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Mortality patterns in St. Lawrence Estuary beluga (*Delphinapterus leucas*), inferred from the carcass recovery data, 1983-2012

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

A total of 469 beluga was found dead in the Estuary or Gulf of St. Lawrence between 1983 and 2012. The number of cases reported varied among years, with a median of 15 beluga annually. Beluga deaths were mainly reported in the St. Lawrence Estuary (SLE), between April and November, and peaked in May to August. Over the first 24 years of the study period, newborn deaths varied from 0 to 3 beluga per year, and followed a 3–4 year cycle. In 2008, this cycle changed to biennial peaks, and was accompanied by annual report rates 3 to 5 times higher than the maxima observed previously. Mortality patterns among adults followed no clear temporal trends over the study period. There was an equal probability of finding an adult male or an adult female regardless of season or year of study. Age distribution of collected carcasses followed a U-shaped distribution typical of long-lived mammals, with the highest mortalities in the first year of life, and among the older (35+ growth layer groups [GLGs]) age classes. The oldest individual had 72 GLGs. Age-at-death distributions were similar among adult males and females. A comparison of cumulative frequency distributions of age-at-death between the periods 1983–1999 and 2000–2012 indicates beluga died at a younger age in the latter period, and that deaths of adult females but not males were responsible for this pattern. Finally, the relationship between age and standard length of SLE beluga confirmed sexual dimorphism with males reaching an asymptotic standard length longer than females (416 cm vs 365 cm). SLE beluga are intermediate in size compared to other beluga populations.

Mortalité chez les bélugas du Saint-Laurent (*Delphinapterus leucas*) déterminée à partir des carcasses retrouvées de 1983 à 2012

RÉSUMÉ

Au total, 469 bélugas ont été retrouvés morts dans l'estuaire et le golfe du Saint-Laurent entre 1983 et 2012. Le nombre de cas variait d'année en année, se situant autour d'un nombre médian de 15 bélugas par an. Les mortalités ont été rapportées principalement dans l'estuaire du Saint-Laurent (ESL) entre avril et novembre, atteignant un pic de mai à août. Au cours des 24 premières années de la période d'étude, le nombre de veaux retrouvés variait de 0 à 3 par an, et suivait un cycle de 3-4 années. En 2008, la périodicité des pics de mortalités s'est altérée vers des cycles biannuels, et le nombre de veaux annuellement rapporté fut de 3 à 5 fois celui observé auparavant. La mortalité chez les adultes n'a montré aucune tendance temporelle durant la période d'étude. La probabilité de retrouver une carcasse de béluga adulte était la même quel que soit le sexe de l'animal ou l'année de la période d'étude. La distribution d'âge des bélugas retrouvés suivait une courbe en U typique des mammifères à longue durée de vie, avec les plus fortes mortalités observées durant la première année de vie et chez les classes d'âge de 35+ groupes de couches de croissance (GCCs). Le plus vieil animal comptait 72 GCCs. La distribution de l'âge à la mort était semblable chez les mâles et les femelles adultes. Une comparaison des périodes 1983–1999 et 2000–2012 indique que les bélugas adultes mouraient plus jeunes au cours de la seconde période, et que cette tendance provient des femelles et non des mâles. Finalement, la relation entre l'âge et la longueur standard des bélugas de l'ESL confirme le dimorphisme sexuel chez cette espèce, où les mâles atteignent une longueur standard asymptotique plus élevée que les femelles (416 cm vs 365 cm). Les bélugas de l'ESL sont de taille intermédiaire relativement aux autres populations de bélugas.

INTRODUCTION

The beluga (*Delphinapterus leucas* Pallas, 1776) is a medium-sized toothed whale (odontocete) with a circumpolar distribution limited to seasonally ice covered Arctic and sub-Arctic seas (Reeves 1990). Life expectancy can reach 75-80 years (Lockyer et al. 2007; Luque and Ferguson 2010; this study), although estimates are likely biased downward, owing to the difficulty of reading the occluded and worn teeth of old animals. Females usually give birth to a single calf during summer after a 14-15 mo gestation period (reviewed in Heide-Jørgensen and Teilmann 1994). Lactation lasts 20-24 mo and may overlap the following gestation, the occurrence of which suggests a three-year reproductive cycle (Vladykov 1944; Brodie 1971; Sergeant 1973; Burns and Seaman 1985; Doidge 1990; Heide-Jørgensen and Teilmann 1994).

Beluga in the St. Lawrence Estuary (SLE) are at the southern limit of the species distribution. The SLE population is greatly reduced from historical levels as a result of overhunting in the 1800s and 1900s (Reeves and Mitchell 1984), and is protected from hunting by the Fisheries Act since 1979. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated this population as *Endangered* in 1983, and reaffirmed this status in 1996. Eight years later, the COSEWIC changed the status to *Threatened* when revised correction factors for abundance estimates indicated a population larger than previously thought (COSEWIC 2004).

In the early 1980s, a research program was progressively put in place to monitor population growth, and obtain information on beluga ecology and social organization, as well as potential threats to the population. A program for monitoring beluga deaths and sampling carcasses was initiated in 1982, and fully implemented in 1983. This program is still ongoing, and has allowed the collection of various population parameters and tissues from accessible carcasses, the most fresh of which were transported to a veterinary laboratory for complete necropsy.

In this document, we infer mortality patterns and other population parameters using data from beluga found dead in the Estuary and Gulf of St. Lawrence between 1983 and 2012. Some of the reviewed information is used to inform a model of population dynamics (Mosnier et al. 2014).

MATERIALS AND METHODS

The program for collecting beluga carcasses was advertised each spring through a publicity campaign mainly targeting the SLE, and requesting the public to report dead beluga. While the program was initiated in 1982, this year was excluded from the analysis as a result of known incomplete reporting. Every effort was made to investigate each case and confirm species identity. The call center to which the public could report a dead beluga was handled by different organizations over the years, and in some years included other species of marine mammals. However, standards for confirmation of beluga cases remained relatively consistent over time, requiring either photos or visual confirmation by an expert. Only cases confirmed as beluga are included in the analysis. At a minimum, information collected on each carcass included date of observation and location, sex and standard length, i.e., the distance in a straight line from the anterior extremity of the snout to the notch in the fluke. At least one tooth (or the entire lower jaw when possible) was also collected for age determination. Carcasses that were relatively fresh in external appearance were taken for complete necropsy at the *Faculté de médecine vétérinaire* of the *Université de Montréal*, in *Saint-Hyacinthe* (Lair et al. 2014). Field data and samples were collected by a limited (3–4) number of experts over the 30-y study period, while the necropsies were conducted by five veterinary pathologists.

Beluga found dead in the St. Lawrence (SLE and Gulf), around Newfoundland or on the Scotian Shelf, including the Bay of Fundy, were considered as originating from the SLE beluga

population. Only three cases, for which origin was determined to be the Arctic based on contaminant loads or cadmium levels, were excluded from analysis.

Mortality patterns were examined separately for neonates (< 1 y), juveniles (1–7 y), and adult males and females (8+ y). Beluga neonates (also referred to as newborns) were identified on the basis of size, the presence of an umbilical cord, and/or embedded teeth, with neonatal dentinal layer. Total standard length (Brodie 1971; Robeck et al. 2005; Suydam 2010) was used in combination with carcass observation date, and signs of emergence of teeth (Brodie 1971) to identify one- or two-year old calves potentially misclassified as newborn or juveniles. Sexual maturity (i.e., evidence of ovarian activity in females, and mature testes in males) occurs at an earlier age in female than in male beluga, i.e., 6–14 y in females vs. 16–22 y in males, assuming deposition of 1 growth layer group per year (Brodie 1971; Sergeant 1973; Ognetov 1981; Finley et al. 1982; Burns and Seaman 1985; Heide-Jørgensen and Teilmann 1994; Robeck et al. 2005; Hobbs et al. 2008; Suydam 2010). In SLE beluga, the youngest female found dead and carrying a fetus was 7 y-old (Lair et al. 2014), but it is unknown what proportion of females at this age conceive, carry to term or wean a calf. Age 8 was used as the minimum for adulthood, or sexual maturity in females (Robeck et al. 2005; Suydam 2010).

Ages were estimated from growth layer groups (GLGs) of dentine in teeth, using a longitudinal midline section or half tooth, and high-resolution (4800 dpi optical resolution, 24-bit color) digital imagery (Epson scanner Perfection V500 photo) to allow for magnification, light and contrast adjustments. One GLG was assumed to be deposited each year (Stewart et al. 2006; Lockyer et al. 2007; Luque et al. 2007)¹. A tooth was considered ‘worn’ when the neonatal layer was not present. In older beluga, tooth wear, reduced growth, or tooth loss hinder age determination, or lead to age underestimation (Sergeant 1973). While this could not be corrected for in the current analysis, potential biases in aging related to changes in reading methods or readers over the study period were addressed by re-examining teeth using a standardized method (digital imagery) and a single experienced reader performing a minimum of 3 blind replicate readings. Thirty (or 7%) teeth, all sampled prior to 2001, had been lost and could not be reread. Based on a subset of 179 teeth sampled prior to 2001, and aged by a number of previous (NP) readers, and more recently re-aged by a single experienced (SE) reader, there was a tendency for the SE reader to estimate younger ages than the NP readers for beluga teeth with less than 25 GLGs (Figure 1). Given that 26 of the 30 lost teeth were in the age bracket where there was no difference in age between the SE and NP readers, biases in the time series by inclusion of the 30 lost teeth is likely to be negligible. Nevertheless, trends in age composition of mortalities were re-examined excluding the 30 teeth with no recent reading to insure consistency in the time series.

