

# Age structure, growth, mortality, and density of belugas (*Delphinapterus leucas*) in the Canadian Arctic: responses to environment?

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**Abstract** Environmental constraints on life-history traits are expected to increase with seasonality in resources such as food and appropriate breeding habitat. Seasonality is highest at polar latitudes, where environmental constraints can be stronger than biotic factors, such as density and its effect on intraspecific competition. In this study, the age structure, body-length distribution, mortality, and density were studied and compared among five beluga populations of the Canadian Arctic: eastern Beaufort Sea (EBS), Baffin Bay (BB), Cumberland Sound (CS), western (WHB), and eastern Hudson (EHB) Bay, to test the prediction that density-dependent effects on these life-history traits should be inversely related to latitude. Growth, but not mortality, showed a significant positive relationship with latitude. Winter density also increased with winter latitude, consistent with the prediction of greater risk of mortality associated with density-independent effects, such as ice entrapment in winter. Age distributions differed among populations, with animals harvested at the highest-latitude population (EBS) being the oldest and attaining the longest adult body lengths, compared to lower-latitude populations (WHB and EHB). The latitudinal variation in growth, adult

body size, and winter density is congruent with the hypothesis that environmental seasonality may impose stronger constraints on life-history traits of beluga with increasing latitude.

**Keywords** Adaptation · Bergmann's rule · Conservation · Environmental forcing · Home range · Life history · Predictability · Seasonality

## Introduction

Polar and subpolar marine ecosystems display the world's largest seasonal variations and extremes in physical characteristics of the environment (Foster 1978; Valiela 1995). Thus, compared to ecosystems elsewhere, the physical environment imposes stronger constraints on life histories than biological factors (Pörtner 2002; Peck et al. 2006). Where the environment is such a strong force, life-history strategies are often viewed as adaptations to different degrees of seasonality and/or predictability of resources (Boyce 1979; Stearns 1981; Zammuto and Millar 1985; Stearns 1992; Ferguson and Larivière 2002), typically food. Indeed, growth and reproductive parameters covary closely with seasonality and "harshness" of climatic conditions across a broad range of species (e.g. Trites and Antonelis 1994; Sand 1996; Ferguson and Higdon 2006; Hadley et al. 2007). Numerous studies suggest that environmental variation also plays a major role in shaping major life-history traits at the intraspecific level (Fowler 1981; Ferguson and McLoughlin 2000; Gaillard et al. 2000; De Roos and Persson 2002). However, fewer studies testing whether the relationship holds among populations of arctic marine mammals are available (Stirling and Lunn 1997; Ferguson et al. 2005), notwithstanding their

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importance for implementing adequate management and conservation measures under expected climate change (Laidre et al. 2008).

Belugas (*Delphinapterus leucas*, Pallas 1776) are an interesting model species for understanding how environmental variation may have affected the evolution of major life-history traits at the population level. They have a nearly circumpolar distribution with two major populations in the North American Arctic (O’Corry-Crowe et al. 1997; Brown Gladden et al. 1999) and a complex stock structure (Reeves et al. 1994; Innes et al. 2002a; de March and Postma 2003; Brennin et al. 1997). They are found from 47°N to about 78°N and across all longitudes in Canadian waters (Richard et al. 1988); a range where oceanographic characteristics, ice conditions, and biodiversity, may differ considerably in terms of predictability and seasonality (Grebmeier et al. 2006; Michel et al. 2006). They inhabit shallow estuarine areas in spring and summer for reproducing, and may traverse deep oceanic areas during their fall migration to wintering areas where, for at least some populations, feeding is thought to be concentrated (Smith and Martin 1994; Richard et al. 1997, 2001a). However, comparisons of age structure and growth among purported beluga populations have been limited in geographical scope to test predictions about the influence of environmental factors and density (Doidge 1990; Stewart 1994; Harwood et al. 2002). A comprehensive comparison is needed, considering that two of the Canadian stocks (eastern Hudson Bay and Ungava Bay) are classified as “endangered”, two (St. Lawrence estuary and Cumberland Sound) as “threatened”, and two (western Hudson Bay and eastern High Arctic-Baffin Bay) as of “special concern”; i.e., six out of eight stocks have at least a “special concern” status according to the most recent report of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004a).

In Canada, belugas are hunted by Inuit throughout the majority of their range, and there is considerable variation in the composition of the harvest, in terms of the age and sex of animals. For example, the median age<sup>1</sup> of animals harvested in the Mackenzie River delta during the early 1990s was approximately 24 for both males and females, while males were about twice as numerous as females (Harwood et al. 2002). In contrast, the median age of belugas harvested in eastern Hudson Bay was reported at 8.5 years during approximately the same time period, although significant reductions in age were observed in the entire Nunavik region, compared to animals harvested in the 80s (Lesage and Doidge 2005). Compared with eastern Beaufort Sea belugas, eastern Hudson Bay beluga

abundance may have been negatively affected by past 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 harvests, relative to years prior to peak harvests (Hammill et al. 2005).

Although some patterns have emerged when comparing growth of belugas harvested at various eastern Arctic communities, no comprehensive analysis has been done to tease apart the factors that generated them. Previous studies suggest that belugas from eastern Hudson Bay tend to be smaller than those from most other eastern High Arctic locations (Doidge 1990). 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 among 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). As with most life-history traits, observed growth rates are a trade-off between conflicting demands, mediated by the environment: large adult body size tends to increase reproductive success in many populations, but fast growth may be associated with greater risk of juvenile mortality due to reduced ability to survive during periods of poor feeding conditions (Case 1978; Arendt 1997). Therefore, the observed pattern leads to the question: are differences in intraspecific life-history traits related to differences in environments?

Here we compare the growth, mortality, age and sex structure, and density of beluga populations in the Canadian Arctic. We used density, calculated from the best available estimates of abundance and areas where belugas concentrate their activity, to test the prediction that density-dependent effects on mortality and growth should decrease with increasing latitude. Beluga mortality and growth in populations at higher latitudes should be more strongly affected by density-independent effects due to abiotic factors. Assuming that hunter selectivity is similar across populations, the spatial and temporal coverage of this analysis can help identify common mechanisms controlling the response of beluga to differences in environmental influences that are relevant to conservation.

