An Emerging Pattern of Declining Growth Rates in Belugas of the Beaufort Sea: 1989–2008

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ABSTRACT. Standardized, hunter-based sampling of harvested beluga whales was initiated in the three main harvesting areas of the Mackenzie River delta (Shallow Bay, Kendall Island, Kugmallit Bay) in 1980 and near Paulatuk, Northwest Territories, in 1989. Standard length and sex of landed whales have been recorded for 90 to 110 belugas per year since 1980, and ages have been determined since 1988. Hunters select larger and older belugas; males outnumbered females 2.0 to 1 between 1980 and 1989, 3.0 to 1 between 1990 and 1999, and 3.6 to 1 between 2000 and 2009. Age classes younger than 10 growth layer groups (GLGs) were essentially absent from harvests both in the Delta and near Paulatuk. Asymptotic lengths, calculated using GLG counts from teeth of 839 males and 225 females sampled over 16 seasons (1989, 1993–2008), were 435.3 cm (SE 2.0) for males and 380.1 cm (SE 1.8) for females. Males were 14.5% longer than females. Belugas landed in the Delta and Paulatuk were mainly mature adults (by hunter selection). Mature belugas landed by Paulatuk hunters were younger and shorter than those taken in the Delta because of age and sex segregation in the hunting areas. There was no difference in the size-at-age relationships for belugas landed at Paulatuk vs the Delta. The linear trend in size-at-age indicated a decline of 0.08% (SE 0.038%) per year, or 1.75% over the 19 year time series. The 314 male belugas landed in the Delta between 2000 and 2007 showed statistically significant differences in blubber thickness among years, but only a slight downward trend over this short period. Mean blubber was thickest in 2002 and 2003 and thinnest in 2005. The thinness of belugas in 2005, and subtle changes in growth of the belugas over the time series, may reflect ecosystem changes that have reduced the availability or quality and quantity of their prey in recent years. Further research, including isotope and fatty acid profiling, would be helpful in substantiating the declining trend in growth and elucidating the causative factors.

Key words: Beaufort Sea beluga, Mackenzie Delta, Paulatuk, harvest, length, GLG, size-at-age, growth, blubber thickness

RÉSUMÉ. Des échantillons standardisés provenant de pêcheurs ayant capturé des bélugas ont été prélevés dans trois lieux de capture principaux du delta du fleuve Mackenzie (baie Shallow, île Kendall et baie Kugmallit) en 1980 et près de Paulatuk, dans les Territoires du Nord-Ouest, en 1989. La longueur standard et le sexe des baleines débarquées ont été enregistrés dans le cas de 90 à 110 bélugas par année depuis 1980, et les âges ont été déterminés depuis 1988. Les pêcheurs choisissent les bélugas qui sont plus gros et plus âgés. Le nombre de mâles a dépassé le nombre de femelles dans une mesure de 2,0 contre 1 entre 1980 et 1989, de 3,0 contre 1 entre 1990 et 1999, et de 3,6 contre 1 entre 2000 et 2009. Les classes d'âge plus jeunes que dix groupes de couches d'accroissement (GCA) étaient pour ainsi dire absentes des récoltes du delta et de la proximité de Paulatuk. Les longueurs asymptotiques, calculées au moyen des dénombrements de GCA à partir des dents de 839 mâles et de 225 femelles échantillonnés au cours de 16 saisons (1989, 1993-2008) étaient de 435,3 cm (ET de 2,0) chez les mâles et de 380,1 cm (ET de 1,8) chez les femelles. Les mâles étaient plus longs que les femelles dans une mesure de 14,5 %. Les bélugas débarqués dans le delta et à Paulatuk étaient surtout des adultes en pleine maturité (en raison du choix des pêcheurs). Les bélugas adultes débarqués par les pêcheurs de Paulatuk étaient plus jeunes et moins longs que ceux capturés dans le delta en raison de la ségrégation entre les sexes et de l'âge dans les zones de pêche. Il n'y avait pas de différence dans les relations en fonction de la taille selon l'âge pour les bélugas débarqués à Paulatuk par rapport à ceux débarqués au delta. La tendance linéaire dans la taille selon l'âge a fait ressortir un déclin de 0,08 % (ET de 0,038 %) par année, soit 1,75 % pour la série temporelle de 19 ans. Les 314 bélugas mâles débarqués dans le delta entre 2000 et 2007 ont affiché d'importantes différences statistiques sur le plan de l'épaisseur du lard au fil des ans, mais seulement une faible tendance à la baisse pendant cette courte période. L'épaisseur moyenne du lard était à son point le plus élevé en 2002 et en 2003, et à son point le plus faible en 2005. La maigreur des bélugas en 2005 et les changements mineurs sur le plan de la croissance des bélugas au cours de la série temporelle pourraient être le reflet de changements caractérisant l'écosystème, changements qui ont eu pour effet de réduire la disponibilité ou la qualité et la quantité des proies des baleines ces dernières années. Des recherches plus poussées, prenant notamment la forme du