An apparent shift from a cold to a warm period was observed in the St. Lawrence system around year 2000 (Plourde et al. 2014). To account for potential effects of this change on beluga population dynamics, mortality patterns were compared between the periods 1983-1999 and 2000-2012.

Finally, the length-at-age data were fitted to the Gompertz growth model:

$$L(t) = A \cdot \exp[-b \cdot \exp(-k \cdot t)]$$

¹ While the traditional annual deposition rate of 2 GLGs was recently upheld based on an analysis of data on growth and reproduction of Cumberland Sound and captive beluga (Brodie et al. 2013), evidence in support of this hypothesis was criticized on a number of accounts during a workshop on age estimation in monodontids (Tampa Convention Center, Nov. 2011).

$L(t)$ is the length at age t in centimeters, A is the asymptotic value, e is Euler's number (2.7183) or base of natural logarithms, b is the integration constant, k is the growth rate constant, and t is age in years (or GLGs).

Cumulative age and seasonal death distributions were compared between sex or time periods using Kolmogorov-Smirnov tests. Statistical analyses were conducted using the programming language R (R Development Core Team 2009). Statistical significance was set at $\alpha = 0.05$.

RESULTS

SEASONAL MORTALITY PATTERNS

Beluga deaths were mainly reported between April and November (95.3%), and in the SLE (87.5% of cases), with peak reporting from May to August (Figure 2). The seasonal distributions of carcass observation dates were similar in adult males and females, indicating that there was an equal chance of either sex being reported at any time of year (K-Smirnov test: $D = 0.12$, $p = 0.23$) (Figure 3).

ANNUAL MORTALITY PATTERNS

A total of 469 beluga was found dead between 1983 and 2012, with a median of 15 beluga annually (Figure 4). The number of confirmed cases varied among years, ranging from 9 to 28 beluga ($CV = 28\%$) including 0–16 newborn calves ($CV = 155\%$). Over the first 24 years of the study period, newborn deaths varied annually from 0 to 3 beluga around a median of 1 beluga, and followed a 3–4 year cycle (Figure 4). In 2008, this apparent cycle changed to biennial peaks, and was accompanied by annual reporting rates 3 to 5 times higher than the maxima observed previously. As a result, trends in newborn deaths and total number of beluga deaths were non-linear, and mainly driven by the particularly high newborn mortalities reported in 2008, 2010, and 2012.

Juvenile (1–7 y) mortality followed no trend over the study period, with a total of 36 cases, and 0 to 4 beluga per year (mean = 1.2 individuals; Figure 5). Similarly, mortality patterns among adults also followed no clear trends over the study period ($R^2 = -0.04$, slope = 0.00, NS), with a median of 10.5 beluga per year ($CV = 26\%$) (Figure 6). While female mortality tended to be above average and male mortality below average over the last 4–5 years of the study period (Figure 7), trends in number of deaths over time were non-significant for adult males and females ($R^2 = 0.03$ and 0.05 , respectively; slope = 0.08 and 0.06; both NS).

SEX RATIO

Sex ratio among adult beluga was unbiased in most years (F:M median = 1.09), except in 1988 and 2000, and the period 2006–2012 when a bias was observed toward adult females (Figure 8). These characteristics resulted in a poor fit and heteroscedasticity of residuals and thus, in an invalid relationship.

AGE DISTRIBUTION

Age was determined for 409 of the 469 beluga. Tooth wear was observed starting at 17 GLGs, and was predominant in beluga teeth aged 20 GLGs or older. The oldest animal with unworn teeth had 32 GLGs (Figure 9).

Age distribution of collected carcasses followed a U-shaped distribution typical of long-lived mammals, with the highest mortalities in the first year of life, and in the 35+ GLGs age classes (Figure 9). Mortality decreased dramatically after the first year of life. The oldest individual had

72 GLGs. Age-at-death distributions were similar among adult males and females ($D = 0.10$, $p = 0.41$).

A comparison of cumulative frequency distribution of age-at-death between the periods 1983–1999 and 2000–2012 indicates that beluga died at a younger age in the latter period ($D = 0.24$; $p < 0.0001$). The exclusion of newborn calves and juveniles from the analysis, and examination of adult mortality separately for each sex indicates that this pattern (i.e., death at younger age in 2000–2012 compared to 1983–1999) is seen in adult females only (Adult female: $D = 0.26$, $p = 0.009$; Adult male: $D = 0.19$, $p = 0.19$; Figure 10), and is not related to the unusual mortalities of 2008, 2010, 2012 (Adult females excluding years 2008, 2010, 2012: $D = 0.27$; $p = 0.02$). This pattern was also not attributed to differences in tooth reading methods or readers between the two periods, as these differences remained statistically significant when excluding the 30 teeth (all sampled prior to 2001) that could not be reread (data not shown). Examination of raw age data indicated that this change in distribution is not associated with a particular year, but more to a general increase in the annual number of younger adult female deaths (Figure 11).

GROWTH

The relationship between age and standard length of beluga was adequately described by a Gompertz function (r -squared=0.96 and 0.94 for males and females, respectively). Growth rate was sex-specific, indicating a sexual dimorphism with an asymptotic standard length of 416 cm in males (95% CL = 370–462 cm) and 365 cm in females (95% CL = 328–402 cm), and which is reached approximately 5 years later in males than in females (Figure 12; Table 1). The predicted standard length at birth was 162 cm for males and 158 cm for females. Standard length appeared to remain similar in males and females until approximately 8 GLGs.

DISCUSSION

Only a few carcasses were reported outside of the SLE or during periods of ice coverage. While beluga concentrate in the SLE during summer, an unknown proportion of the population ventures into the northwestern Gulf of St. Lawrence and possibly further during the fall, winter and spring (reviewed in Lesage and Kingsley 1998; Mosnier et al. 2010). Whether beluga carcasses have an equal probability of being found inside or outside of the SLE is difficult to assess. Communities from the Gulf of St. Lawrence may be less likely to report a dead beluga, being less familiar with the Quebec carcass recovery program, for which publicity campaigns target mainly SLE communities. The absence of death reports during winter months likely results from a reduced probability of finding carcasses as a result of several factors, including the presence of land-fast ice, fewer people walking along shore, and shift in beluga distribution toward the East into, larger more open areas (e.g., Gulf of St. Lawrence). Assuming the maxima in carcass detection rates observed in May to August (1.6 adults/month or 48 adults/month for the 30 years of study; Figure 2) apply to the rest of the year, and that mortality rate is not season-dependent, then a total of 19.2 (1.6 x 12 month) adults would be expected to be found each year. This is approximately double the median number of adults (10.5 individuals) reported each year. In other words, approximately half of the carcasses may be missed due to unequal probability of detection across months. How this relates to the annual mortality rate also depends on population size and proportion of adults, which likely varied over the study period (see Mosnier et al. 2014).

Body condition of beluga is also likely to influence the probability of a carcass floating and being found adrift or on shore. In spite of a relatively large body of literature on beluga ecology and life history, little is known about variability in food intake, energy reserves and body condition with season or age class. In northern Quebec for instance, hunters from Hudson Strait report a tendency for beluga to sink rapidly in the fall (October–November), and to float in the spring

(May-June) (K. Breton-Honeyman et al.², unpublished data), suggesting a thicker blubber layer in the spring than in the fall, although seasonal changes in water density may to some extent also affect carcass floatability. In beluga from Cumberland Sound, females in late pregnancy and early lactation were found to be unusually fat (Sergeant and Brodie 1969), suggesting that spring and possibly winter feeding are periods particularly important for adult female beluga. In the SLE, hunter reports suggest that beluga are thin during winter, i.e., November to March, that they put on most of their fat in May to June, gaining 5–6 inches (12.7–15.2 cm) of fat in less than 10 days, and that they remain fat during summer (Casgrain 1873, cited in Vladykov 1944). Hunter reports also suggest large inter-annual variability in blubber thickness, with beluga floating in one year, and sinking at the same period in others (Vladykov 1944). A study from the 1930s based on a small sample size suggests that SLE beluga have a thicker blubber layer in the spring than other seasons, supporting the hypothesis of spring, specifically May to June, or late winter as being particularly important feeding periods for this population. SLE beluga data also indicate an increase in blubber thickness from 2–3 inches (5.0–7.6 cm) in calves, to 4 inches (10.1 cm) in yearlings, and to 6–7 inches (15.2–17.8 cm) in adults, with no clear difference in blubber thickness between adult males and females of similar length (Vladykov 1944). Comparing fat deposition rates from the hunter reports (Casgrain 1873, cited in Vladykov 1944) with blubber thicknesses measured by Vladykov (1944) suggests that SLE beluga return from their winter journey with basically no fat left, which is unlikely. However, both sources suggest that beluga put on most of their blubber fat reserves in the spring. Based on this evidence, beluga carcasses would be more likely to sink in the fall or winter than during late spring or summer, further reducing chances of finding a carcass outside of the May to August period.