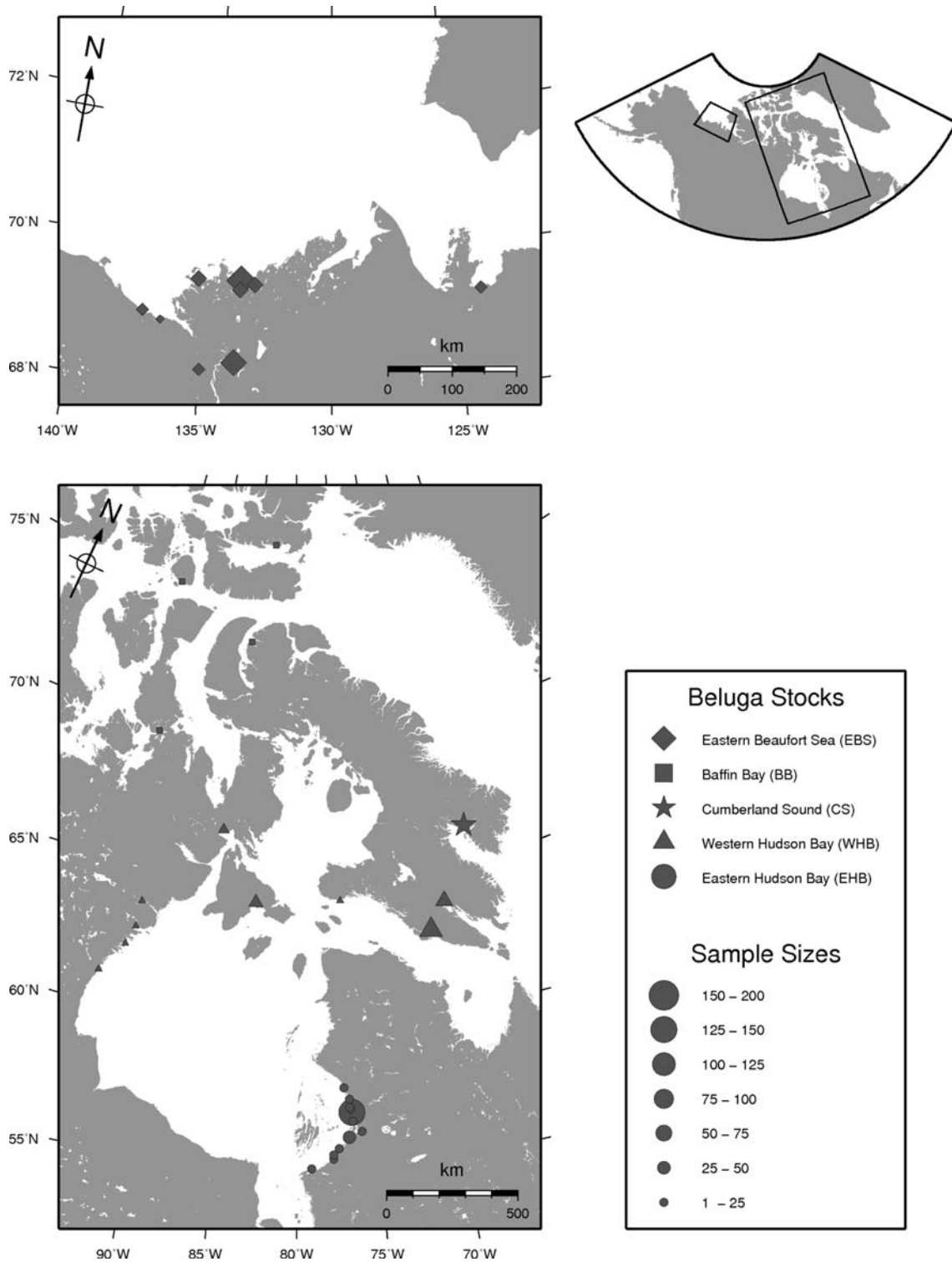
## Materials and methods

Morphometric and age data have been maintained by the Fisheries Joint Management Committee (FJMC) and the Department of Fisheries and Oceans (DFO), in collaboration with hunters and members of local Inuit

<sup>1</sup> Values follow the assumption that two dentinal growth layer groups are deposited per year, following the corresponding references.

communities, over almost three decades. The whales were hunted during subsistence harvests carried out annually throughout arctic communities (Fig. 1). Data were examined for accuracy in the sex of individuals (de March and Postma 2003).

We used data with the most extensive morphometric data and matching age estimates, which included data from five of the eight stocks recognized in Canada. Collections of subsistence harvests were approved under Fisheries and Oceans Canada licenses to fish for scientific purposes.



**Fig. 1** Location of communities where belugas were harvested for local subsistence and corresponding populations

## Putative beluga populations

Eastern Beaufort Sea belugas are relatively isolated from individuals in the eastern Canadian Arctic (O’Corry-Crowe et al. 1997; Brown Gladden et al. 1999). Information on the population structure of eastern Canadian Arctic belugas is less clear (Koski et al. 2002; Richard et al. 1990; Stewart 1994; O’Corry-Crowe et al. 1997; Innes et al. 2002a), but allows the definition of four relatively discrete areas that represent different groups of belugas forming separate management units, or stocks (Fig. 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’ harvests is consistent with available information of spatio-temporal movements of belugas in these regions (Smith and Martin 1994; Richard et al. 1998, 2001a, b; Suydam et al. 2001; Koski et al. 2002).

Samples were collected between 1993 and 2004, except for CS and WHB, where collection started in 1991 and 1989, respectively.

## Aging

Details of the process of age determination for the samples analyzed here have been described previously (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 mounting it onto wooden blocks for longitudinal sectioning and counting of growth layer groups. Evidence from radiocarbon marking (Stewart et al. 2007), aquarium-raised individuals (Robeck et al. 2005), and life-history relationships (Luque et al. 2007) lend support to the hypothesis of one dentinal growth layer group (GLG) being deposited annually in beluga. Therefore, ages were assigned to animals using one GLG per annum (i.e. age equals the GLG count for any given individual) in the present study. All dentine counts were performed by one reader (Barbara Stewart, Sila Consultants, Howden, Manitoba, Canada) for samples collected after 1993, except for a few individuals, but by different readers for samples collected previously. Therefore, only samples collected after 1993 by the single reader were used in all subsequent analyses, resulting in a sample of 1,397 belugas for five populations (Table 1).

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 may obscure the underlying distribution, including small numbers of frequency classes. To test for differences

**Table 1** Number of known age belugas harvested from five beluga populations (yearly mean catch) for which GLG counts were available from the same reader

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)
WHB	171 (17.1)	203 (20.3)
EHB	109 (7.8)	104 (7.4)
All	502 (22.8)	895 (40.7)

among 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.

## Morphometry and growth

Morphometric measurements, including body mass, standard length, and girth were obtained from the 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 1983; LaBarbera 1989), we used standard length as an index of body size for belugas in this study.

To compare growth of individuals between populations and sexes, a Gompertz model was used:

$$l_t = A \cdot e^{-b \cdot e^{-kx}} \quad (1)$$

where  $l_t$  represents length at age  $t$ ,  $A$  represents asymptotic length,  $k$  represents the rate of exponential growth decay,  $b$  is a constant describing initial growth (Windsor 1932; Winship et al. 2001), and  $x$  is observed age. This model and an alternative von Bertalanffy model provided indistinguishable results, whereas a linear model on the semi-log transformed relationship did not accurately describe the growth data, as linearity assumptions were violated (Zar 1996). For comparison with previously published reports, the Gompertz model was chosen to describe growth.