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profilage des isotopes et des acides gras, aideraient à valider la tendance à la baisse en matière de croissance et à élucider les facteurs causaux.

Mots clés : béluga de la mer de Beaufort, delta du Mackenzie, Paulatuk, récolte, longueur, GCA, taille selon l'âge, croissance, épaisseur du lard

INTRODUCTION

As long-lived and wide-ranging oceanic predators, marine mammals can act as indicators of the state of the ecosystem (Boyd, 2002; Moore, 2008; Williams et al., 2013; Moore et al., 2014), providing evidence of changes to the food web and ecosystem structure. They respond to ecosystem variation with changes in body condition, which is directly linked to the year-to-year availability and quality of their prey. Changes in condition can eventually affect reproduction, growth rates, and survival of individuals, all of which can have impacts on populations (Smith, 1987; Kingsley and Byers, 1998; Stirling, 2002; Moore, 2008; Harwood et al., 2012; Williams et al., 2013).

The belugas (*Delphinapterus leucas*) of the Beaufort Sea stock winter in the Bering Sea and migrate each spring along the north coast of Alaska to summering areas in the Mackenzie Estuary, as well as the offshore Beaufort Sea and Amundsen Gulf (Fig. 1; Fraker, 1979; Richard et al., 2001). This stock, shared with Alaska and Russia, is the second largest in Canada, and it was most recently assessed as stable or increasing (DFO, 2000). Using aerial survey data from 1992, Hill and DeMaster (1999) calculated an abundance estimate for the Beaufort Sea beluga stock of 39 258 (CV = 0.229).

The Inuvialuit of the Western Arctic have a long history of hunting belugas for food during the summer, when the whales aggregate in the shallow estuarine waters of the Mackenzie River (Nuligak, 1966; McGhee, 1988; Day, 2002; Harwood and Smith, 2002). Present-day harvesters from the communities of Inuvik, Aklavik, and Tuktoyaktuk travel by small boat to seasonal whaling camps clustered on the coast of the Mackenzie River delta (hereafter called "the Delta"), mainly on the shores of Kugmallit Bay, Kendall Island, and Shallow Bay (Fig. 1). Beluga hunting occurs mainly during a four-week period in July (Fraker et al., 1979; Norton and Harwood, 1986; Harwood et al., 2002). Harvesters from Paulatuk, a small Inuvialuit community 350 km to the east of the Mackenzie delta, also regularly hunt belugas near their community, but usually later in the season after the belugas' estuarine aggregation period (Norton and Harwood, 1985). Harvest levels are regulated locally by the hunters (FJMC, 2013) and were last assessed as sustainable (DFO, 2000).

As apex predators, marine mammals can provide a means to assess marine ecosystem shifts from a top-down perspective. However, attempts to relate environmental change (Melling et al., 2005; Serreze et al., 2007; Walsh, 2008; Barber et al., 2008) to a marine mammal's responses
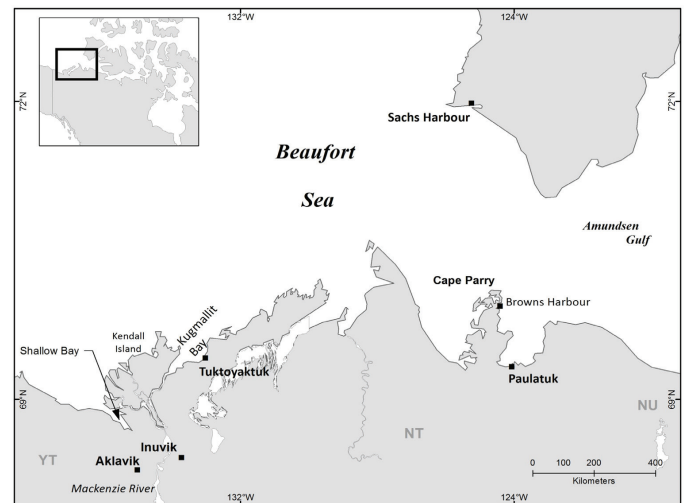

