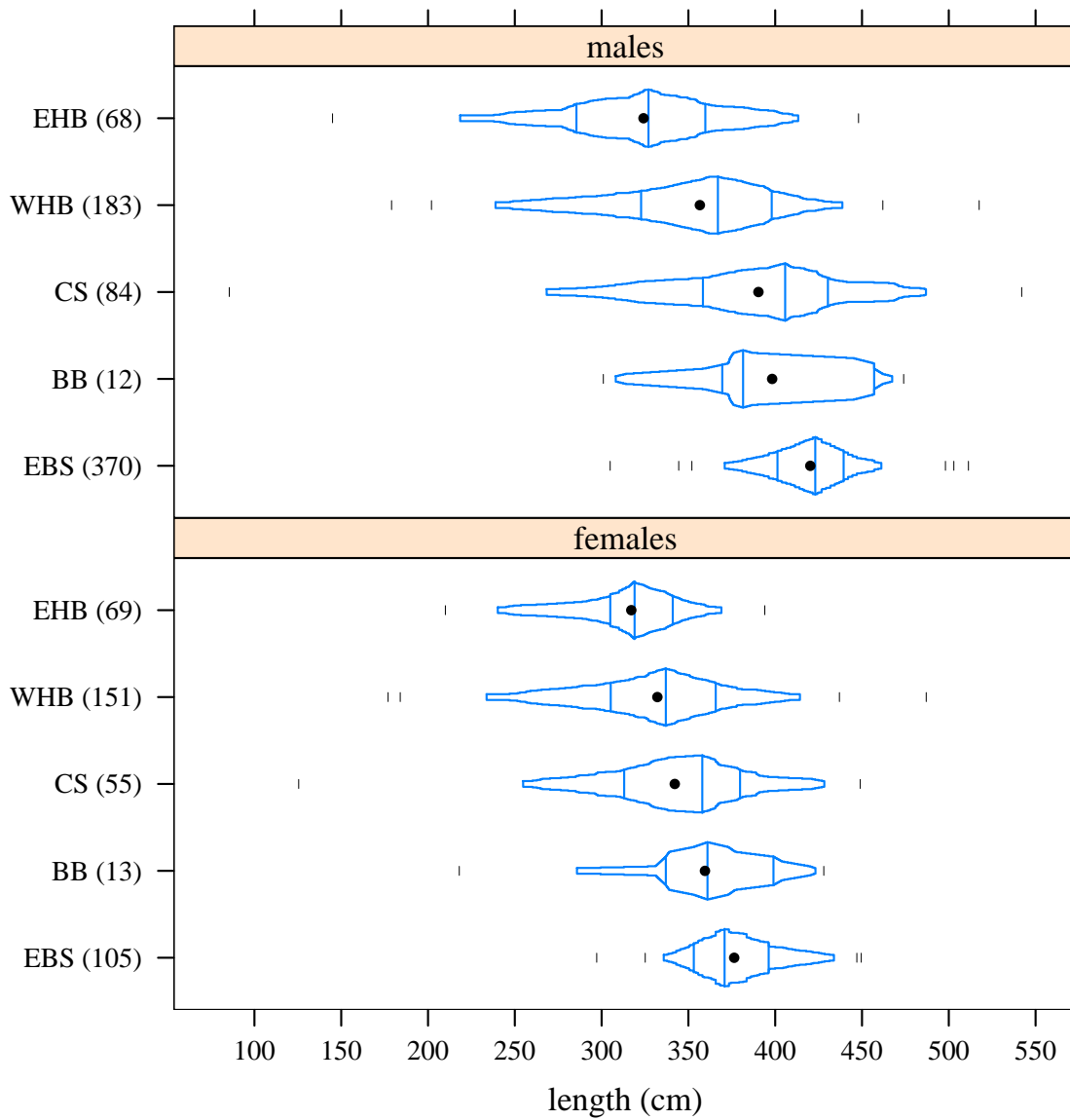


Figure 3.3. Length distribution of male and female beluga collected from five populations across the Canadian Arctic between 1993 and 2004 (except for CS and WHB, where collection started in 1991 and 1989, respectively). See Figure 3.1 for explanation of box-percentile information displayed.