While the blubber layer is thinner in calves and juveniles than it is in adults, it remains unclear how blubber thickness relates to total mass and floatation. Only five yearlings (1 GLG) were found stranded over the 30-y study period, resulting in an annual rate of death for this age class much lower than the median of 1 for young-of-the-year (YOY) (GLG<1). This may indicate a greater survival of yearlings compared to YOY, a higher probability of sinking in yearlings than YOY, or both. While there is no reliable estimate of mortality rate for these age classes (reviewed in Lesage and Kingsley 1995), a smoothed age-structured model (Caughley 1966) applied to a large hunted beluga sample from the Beaufort Sea ($n = 528$) suggests mortality rates (q_x) of 0.294, 0.107, 0.084 and 0.073 for beluga of 0, 1, 2 and 3 years of age. Thus, mortality rates for yearlings and older juveniles would be approximately one-third that of YOY (Burns and Seaman 1985). While these results need to be interpreted with caution given that the life table was produced while assuming deposition of two GLGs per year, age-specific mortality rates produced from our sample were still much lower than these estimates for SLE beluga of 0, 1 and 2 years of age at 0.154, 0.014 and 0.024, respectively. Yearlings, and possibly also beluga of age 2, may be under-represented in our sample (perhaps less likely to be found) compared to YOY or older age classes. Yearlings are still nursing, although probably starting to feed during the second year of life (Vladykov 1944; Brodie 1971; Sergeant 1973). Mass-specific energy gain in terms of fat reserves may be less in yearlings than YOY, making them more likely to sink relative to the latter.

Seasonal patterns in adult male and female deaths revealed no differences in the likelihood of finding one sex over the other during the ice-free period, a finding which suggests an unbiased sampling of adults of the two sexes. Biases would be expected if mortality rate, seasonal floatability and distributions differed among the sexes. While there is no data supporting a difference in mortality rate or seasonal floatability among sexes, area of occupancy is known to differ among sex and age classes at least during summer, with males occupying deeper waters

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with steeper shorelines than females with calves or juveniles (Michaud 1993). However, the probability of a beluga stranding on shore and being found is also influenced by local tides, currents, gyres, shore use by people, and weather. Any bias related to distribution is therefore difficult to measure.

There was no trend detected in the number of adult or juvenile beluga found dead over the study period (Figures 5, 6), an observation which supports survey results indicating a population showing little change up to the early 2000s, then a progressive decline likely associated mostly with calf mortality (Hammill et al. 2007; Mosnier et al. 2014). There was a 3 to 4 year cycle in newborn calf mortality, a trend which is consistent with a three-year reproductive cycle in beluga (Heide-Jørgensen and Teilmann 1994), and reproductive synchrony among females, a pattern widespread among plants and animals for seasonal reproductive timing (Ims 1990), but also for inter-year timing in species with inter-calf intervals above one year (e.g., brown bears: Ordiz et al. 2008). The high calf mortality observed on a two-year cycle in 2008, 2010 and 2012 could result from a combination of factors. Good environmental conditions may have shortened the calving interval, as observed in species such as right whales when food was abundant (Miller et al. 2011; Greene et al. 2013). Alternatively, high calf mortality shortly after birth may have interrupted the two-year lactation, leaving females available to mate one year earlier than normal. This would have increased production two years later. However, a combination of these two phenomena could not explain the 8-16 fold increase in calf mortality observed in those years; mortality rates were likely abnormally high for calves. A red tide in August 2008 caused a die-off of large numbers of marine invertebrates, birds, fish, and mammals (Scarratt et al. 2014; see also Truchon et al. 2013), including beluga (Figures 4, 6), and may have triggered an increased calf production in 2010. However, the high calf mortalities in 2010 and 2012 remain largely unexplained, although abnormally high sea surface temperature and low ice coverage, coupled with low abundance of some potential beluga prey occurred concurrently with these mortalities (Plourde et al. 2014). Mechanisms leading to calf deaths are however, unknown.

Mortality patterns also changed during the 2000s, with more adult female beluga dying at a younger age compared to the 1990s. This may have been caused by an increase in the relative proportion of young adult females in the population, the appearance of new causes of death or changes in environmental factors affecting this particular segment of the population. An age-structured population model based on carcass recovery data, aerial survey abundance estimates and indices of calf production suggests an increase in the relative proportion of mature beluga in the population in the early 2000s (Mosnier et al. 2014). However, adult male and female mortalities during that period appeared rather stable (Figure 6), although generally above median in the case of adult females (Figure 7a), and below median in the case of adult males (Figure 7b). Dystocia (adult female death associated with complications during parturition) increased substantially in the 2010-2012 period (Lair et al. 2014), but the persistence of a significant difference in age distribution between the 1990s and 2000s even when excluding the period with high dystocia suggests that relatively earlier deaths of adult females do not result from an increase in this single cause of death. A sex-specific analysis of causes of death vs. age is required to clarify this question. Environmental factors affecting body condition or health may also be responsible for the observed pattern of mortalities. Change in environmental conditions from a cold to a warm period in the late 1990s, and from plankton communities dominated by different phytoplankton and zooplankton species in 2003, concomitant with changes in biomass of various fish species were observed in the Gulf of St. Lawrence (Plourde et al. 2014). A parallel change in the trophic ecology of the beluga was observed during the same period (Lesage 2014). Whether this change affected young adult females differently from other segments of the population is difficult to assess given the uncertainty related to the specific nature of this trophic change (Lesage 2014) and general lack of information on body condition and health of live beluga.

In spite of these temporal trends, age-specific mortality rates were similar in adult males and females over the study period, a result which was somewhat unexpected. In mammalian populations with polygamous mating systems and competition among males, females often have a higher survival rate than males, largely as a result of the costs of sexual selection for males (Ralls et al. 1980). While the mating system of beluga is unknown, males do compete for females and thus may die at an earlier age than females. SLE beluga also have high levels of contaminants, males more so than females as males are unable to transfer their contaminant burden to calves through the placenta or lactation (Lebeuf et al. 2007; 2009; 2014). Contaminants are suspected to play a role in the non-recovery of the SLE beluga population (Martineau et al. 1994) through possible impairment of the immune system, reproduction, and general health (de Guise et al. 1995; Wilson et al. 2005). Given their higher contaminant burdens, effects of contaminants on male health would be expected to be stronger than in females. However, mobilization of contaminants (from blubber to milk) during lactation may also affect female health. Tooth wear impairs age determination in beluga, particularly for animals older than 33 GLGS (Figure 2), and shows more in males than females as a result of male competition for females (Sergeant 1973; Stewart and Stewart 1989; Heide-Jørgensen et al. 1994). As a result, ages are underestimated and age distributions truncated, which may explain the lack of sex differences in mortality patterns in older age classes in our sample.

This study corroborates results indicating a sexual dimorphism in wild beluga (see Table 1 for a review), with males being larger than females but growing at a slower rate. While small sample sizes may impair some of the studies conducted in other areas, comparison of asymptotic standard length among males and females suggests that beluga from the SLE are intermediate in size, and more similar to beluga living in the Eastern Beaufort Sea. Beluga from West Russia, Greenland, and Cumberland Sound (Baffin Island) are the largest, whereas beluga from Hudson Bay appear smaller than those from most other populations. A study comparing growth curves among some of these populations has concluded that growth, but not asymptotic standard length, was a function of latitude, growth rates progressively increasing with latitude and shortening of the productive period (Luque and Ferguson 2010). The data presented here, and which included growth parameters for beluga from Russia, Greenland and the SLE in addition to the populations examined in Luque and Ferguson (2010) do not support these conclusions.

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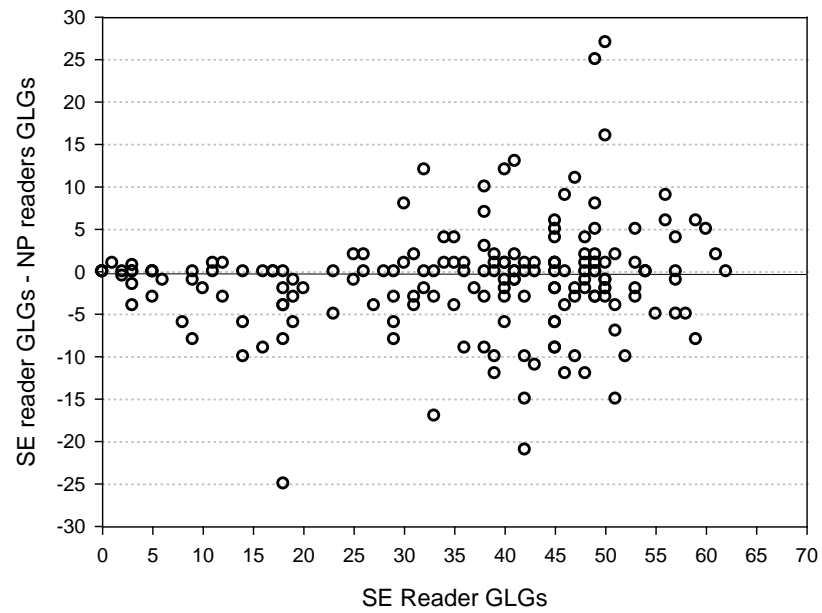


Figure 1. Comparison between age determination (in GLGs) made by a number of previous (NP) readers and a single experienced (SE) reader for a subset ($n = 179$) of teeth sampled prior to 2001.