FIG. 1. Map showing Mackenzie Estuary harvesting areas, the Beaufort Sea, and other place names mentioned in text.

to that change are often constrained by a lack of baseline information about the species, its life history, and its prey (Moore et al., 2014). Harvested belugas have been measured and sampled from the Mackenzie Estuary harvest since 1980 (Strong, 1990; Weaver, 1991; Harwood et al., 2002), and these opportunities are expected to continue for the foreseeable future (FJMC, 2013). Also, recent diet studies have revealed that Beaufort Sea beluga feed mainly on Arctic cod (*Boreogadus saida*), at least during their spring migration to the Beaufort Sea (Quakenbush et al., in press). This information, coupled with the more comprehensive picture of their seasonal movements from research using satellite telemetry (Richard et al., 2001), makes Beaufort Sea belugas possible candidates for studying long-term changes in the Beaufort Sea marine ecosystem.

Our study, which used hunter-collected data on the sex, length, age, and blubber thickness of landed belugas, had the objective of examining beluga growth rates and condition, specifically for indications of temporal trends that could ultimately be linked to environmental change. We used 1980–99 data previously summarized by Harwood et al. (2002), although not analyzed with the approach we use here, as well as a decade of new data collected from 2000 to 2009. We examine the entire database for trends and clues as to the nature, direction, and magnitude of environmental changes (Walsh, 2008) that might be reflected in the belugas.

METHODS

Field Sampling

Biological data have been collected from belugas landed in the Mackenzie Delta harvest since 1980 and from Paulatuk harvests since 1989, as described in Harwood et al. (2002). Annual sampling and measuring of landed whales has continued since that time, and here we augment the database with 1018 records for 2000–09, giving a database of 3422 whales harvested from 1980 to 2009.

The beluga harvest monitors were stationed in the seasonal whaling camps for the duration of the whaling season. They examined as many of the landed whales as possible, collected the lower jaws for ageing purposes, determined the sex of the landed whales by palpation of the genitalia, and measured standard length using a cloth tape measure (American Society of Mammalogists, 1961). Blubber thickness at the sternum was measured between the foreflippers on 314 male belugas landed at Kendall Island and in Kugmallit Bay from 2000 to 2007. Other data collected during the monitoring program, including information about the harvest (size, timing, and struck-and-lost rates) and reproductive status of adult females, are available separately (L. Harwood, unpubl. data).

In the laboratory, we extracted and prepared teeth for age estimation according to Wainright and Walker (1988). Over the years 1988–2008, three different people counted dentinal growth layer groups (GLGs) in tooth sections, and samples collected before 1988 were not aged. A growth layer group consists of two adjacent growth layers, one light and one dark (Perrin and Myrick, 1980). Total GLGs present in the dentine and cementum were read following sectioning, as previously described in Perrin and Myrick (1980). There continues to be disagreement in the literature about whether one or two GLGs are deposited annually (Brodie, 1982; Goren et al., 1987; Stewart et al., 2006; Brodie et al., 2013). Here we report "age" as equivalent to one GLG per year. A further confounding factor is that GLGs are lost through normal tooth wear, especially in older animals (Suydam, 2009).

GLG readings and standard length measurements were available for 1411 belugas taken by hunters in the Canadian Beaufort Sea in the western Canadian Arctic between 1988 and 2008. Sex was recorded as female for 303 whales, while the remaining 1108 were males.

GLGs in sectioned teeth had been read by three different readers: reader 1 read 881; reader 2, 377; and reader 3, 178. Few had been read by more than one reader (23 by readers 1 and 2; one by readers 1 and 3; one by readers 2 and 3; and one by all three readers). Two outliers were rejected.

The annual distributions of GLG readings by the three readers were compared, both between years for each reader and between readers, in order to establish a reliability assessment for the data generated by the different readers. To evaluate the validity of using data from different readers, we compared the distribution of their individual GLG readings, by year, on a scatterplot. We then prepared cumulative distributions of GLG readings, by reader and year, for a visual comparison and qualitative decision on comparability.