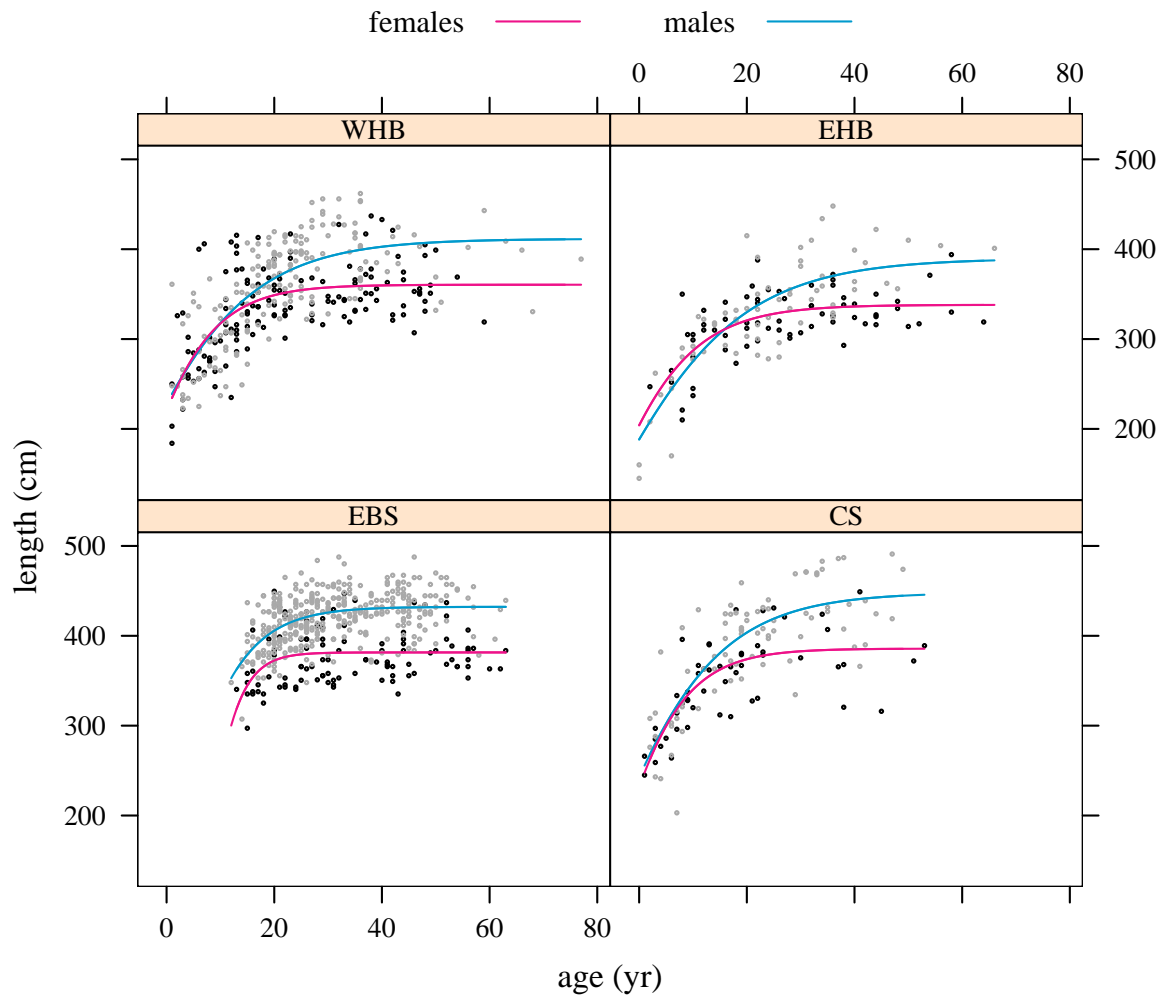


Figure 3.4. Relationship between body length and age for five Canadian beluga populations, including Gompertz model fit. See Table 3.1 for fitted values.

