

DRAFT submitted for publication. DO NOT CITE!

Age estimation for young bowhead whales (*Balaena mysticetus*) using annual baleen growth increments and their rates of change

S. C. LUBETKIN, *University of Washington, Quantitative Ecology and Resource Management, Box 352182, Seattle, WA, 98195-2182, lubetkin@u.washington.edu*

J. E. ZEH, *University of Washington, Department of Statistics, Box 354322, Seattle, WA, 98195-4322, zeh@stat.washington.edu*

C. ROSA, *Department of Wildlife Management, North Slope Borough, Barrow, AK, 99723, Cheryl.Rosa@north-slope.org*

J. C. GEORGE, *Department of Wildlife Management, North Slope Borough, Barrow, AK, 99723, Craig.George@north-slope.org*

ABSTRACT

We compiled age estimates and baleen plate $\delta^{13}\text{C}$ data from 86 bowhead whales (*Balaena mysticetus*, L., 1758). We used previous whale age estimates based on aspartic acid racemization (AAR) and corpora counts to extend the use of $\delta^{13}\text{C}$ data for age determination from cycle counting to a modified exponential model using annual baleen growth increments and their rate of change with age. Our two-fold approach used the growth increment data from individual whales in a non-linear mixed effects model to assess both population level and whale specific growth parameters, and used the rate of change in the annual baleen growth rate to check the model for internal consistency and effectively estimate standard errors for whales that we estimated ages for. Although age estimates from baleen based models become less precise as the whales age, and baleen growth and length near steady state, the growth increment and rate of change models show promise in estimating bowhead whale ages, especially in bowhead length ranges where other techniques are less precise or the data are scarce.

INTRODUCTION

Historically, bowhead whale (*Balaena mysticetus*, L., 1758) ages have been difficult to determine, and, as a result, many of their life history parameters are better known in terms of length than age. Bowheads are difficult to tag, and photographic identification has been limited by lack of identifying marks, especially in young whales. In addition, even when animals are marked, it is difficult to obtain repeated observations of individuals from large populations that range over large, remote areas. Current techniques allow reasonable age estimation of mature whales using aspartic acid racemization (AAR) (George et al. 1999; Rosa et al. 2004) and counts of corpora albicantia and ovulation rates in sexually mature females (George et al. 2004). While age at sexual maturity is estimated to be in the late teens to late twenties (Schell and Saupe 1993; Zeh et al. 1993; George et al. 1999, 2004), it is more clearly known as occurring when whales reach 12-14m in length (Koski et al. 1993), with females probably sexually

mature at 13-13.5m and males at 12-13m (Koski et al. 1993, Zeh et al. 1993; O'Hara et al. 2002; George et al. 2004).

Baleen length and body length are not well correlated in bowhead whales less than 9m long or with baleen less than 200cm (Schell et al. 1989a). For these young whales, baleen length is a better indicator of age than body length, particularly if we assume that in the first few years of life, growth resources are dedicated to forming the baleen structure that will enable them to feed, with body length increases occurring later. Schell and others (Nerini et al. 1987; Schell et al. 1989 a,b; Withrow et al. 1992; Schell and Sauepe 1993) have investigated using baleen plate isotopic patterns as a tool for determining ages of bowhead whales. Most bowheads in the western Arctic population migrate annually from wintering areas in the Bering Sea to their spring and summer grounds in the Beaufort Sea. In simplified terms, plankton from the Bering and Chukchi Seas have a more enriched (higher) $\delta^{13}\text{C}$ than plankton from the Beaufort Sea. Baleen grows throughout the life of a bowhead and reflects the isotopic composition of the food the whale ingested over a lifetime. As the whales migrate from the Bering and Chukchi Seas in spring to the Beaufort Sea in summer and return to the Bering and Chukchi Seas in fall, they eat plankton with distinctly different isotopic signatures, and those differences are reflected in the baleen isotopic signatures. The regular $\delta^{13}\text{C}$ peaks (winter feeding) and valleys (summer feeding) in older whales' baleen isotopic records are thought to be indicative of feeding in locations with isotopically different food sources. If so, by counting the number of peaks (or valleys), the age of the baleen can be estimated. However, baleen age estimates can be misleading as baleen is continuously worn away. This wear may cause the number of cycles in the baleen to under-represent the whales' ages. Also, occasionally, a bowhead may not migrate to the Beaufort Sea in spring, and thus, the baleen signature will be missing evidence of that annual migration.

The purpose of this work is to use annual baleen growth increments and their rates of change to estimate ages of bowhead whales for which other aging techniques are impossible or inaccurate. Specifically, we wish to close the gap in age estimate coverage between mature whales for which AAR- and/or corpora count-based estimates are reliable and the younger whales for which annual baleen growth increments can simply be counted. In a practical sense, this means we wish to use baleen based techniques up to a maximum baleen length of about 250cm. Whales with longer baleen will be at a point where the baleen based techniques are becoming less precise and where other techniques are available and preferable.