Nonlinear mixed effects models (mixed models, hereinafter) were used to allow growth parameters to vary randomly among populations and sexes while accounting for any fixed effects between these factors (Pinheiro and Bates 2000). A stepwise procedure was used to select the best model describing growth and the influence of population and sex on growth parameters. We began model building with the most general model, where all Gompertz growth parameters were allowed to vary randomly between population and sex combinations, without considering any

fixed effect for both factors. In this case, a single coefficient for each parameter was estimated (the intercept). Random effect terms showing strong correlation were selected for removal based on their coefficient of variation. Fixed effects terms and their interactions were subsequently added based on the relationship between random effects and the corresponding factors (population and sex), testing the significance of terms using Wald tests. Models were compared using Akaike Information Criterion (AIC) without correcting for small sample bias because samples were not small enough to make a difference. We used the GNU R package `nlme` to fit and compare models via maximum likelihood techniques (Pinheiro et al. 2004), allowing for heteroscedasticity in residual variance. We assessed the statistical significance of terms in the models using Wald tests.

#### Adult mortality

Mortality was estimated using the methods outlined by Chapman and Robson (1960) and 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 (frequency >0) was performed by increasing class width from 1 to 10 years and plotting the frequency against the corresponding age classes. Analysis of covariance (ANCOVA) was subsequently used to test for parallelism of regression lines among populations (Zar 1996).

#### Determination of density

Belugas were instrumented with ARGOS Platform Transmitter Terminals (PTTs) to determine their at-sea position and movements, following methods described in Orr et al. (2001). Data were collected from July through April, during 1998–1999 for CS ( $n = 13$ ), and 2002–2005 for EBS ( $n = 13$ ) and eastern Arctic populations (WHB:  $n = 27$ , EHB:  $n = 11$ ) (Pierre Richard, pers. comm., except EHB: Hammill, pers. comm.). Individual tracks were filtered using a three-stage algorithm designed to eliminate locations that are likely to be erroneous, based on the animals' speed and distance between successive locations (Austin et al. 2003). Any remaining land locations were eliminated, as they were obviously erroneous, although the filtering process could not detect them as such. A regular time series of each beluga track thus filtered was created by

interpolating locations through an equal time interval of 1 h, assuming straight-line travel between successive locations. The interpolated tracks were subsequently projected to an Albers Equal Area coordinate system with local central meridians and standard parallels chosen using the “one-sixth rule” (Snyder 1987).

The projected data were used to build a spatial raster composed of  $2 \times 2$  km cells with the time spent per unit area ( $\text{h}/\text{km}^2$ ) (BirdLife International 2003; Bradshaw et al. 2003; Terauds et al. 2005) by belugas from each population; i.e., a separate raster for each population, weighting each cell of the raster by the number of individuals. Because belugas travel long distances between their summering and wintering areas (Richard et al. 2001a, b), when density-independent effects may be strongest, separate rasters were also built for winter (January–March, inclusive). The bandwidth for the kernel density estimator was set to 15 km for all rasters, which is approximately the average error of ARGOS satellite locations (Vincent et al. 2002), to allow comparisons among the populations.

Areas of core use by belugas were defined as those areas of the rasters where time spent per unit area was larger than or equal to the 0.95 quantile of the distribution and area ( $\text{km}^2$ ) within those contours, minus any land area. The weighted average latitude of these contours was interpreted as the latitude at which belugas concentrated their activity.

Beluga abundance estimates were obtained from published aerial survey results (Harwood et al. 1996; Hammill et al. 2005; DFO 2005; Richard 2005). Because the EBS abundance estimate did not include corrections for diving animals, we multiplied the estimate by 2, following corrections used in reports for the other populations. Density was, thus, calculated by dividing the population size estimate by area.

## Results

### Age structure

Male median age ranged from 15 for BB to 29 years for EBS animals, while it ranged from 17 for CS to 31 years for EBS females. Maximum ages were found in the WHB samples with values of 77 years for males, and 74 years for females. Within each population, there were no age differences between males and females. Despite the extensive overlap in the distributions, there were significant differences in median ages among populations (Kruskal–Wallis test  $\chi^2_3 = 75.53; 67.74, P < 0.01$  both), due to EBS animals being significantly older than those from CS and WHB (Behrens-Fisher test,  $P < 0.01$ , both males and females).

The kernel-smoothed age distributions were not homogenous 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 years of age (Fig. 2), except for BB males whose most abundant age frequency was 10 years. A second, much weaker, “peak” was observed for EBS males, which probably explains their significantly older median age, at about 45 years of age. Males from other populations also displayed this second increase in frequencies, but they were much more tenuous and occurred at ages ranging from 37 to 40 years. Compared to males, variability among distribution shapes was considerably larger for 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 years (CS), to 18 years (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 years (EHB), to a maximum of 54 years (EBS).

## Growth

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 (Eq. 1). Seven

different mixed models were built to select the most parsimonious model of growth of belugas. Analysis of the first model revealed that random effects for parameters  $b$  and  $k$  were strongly correlated, so the random effect for  $b$  was removed, based on its low coefficient of variation and the lack of data from young whales in some populations. Interactions between fixed effects for population and sex were not significant in any of the models (Wald test  $P > 0.05$ , all models), and the most parsimonious model consisted of additive fixed effects for population and sex with respect to both  $A$  and  $k$ . However, a random-effect term was necessary for  $A$  (Table 2). Therefore, growth differed significantly between sexes and populations only with respect to parameters  $A$  and  $k$  (Table 3).

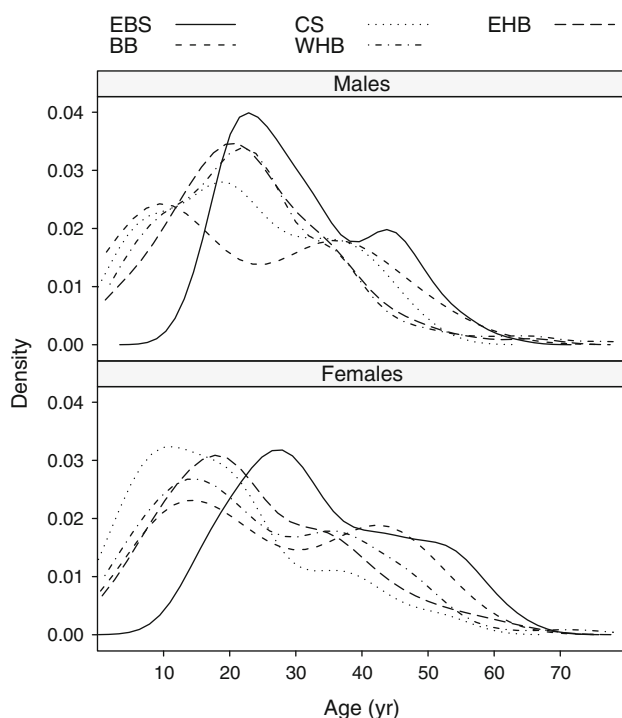
The selected model adequately described growth for each population and sex (Figure 1, supplementary material). Asymptotic length, estimated from the best model, showed large differences among populations, ranging from 392 (EHB) to 441 cm (CS) for males (Fig. 3). Asymptotic length of females varied from 338 (EHB) to 387 cm (CS) (Table 3). Similarly, the growth constant ( $k$ ) ranged from 0.06 (EHB) to 0.11 (EBS) for males, and from 0.13 (EHB) to 0.18 (EBS) for females (Fig. 3). Given that no interactions were found for the Gompertz growth parameters, the population average equations were as follows:  $407.5 \cdot e^{-0.62 \cdot e^{0.14 \cdot x}}$  (EBS),  $413.9 \cdot e^{-0.62 \cdot e^{0.13 \cdot x}}$  (CS),  $385.7 \cdot e^{-0.62 \cdot e^{0.12 \cdot x}}$  (WHB),  $364.9 \cdot e^{-0.62 \cdot e^{0.10 \cdot x}}$  (EHB).