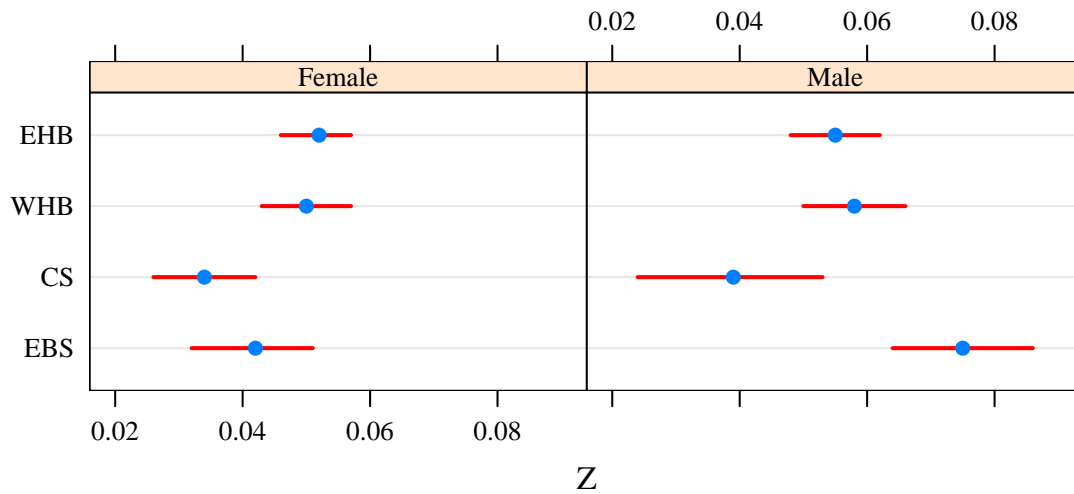


Figure 3.5. Beluga mortality estimates ($Z \pm SE$) in relation to population of origin.

3.3 Mortality

Variation in estimates of mortality, derived from catch curves, among beluga populations was relatively small (Figure 3.5). Confidence intervals around CS male mortality estimates were particularly large. Mortality estimates ranged from 4% (Cumberland Sound) to 8% (EBS) among males, and from 3% (CS) to 5% (EHB and WHB) among females. However, there was a large overlap in confidence intervals around each estimate, and ANCOVA showed that differences were not significant ($P > 0.2$ males and females).

4 Discussion

Compared to previous reports, the age distribution of the beluga catch in the eastern Beaufort Sea in our study provides considerably younger median ages for belugas of both sexes. Harwood *et al.* (2002) provided median ages of 23.5 and 24 yr for females and males, respectively, using 2 GLGs per annum to obtain those estimates. This would correspond to 47 and 48 yr using our assumption of 1 GLG per annum in our study, whereas we found median ages of 31 and 29 yr for females and males, respectively. Although the data from our study include those in Harwood *et al.* (2002), the temporal coverage of the catches, and hence sample sizes are different. Eastern Beaufort beluga age information available in 2001 was restricted to animals caught between 1988 and 1994, whereas those currently available are from 1988 to 2003. Therefore, it is possible that the discrepancy may be due to the use of different sampling periods between both studies. However, such large differences (16 and 19 yr) would not be expected from the currently available data. An additional factor is hinted at from our finding of large reader effects on age estimates and variability (Figure 2.2). Age estimates for animals caught prior to 1993 were performed by readers that systematically overestimated median age by about 10 yr, compared to the reader who aged other beluga teeth more recently. Either of these factors, or their combination, may have been responsible for the discrepancy in median age estimates.

A common pattern observed in all five beluga populations was the presence of two peaks in age frequencies. Most large vertebrates show relatively constant adult survival rates (Charnov 1986), so steadily decreasing frequencies in adult age were expected for belugas. The reasons for this pattern are not clear, but the trough between these peaks could indicate past reductions in natality, such that animals of those cohorts were relatively less abundant. A possible explanation is that the troughs indicate an unusually large number of individuals taken from the populations in the past, which could therefore not reproduce during particular years. Reductions in adult survival have been associated with increased hunting pressure in sperm whales (Evans and Hindell 2004), a species with similar life history. A second possibility is large scale changes in the environment leading to increased adult mortality or reduced fecundity (e.g. Davis *et al.* 2002, Coulson *et al.* 2000). Historical catch records and indices of ecosystem change, together with the data used in this study may help test these hypotheses.

The age structures of populations considered in this study indicate that belugas caught in the EBS are older than those caught in the eastern Arctic. Not only was the median

age of belugas in the EBS population significantly older, but animals older than this age were being caught with higher probability in this population than in others. If the catches accurately reflect available beluga populations, then these results suggest that the eastern Beaufort Sea beluga population is in better condition than populations in the eastern Arctic, as the relative abundance of old individuals in a population is considered an indication of the level of recruitment of immature individuals and how long they remain in the reproductive portion of the population (Caughley 1977, Laws 1978, Boyd *et al.* 1995). Our results, therefore, are consistent with the suggestion that the eastern Beaufort Sea beluga population is in healthy condition, based on how it compared to other populations in Canada, in terms of its age structure.