MATERIALS AND METHODS

Data used

Our data are a compilation of $\delta^{13}\text{C}$ measurements at incremental lengths from the baleen plates of 86 whales, 40 of which had age estimates available for fitting the growth increment model based on $\delta^{13}\text{C}$ cycle counts, AAR and/or corpora counts (Rosa et al. 2004; George et al. 2004, Table 1). Portions of the isotopic data were provided by Don Schell (University of Alaska Fairbanks), and David Withrow (NOAA). Other baleen plates were sampled by Rosa. Lubetkin transcribed an additional three plates (whales 66B, 68B, and 71B) from published plots of isotopic data (Nerini et al. 1987; Schell et al. 1989b).

Baleen isotopic analysis

The collection, sampling and isotopic analysis methodology for the data from Withrow and Schell are presented in their previous works (Schell et al. 1989 a,b; Schell 1992; Withrow et al. 1992). For the new data shown here, single baleen plates were collected from 31 bowhead whales over an eight year period (1990 and 1997-2003). All samples were obtained via the Inupiat bowhead whale subsistence hunt at Barrow, Alaska, and Kaktovik, Alaska.

Each baleen plate was soaked and subsequently cleaned (superficially) with steel wool. Samples were obtained from the outside (“non-haired”) edge of the baleen with an engraving tool at 1cm or 2cm intervals, starting at the base of the plate (below the gumline). The samples were then weighed in tin cups and $\delta^{13}\text{C}$ measured via elemental analysis-isotope ratio mass spectrometry (EA-IRMS). This method utilizes a Costech Elemental Analyzer (ESC 4010), and Finnigan MAT Conflo III interface with a Delta+XL Mass Spectrometer. The combustion reactor consists of a reaction tube packed with chromium oxide and silver/cobalt oxide. The reduction tube was packed with reduced copper wire. Other elemental analyzer (EA) conditions are listed in Table 2.

Dried, homogenous samples were placed in tin capsules. The tin capsules were then closed and placed in the EA autosampler. The samples were then dropped into the EA where they were combusted. The CO_2 combustion gas was separated chromatographically and then transferred to the IRMS, where the isotopes were measured. $\delta^{13}\text{C}_{\text{PDB}}$ values were reported in reference to international isotope standards.

The QA/QC scheme involved analyzing tin capsule blanks and laboratory working standards. Blanks were analyzed every twenty samples and working standards (Peptone: No. P-7750 meat based protein. Sigma Chemical Company Lot #76f-0300) were analyzed every ten samples. Twice a year the laboratory working standards are compared to NIST standards to confirm quality assurance.

$\delta^{13}\text{C}$ cycle sampling idiosyncrasies

The baleen isotopic data had sampling inconsistencies. First, not all of the plates were sampled along their entire lengths. Second, the sampling interval varied both by and within component data sets. Some plates were sampled as finely as every 1cm for the entire plate length, others every 5cm. The plates prepared by Rosa were the most finely sampled on a consistent basis, with intervals of 1 or 2cm for all whales. The data from Schell also contained some plates sampled every 1 or 2cm, but usually only for a short section of baleen. Most of the Schell plates were sampled every 2.5cm, although some sampling was at 5cm intervals. The Withrow plates were sampled every 2.5 or 5cm. When possible the baleen plates sampled were the longest ones for each whale. Samples from neighboring plates and plates across from one another in the mouth confirm that isotopic patterns are internally consistent within each whale (data not shown).

Modeling overview

We aged the smallest whales by examining the $\delta^{13}\text{C}$ patterns in the baleen, counting the number of cycles present and adjusting this value by the number of early growth cycles that appeared to be missing or partial. Slightly older whales were aged by fitting a growth model to the baleen growth increments, using the youngest whales to characterize the initial decrease in baleen growth rate and older whales with age estimates from AAR or corpora counts to estimate the eventual asymptotic baleen growth rate.

We used two complementary ways of looking at the changing baleen growth rate and required that they have consistent estimates of the parameters governing baleen growth. Once we had internally consistent estimates of those values, we were able to use them with growth increment and rate of change data from whales with up to 250cm baleen to arrive at age estimates and associated standard errors. All modeling and statistical calculations were performed using S-PLUS.

Young whales – age estimates and age-specific baleen growth increments

It is critical to eliminate as much subjectivity and reader bias as possible from counting the number of cycles in the baleen (Lawson et al. 1992; Hohn and Fernandez 1999). Lubetkin and Rosa independently used patterns in the $\delta^{13}\text{C}$ from 24 (12 male and 12 female) of the smallest (and presumably youngest) whales to estimate their ages (Table 3). Lubetkin estimated the ages of the remaining 35 young whales (20 male and 15 female). The subset of whales with two age estimates allowed us to evaluate the consistency of ages estimated by different examiners working independently and to calculate standard errors of the estimated ages.