## Adult mortality

A class width of 5 years was deemed optimal for defining the catch curves (Fig. 4a). Variation in estimates of mortality, derived from these curves, among beluga populations was relatively small (Fig. 4b). Confidence intervals around CS male mortality estimates were particularly large. Mortality estimates ranged from 4% (CS) to 8% (EBS) for males, and from 3% (CS) to 5% (EHB and WHB) for females. However, there was a large overlap in confidence intervals around each estimate, and an ANCOVA showed that differences were not significant ( $P > 0.2$  males and females, Fig. 4a).

## Relationships with density and latitude

There were large differences between the summer–winter and winter distributions of belugas for all populations. The smallest areas of core use were found for CS and the largest for EBS animals during the entire period they were tracked, but these areas were drastically reduced during the winter (Fig. 5). The corresponding summer–winter density estimates (Table 4) did not show any significant relationship with summer–winter latitude (Pearson product-moment correlation,  $t = 0.25$ ,  $P > 0.1$ ). However, winter density



**Fig. 2** Smoothed age distribution of belugas had a strong and a weak peak for all populations, with the latter being at higher ages for EBS

**Table 2** Summary of stepwise procedure for selection of most parsimonious mixed effects model of Gompertz growth (Eq. 1) parameters and their variation among sexes and four beluga populations of the Canadian Arctic

$A^a$	$b^a$	$k^a$	Log-likelihood	AIC	$\delta AIC$
1 + $u_1$	1 + $u_2$	1 + $u_3$	10,335	5,157	0
1 + $u_1$	1	1 + $u_3$	10,333	5,158	-1
1 + population + sex + $u_1$	1	1 + $u_3$	10,308	5,142	-16
1 + population + sex + $u_1$	1	1	10,323	5,151	9
1 + population + sex + $u_1$	1	1 + population $\times$ sex + $u_3$	10,292	5,127	-24
1 + population + sex + $u_1$	1	1 + population + sex + $u_3$	10,289	5,128	1
1 + population + sex + $u_1$	1	1 + population + sex	10,285	5,128	0

<sup>a</sup> Models describe each growth parameter by an intercept (1), and predictors for changes in population and sex of each whale, plus a random component ( $u$ ) for each parameter. The intercept corresponds to the average for all populations and sexes if no fixed effects are included, else to a baseline population (EBS) and sex (female). + indicates additive effects, and  $\times$  indicates additive effects plus interaction

**Table 3** Estimated parameters from best AIC-ranked mixed model (Table 2) for variation in growth (Eq. 1) among sexes and four beluga populations of the Canadian Arctic

Parameter <sup>a</sup>	Estimate	SE	t-value	P-value
A: intercept	380.4	2.951	128.90	< 0.01
A: CS	6.3	5.605	1.13	0.26
A: WHB	-21.8	4.083	-5.34	< 0.01
A: EHB	-42.6	5.811	-7.34	< 0.01
A: Male	54.2	3.446	15.74	< 0.01
k: intercept	0.18	0.014	13.02	< 0.01
k: CS	-0.01	0.011	-0.92	0.36
k: WHB	-0.02	0.008	-2.78	< 0.01
k: EHB	-0.05	0.009	-5.11	< 0.01
k: Male	-0.07	0.012	-5.69	< 0.01
b	0.62	0.035	17.69	< 0.01

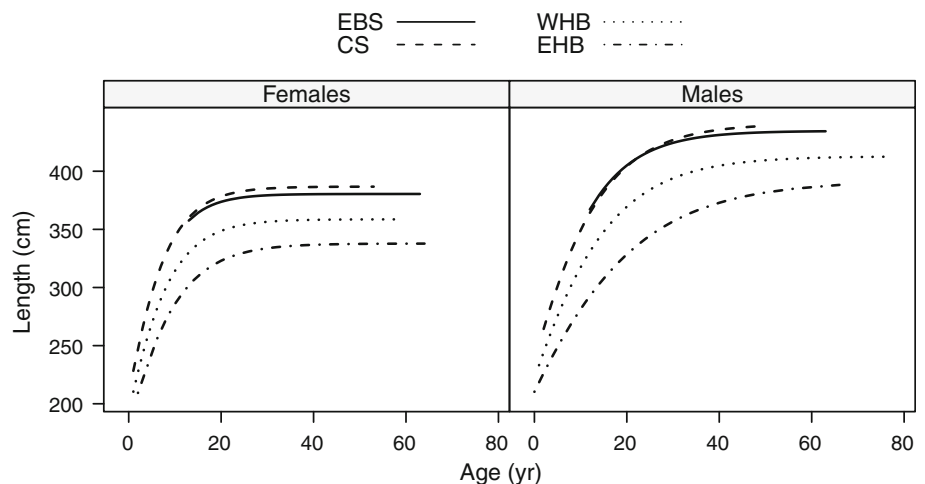
<sup>a</sup> Intercept represents baseline population (EBS) and sex (female), and the other population or sex indicators represent differences between them and the baseline level. For example, “A: CS” represents the difference:  $A_{CS, female} - A_{EBS, female}$

was positively related to winter latitude (Fig. 6a). Mortality was not significantly related to density in males nor females, regardless of study period ( $P > 0.05$ , summer-winter and winter). Similarly, neither mortality nor  $A$  or  $k$  showed any relationship with density ( $P > 0.05$ , summer-winter and winter). Asymptotic length ( $A$ ) and growth decay constant ( $k$ ) were positively related to latitude (Fig. 6b), although the relationship was significant only for  $k$  during summer-winter ( $t = 5.04$ ,  $P = 0.03$ ).