Our finding that Hudson Bay belugas are smaller than those from other eastern Arctic populations is consistent with previous comparisons of animals from these populations (Stewart 1994, Doidge 1990). However, there was an apparent geographical gradient of body size in a north, northwest direction in body length observed in the animals in the present study, that was not evident in previous reports. This gradient was unexpected, based on the comparisons of age distributions, but was in agreement with variation in growth among populations. Belugas from EHB had smaller asymptotic lengths than those from WHB, which in turn were smaller than those of belugas from CS or EBS. If this pattern is the result of differing responses of belugas to changes in hunting pressure, we would expect to see a similar pattern in the catches from these populations. Comparable catch records from all these populations have not yet been properly assembled, but partial records from CS, EBS, and WHB provide some indications that this may be the case (Figure 4.1). Cumberland Sound belugas have had the lowest numbers of animals killed since 1978, while the opposite is true for WHB belugas. Catch record numbers for EBS are intermediate between these numbers. Therefore, there is some association between asymptotic length and hunting pressure among these three populations.

Comparable beluga survival estimates from the populations studied here is, to the best of our knowledge, not available. The estimates were, however, marginally higher overall than those reported for West Greenland (Heide-Jørgensen 1994). Heide-Jørgensen (1994) provided survival estimates ranging from 0.81 to 0.86, using the same method used in this study (Robson and Chapman 1961). Our lowest estimate corresponds to 0.92 annual survival rate among males from EBS, while the highest annual survival rate was 0.97 for females from CS. The difference may reflect the history of more intensive hunting of West Greenland belugas, compared to Canadian Arctic populations (Heide-Jørgensen 1994).

The age structure, growth, and beluga mortality patterns raise questions about their inter-relationships with animal abundance and hunting pressure, in populations with similar harvest histories. This is illustrated by the EHB and CS stocks, which have been subject to intensive harvests until the late 80's, when catches became more regulated,

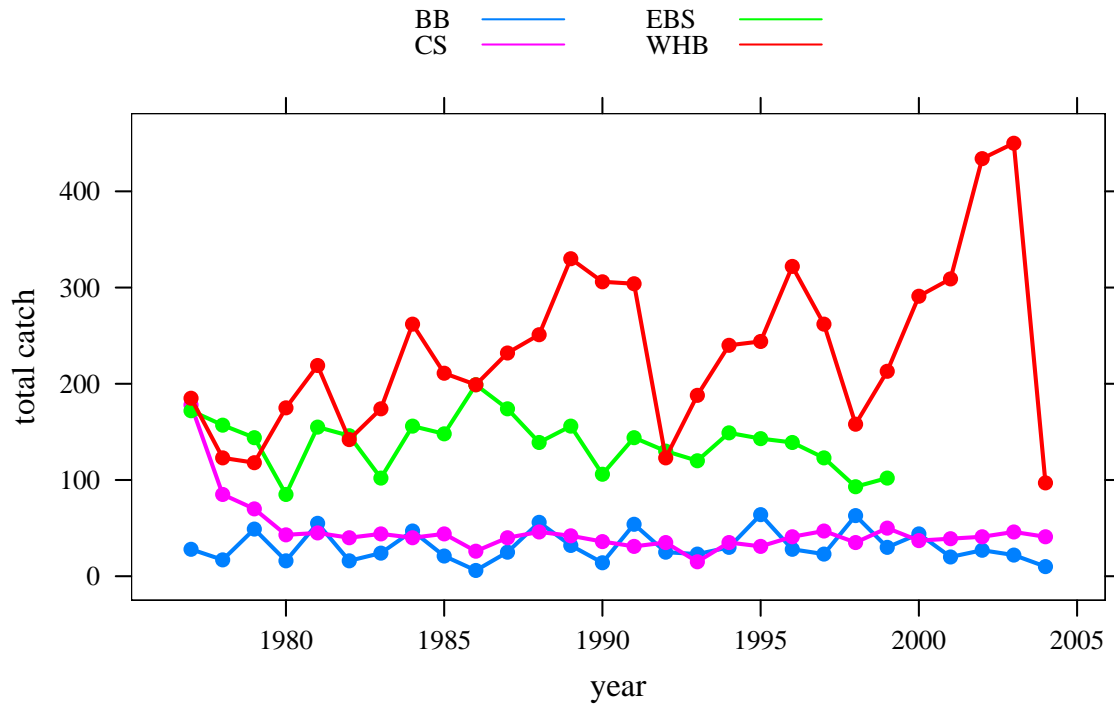


Figure 4.1. Catch history record from aggregated figures belonging to four beluga populations or stocks.