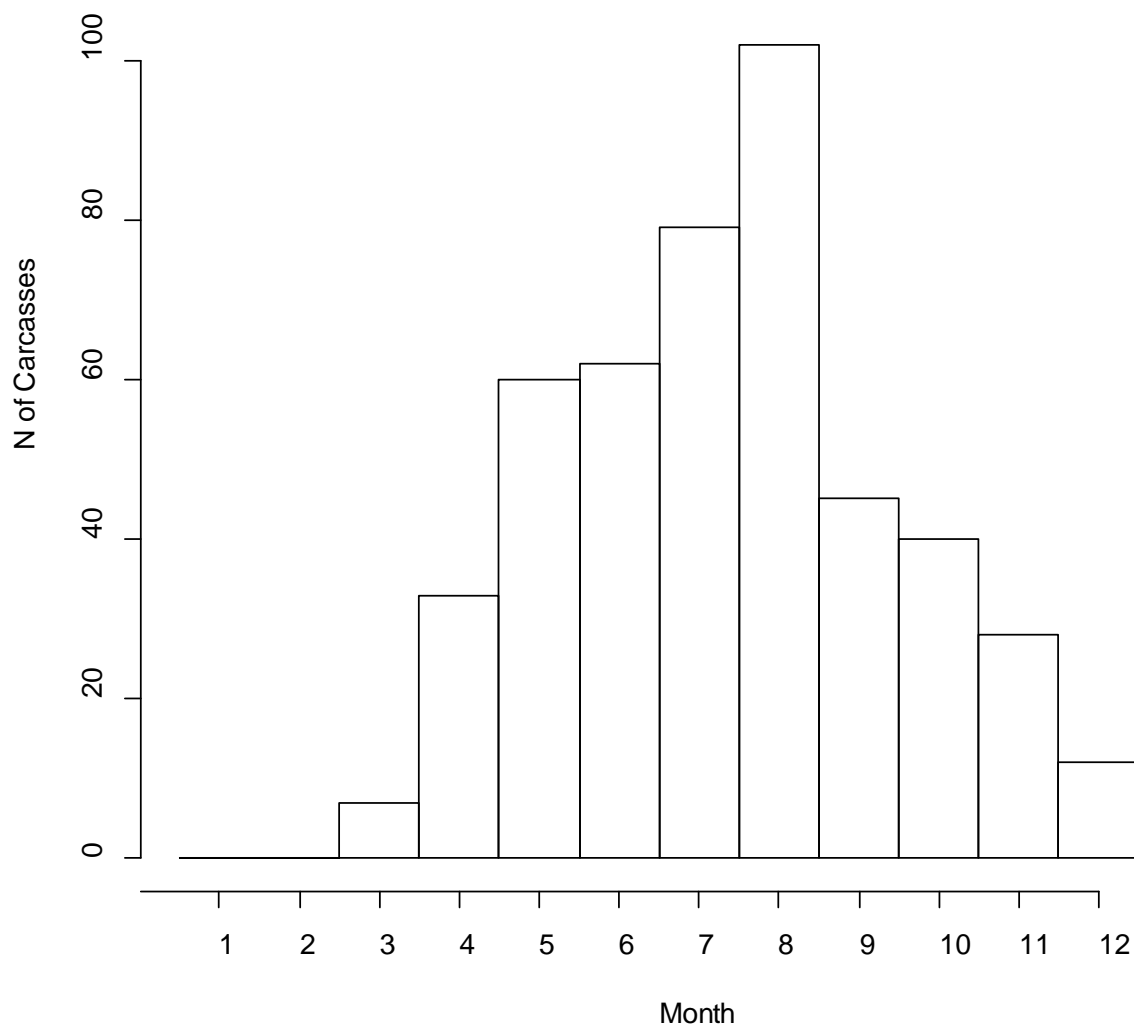


Figure 2. Seasonal distribution of beluga deaths reported ($n = 469$ beluga) in the Estuary and Gulf of St. Lawrence, 1983-2012.

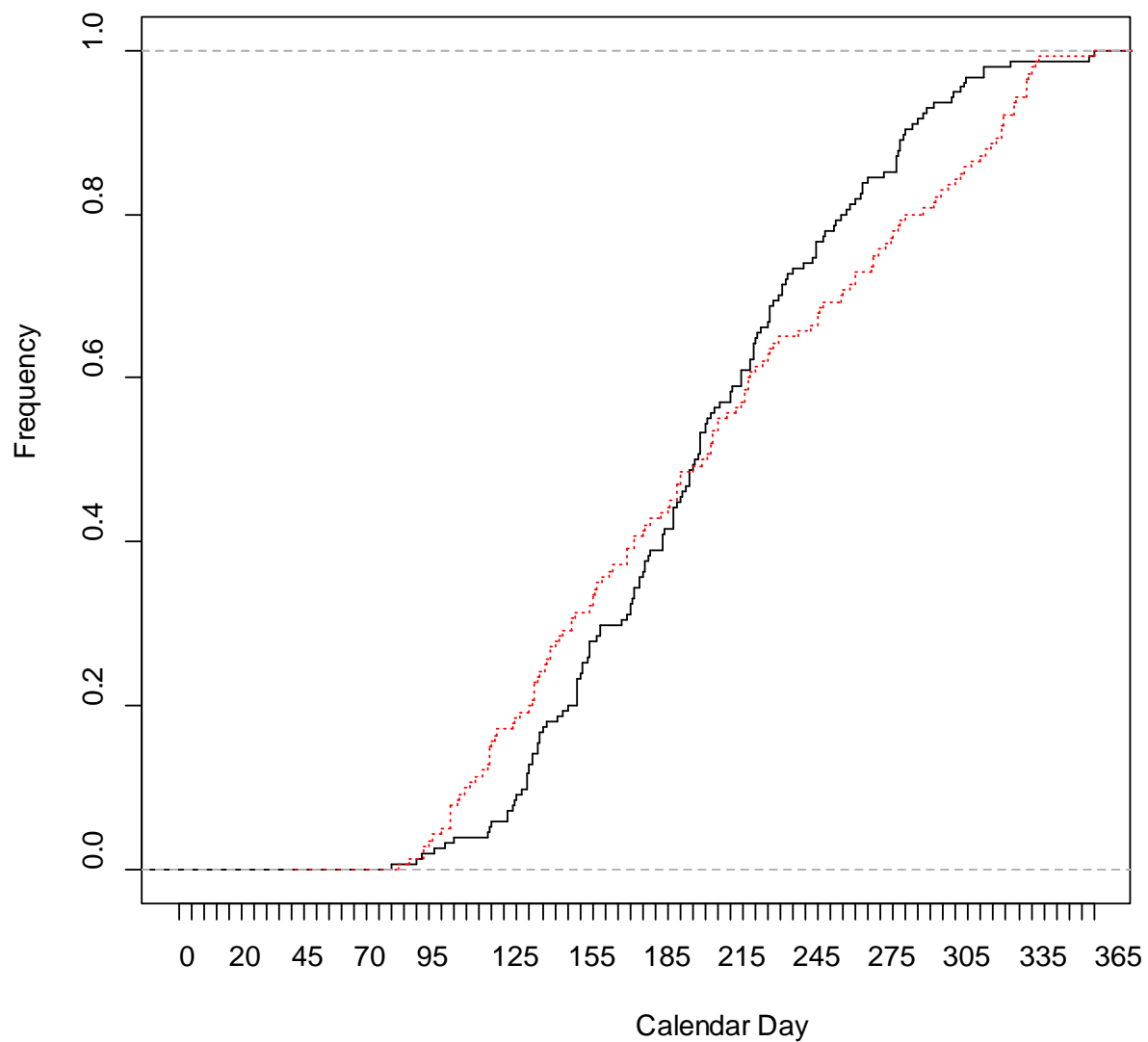


Figure 3. Comparative cumulative seasonal distribution of adult male (solid black curve) and adult female (dotted red curve) beluga deaths reported ($n = 309$) in the Estuary and Gulf of St. Lawrence, 1983-2012.