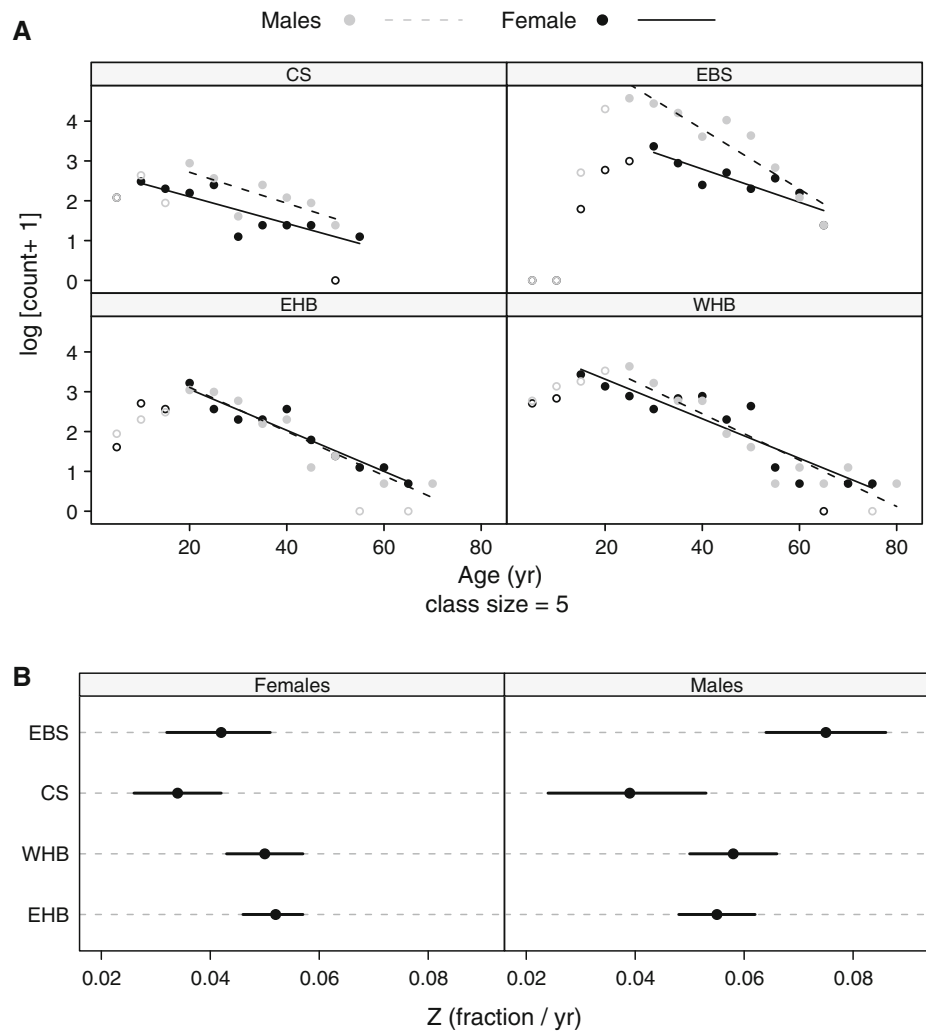
**Discussion**

The central question that this study aimed to answer was whether density-dependent effects on mortality and growth decreased with latitude. This expectation was based on the observation that seasonality and environmental extremes increase with latitude, and evidence that abiotic factors may be a stronger force affecting mortality and growth at high latitudes. Our main findings were that (1) growth, as

**Fig. 3** Beluga growth curves differed significantly among populations, with the largest asymptotic lengths found in EBS and CS belugas, while the smallest were found in EHB animals, irrespective of sex. See Tables 2 and 3 for fitted model and effects. Curves are limited to the range of ages in each population



**Fig. 4** Beluga catch curves (a) were best described using an age class width of 5 years to estimate mortality ( $Z \pm SE$ ) in relation to population of origin (b)