albeit with limited success (Lesage and Doidge 2005, Hammill *et al.* 2005). The EHB population is thought to be declining since the late 80's from 4200 in 1985 to 3100 belugas in 2004, although the rate of decline has slowed (Hammill *et al.* 2005). In contrast, the abundance of CS beluga seems to have increased from a mean of 475 animals in 1990 to a mean of 750 animals counted in 1999 (Richard and Baratin 2005, Alvarez-Flores 2005). Hunting pressure has increased during the mid 90's at EHB, associated with the highest estimated rates of decline for this population. Conversely, hunting pressure at CS has remained relatively low and constant (Figure 4.1). Based on the results from this study, the CS beluga population has shown an increase in abundance associated with: 1. relatively low hunting pressure, 2. increased body size, and 3. low adult mortality, compared to EHB belugas, where numbers have been decreasing. EBS beluga numbers appear to be stable at a minimum of 20,000 animals, an estimate which did not account for animals below the surface and dating from 1992 (Harwood *et al.* 1996). Given that hunting pressure and body size are similar for EBS and CS belugas, why does the former show relatively large adult mortality? This question deserves closer examination in the future, as uncertainties in abundance and mortality estimates remain high.

To summarize, this study has shown that median ages of beluga catches from EBS are significantly older than those from the eastern Arctic (particularly, CS and WHB).

In general, the age distribution of EBS belugas displays older ages compared to other Canadian Arctic populations. The body size of EBS belugas was found to be larger than those caught in Hudson Bay, but similar to that of CS belugas. Furthermore, body size showed a geographical gradient, whereby body size increased from EHB to EBS, in a south, to north, northwest direction. Mortality was similar across populations, but with marginally higher values for EBS belugas. Comparison of these results with animal abundance and hunting pressure suggest that the latter may have played a role in the observed responses. However, an assessment of differences in hunter selectivity between populations is needed, to insure that the patterns are comparable. Such a study has the potential to open up the possibility for the comparative approach used here to interpret spatiotemporal demographic patterns in each of these monitored beluga populations.

Bibliography

- Alvarez-Flores, C., 2005. Risk assessment of the hunt of belugas, *Delphinapterus leucas*, in Cumberland Sound. Technical report, Fisheries and Oceans Canada.
- Bowman, A. and A. Azzalini, 1997. Applied Smoothing Techniques for Data Analysis: the Kernel Approach with S-Plus Illustrations. Oxford University Press, Oxford.
- Boyd, I., J. Croxall, N. Lunn and K. Reid, 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology* 64:505–518.
- Bretz, F., A. Genz and L. Hothorn, 2001. On the numerical availability of multiple comparison procedures. *Biometrical Journal* 43(5):64–66.
- Brodie, P., 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *Journal of the Fisheries Research Board of Canada* 28:1309–1318.
- Brown Gladden, J., M. Ferguson, M. Friesen and J. Clayton, 1999. Population structure of North American beluga whales (*delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. *Molecular Ecology* 8:347–363.
- Caughley, G., 1977. *Analysis of Vertebrate Populations*. Wiley & Sons.
- Chapman, D. and D. Robson, 1960. The analysis of a catch curve. *Biometrics* 16(3):354–368.
- Charnov, E., 1986. Life history evolution in a "recruitment population": why are adult mortality rates constant? *Oikos* 47:129–134.
- Cosens, S. and L. Dueck, 1991. Group size and activity patterns of belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) during spring migration in Lancaster Sound. *Canadian Journal of Zoology* 69:1630–1635.
- Coulson, T., E. Milner-Gulland and T. Clutton-Brock, 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society of London B Biological Sciences* 267:1771–1779.