We also measured the annual baleen growth increments in the youngest whales. First we established “landmarks” in the baleen patterns of the very smallest of these whales, which often did not have baleen lengths of over 120cm and few of the regular cycles that are common in older whales. Following the methodology of Schell and Saupe (1993), we aligned growth increments, measured valley-to-valley, of similar lengths across whales. After aligning growth increments across whales, we calculated average increment lengths of the complete annual cycles. Age estimates in these young whales were the result of the number of complete cycles present in the baleen and how the pattern of baleen cycles and increments aligned with other young whales. The distance from the last $\delta^{13}\text{C}$ valley to the proximal terminal end of the baleen was always considered an incomplete baleen cycle, regardless of its length. Assuming that all whales were born in spring, we adjusted the age estimate of fall-caught whales by 0.5 years (Figure 1). If that last partial (by definition) cycle was over half the length of its preceding cycles, we interpreted the truncated cycle as a portion of the next full $\delta^{13}\text{C}$ cycle and added 0.5yr to the counted cycles to arrive at the age estimate (Whale 98B24, Figure 1a). If the last partial cycle was short, then we interpreted that last partial cycle as noise around the true $\delta^{13}\text{C}$ valley, indicating that the cycle count was too high, and we subtracted 0.5yr from the age estimate (Whale 99B22, Figure 1b). In general the fall-fall increments were easier to measure unambiguously, with the spring $\delta^{13}\text{C}$ peaks being softer than the fall valleys. However, the number of cycles counted remained the same regardless of which counting method was used.

Growth increment and rate of change models

We based our growth increment model on annual growth increments from the youngest whales aged with wear-adjusted $\delta^{13}\text{C}$ cycle counts and from older whales for which we had both isotopic data and an independent estimate of age from AAR and/or corpora counts. These large, old whales were critical for achieving a reasonable estimate of the eventual intrinsic baleen growth rate parameter. Whales 86KK2 and 87B6 had large sections of their baleen sampled every 5cm rather than every 2.5cm. We only used the youngest baleen (grown when the whale was oldest) that was sampled every 2.5cm

from these whales in these analyses. Even with this restriction on the baleen used, we had nine complete cycle lengths from whale 86KK2 and six from 87B6.

We chose a model structure using nonlinear regression. After considering Gompertz, von Bertalanffy, and exponential models, we chose a modified exponential decay equation to model the decreasing baleen growth increments. The modification allowed for an intrinsic baleen growth rate that persists after the initial burst of baleen growth. This growth model does not account for any potential nursing effects that would increase baleen growth in the years 1 and 2. Therefore, for ages $t \geq 3$,

$$\text{[eq'n 1]} \quad \text{Growth (cm/yr)} = G \times (1 + \exp(-k \times t))$$

This intrinsic growth rate G is necessary to preserve baleen length as the distal end is worn away as the whale ages. The parameter k controls the rate at which the exponential function decays. Since the growth rate declines with age, $k > 0$. We used non-linear mixed effects (NLME) models to estimate parameter values, which allowed us to fit each whale's growth curve specifically and see how much variation there was around the population parameters (Pinheiro and Bates 2000). NLME models allowed us to examine how much variability there was around the predicted growth curve by whale, by group (males vs. females), and within the entire population. We were also able to test if there were fixed (i.e., sex) or random effects (whale-to-whale variability) on G and/or k . We examined models with sex effects on G and/or k and random effects on G and/or k together, and chose the best model fit using the Bayesian Information Criterion (BIC), a measure which takes into account the likelihood of the data given the parameter estimates and the complexity of the model, using the formula

$$\text{[eq'n 2]} \quad \text{BIC} = -2 \log \text{Lik} + n_{par} \log(N)$$

where n_{par} is the number of parameters in the model, N is the number of observations, and $\log \text{Lik}$ is the log of the likelihood (Pinheiro and Bates 2000). Smaller BIC values correspond to simpler models with better fits to the data.

If our model of baleen growth is correct, then the growth increment data should also fit the derivative of the baleen growth model. That is, the change in the baleen growth rate over time should also be dependent on whale age. Specifically, the rate of change in baleen annual growth rate is

$$\text{[eq'n 3]} \quad \frac{d}{dt} \text{Growth} = -kG \exp(-k \times t)$$

which can be more easily analyzed by taking the logarithm of the negative (since $k, G > 0$) such that

$$\text{[eq'n 4]} \quad \log\left(-\frac{d}{dt} \text{Growth}\right) = \log(kG) - kt = \log(G) + \log(k) - kt$$

How well Equation 4 describes the baleen data will depend on whether the random effects on G or k or both are significant. If only G has a significant random component, then the slope $-k$ will be the key to fitting the model. If, on the other hand, k is the parameter with significant random effects, then the intercept term will be more

consistent across whales. Finally, if both G and k have significant random effects, then Equation 4 will be impossible to fit with any meaningful parameter values.

We estimated $\frac{d}{dt} Growth$ by fitting a least squares linear regression line to the baleen growth increment lengths over time for each whale (Figure 2). The slope from that regression should be tangent to the growth curve at the midway point, based on the number of growth increments used to find the slope. Therefore, we used the estimated slope at $t_{adj} = t - \frac{n}{2}$, where n is the number of baleen growth increments used in fitting the slope and t is the age of the whale when the last cycle was grown (Figure 2). As in the NLME model, the t estimates all came from independent analyses (cycle counting, AAR, and corpora counts). We were limited in the number of whales we could use in fitting the rate of change model (Table 1) because many had too few cycles to estimate a change in growth rate and some had estimates of the change in growth rate that were positive. All of those whales with baleen growth rates estimated to be increasing were either very old with near asymptotic baleen growth (i.e. whale 00B5, a 17.5m female estimated to be 73.2 years old via a combination of AAR and corpora based ages that was estimated to have a baleen growth rate of change 0.0123cm yr^{-2}) and/or had enough uncertainty about the estimates of their changing baleen growth rates that the slope wasn't significantly different from 0 (i.e., whale 79KK3, a 10.3m male thought to be 10.5 years old based on the number of baleen cycles present, which was estimated to have his baleen growth rate increasing by about 0.30cm yr^{-2} , but with a standard error of 0.52cm yr^{-2}).