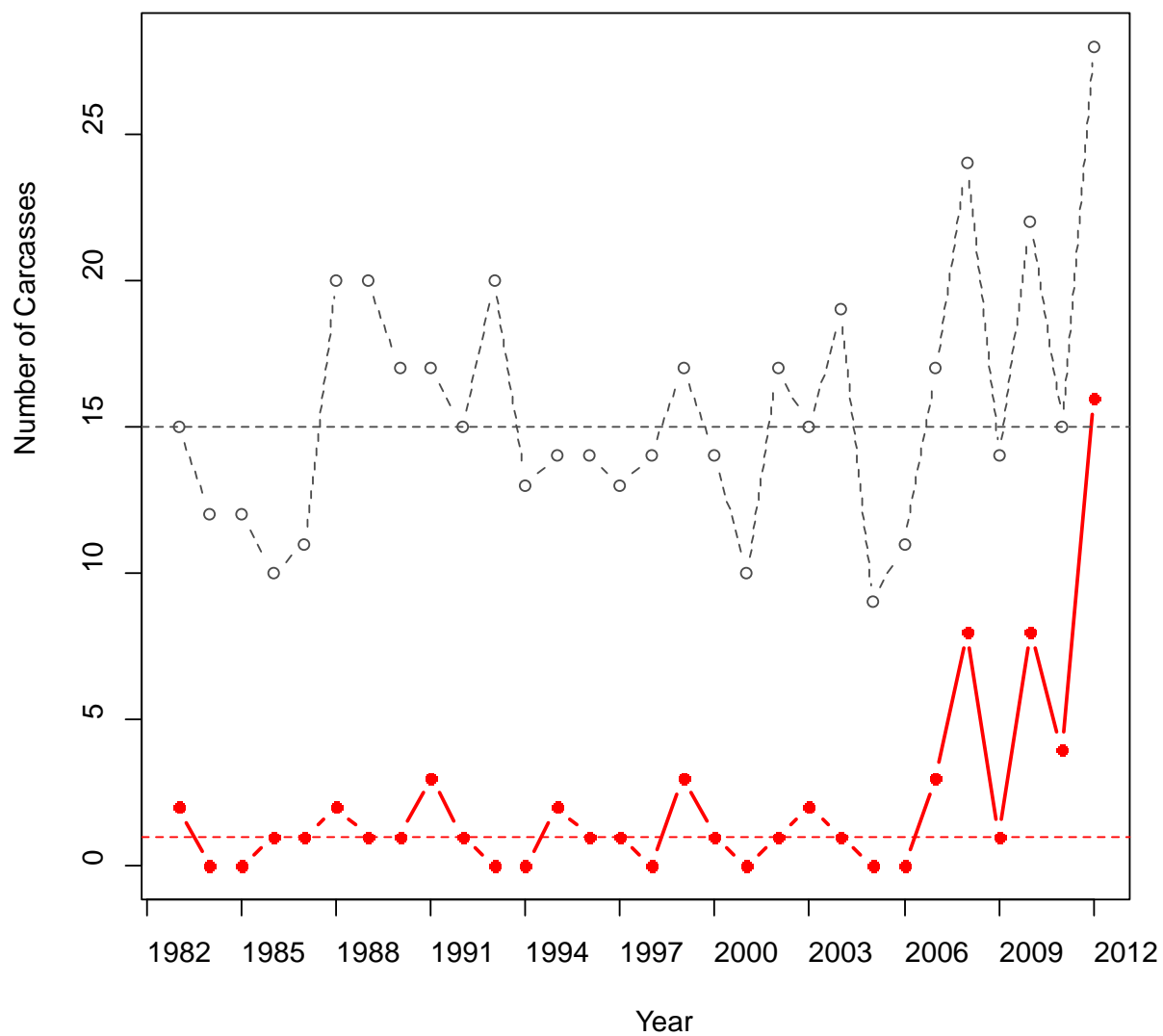


Figure 4. Total (open circle) annual reported cases of dead beluga in the Estuary and Gulf of St. Lawrence, 1983-2012, including newborn calves (closed circles). The solid horizontal lines gives the median for each time series.

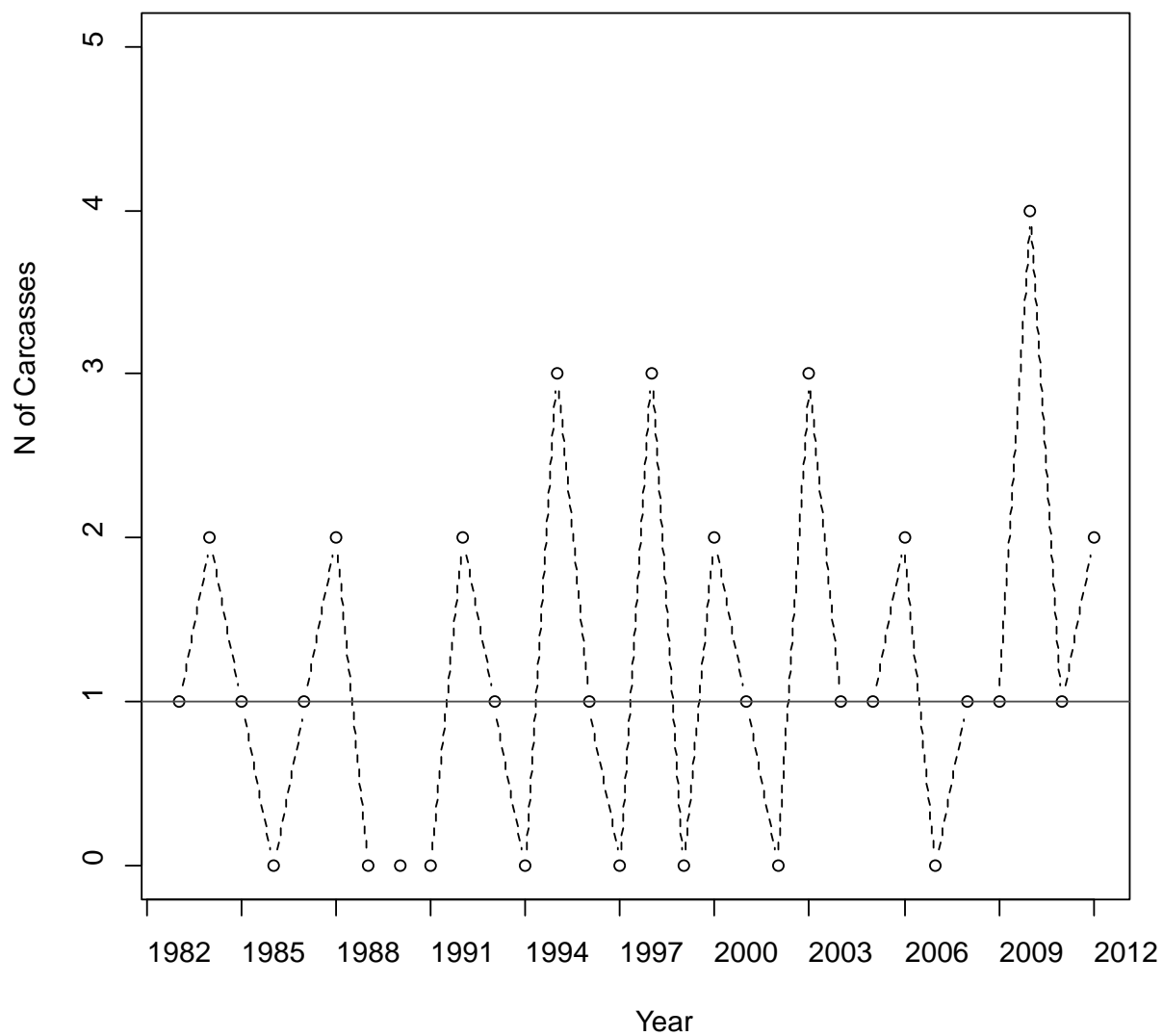


Figure 5. Annual reported cases of dead juvenile (1–7 GLGs) beluga found in the Estuary and Gulf of St. Lawrence, 1983-2012. The solid horizontal line gives the median.