- Davis, S., R. Pech and E. Catchpole, 2002. Populations in variable environments: the effect of variability in a species' primary resource. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 357:1249–1257.
- Doidge, D., 1990. Age-length and length-weight comparisons in the beluga, *Delphinapterus leucas*. In T. Smith, D. St. Aubin and J. Geraci, eds., *Advances in research on the beluga whale, Delphinapterus leucas*, volume 224. Canadian Bulletin of Fisheries and Aquatic Sciences, Ottawa, pages 59–68.
- Evans, K. and M. Hindell, 2004. The age structure and growth of female sperm whales (*Physeter macrocephalus*) in southern Australian waters. *Journal of Zoology (London)* 263:237–250.
- Haddon, M., 2001. *Modelling and quantitative methods in fisheries*. Chapman & Hall.
- Hammill, M., V. Lesage and J.-F. Gosselin, 2005. Abundance of eastern Hudson Bay belugas. Technical report, Fisheries and Oceans Canada. URL <http://www.dfo-mpo.gc.ca/csas/>.
- Harwood, L., S. Innes, P. Norton and M. Kingsley, 1996. Distribution and abundance of beluga whales in the Mackenzie river estuary, southeast Beaufort Sea, and west Amundsen Gulf during late July 1992. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2262–2273.
- Harwood, L., P. Norton, B. Day and P. Hall, 2002. The harvest of beluga whales in Canada's Western Arctic: hunter-based monitoring of the size and composition of the catch. *Arctic* 55(1):10–20.
- Heide-Jørgensen, M., 1994. Distribution, exploitation and population status of white whales (*Delphinapterus leucas* and narwhals (*Monodon monoceros*) in West Greenland. *Meddelelser om Grønland* 39:135–149.
- Innes, S., D. Muir, R. Stewart, M. Heide-Jørgensen and R. Dietz, 2002. Stock identity of beluga (*Delphinapterus leucas*) in Eastern Canada and West Greenland based on organochlorine contaminants in their blubber. *NAMMCO Scientific Publications* 4:51–68.
- Koski, W., R. Davis and K. Finley, 2002. Distribution and abundance of Canadian High Arctic belugas, 1974-1979. *NAMMCO Scientific Publications* 4:87–126.
- LaBarbera, M., 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20:97–117.
- Laws, R., 1978. Monitoring whale and seal populations. In D. Nichols, ed., *Monitoring the Marine Environment*. Institute of Biology, London, pages 115–139.

- Lesage, V. and D. Doidge, 2005. Harvest statistics for beluga whales in Nunavik, 1974-2004. Technical report, Fisheries and Oceans Canada. URL <http://www.dfo-mpo.gc.ca/csas>.
- O'Corry-Crowe, G., R. Suydam, A. Rosenberg, K. Frost and A. Dizon, 1997. Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology* 6:955-970.
- Peters, R., H. Birks and E. Connor, 1983. The ecological implications of body size. Cambridge University Press.
- Richard, A., A. Martin and J. Orr, 2001. Summer and autumn movements of belugas of the Beaufort Sea stock. *Arctic* 54(3):223-236.
- Richard, P. and M. Baratin, 2005. Size and trend of the Cumberland Sound beluga population, 1990 to 1999. Technical report, Fisheries and Oceans Canada.
- Richard, P., J. Orr and D. Barber, 1990. The distribution and abundance of belugas, *Delphinapterus leucas*, in eastern Canadian subarctic waters: a review and update. In T. Smith, D. St. Aubin and J. Geraci, eds., *Advances in research on the beluga whale, Delphinapterus leucas*, volume 224. Canadian Bulletin of Fisheries and Aquatic Sciences, Ottawa, pages 23-38.
- Robson, D. and D. Chapman, 1961. Catch curves and mortality rates. *Transactions of the American Fisheries Society* 90:181-189.
- Scott, D., 1992. Multivariate density estimation. Wiley.
- Sergeant, D., 1959. Age determination of odontocete whales from dentinal growth layers. *Norsk Hvalfangst Tid* 6:273-288.
- Sergeant, D. and P. Brodie, 1969. Body size in white whales, *Delphinapterus leucas*. *Journal of the Fisheries Research Board of Canada* 26:2561-2580.
- Smith, A., 2004. Beluga whale summer use of Cumberland Sound estuaries, Baffin Island, Canada. Technical report, Fisheries and Oceans Canada.
- Stewart, R., 1994. Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. *Meddelelser om Grønland, Bioscience* 39:217-225.
- Suydam, R., L. Lowry, K. Frost, G. O'Corry-Crowe and D. Pikok, 2001. Satellite tracking of Eastern Chukchi Sea beluga whales into the Arctic Ocean. *Arctic* 54(3):237-243.
- Windsor, C., 1932. The Gompertz curve as a growth curve. *Proceedings of the National Academy of Sciences of the United States of America* 18(1):1-8.

Winship, A., A. Trites and D. Calkins, 2001. Growth in body size of the Steller sea lion (*Eumetopias jubatus*). *Journal of Mammalogy* 82(2):500–519.

Zar, J., 1996. *Biostatistical analysis*. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Appendices

A Classification of community catches into putative beluga populations

Table A.1. Number of belugas aged by the same reader, according to the community where the catch was made and population it belongs to.