Cumulative frequency distributions, by sex, were constructed for standard lengths and GLGs of whales landed in the Mackenzie Delta and Paulatuk harvests. The distribution of ages and lengths at the two locations were compared using Kolmogorov-Smirnov tests, by sex. Asymptotic size-at-age curves were fitted to the Richards model by maximum likelihood using Excel Solver. The general Richards curve and the Gompertz and von Bertalanffy cases were fitted to all whales in the database, by sex. Models were parameterized in terms of standard length and size at age zero and asymptotic length (see Appendix I). We compared and selected models using an information criterion composed of the difference between the number of parameters estimated and the log likelihood. We also compared size-at-age for whales landed in Paulatuk versus those landed in the Delta by fitting a von Bertalanffy growth curve for standard length and comparing models by information criterion (Kingsley, 1979).

The observed length l_i was assumed to be related to the predicted length $\hat{l}_i$ by:

$$l_i = \hat{l}_i + \varepsilon_i$$

where the scatter terms ε_i were considered to have independent normal distributions with zero mean and variance:

$$\sigma_i^2 = a^2 \cdot l_\infty^2 \cdot \left(\frac{\hat{l}_i}{l_\infty} \right)^{2b} .$$

This equation defines a power-law relationship between predicted length and the scatter about the fitted relationship, with the parameter a specifying the coefficient of variation (CV) at asymptotic length and the parameter b specifying the relationship between the CV and length. In particular, $b = 0$ specifies a standard deviation about the line, and $b = 1$ is a CV that is independent of length.

To examine temporal trends in size-at-age, we fitted year effects to all parameters of the Gompertz size-age relationship, including standard deviations about the fit: that is, one effect for each year was applied to all parameters. We considered models in which year effects were independent (with a weighted mean of zero) and in which there was a linear trend in the year effect. To our knowledge, temporal trends in beluga growth rates have not been examined previously for this stock. Using an earlier subset of the database, Luque and Ferguson (2010) compared growth rates among various Canadian stocks, relating body size to latitude, and examined the relationship of body size to survival and North Pacific regime shifts (Luque and Ferguson, 2009).

Size-age curves were fitted to yearly collections of cross-sectional data, without regard to the longitudinal properties of the data, and in such an analysis, given the persistence of growth indicators, there is inevitably some linkage between years. In contrast, blubber thickness is independent
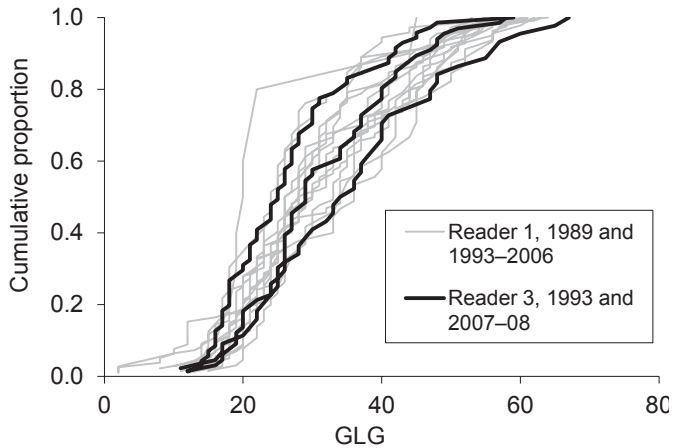
FIG. 2. Cumulative frequency distribution of GLG readings by Readers 1 and 3 for belugas landed in 1989 and 1993–2008.

between years, reflecting an individual's condition in the short term. Therefore, we did not look for or consider relationships between deviations of an individual year from the overall trend in size-at-age and from average blubber thickness, since these features tend to reflect short-term changes in prey availability.

RESULTS

Sex was determined for 95.2% (3026/3179) of the belugas landed in the Delta and Paulatuk harvests between 1980 and 2009. The harvest over the past three decades has been strongly biased toward males and continues to be so. In 1980–89, males outnumbered females in the harvest by 2.0 to 1; in 1990–99, by 3.0 to 1 (Harwood et al., 2002); and in 2000–09, by 3.6 to 1. Trend tests revealed that this diminishing proportion of females in the harvest was statistically significant over the time series (Kendall's tau-b $\tau 0.281$, $p = 0.033$). Over the study period, the proportion of females landed ranged from a low of 19.6% in Paulatuk to 32.4% in the Kendall Island area.