We used an iterative process based on both the growth increment and rate of change models to arrive at estimates of G and k . We initially fit the growth model alone using a NLME model and the multiple observations from each whale for which we had an age estimate and cycle length data. Next we fit the rate of change model to the subset of known aged whales with negative regression slopes. The NLME model estimate of G was then used in the rate of change model to arrive at a new estimate of k , and the rate of change model estimate of k was used in the NLME model to find a new value of G . We continued iterating until both models had the same parameter values.

After fitting the growth increment and rate of change models, we used nonlinear least squares analysis to estimate the ages of whales with less than 250cm baleen individually. We used three versions of the growth models to estimate age. The first two were variants of the NLME model. The first of these used nonlinear least squares on annual growth increments without a random effect on G :

$$\text{[eq'n 5]} \quad \text{Growth (cm/yr)} = G \times (1 + \exp(-k \times (t - \text{CycleDiff})))$$

where CycleDiff was the difference between the position of a given baleen cycle and the last baleen cycle grown. For the newest baleen cycle (produced when the whale was oldest), there is no difference between the whale's age t and the cycle number. None of the cycle lengths was old or long enough to be first or second year baleen. (Had first or second year baleen been present, we would have been able to estimate age via the cycle counting technique.) Our second age estimate used nonlinear least squares analysis on

the annual growth increments with a random effect on G , and yielded estimates of whale age and G_{random} :

$$[\text{eq'n 6}] \quad \text{Growth (cm/yr)} = (G + G_{random}) \times (1 + \exp(-k \times (t - \text{CycleDiff})))$$

Finally, a third age estimate came from the rate of change model by rearranging Equation 4 (including finding the midpoint of the curve) to solve for age t such that

$$[\text{eq'n 7}] \quad t = \frac{\log(kG) - \log\left(-\frac{d}{dt}\text{Growth}\right)}{k} + \frac{n_{cyc}}{2}$$

where n_{cyc} is the number of complete baleen growth increments measured.

We limited our age estimation using Equations 5-7 to whales $\leq 13.5\text{m}$ in length with less than 2.5 m of baleen. Whales exceeding those body and baleen lengths had cycle lengths too uniform to get reasonable age estimates as the baleen growth curve flattens out very quickly (Figs 2 and 3 and Table 4). With the exception of whales 98KK1 and 98KK3 which had only part of their baleen plates sampled, whales with ages estimated using these models had between 6 and 11 complete baleen growth increments. Our purpose in using three methods in estimating the whales' ages was threefold: first, to investigate the effects of including G_{random} in the age estimation process; second, to compare which of the NLME models matched better with the rate of change model; and, third, to have an alternative method for estimating the standard errors of the age estimates.

Because there was uncertainty about the estimates of G and k in the growth increment and rate of change models, we used a parametric bootstrap to estimate their joint distributions and later estimate standard errors around our estimated whale ages. First, we randomly drew 1000 values of k from $N(\hat{k}, SE(\hat{k}))$ and solved for G using the NLME model (Equation 1). This yielded 1000 pairs of G and k , from which we could estimate their joint distribution. Next, we did the same process using the rate of change model (Equation 4), but this time drawing values of G from $N(\hat{G}, SE(\hat{G}))$. Once we had a joint distribution of (G, k) , we were able to use that to find bootstrapped standard errors of the age estimates. For the growth increment model, we drew 1000 pairs of (G, k) and solved for age for each whale. Each combination of G and k yielded a new age estimate for the whale, and the standard deviation of these 1000 age estimates provided the standard error of the age estimate (Table 8) obtained using the growth increment model with the Table 7 values. We repeated this, using a new 1000 samples from (G, k) , for the growth increment model including a random effect on G . Finally, we performed a similar procedure for the rate of change model, but this time in addition to drawing 1000 (G, k) pairs, we also drew 1000 values of $\frac{d}{dt}\text{Growth}$ from $N(\frac{d}{dt}\text{Growth}, SE(\frac{d}{dt}\text{Growth}))$ for each whale. In this way, we were able to take into account the quality of the data available specific to each whale when assessing the reliability of the age estimate. Because 98KK1 and 98KK3 had only 4 and 3 complete cycle lengths measured respectively, we did not use either the growth increment model with a G_{random} component

or the rate of change model on these whales, as there were too few individual points to warrant either estimating two distinct values (t and G_{random}) or a slope and its standard error.