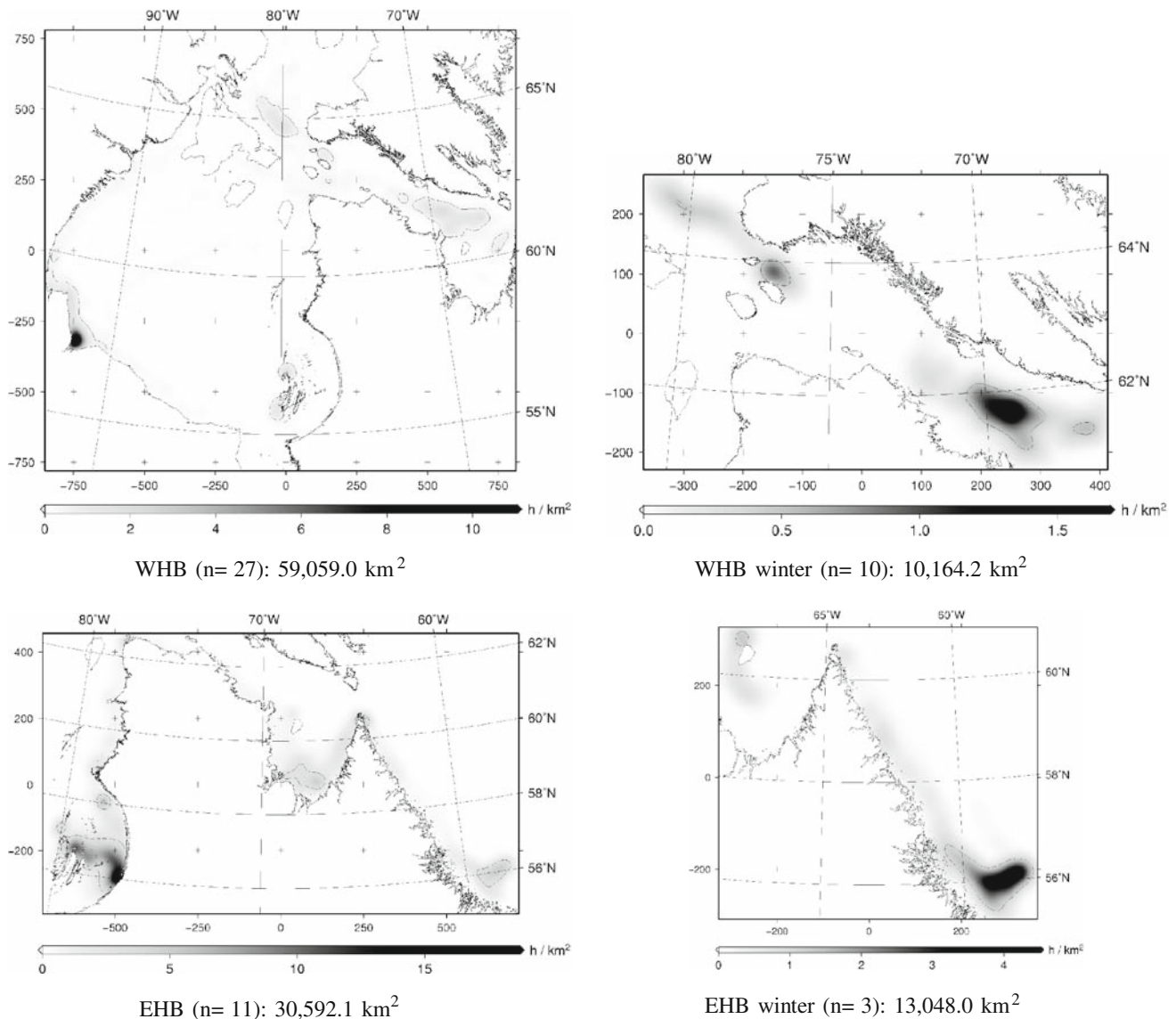


measured by asymptotic length, was related to latitude, but not in a predictable density-dependent fashion, (2) winter density increased with latitude, and (3) mortality was related neither to latitude nor to density. However, before concentrating on the significance of these main findings, a consideration of our comparisons of beluga age structure and body size is needed to adequately interpret them.

Compared with previous reports, the age distribution of the beluga harvests 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 years for females and males, respectively, using two GLGs per annum to obtain those estimates. This would correspond to 47 and 48 years using our assumption of one GLG per annum in our study, whereas we found median ages of 31 and 29 years for females and males, respectively. Although the data from our study include those in Harwood et al. (2002), the temporal coverage of the harvests, and hence sample sizes, are different. Eastern Beaufort beluga age information available to Harwood

et al. (2002) was restricted to animals harvested between 1988 and 1994, whereas those used in our study were harvested between 1993 and 2003. However, such large differences (16 and 19 years) would not be expected from the currently available data. An additional explanation is that different readers affected age estimates and variability. Age estimates for animals harvested prior to 1993 were performed by readers who systematically overestimated median age by about 10 years, compared to the reader who aged beluga teeth more recently (this study). 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



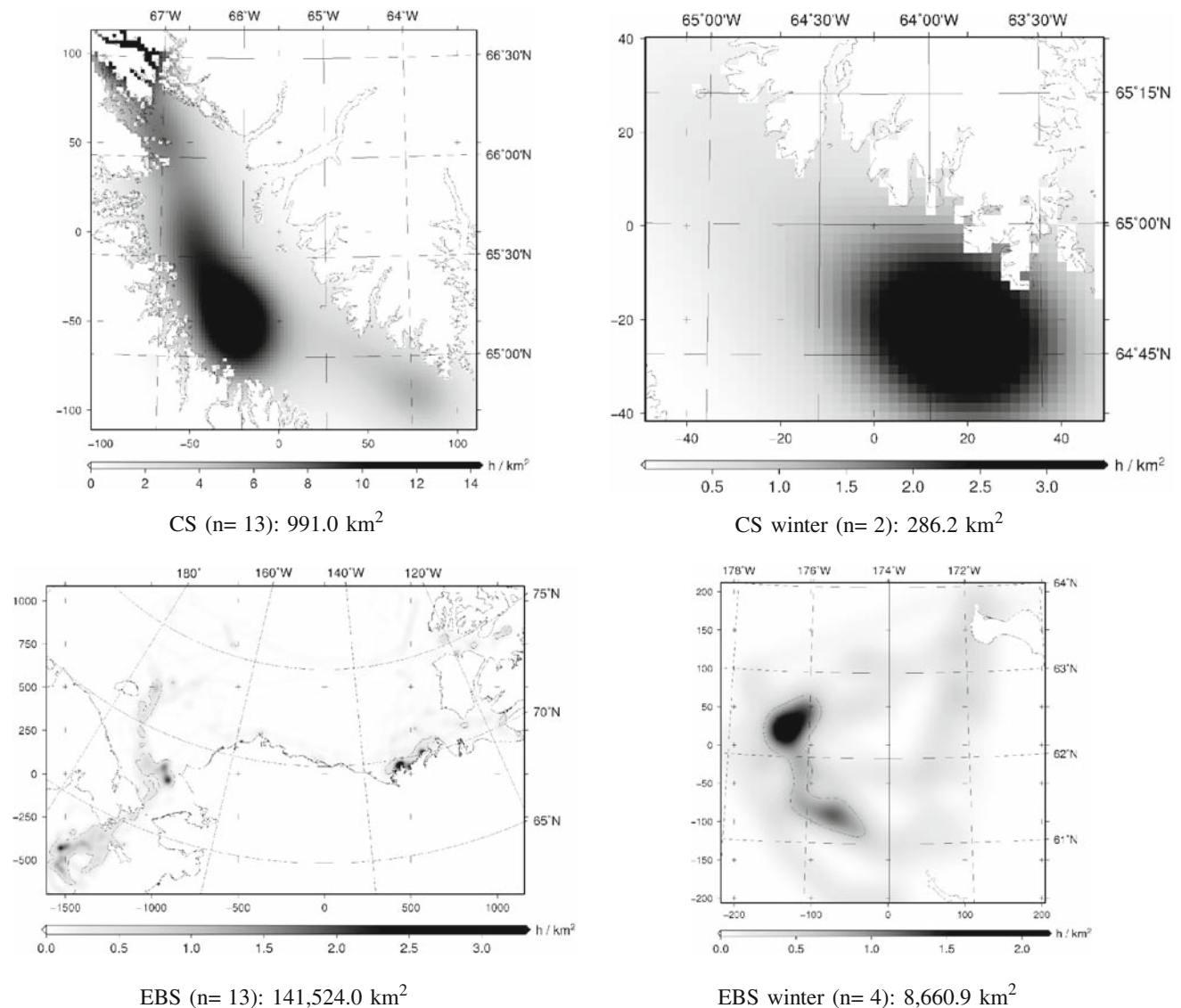
**Fig. 5** Areas of core use (km<sup>2</sup>) by belugas, as determined by satellite ARGOS telemetry, showed that winter distributions (*right panels*) were reduced during winter, compared to pooled summer–winter

distributions (*left panels*). *Top/right* axes show geographical coordinates, and *left/bottom* axes show projected units (km). *n* indicates the number of individuals tracked for each population/period

less abundant. The troughs may indicate an unusually large number of individuals that were not available to reproduce during a particular period. Reductions in adult survival have been associated with increased hunting pressure in sperm whales (*Physeter catodon*, Linnaeus 1758, 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). The median birth year of animals corresponding to these troughs was 1960, 1964, 1963, and 1954, for EBS, CS, WHB, and EHB, respectively. Comparing these birth years with available historical harvest records (Strong 1989; Lesage et al. 2001; Harwood et al. 2002; Lesage

and Doidge 2005) suggests that hunting pressure may have played a role in EBS and CS, but not in WHB, whereas insufficient data preclude any assessment for EHB (Fig. 7).