The information available did not permit a satisfactory reconciliation of the age data from all three readers. Reader 2 had distributions of GLG readings that were different from those of the other readers, and for all 23 teeth that were read in common by Reader 1 and Reader 2, Reader 2 consistently read about eight layers more than Reader 1. Owing to the difficulty of resolving these problems, the readings from Reader 2 were not used in any of the analyses. Distributions of GLG counts produced by Reader 3 were similar to those of Reader 1, and their year-to-year variation fell within the spectrum of the year-to-year variation of Reader 1 (Fig. 2). Data from Reader 3 were thus included in the analyses without modification. This procedure created a reconciled dataset of 1064 GLG readings (225 females, 839 males), covering the years 1989 and 1993 to 2008. The GLG counts for females in the sample ranged from 10 to 63 and those for males from 8 to 67.
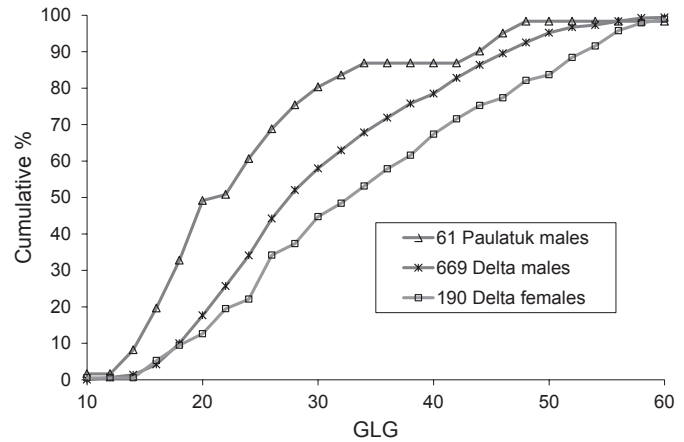

FIG. 3. Cumulative frequency distribution of GLG readings of male and female belugas landed in the Mackenzie Delta and Paulatuk subsistence harvests, 1993–2008.
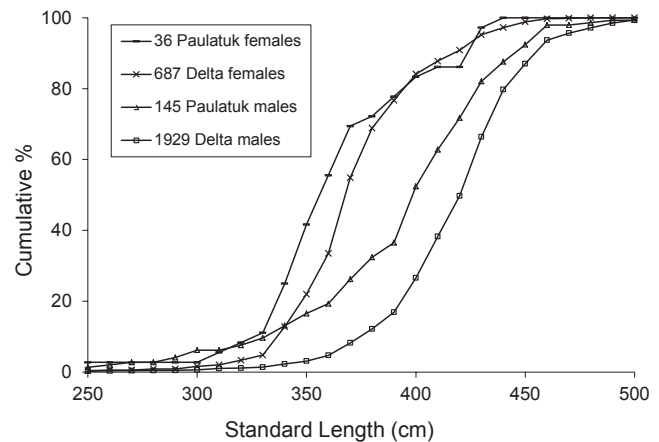

FIG. 4. Cumulative frequency distribution of standard length of male and female belugas landed in the Mackenzie Delta and Paulatuk subsistence harvests, 1993–2008.

On average, females landed in the Delta were older than landed males (Fig. 3), with median GLG counts of 34 and 28, respectively. The maximum difference in cumulative proportion was 14.7% ($p < 0.01$) at 34 GLGs. Male belugas from Paulatuk were on average younger than Delta males, with a median GLG count of 22; the maximum difference in cumulative proportion was 31.5% ($p < 0.001$) at 20 GLGs (Fig. 3). GLG readings were available for only nine females landed at Paulatuk, too few for analysis of cumulative proportion.

Belugas of both sexes landed in Paulatuk were younger and shorter than those taken in the Delta (Fig. 4). Median length for females was 356 cm at Paulatuk and 368 cm in the Delta. For males, it was 398.5 cm and 420 cm, respectively. The maximum difference in cumulative proportion was 22% ($p > 0.05$) for females, at 360 cm length, and 26% ($p < 0.001$) for males, at 400 cm.

Age (GLG readings), standard length, and sex were estimated for 1059 belugas sampled in 1989 and in 1993–2008. Asymptotic lengths were calculated (Table 1) for each of the three models (Fig. 5). Males were 14.5% longer than females.

TABLE 1. Parameters of Richards, Gompertz, and von Bertalanffy size-age relationships fitted to data for 224 female and 835 male belugas taken by hunters in the Mackenzie Delta and at Paulatuk in 1989 and 1993–2008.