Having three different but not independent estimates of age for each whale is almost as useless as not having any estimate of age at all. Our next task was to examine the strengths of each age estimation technique, including how well the bootstrapping captured the precision of the estimates, and then combine them into one composite estimate. Two of the techniques, the growth increment model with an estimated G_{random} and the rate of change model, had very similar age estimates for the whales but standard errors that often differed by an order of magnitude. Since these two methods both rely more heavily on k than G and provided such similar results, we chose to average their estimates to arrive at more reasonable standard errors. Here we used the fact that for any two random variables X and Y and any two constants a and b

$$\text{[eq'n 8]} \quad \text{Var}(aX + bY) = a^2\text{Var}X + b^2\text{Var}Y + 2ab\text{Cov}(X,Y)$$

where

$$\text{[eq'n 9]} \quad \text{Cov}(X,Y) = \rho_{XY}\sigma_X\sigma_Y$$

where ρ_{XY} is the correlation coefficient between X and Y , and σ_X and σ_Y are their respective standard deviations (Casella and Berger 1990). In this case we used $a = b = 1/2$. Once these two estimates were combined, we repeated this procedure by finding the mean and variance of that estimate combined with the growth increment model estimate that did not include G_{random} . This may appear to unfairly weight the composite estimate to the result from the simplest growth increment model. However, the rate of change model loses a lot of data by reducing the individual growth increment lengths down to one slope estimate, and we fear that the version of the growth increment model with G_{random} may be over-parameterized.

RESULTS AND DISCUSSION

Young whales – age estimates and age-specific baleen growth increments

Using a paired t -test, we found that the age estimates by Lubetkin and Rosa (Table 3) were not significantly different ($p = 0.85$). An F -test on the variances of those whales with average age estimates less than 5yr and those with average age estimates greater than 5yr showed a significant difference ($p < 0.001$). Whales with average estimated ages less than 5yr had residual SE = 0.42yr from an analysis of variance, and whales with average estimated ages greater than 5yr had residual SE = 1.51yr. These values provide rough estimates of SE for age estimates based on cycle counting in the ranges 1-4.5yr and 5-10.5yr, respectively.

Whale 01KK1 is listed in the database as being 13.2m long with 1.48m baleen. This pair of baleen and body lengths is an outlier from the trend shown by the other young whales (Table 3). It is possible that the baleen plate assigned to 01KK1 was mislabeled. We have shown the two independent age estimates for that whale based on the $\delta^{13}\text{C}$ patterns in the plate but excluded it from further analyses.

Based on the average lengths of complete cycles, we characterized early growth for males and females (Table 4). First year baleen is distinct from other baleen cycles in two respects: it is significantly longer (often around 50 cm, Table 4), reflecting the greater baleen growth rate of very young whales, and its $\delta^{13}\text{C}$ cycle is smoother (Fig. 1b). This smoothness is partly a result of its greater length and partly due to the isotopic averaging that occurs in the production of the mother's milk. After the first year, the baleen isotopic cycles have a fairly uniform pattern regardless of the number of cycles present. The second year baleen serves as a transition between the shallow (almost non-existent) cycles of the first year baleen growth and the regular cycles that are present subsequently. It is also distinct on the basis of its length (Table 4).

Growth increment and rate of change model fitting

We compared variations of the growth increment model with no sex effects, with sex effects on G alone or k alone, and with sex effects on both G and k . For each variation, we considered models with random effects on just G , just k , and on both G and k . We found that the best model for baleen growth rate (as determined using BIC) did not have sex effects on G or k , and included random effects on G , but not on k , indicating that while the shape of the decline in baleen growth with time remains basically the same across whales, there is significant variability in the asymptotic baleen growth rate. We found that when we included sex effects on just G or k , they were not statistically significant. Interestingly, although sex effects were statistically significant when present on both G and k , the best overall model was the one which had no sex effects (Table 5). The oldest males and females used in fitting the growth increment model did not have significantly different average annual baleen growth rates (two-sample t -test with $G_{female} = 17.3\text{cm yr}^{-1}$, $G_{male} = 15.6\text{cm yr}^{-1}$, and 4 females and 3 males had $t = 1.7375$, and $p = 0.1428$). While it appears that females may have slightly greater annual baleen growth as adults, we have too few observations to merit including sex effects in the model. Using the baleen growth increment model by itself we found $(G, k) = (16.66\text{cm yr}^{-1}, 0.215)$.

When we fit the rate of change data against age, we again found that the best model did not have sex effects (Table 6). However, the estimates of G and k were very different from those found using the growth increments, with $(G, k) = (29.87\text{cm yr}^{-1}, 0.126)$. While it is difficult to have an intuitive grasp of whether a value of 0.2 or 0.1 is more appropriate for k , it is clear that the asymptotic baleen growth rate is not near 30cm yr^{-1} (Figure 3). Our next method of fitting the rate of change model used $G = 16.66\text{cm yr}^{-1}$, as determined by the NLME model (Table 7). With that parameter fixed, we estimated $k = 0.109$ (SE = 0.019), which was not significantly different than the value estimated for k when G wasn't previously determined. The growth increment model showed significant random effects on G , indicating that the rate of change model should be more precise in its determination of slope (k) than intercept ($\log(Gk) = \log(G) + \log(k)$), so the stability of the estimate of k in the face of two very different values for G is not surprising. We also re-fit the NLME model of the growth increments, this time with $k = 0.126$ from the initial rate of change model estimations. This yielded an estimate of $G = 15.31\text{cm yr}^{-1}$. In both cases, refitting the model with either G or k predetermined led to only slight changes in the estimate of the other parameter. This indicates that each technique is better at fitting one or the other component of the growth model. Our continued iterations led to only slight changes in the estimate of G , from 15.31 cm yr^{-1} to 14.95 cm yr^{-1} , in the NLME model and in estimates of k in the rate of change model,

from 0.109 to 0.107 (Table 7). The differences in residual error, BIC and logLik between the best NLME model and the final one are very small (Table 7 and Figure 3). Similarly, while the best NLME parameters do not fit the rate of change data well (Figure 4), there is little loss of fit quality in going from the best rate of change model to the set of parameters that also fit the NLME data well (Table 7).