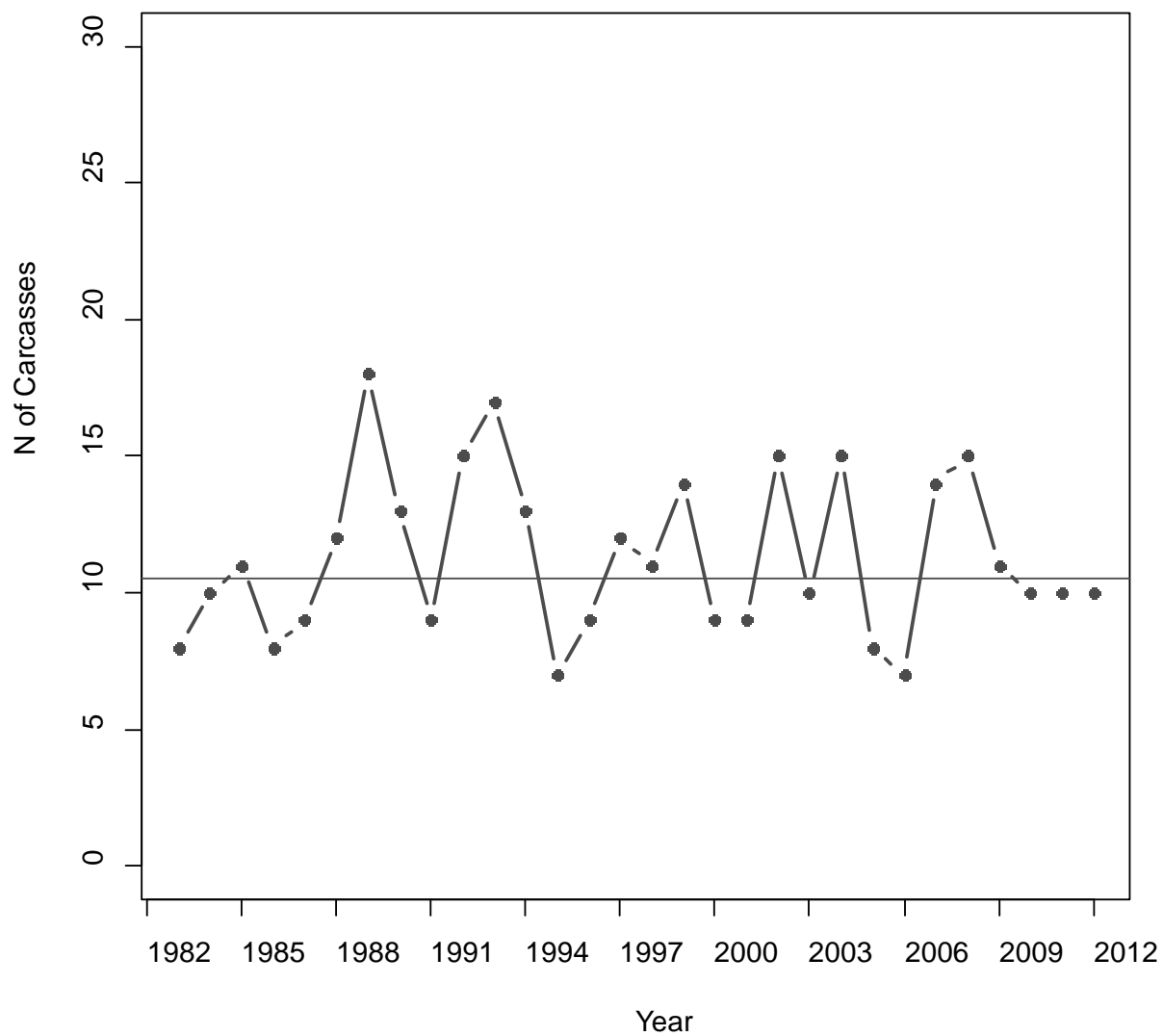


Figure 6. Annual reported cases of dead adult (8+ GLGs) beluga found in the Estuary and Gulf of St. Lawrence, 1983-2012. The solid horizontal line gives the median.

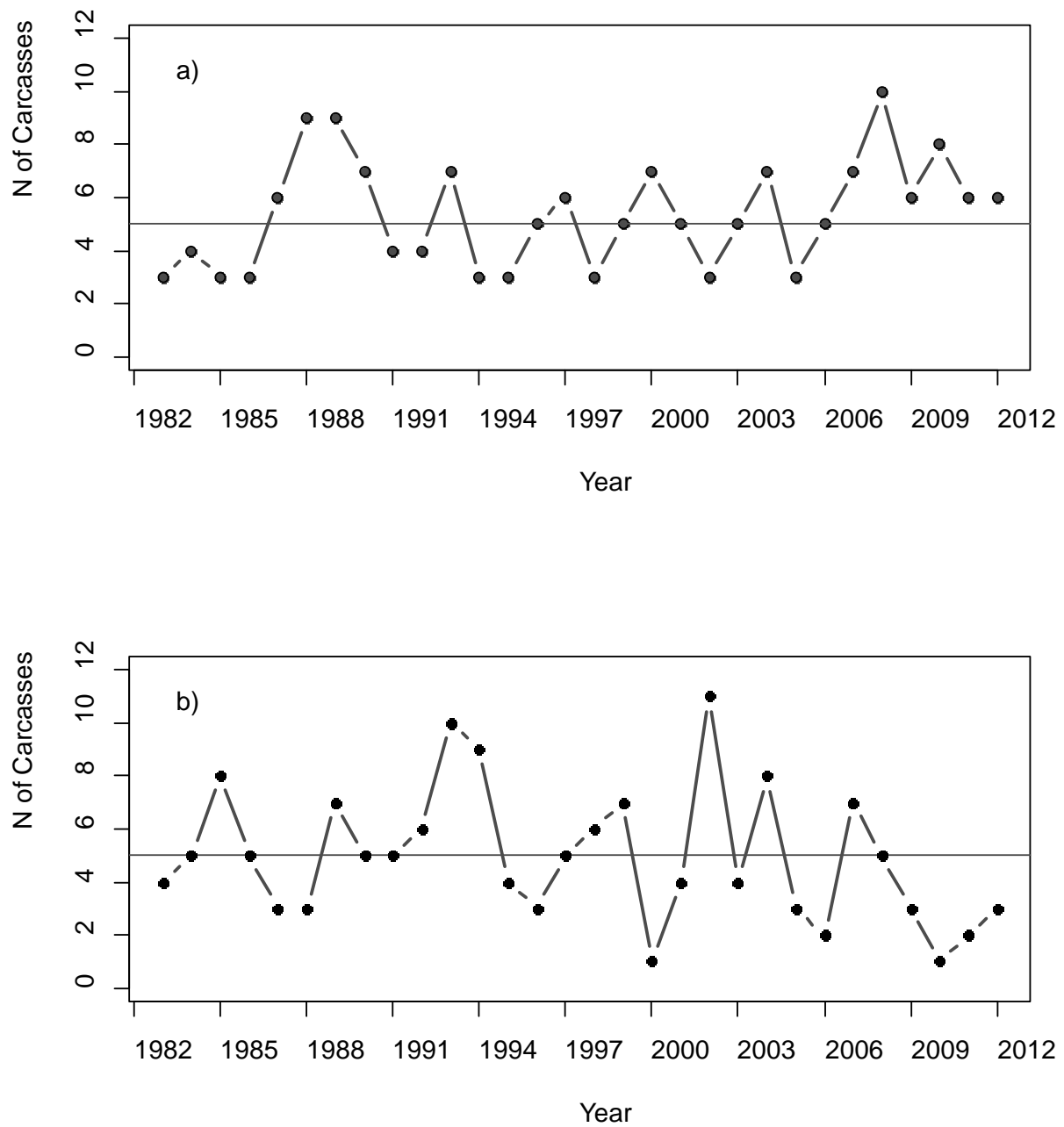


Figure 7. Annual reports of dead adult (8+ GLGs) a) female and b) male beluga found in the Estuary and Gulf of St. Lawrence, 1983-2012. The solid horizontal lines give the medians.

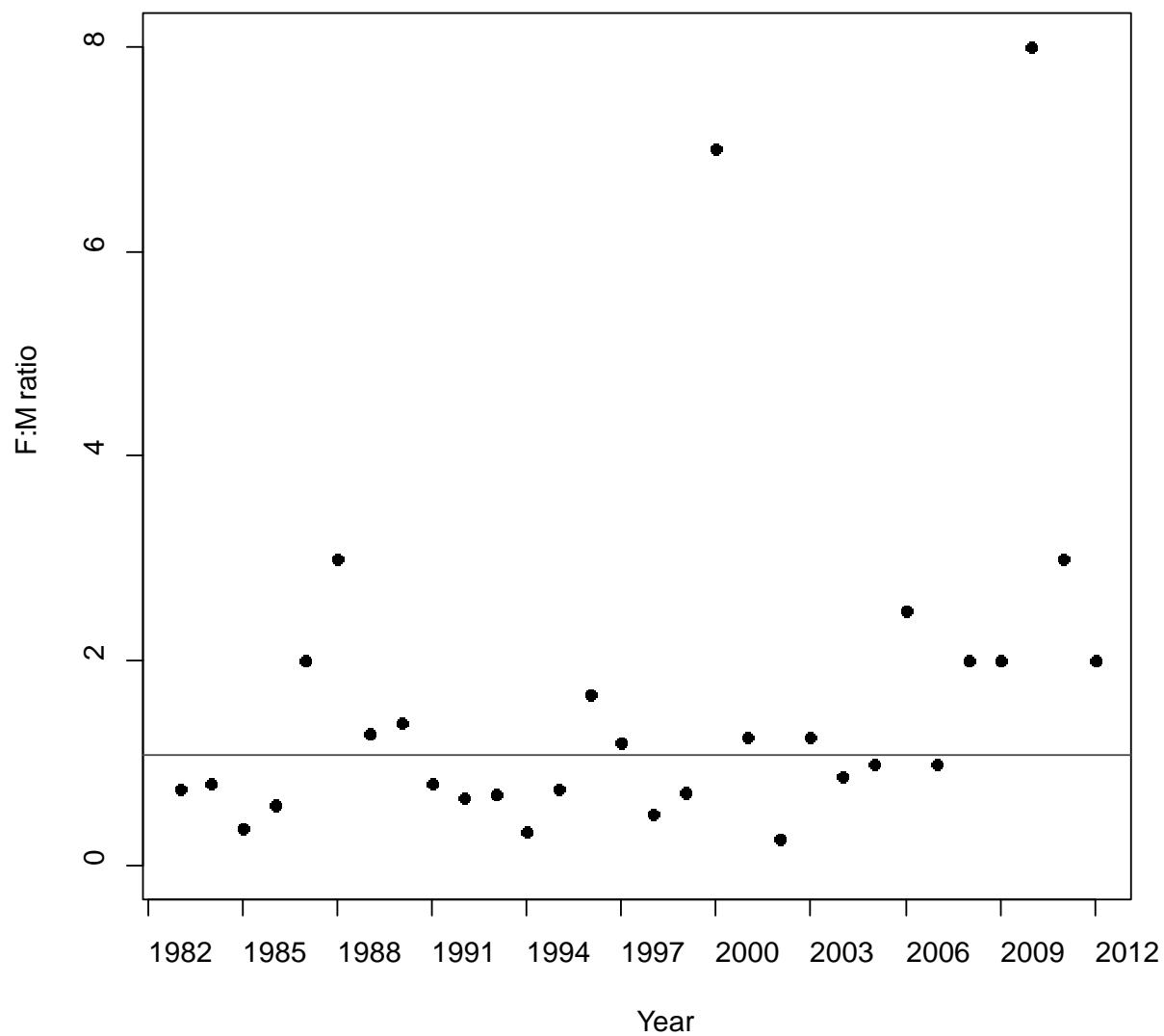


Figure 8. Female to Male (F:M) ratio among adult beluga found dead annually in the Estuary and Gulf of St. Lawrence, 1983-2012. The solid horizontal line gives the median.