	General Richards	Gompertz	von Bertalanffy
Shape parameter	1.91 (1.03)	1	0
Male asymptotic length (cm)	432.3 (2.0)	433.5 (2.0)	435.3 (2.0)
Female asymptotic length (cm)	379.5 (2.0)	379.8 (1.6)	380.1 (1.8)
Length at zero age (cm)	187.2 (16.6)	174.3 (11.8)	154.9 (14.9)
Growth at zero age (cm/GLG)	15.73 (3.9)	20.1 (1.1)	30.2 (2.8)
SD Reader 1 (cm)	25.24	25.25	25.3
SD Reader 3 (cm)	30.02	30.02	30.03
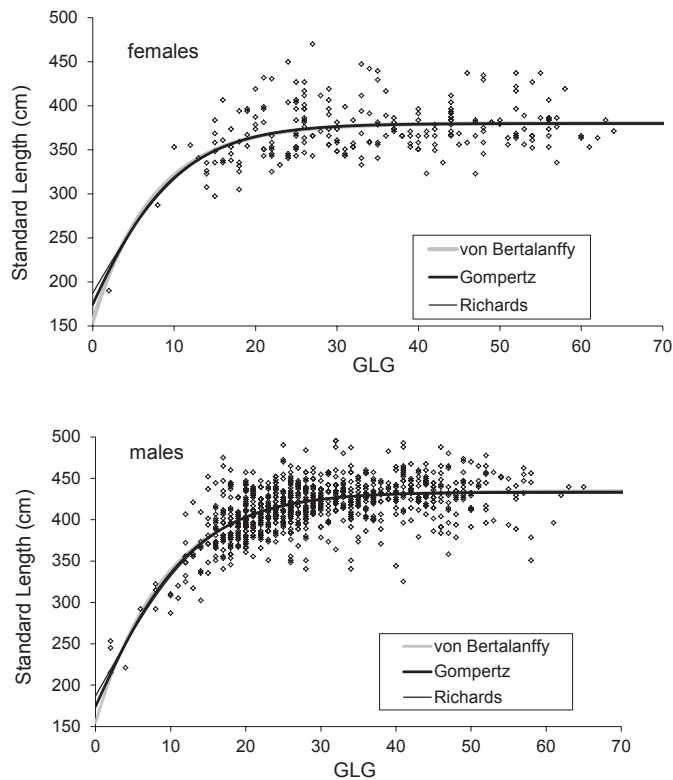
FIG. 5. von Bertalanffy, Gompertz, and Richards-modeled curves for male and female belugas landed in the Delta and Paulatuk subsistence harvests in 1989 and 1993–2008.

The different growth models—general Richards, Gompertz and von Bertalanffy—differed most at the left side, i.e., for the youngest animals, from which few data were available (Fig. 5). We present results for all three models to allow comparison with other studies (Table 1). For all models, common values of the length and the growth rate at age zero were fitted to the two sexes. There was no indication that the size-at-age relationship for belugas taken at Paulatuk differed from that of belugas from the Delta (Table 2).

Length-independent standard deviations fitted best to the data. Lengths associated with GLG readings from the two readers had different scatter about the fitted models, but models in which the sexes had the same values for standard deviation fitted better than models in which they had the same CV.

TABLE 2. Constant ratio (fitted at 1.002442) between size parameters of von Bertalanffy length-age relationships between whales taken at Paulatuk and in the Delta.

	Delta	Paulatuk
Female asymptotic length (cm)	380.1	379.1
Male asymptotic length (cm)	435.3	434.2
l0 (cm)	154.9	154.5
k0 (cm/GLG)	30.2	30.1
SD Reader 1 (cm)	25.3	
SD Reader 3 (cm)	30	
ln Likelihood	−4954.6	

The free Richards curve fitted was close to a logistic curve. As the shape parameter was brought down from 1.91 to 1 for the Gompertz curve and to 0 for the von Bertalanffy curve, the length at zero age was greatly reduced, and the growth rate correspondingly increased. Asymptotic lengths were affected, but only slightly, by the change in the shape parameter. Since most whales landed were adults, the asymptotic lengths were precisely estimated, but length and growth rate at zero age were imprecise and sensitive to the choice of model.

A possible temporal trend in size-at-age was investigated by fitting a linear trend with time to all size parameters—asymptotic lengths for both sexes and length and growth rate at age zero, and the standard deviations—for the Gompertz model (Table 3). Year-to-year differences were small, ranging from +2% in 1994 to −2% in 2003, and were not statistically significant among the different years tested. The linear trend was a decline of 0.08% (SE 0.038%) per year (Fig. 6). The linear-trend model was selected by the information criterion and its gross change in likelihood was statistically significant at 5%, although not when tested against the residual variation between years.