Location	Putative population	N
Aklavik	EBS	25
East Whitefish	EBS	58
Hendrickson Island	EBS	195
Inuvik	EBS	141
Kendall Island	EBS	74
Paulatuk	EBS	36
Shingle Point	EBS	36
Tuktoyaktuk	EBS	54
West Whitefish	EBS	9
Arctic Bay	BB	10
Arviat	WHB	22
Cape Dorset	WHB	22
Chesterfield Inlet	WHB	10
Coral Harbour	WHB	69
Grise Fiord	BB	7
Iqaluit	WHB	86
Kimmirut	WHB	125
Pangnirtung	CS	144
Rankin Inlet	WHB	2
Repulse Bay	WHB	28
Resolute	BB	6
Taloyoak	BB	15
Whale Cove	WHB	10
Cott	EHB	1
GWR	EHB	5
Inujjuaq	EHB	2
Iqirasak	EHB	1
Iqirasaruq	EHB	1
Kuujjuaraapik	EHB	3
Little Whale River	EHB	25
Long Island	EHB	11
Nastapoka	EHB	136
Out-in-the-Bay	EHB	4
Patiqtuq	EHB	10
Pte Baleine Blanche	EHB	6
Richmond Gulf	EHB	4
Umiujaq	EHB	4
All		1397

B Determination of age class width for catch curve analyses

An age class width of 5 yr was determined by optimizing the representation of age classes, as class width was increased from 1 to 10 yr, with respect to the r^2 value of the fitted regression (Figure B.1). The resulting catch curve is shown in Figure B.2.