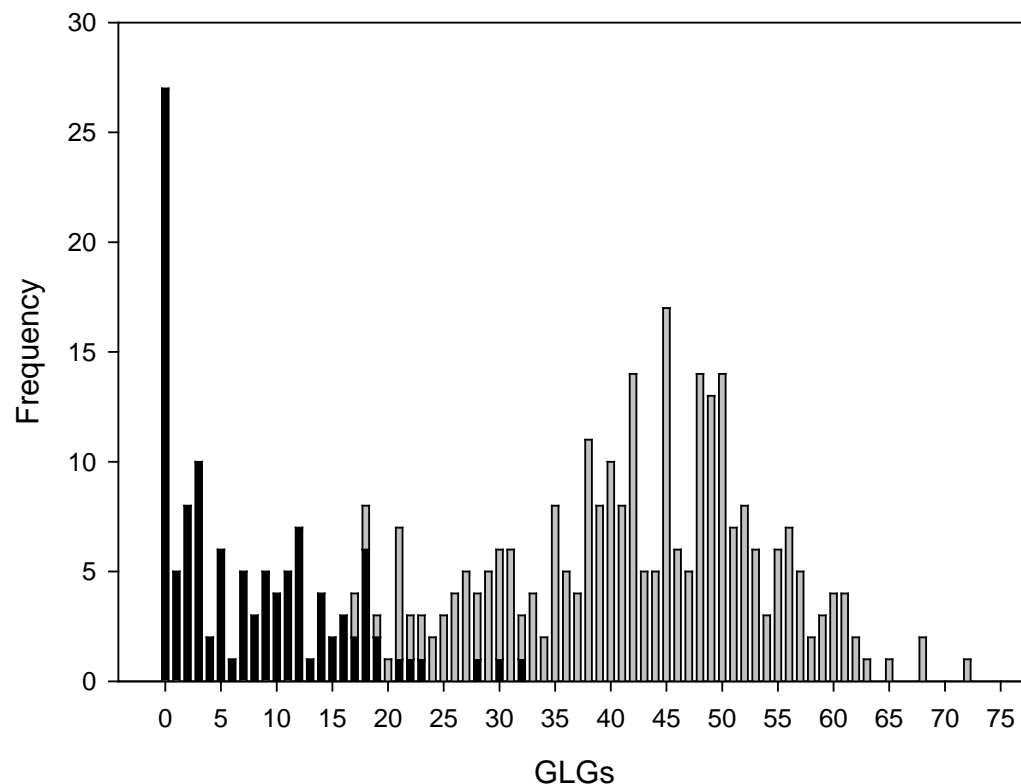


Figure 9. Age-frequency of the dead beluga ($n = 409$) found annually in the Estuary and Gulf of St. Lawrence, 1983-2012. Teeth used for determining ages (in GLGs) showed wear in older animals (grey bars; not corrected for missing layers). A tooth was considered worn when the neonatal layer was not present.

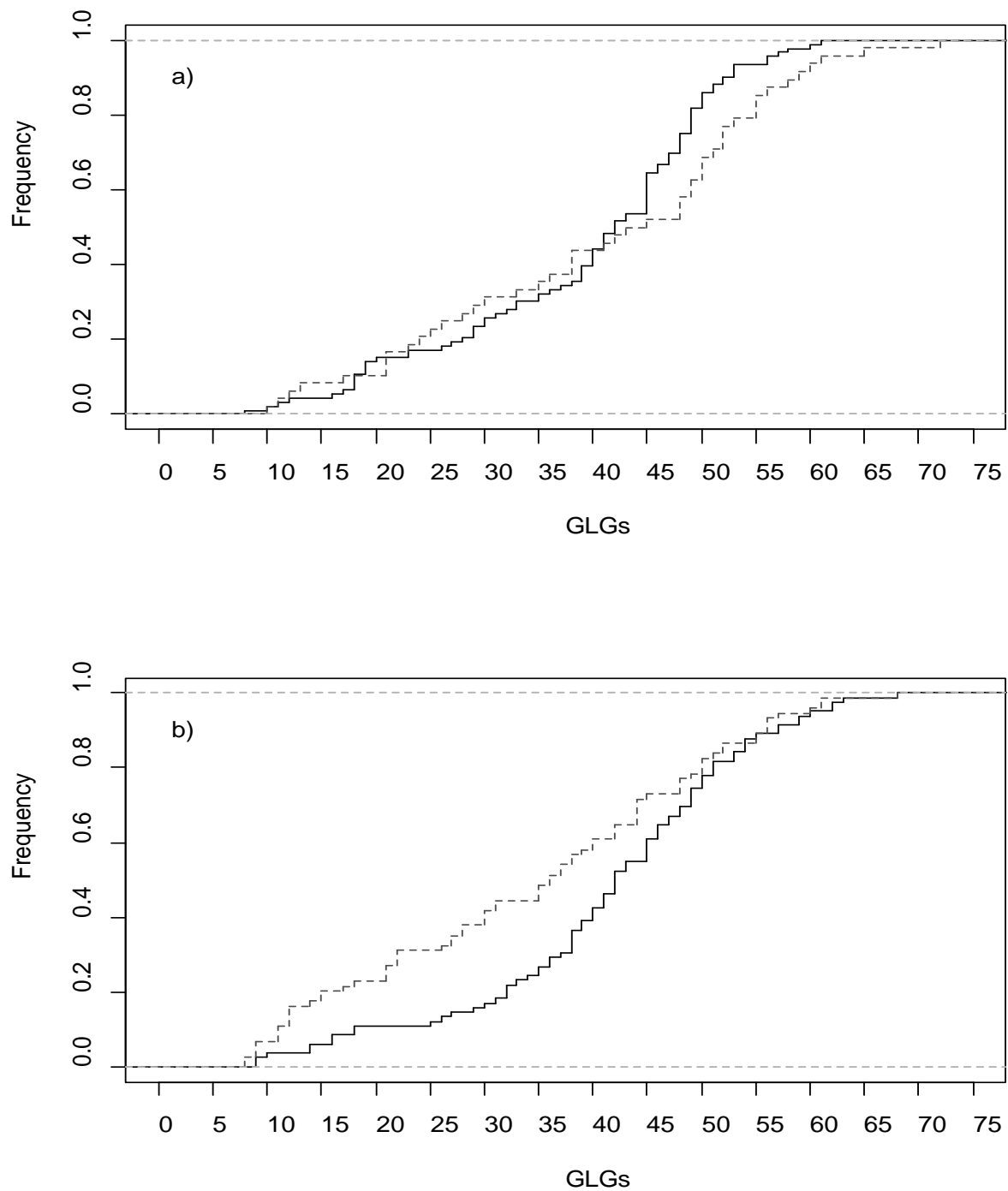


Figure 10. Comparative cumulative age-frequency distribution of a) adult males and b) adult female beluga found dead annually in the Estuary and Gulf of St. Lawrence, for the periods 1983-1999 (solid line) and 2000-2012 (dashed line).