Trends in blubber thickness were evaluated using a general linear model in SAS. Effects of length, then age, were added to the model, and both were retained because they were significant. No significant linear trend related to calendar date was detected: male belugas got neither fatter nor leaner progressively from early to late summer. However, there was a significant curved relationship, and it appeared that they were fatter both early and late in the season than they were in mid-season. The date of minimum average blubber thickness was estimated as July 20.

Overall, there was a weak downward trend in blubber thickness of adult males, but this was not statistically

TABLE 3. Fit statistics for year dependence of the parameters of Gompertz size-age relationships fitted to data from belugas harvested in the Delta and near Paulatuk, Northwest Territories.

Year effects fitted	log. Likelihood	No. of parameters	Information
None	−4952.87989	6	4958.88
Independent, with zero mean	−4941.09667	22	4963.097
Linear with time	−4950.54024	7	4957.54
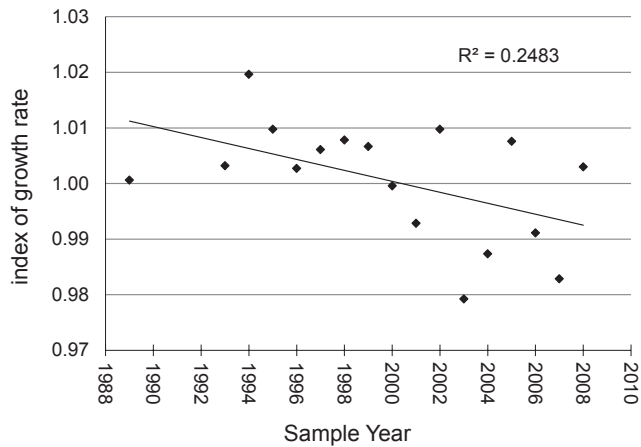
FIG. 6. Temporal trend in size-at-age of belugas landed in Delta and Paulatuk subsistence harvests in 1989 and 1993 – 2008.

FIG. 7. Year-to-year variation in mean sternal blubber thickness (cm) of adult male belugas (n = 314) sampled from subsistence harvests during July at Kendall Island and Kugmallit Bay from 2000 to 2007.

significant at 5% (Fig. 7). There were, however, significant differences among years ($p < 0.05$): blubber was thickest in 2002 and 2003 and thinnest in 2005.

DISCUSSION

Inuvialuit hunters select larger, older animals, primarily males (Strong, 1990; Weaver, 1991; Harwood et al., 2002). This bias continued through 2000 – 09, and obviously limits the types of analysis that can be done with these data. On the other hand, the growth rates and blubber thickness that we have documented are not influenced by hunter selection (Suydam, 2009).

We checked whether belugas landed in Paulatuk had different growth rates from those taken in the Mackenzie Delta and were unable to conclude that they did. This result fits with our understanding that the whales occurring and harvested at Paulatuk are a subset of the same stock (Richard et al., 2001), although they tend to be younger and shorter because of size and sex segregation during the August feeding period (Richard et al., 2001).

Belugas sampled in early summer, just after arriving from their Bering Sea wintering areas and the Chukchi/Beaufort spring migration, showed a weak but sustained trend of declining growth rate beginning in 2000. This declining growth trend points to the possibility that longer-term changes are occurring in the marine ecosystem (Tynan and DeMaster, 1997; Barber et al., 2008; Laidre et al., 2008), which appear to be influencing the beluga's prey base. In a much larger, longer-term sample (n = > 2200; 20

years), ringed seals exhibited a significant and sustained decline during the same period; belugas might well be undergoing the same effects although they are less measurable in the shorter data set (Harwood et al., 2012).

Although the slight downward trend in blubber thickness of 314 adult beluga males from 2000 to 2007 was not statistically significant, there was significant year-to-year variation in blubber thickness. Substantial year-to-year variation in body condition (as measured by fat stores) has been well documented for several species of Arctic animals and linked to temporary variations in their environment (Boyd, 2002; Miller et al., 2011; Williams et al., 2013). We note that in 2005, the year when male beluga blubber was thinnest, 70% of the adult female ringed seals in neighboring east Amundsen Gulf failed to ovulate, and seal body condition indices were at their lowest point in two decades (Harwood et al., 2012). The coincident downturns in these two species in 2005 might indicate that a common factor was operant, which was most likely related to availability of their common winter food, the Arctic cod. During the same period (2004–06), polar bears in the southern Beaufort Sea were nutritionally stressed. The underlying causes of observed changes in polar bear body condition and foraging behaviour were unknown, but the most likely explanation was major changes in the sea ice and marine environment (Stirling et al., 2008). Linkages to downturns in the seal population were also suggested as a possible explanation.