The more robust estimate of the correlation coefficient of G and k came from the bootstrapping procedure that used the NLME model, and led to a correlation coefficient of 0.994. This coefficient of correlation is higher than those estimated by either the initial NLME or rate of change models, which estimated the correlation of G and k to be 0.801 or 0.545, respectively (Table 7), and results from specifying the range of values G or k was drawn from. The higher correlation coefficient leads to a higher covariance estimate (Equation 8) and very slightly higher age estimate standard errors from the bootstrapping procedure.

Age estimates for whales up to 13.5m in length

Age estimates from the baleen growth increments and their rates of change have little correlation with body or baleen length (Table 8). Individual age estimates ranged from 4.0 (whale 79KK5, a 10.7m male with 200cm baleen containing 6 complete growth increments) to 35.0yr (whale 86B6, a 12.3m female with 230cm baleen containing 11 complete growth increments). Standard errors from the bootstrap procedures were either surprisingly and unrealistically small, ranging only as high as 3.0yr for whale 86B6 using the growth increment model or disproportionately large, up to 11.2yr for whale 02B21, when we used the rate of change model. There was no significant increase in standard error with increasing age estimate, in part because older whales with longer baleen plates have more growth increments to use in estimating whale age.

Perhaps the most striking trend in the age estimates from the three model variations is that the growth increment model with an estimated G_{random} and the rate of change model were a very good match, while the growth increment model age estimates without concomitant estimate of G_{random} were often quite different (Table 8). The agreement between the growth increment age estimates with G_{random} and rate of change age estimates gives insight into what the driving factor is in estimating age using the growth increment model more than it serves as evidence that those two estimates are more reliable than the growth increment model without G_{random} .

When we estimated whale age and G_{random} with the growth increment model, we saw the suggestion that females have larger asymptotic baleen growth rates. All four females we used the model on had positive G_{random} , and three had a difference between the population mean G and their asymptotic growth rate of more than 2.4cm yr^{-1} (Table 8). Of the nine males, only three had random effects that were greater than 0, and two of those were more than 2cm yr^{-1} . The random effects were estimated with remarkable consistency across all the whales we estimated ages for, with all the G random effects having standard errors ranging from 0.12-1.05 cm yr^{-1} .

The growth increment model with G_{random} and rate of change model estimates had a correlation coefficient of 0.9814. The resulting averaged age estimates had a correlation coefficient of 0.4010 with the growth increment model estimates that did not have a random component. Our final composite age estimates both showed a general increase with body and baleen length, although estimated ages for females tended to be higher than those for similarly sized males (Table 8). The standard errors from the

composite age estimates look quite reasonable, with coefficients of variation ranging from 12 to 20% for all but one individual (whale 79KK5, with a CV of 47%, but with a much lower age estimate than the other whales in this sample). The standard errors are fairly accurate assessments of how precise we feel the age estimates are, with the exception of whales where the three techniques had very different individual estimates (i.e. whales 02B21, 86B6, 02B20, and 90B8). In these four cases there is a minimum of 8 years difference between the lowest and highest age estimates, a significant discrepancy for whales estimated to be in their late teens to mid-20s, but not one that is caught when using Equation 8. Overall, we place more confidence in the composite age estimates and standard errors for those whales where the individual techniques resulted in similar estimates than we do in those cases where the growth increments and slopes showed unexpected patterns. Surprisingly, we saw little effect of the sampling interval on either $SE(\frac{d}{dt} Growth)$ or the precision of the individual or composite age estimates (Table 8).

It appears that the overall shape of the growth increments is captured even with fairly coarse sampling. In addition, there is enough whale-to-whale and interannual variability (perhaps related to weather and ice conditions) that even the growth increment lengths from finely sampled baleen plates don't exactly follow the predictions from the models.

The composite age estimates are in line with AAR-, corpora count- and cycle count-based estimates for similarly sized whales with similar baleen lengths up to baleen lengths of about 2.50m and body lengths to roughly 13.5m (Figs 5 and 6). For example, the smallest males on which we used all three growth models were 10.7m long with 2.00m baleen and estimated to be 6.4 and 11.0 years old (Table 8). Other males ranging from 10.5 to 10.9m with 1.74 to 1.93m baleen were estimated to be 9.6 to 13.3 years old via cycle counting (Table 3) and/or AAR (Figs 5 and 6). (It should be noted that whale 79KK5, which had a surprisingly low age estimate, had the steepest slope on which we used the rate of change model and the largest standard error around its rate of change estimate. These two factors put this whale in the region where the random effects around G play a large role (Figure 4) and increase the SE associated with the rate of change model age estimate.) The largest male we applied the growth increment model to was 13.5m with 2.15m baleen with an estimated age of 18.2yr (Table 8). This estimate was lower than AAR age estimates for whales of similar body lengths, which fell between 20 and 60 years, but closer to age estimates of whales with baleen lengths between 2.1 and 2.2m, which ranged from 8-34yr based on AAR (Rosa et al. 2004).