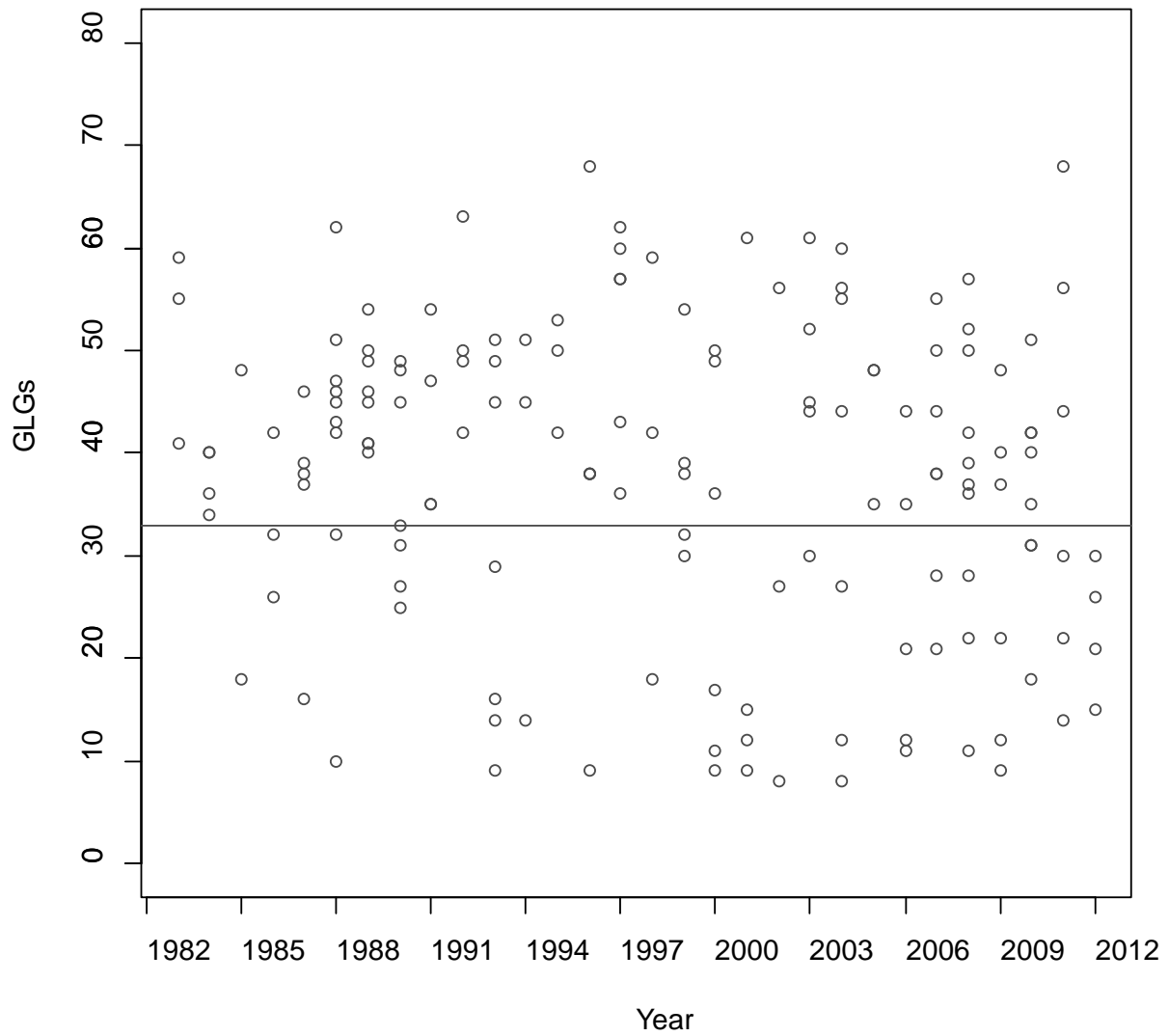


Figure 11. Age (GLGs) at death for adult female beluga found in the Estuary and Gulf of St. Lawrence, for the periods 1983-2012. Solid line represents the age (in GLGs) beyond which all teeth show sign of wear.

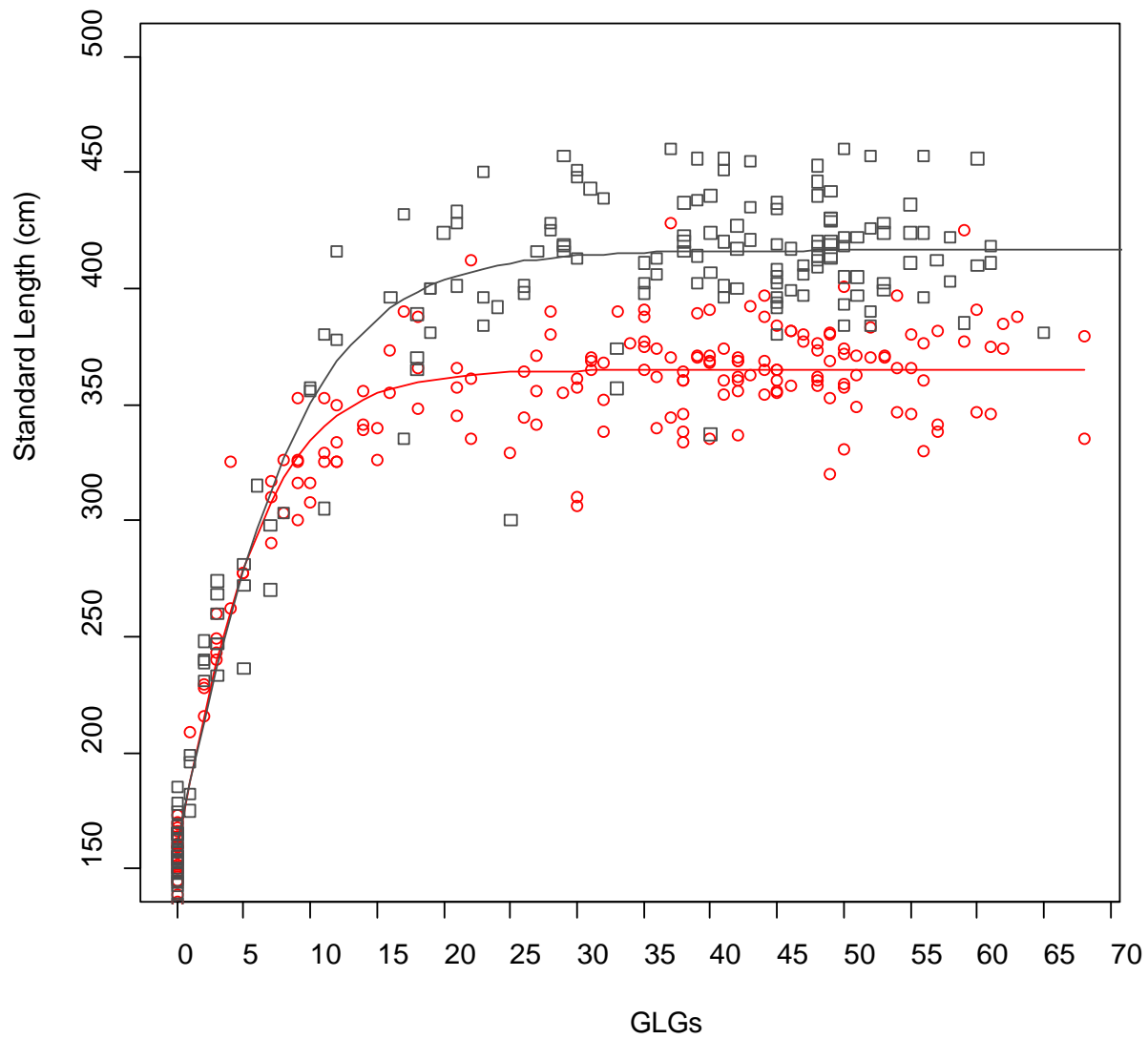


Figure 12. Growth curves for male (square) and female (circle) beluga from the Estuary and Gulf of St. Lawrence. The curves are fitted by the Gompertz model (see Table 1 for parameters).

Table 1. Growth constants (b , k) and asymptotic standard length (T_{∞}) of male and female beluga from various regions. Parameters are fitted to the Gompertz growth model. Numbers in brackets indicate 95% confidence intervals. N indicates sample size. B parameters for studies prior to 2006 are not comparable to those from later studies because of differences in age determinations. However, k parameters were corrected (halved) based on results from Stewart (1994) and Stewart et al. (2006) using the same dataset.

	Location	Males				Females			
		n	T_{∞}	b	k	n	T_{∞}	b	k
Heide-Jorgensen and Teilmann 1994	West Greenland	130	483 (458-509)	0.95 (0.89-1.01)	0.11a (0.09-0.13)	166	386 (374-398)	0.62 (0.56-0.67)	0.135 ^a (0.105-0.16)
Heide-Jorgensen and Teilmann 1994	White Sea and Kara Sea	312	434 (427-441)	0.75 (0.71-0.79)	0.105 ^a (0.095-0.115)	258	375 (370-379)	0.65 (0.60-0.70)	0.155 ^a (0.135-0.17)
Brodie 1971	Cumberland Sound	40	427			51	362		
Suydam 2010	Eastern Chukchi Sea	83	436 (420-453)	0.61 (0.54-0.76)	0.08 (0.07-0.11)	130	362 (355-368)	0.54 (0.44-0.64)	0.13 (0.11-0.17)
Suydam 2010	Kotzebue Sound	48	432 (416-449)	0.73 (0.64-0.82)	0.06 (0.05-0.08)	65	357 (350-363)	0.74 (0.62-0.86)	0.16 (0.13-0.19)
Suydam 2010	Cook Inlet	28	432 (401-461)	1.01 (-0.2-2.2)	0.16 (0.02-0.30)	17	361 (351-370)	0.84 (0.57-1.11)	0.35 (0.09-0.61)
Suydam 2010	Bristol Bay	13	405 (385-424)	1.02 (0.92-1.12)	0.15 (0.11-0.17)	9	351 (298-403)	0.69 (0.39-0.98)	0.13 (0.01-0.26)
Harwood et al. (2002)	Mackenzie River	3282	432 (427-437)			379	386 (377-395)		
Burns and Seaman 1985	Northwest Alaska	56	427	0.74	0.07 ^a	51	359	0.68	0.15 ^a
This study	St. Lawrence Estuary	178	416 (412-421)	0.94 (0.89-1.00)	0.17 (0.15-0.19)	191	365 (362-368)	0.84 (0.79-0.88)	0.23 (0.20-0.25)
Doidge 1990	Northern Quebec	44	349	0.71	0.14 ^a	55	330	0.60	0.135 ^a
Stewart 1994; Stewart et al. 2006	Western Hudson Bay	70	388		0.105 ^a	52	330.9		0.156 ^a

^a Corrected (divided by half) to account for change from annual deposition rate of 2 to 1 GLG (see Stewart 1994 vs. Stewart et al. 2006).