The age structures of populations considered in this study indicate that belugas harvested in EBS are older than those harvested in the eastern Arctic. Not only was the median age of belugas in the EBS population significantly older, but also animals older than this age were being harvested with higher probability in this population than in others. If the harvests accurately reflect available beluga populations, then these results are consistent with the suggestion that EBS belugas are under lower hunting pressure than those in eastern Arctic populations, as the



**Fig. 5** continued

relative abundance of old individuals in a population is considered to be 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). Furthermore, survivorship and growth of this population have not shown effects of previous large-scale ecosystem regime shifts in the North Pacific (Luque and Ferguson 2009).

The age structure, body size, 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 80s, when hunting became more regulated (Lesage and Doidge 2005; Hammill et al. 2005).

The EHB population is thought to be declining since the late 80s from 4,200 in 1985 to 3,100 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 estimated in 1999 (Richard and Baratin 2005). Hunting pressure has increased during the mid 90s at EHB, associated with the highest estimated rates of decline for this population. Conversely, hunting pressure at CS has remained relatively low and constant (COSEWIC 2004b). 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. Given that

**Table 4** Population density estimates did not vary with latitude for four beluga populations of the Canadian Arctic

Population	Abundance (95% CI)	Summer–winter latitude	Winter latitude	Summer–winter density (belugas/km <sup>2</sup> )	Winter density (belugas/km <sup>2</sup> )
EBS	39,258 (30,268–48,250) <sup>a</sup>	69.91	61.86	0.28	4.53
CS	2,018 (1,553–2,623) <sup>b</sup>	65.24	64.80	2.04	7.05
WHB	57,300 (37,700–87,100) <sup>c</sup>	61.25	62.39	0.97	5.64
EHB	3,100 (1,532–4,668) <sup>d</sup>	57.88	56.81	0.10	0.24

<sup>a</sup> Harwood et al. (1996). Original estimate was multiplied by 2, to correct for diving belugas

<sup>b</sup> DFO (2005)

<sup>c</sup> Richard (2005)

<sup>d</sup> Hammill et al. (2005)

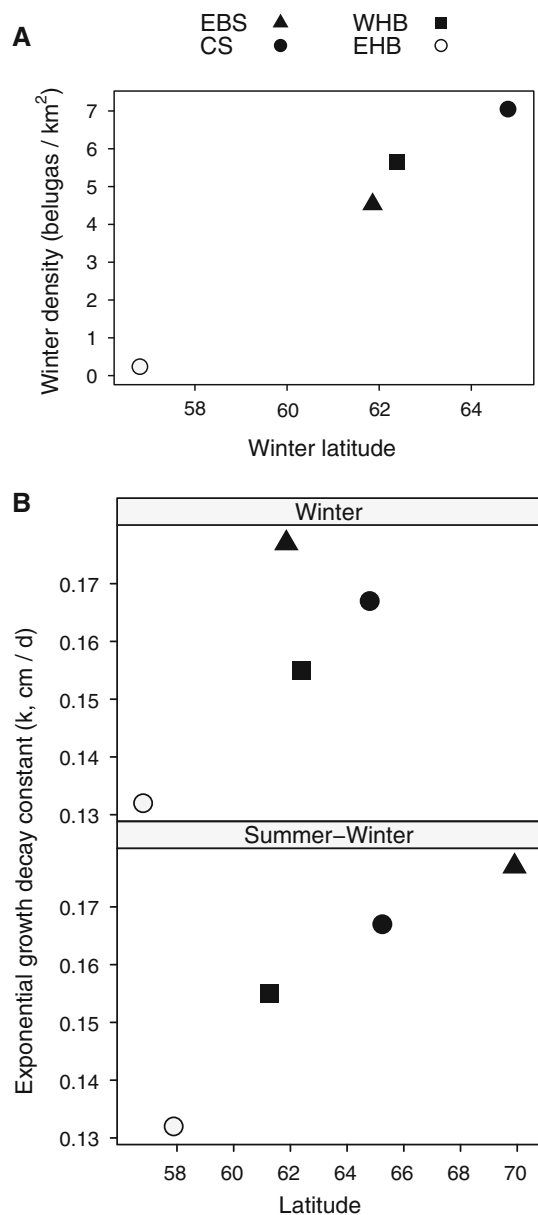
hunting pressure and body size are similar for EBS and CS belugas, why does the former show relatively large adult mortality? One explanation is that with more constant hunting pressure over time, the EBS population has retained the natural age structure associated with evolutionary adaptations to their high-latitude variable environment. Predicted adaptations would include longer life span (Philippi and Seger 1989) and variation in adult mortality associated with unpredictable environmental events such as density-independent ice entrapment.

We hypothesized that growth and mortality should show weaker density dependence in high-latitude populations, but we found that both life-history traits were unrelated to density along a latitudinal gradient. The small number of populations (5) for comparisons may have reduced the power to discern patterns in the density estimates, making it difficult to assess density relationship to growth and mortality. Differences in tooth wear may also have contributed to imprecision in our mortality estimates (Heide-Jørgensen and Lockyer 2001), although growth curves suggest that old whales were sufficiently represented in all populations to properly construct catch curves. Moreover, we were unable to separate hunting from natural mortality with the available data, so our comparisons of this variable may have been biased by different hunting selectivity among populations. Nonetheless, the relatively large spatial scale of our analyses, which included a 10-degree range in latitude, should have minimized these potential biases.

A basic premise of our hypothesis is that seasonality and environmental extremes increase with latitude. Density was significantly related to latitude, when estimated for winter, when their ranges become reduced and belugas may be more susceptible to ice entrapment (Heide-Jørgensen et al. 2002). The summer–winter areas of core use by belugas were different and larger than winter areas for all populations, reflecting seasonal movement patterns (Richard et al. 1990, 1997, 1998, 2001a; Innes et al. 2002b). In the case of the high-latitude populations (CS and EBS), summer to

winter migration involved a net southward movement, while the opposite or little change in latitude between seasons was observed for the Hudson Bay populations. Hudson Bay freezes completely over in winter (Saucier et al. 2004; Michel et al. 2006), so it is not surprising that belugas move to areas outside the bay, and hence avoid heavy and dangerous ice concentrations that may lead to ice entrapment (Harwood and Smith 2002; Heide-Jørgensen et al. 2002). This may explain why the relationship between winter density and latitude did not reflect the relationship between asymptotic length and latitude. However, our comparisons for winter are based on small numbers of satellite-tracked individuals (Fig. 5), so these results should be interpreted with caution. Latitude was used as a proxy for environmental seasonality in this study, but direct indices may need to be developed to evaluate the influence of this factor on the strength of density-dependent effects on life-history traits.