For the females, the smallest whale we aged with all three techniques was 02B21, a 10.0m whale with 1.92m baleen, which we estimated to be 17.4 years old. That age estimate may seem high, especially when compared to cycle counting age estimates of similarly sized whales that are closer to 5 or 6 years, but AAR age estimates for whales that size range from 6 to 46. The largest female aged using growth increment models was 86B6. This 12.3m whale with 2.30m baleen had an age estimate of 25.7yr, within the 24 to 32yr range seen for females between 12.1 and 12.6m in length aged by AAR (Rosa et al. 2004).

Whales with matching body and baleen length measurements may be estimated to have different ages based on their unique annual growth increments, as 86B7 and 79KK5 were (Table 8). These two males have surprisingly different age estimates, especially when age is estimated using the growth increment model. Individual variation around the

average growth curve led to these different age estimates, which would not have been seen using an equation based solely on body or baleen length.

It is clear from Table 1 and Fig 3 that more data are needed to fully characterize the growth increment curve. In particular, whales between 9.5 and 13.5m in length with age estimates are needed. Whales in this age range should still have enough change in their growth increments to delineate the growth model as the curve becomes more shallow.

Age at sexual maturity

Baleen growth increments are only useful for age estimation until those increments reach their asymptotic values, and, thus, these techniques have limited use in making inferences about bowhead age at sexual maturity. We considered males 12.3-13.1m long as mature, with baleen lengths ranging from 210-243cm. These individuals had composite age estimates ranging from 15.8-17.7yrs (Table 8). For the females, sexual maturity is attained around body lengths 13-13.5m, when baleen lengths range from 236-260cm. These measurements exceeded the whale sizes where the growth increment models can provide reliable age estimates. Since the largest female we used the models on was estimated to be 25.7 years old, our only indication from this model is that females attain sexual maturity in their mid-20s (Table 8).

Recommendations for the use of these models

For whales under 10m in length, cycle counting appears to be the best method for determining age. The first years of baleen growth are quite distinctive and reader bias appears low. Baleen growth increment modeling is effective until the whales reach a body length exceeding 13.5m and/or a baleen length of 250cm or more. For smaller whales with shorter baleen plates, the relationship between baleen length and age is clearer (Figs 6a,b). However, the whale to whale variability is so high that baleen length alone is not a good predictor of age except for whales with 105cm of baleen or less, who are only a year or two old (Table 3). Overall, the composite estimate from the growth increment-based models provides a good bridge between counting cycles in the baleen and using techniques such as AAR and corpora counts that are effective in older whales.

ACKNOWLEDGMENTS

The authors extend their thanks to the North Slope Borough Department of Wildlife Management, the Cooperative Institute for Arctic Research, the University of Alaska Fairbanks Experimental Program to Stimulate Competitive Research, and NOAA for their support and funding. They would also like to thank the Inupiat subsistence hunters in Barrow and Kaktovik for graciously allowing us to collect these samples. The authors are indebted to Norma Haubenstein, Tammy Massie and Tim Howe for laboratory support. Finally, they thank all those who shared their historical isotopic data, especially Don Schell and David Withrow.

REFERENCES

- Casella, G., and Berger, R. L. 1990. *Statistical Inference*. Duxbury Press, California.
- George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77:571-80.
- George, J.C., Follman, E., Zeh, J., Sousa, M., Tarpley, R. and Suydam, R. 2004. Inferences from bowhead whale ovarian and pregnancy data: age estimates, length at sexual maturity and ovulation rates. Paper SC/56/BRG8 presented to the IWC SC, June 2004.
- Hohn, A. A., and S. Fernandez. 1999. Biases in dolphin age structure due to age estimation technique. *Mar. Mammal Sci.* 15: 1124-1132.
- Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. *In The Bowhead Whale Special Publication No. 2 of the Society for Marine Mammalogy. Edited by J. J. Burns and J. J. Montague and C. J. Cowles.* Allen Press, Inc., Lawrence, Kans. pp. 239-274.
- Lawson, J. W., Harrison, G. D., and Bowen, W. D. 1992. Factors affecting accuracy of age determination in the harp seal, *Phoca groenlandica*. *Mar. Mamm. Sci.* 8: 169-171.
- Nerini, M.K., Brooks, J.M., and Pflaum, R. 1987. Preliminary examination of carbon isotope composition of bowhead whale baleen plates. Paper SC/39/PS23 presented to the IWC SC, June 1987 (unpublished).
- O'Hara, T.M., George, J.C., Tarpley, R.J., Burek, K., and Suydam, R.S. 2002. Sexual maturation in male bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas stock. *J. Cetacean Res. Manage.* 4(2):143-8.
- Pinheiro, J. C., and Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York.
- Rosa, C., George, J. C., Zeh, J., Botta, O., Zauscher, M., Bada, J., and O'Hara, T.M. 2004. Update on age estimation of bowhead whales (*Balaena mysticetus*) using aspartic acid racemization. Paper SC/56/BRG6 presented to the IWC SC, June 2004.
- Schell, D. M. 1992. Stable isotope analysis of 1987-1991 zooplankton samples and bowhead whales tissues. OCS Study MMS 92-0020, report to U.S. Minerals Management Service.
- Schell, D. M., and Saupe, S. M. 1993. Feeding and growth as indicated by stable isotopes. *In The Bowhead Whale Special Publication No. 2 of the Society for Marine Mammalogy. Edited by J. J. Burns and J. J. Montague and C. J. Cowles.* Allen Press, Inc., Lawrence, Kans. pp. 491-509.
- Schell, D. M., Saupe, S. M., and Haubenstock, N. 1989a. Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}\text{C}$ techniques. *Mar. Biol.* (Berl.), 103: 433-443.