Concurrent declines in growth, condition, and reproduction in seals and belugas likely reflect changes that are occurring in the Arctic marine ecosystem. Thus belugas,

like seals, appear to be a candidate indicator species for measuring environment change particularly by examining their growth rates, especially when results of different species are interpreted collectively. Concurrent changes in seals and polar bears, which are also mirrored, date back to at least the 1970s and were largely attributed to severe ice conditions in winter 1974–75 (Stirling et al., 1977, 2008). However, concurrent changes in belugas and seals are informative in a different way because these two species feed on a common prey, Arctic cod, of which we know very little (Bradstreet et al., 1986; Benoit et al., 2010; Crawford et al., 2012). While the seal-polar bear link is influenced by sea ice cover and quality (Stirling, 2002), the beluga-seal link may indicate more subtle climatic and oceanographic changes occurring lower in the trophic pyramid that could have cascading and profound ecosystem impacts.

Our results point to the need for more detailed study to confirm and monitor observed signals in the growth rate of belugas and to further describe trends and year-to-year variation in blubber thickness. Ideally, sampling of Arctic cod biomass would be the study of choice, but the size and location of the wintering habitats used by belugas present formidable sampling challenges insofar as obtaining data at a scale relevant to beluga feeding. Direct collection of field data to examine changes in the prey base and food web structure would be impractical and inordinately expensive in such vast, remote locations during winter, particularly given that the belugas use prey patches and that variation exists among seasons, individuals, and different parts of their vast annual range. Future studies, including continued harvest-based monitoring of the Mackenzie Estuary beluga harvest (Bell and Harwood, 2012), are important to continue to monitor the trends we have observed. To infer dietary change, these studies could be coupled with diet profiling studies using fatty acids (e.g., Dahl et al., 2000; Theimann et al., 2008) and stable isotopes (Kelly, 2000; Chambellant et al., 2012), provided that appropriate calibration coefficients could be determined (Rosen and Tollit, 2012). Such studies in turn would contribute to our understanding of feeding strategies and eventually provide a quantitative assessment of the time and location of resources selected by belugas throughout their range. This assessment could also be coupled with projects that deploy CTD-equipped satellite tags on belugas (Smith, 2001; Lydersen et al., 2002, 2004; Fedak 2004) to monitor the oceanographic characteristics of their wintering habitats and their prey concurrently. The advantage of using the marine mammals themselves as sampling platforms is that they are specialists in feeding at various trophic levels. Using their evolved ability to locate and feed on Arctic marine resources would produce a sampling strategy that is based on millions of years of natural selection and adaptation to acquiring resources in a changing Arctic marine ecosystem.

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APPENDIX I: SIZE-AGE CURVES PARAMETERIZED WITH ZERO-AGE PARAMETERS

The general Richards size-age function, parameterized at zero age, is:

$$l(t) = l(\infty)\left(1 - \left(1 - \frac{l(0)}{l(\infty)}\right)^{(1-m)} \exp\left(\frac{-kt(1-m)}{l(0)\left(\left(\frac{l(0)}{l(\infty)}\right)^{(m-1)} - 1\right)}\right)\right)^{1/(1-m)}$$

where $l(t)$ is the size at age t, k is the growth rate at zero age, and m is the shape parameter. Common standard special cases are the logistic, with m equal to 2; the Gompertz, which is the limiting case as m tends to 1; and the von Bertalanffy for length with $m = 0$.

The simplified form for the logistic is:

$$l(t) = l(\infty) \left/ \left(1 + \left(\frac{l(\infty)}{l(0)} - 1\right)\exp\left(\frac{-kt}{l(0)\left(1 - \frac{l(0)}{l(\infty)}\right)}\right)\right)\right.$$

For the Gompertz:

$$l(t) = l(\infty)\left(\left(\frac{l(0)}{l(\infty)}\right)^{\exp\left(kt / l(0)\ln\left(\frac{l(0)}{l(\infty)}\right)\right)}\right)$$

And for the von Bertalanffy:

$$l(t) = l(\infty)\left(1 - \left(1 - \frac{l(0)}{l(\infty)}\right)\exp\left(\frac{-kt}{l(\infty) - l(0)}\right)\right)$$

These expressions can be used with any standard non-linear fitting method to produce parameter estimates, with standard errors, that are comparable between different models and are susceptible to being reconciled with observable features of species biology.