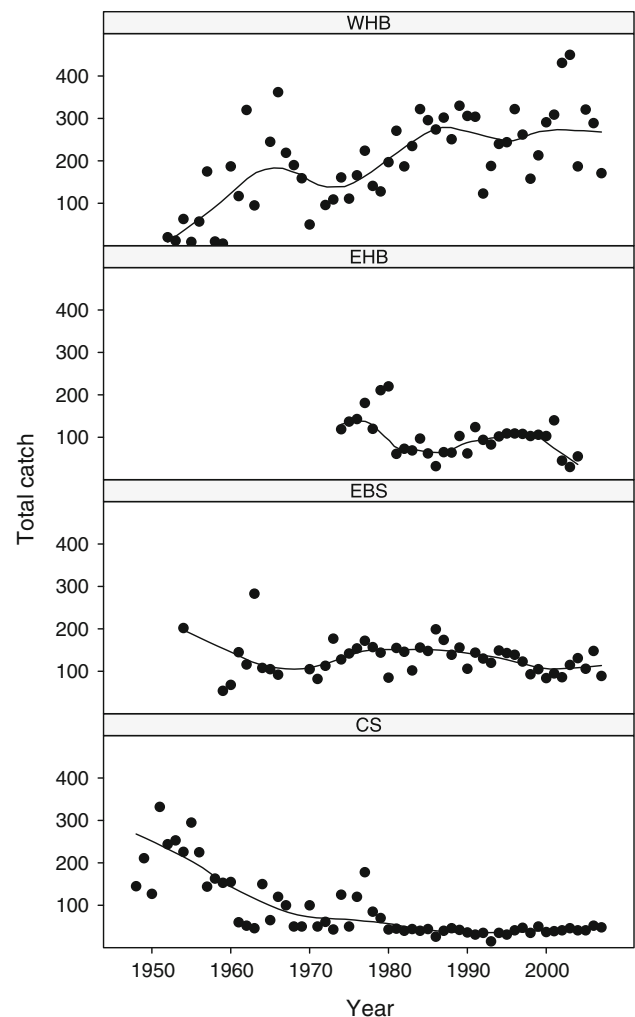
Larger body size confers mammals greater fat storage capabilities (Lockyer et al. 1987; Costa 1993; Costa and Williams 1999), in addition to better thermal insulation properties (Schmidt-Nielsen 1972, 1984; Peters 1983), which are expected to be beneficial in cold and strongly seasonal high-latitude environments. The geographical gradient whereby beluga asymptotic body length increased in a south to north direction has not been previously reported (Doidge 1990; Stewart 1994), and is consistent with this argument. Belugas from EHB had smaller asymptotic lengths than those from WHB, which in turn were smaller than those of belugas from CS or EBS. This gradient was unexpected, based on the comparisons of age distributions, but was in agreement with variation in growth among populations. This result is suggestive of Bergmann's rule (Mayr 1956), the increase in body size with latitude observed in many organisms (Meiri and Thomas 2007; Meiri and Dayan 2003), which is usually explained as a thermoregulatory adaptation to lower temperatures at higher latitudes/altitudes. Although the



**Fig. 6** Winter density was significantly related to winter latitude (a, Pearson product-moment correlation:  $t = 13.16$ ,  $P < 0.01$ ). The growth decay constant ( $k$ , Eq. 1) was positively related to latitude in four beluga populations only during summer–winter (b, Pearson product-moment correlation:  $t = 5.04$ ,  $P = 0.03$ ).

explanation for Bergmann's rule has been repeatedly criticized (Scholander 1956; McNab 1971; Geist 1988) due to its inability to predict body size with ambient temperature both intra- and interspecifically, the rule holds for birds and some mammals (Ashton et al. 2000; Ashton 2002; Meiri and Dayan 2003), especially in the largest species inhabiting very cold environments, and may be explained by environmental predictability (Ferguson and Larivière 2008).

Alternatively, or in combination with this explanation, the pattern may reflect different responses of belugas to



**Fig. 7** Catch history record from aggregated figures belonging to four beluga populations from 1948 to 2007. A locally weighted smoothing line was fit to data from each population, showing that the number of belugas harvested has remained relatively stable during the past 30 years for all populations, although reductions are evident for EHB and high interannual variation occurs for WHB

changes in hunting pressure relative to population size. The four study populations have been subject to past commercial and subsistence harvests, and both CS and EHB populations may have been relatively small prior to periods of intense hunting, compared with EBS and WHB, suggesting that hunting pressure has been relatively higher for these smaller populations (Reeves and Mitchell 1988; COSEWIC 2004b). However, harvests of belugas at CS have been considerably reduced during more than two decades, so the availability of old, large individuals in the population may be greater than at EHB.

Considering biotic interactions alone, reductions in population density are associated with increases in adult body size (body mass and length) (Scheffer 1955; Trites and Bigg 1992) and reductions in mortality, via increases

in per-capita energy availability and hormonal and behavioral mechanisms (Christian 1971; Peters 1983). However, density-dependent effects are more pronounced when density fluctuates close to the environment's "carrying capacity" (Fowler 1981), which may vary across populations. The lack of relationship between population density and these life-history traits may, thus, indicate differences in how far each population's density is from its respective "carrying capacity". Accurate, long-term, population abundance surveys and habitat use of belugas are required to address this possibility. Data on some aspects studied here for other beluga populations are available in a fragmentary manner for western Greenland (Heide-Jørgensen and Teilmann 1994; Heide-Jørgensen and Lockyer 2001), Gulf of St. Lawrence (COSEWIC 2004a), Alaska (Hobbs et al. 2000; Vos 2003; Hobbs et al. 2005), and Russia (Heide-Jørgensen and Teilmann 1994), using different methodology. Therefore, consideration of abiotic factors using a unified approach encompassing a larger number of beluga populations may provide future tests to explain the observed patterns in adult body size and mortality.

To summarize, this study has shown differences in age structure, growth, and density of belugas among four populations distributed over 10 degrees of latitude, where differences in seasonality and environmental predictability are likely to influence these life-history traits. We predicted that density-dependent effects on growth and mortality should diminish with latitude. Growth, but not mortality, showed a significant relationship with latitude, and density did not appear to be an important explanatory factor for growth and mortality. In general, the age distribution of EBS belugas displayed older ages compared to other Canadian Arctic populations. Adult body size of EBS belugas was found to be larger than that of whales harvested in Hudson Bay, but similar to that of CS belugas. Body size of belugas increased from south to north, being smallest for EHB and largest for EBS animals, consistent with stronger environmental constraints expected at higher latitudes. Winter density of beluga populations increased with latitude, suggesting that high-latitude populations are at higher risk of density-independent mass mortality events such as ice entrapment in winter. However, comparison of these results with animal abundance trends and past commercial harvests suggest that the latter may have played a role in the observed responses. An assessment of differences in hunter selectivity and a separation of natural versus hunting mortality among populations are required to take full advantage of the comparative approach used in this study. Such studies can help understand the spatio-temporal demography and life-history patterns of these monitored beluga populations.

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