Appendix B. Determination of age class width for catch curve analyses

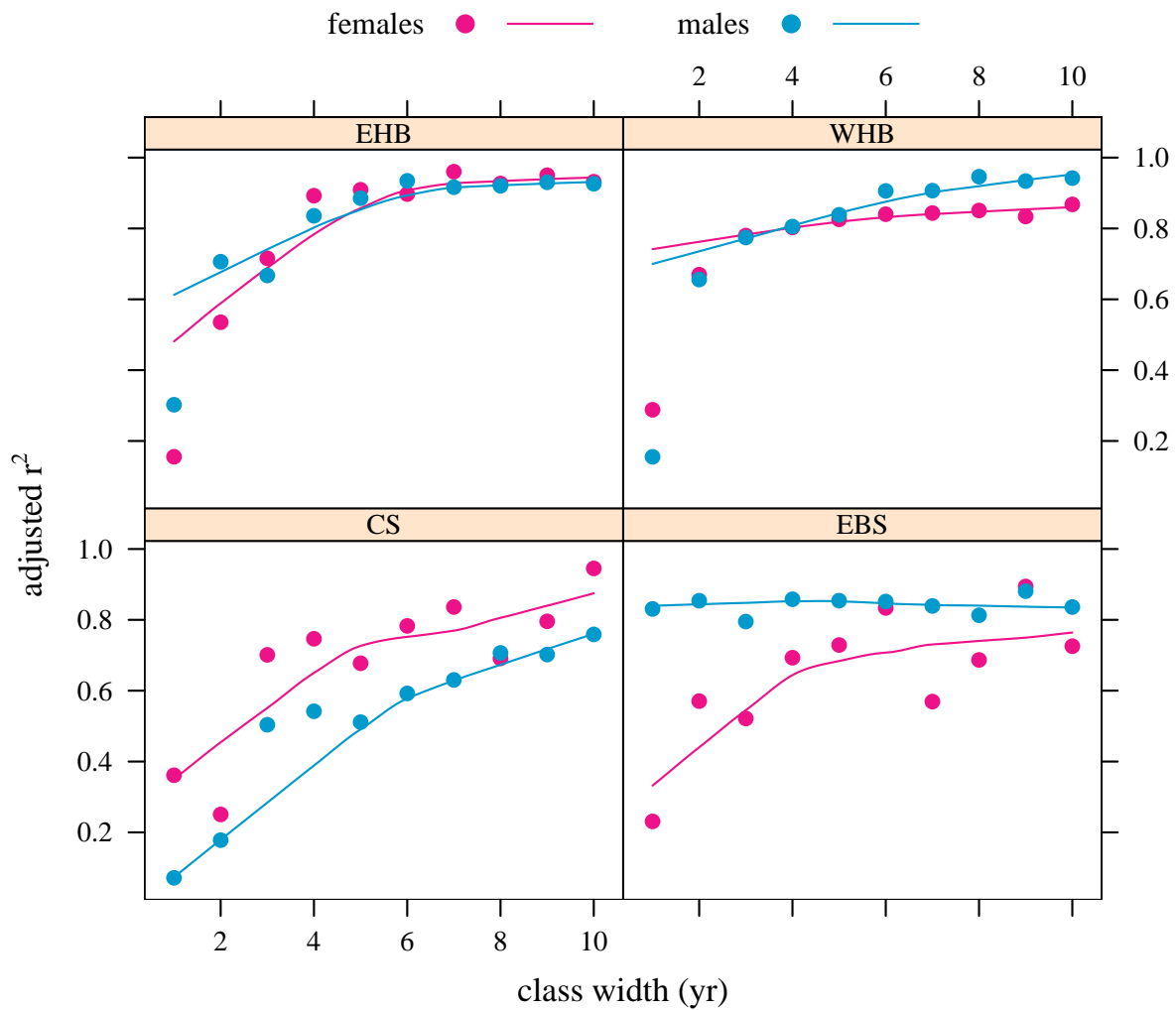


Figure B.1. Changes in r^2 of the regression of log transformed frequency on age class through the descending limb of catch curves, as age class width was increased from 1 to 10, at different beluga populations. The resulting curve from a local regression model (LOESS), used to detect the trend, is also shown.

Appendix B. Determination of age class width for catch curve analyses

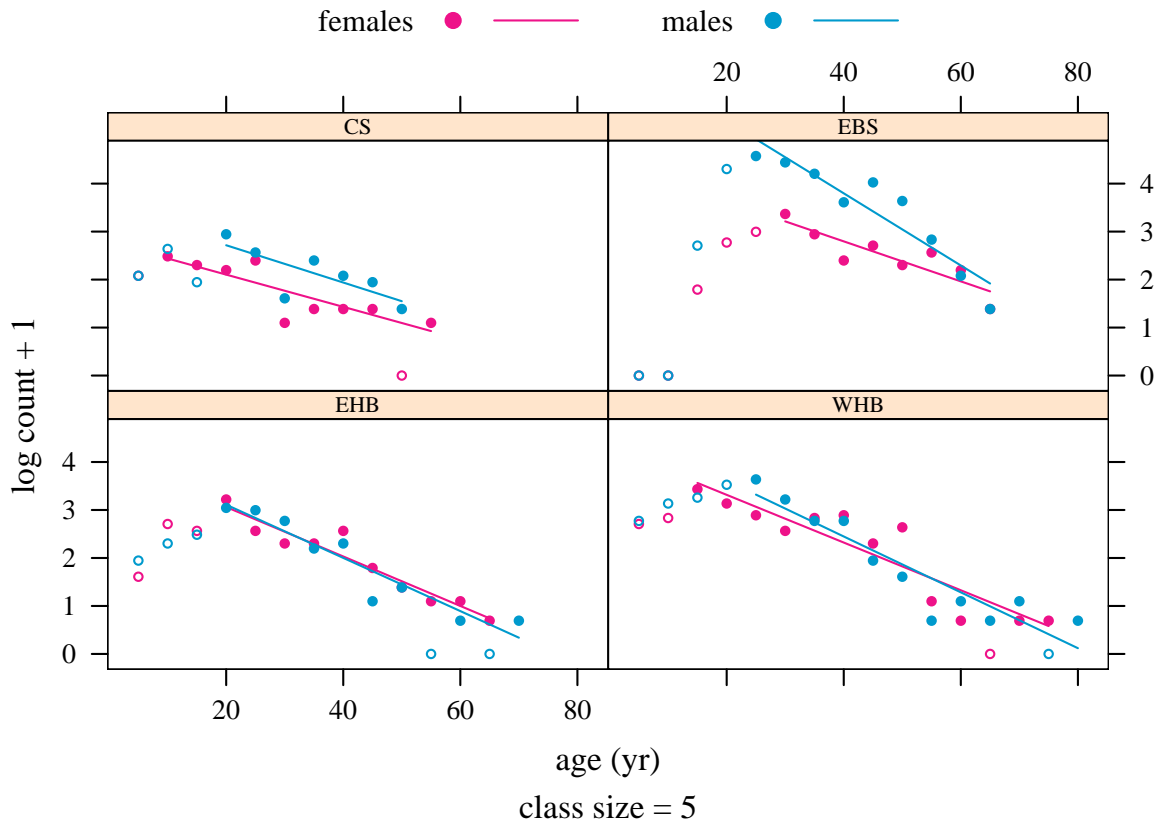


Figure B.2. Catch curves estimated for each beluga population, showing the points included in the estimation of the regression (filled circles), and those excluded (empty circles).