- Schell, D. M., Saupe, S. M., and Haubenstein, N. 1989b. Natural isotope abundance in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. *In Stable Isotopes in Ecological Research*. Edited by P.W Rundel, J. R. Ehleringer and K. A. Nagy. pp. 260-269
- Withrow, D., Burke, R., Jr., Jones, L., and Brooks, J. 1992. Variations in $\delta^{13}\text{C}$ carbon isotope ratios in bowhead baleen plates used to estimate age. *Rep. int. Whal. Commn.* 42: 469-473.
- Zeh, J. E., Clark, C. W., George, J. C., Withrow, D., Carroll, G. M., and Koski, W. R. 1993. Current population size and dynamics. *In The Bowhead Whale Special Publication No. 2 of the Society for Marine Mammalogy*. Edited by J. J. Burns and J. J. Montague and C. J. Cowles. Allen Press, Inc., Lawrence, Kans. pp 409-489.

Table 1. Age estimates used in fitting the growth increment and rate of change models.

Growth increment model	n	Length Range (m)		Estimated Age Range (yrs)
		Body	Baleen	
Cycle counting				
Males	14	7.6-10.4	1.18-1.90	4-11
Females	10	7.5-10.3	1.30-1.92	3.5-9
AAR				
Males	3	14.5-17.4	2.89-3.84	57-172
Cycle counting and AAR				
Males	2	10.5-10.9	1.74-1.92	9.6-9.8
Females	1	9.7	1.75	5.2
Corpora counts	8	13.6-17.7	2.60-3.56	27.5-52
Females				
Corpora counts and AAR	2	14.5-17.5	2.73-3.31	31-73.2
Females				
Total	40			
Rate of change model	n	Length Range (m)		Estimated Age Range (yrs)
		Body	Baleen	
Cycle counting				
Males	6	8.9-10.4	1.30-1.90	7.25-11
Females	2	8.9-9.3	1.82-1.85	6.75-9
Cycle counting and AAR				
Females	1	9.7	1.75	5.2
Corpora counts and AAR				
Females	1	14.5	2.73	31
Corpora counts				
Females	6	14.9-17.7	2.97-3.56	27.6-52
Total	16			

Table 2. Elemental analyzer conditions (ESC 4010)

Combustion tube temperature	1020°C
Reduction tube temperature	700°C
He flow rate	120 mL/min
GC column	3m 5Å mol sieve
GC oven temperature	70°C
Water trap	magnesium perchlorate

Table 3. A subset of 24 young whales for which Lubetkin and Rosa independently estimated ages (in years) from $\delta^{13}\text{C}$. Whales are ordered by increasing average age. SL indicates that Lubetkin estimated the whale's age to be this many years. CR indicates that Rosa made that age estimate.

Whale	Sex	Body Length (m)	Baleen Length (m)	Age Estimates			
				SL	CR	Ave.	Diff.
99B19	F	8.1	0.74	1.5	1.0	1.25	0.5
98B14	M	8.2	0.74	1.5	1.5	1.5	0
01B23	F	8.0	0.84	1.5	1.5	1.5	0
01B16	M	8.6	0.94	1.0	2-2.5 ^a	1.63	-1.25
01B22	F	8.2	0.87	2.0	1.5	1.75	0.5
99KK1	F	7.7	0.85	1.5	2.5	2.0	-1.0
01B13	F	8.2	0.94	2.0	2.0	2.0	0
99B20	F	9.0	0.98	2.5	2.0	2.25	0.5
00KK3	F	8.8	1.12	2.5	2.5-3 ^a	2.63	-0.25
03B3	F	9.0	1.18	3.0	2.5-3 ^a	2.88	0.25
01B10	M	8.1	1.26	3.0	3.5	3.25	-0.5
01B12	M	9.1	1.41	3.0	3.5	3.25	-0.5
98B13	M	9.3	1.38	3.5	3.0	3.25	0.5
01KK1	F	13.2	1.48	3.5	4.5	4.0	-1.0
01B21	M	8.9	1.41	4.5	4.5	4.5	0
99KK3	M	8.3	1.30	3.5	7.0	5.25	-3.5
99B22	F	9.7	1.42	5.5	5.0	5.25	0.5
98B24	F	10.3	1.75	7.5	5.5	6.5	2.0
02B17	F	9.3	1.85	5.5	8.0	6.75	-2.5
02B19	M	9.4	1.63	7.5	6.5	7.0	1.0
00B13	M	9.4	1.76	6.5	8.0	7.25	-1.5
02B10	M	9.5	1.76	8.5	8.0	8.25	0.5
99B23	M	10.9	1.60	10.5	8.0	9.25	2.5
99B21	M	10.5	1.74	10.5	8.5	9.5	2.0

^a In cases where Rosa left the estimate as an age range, we used the midpoint of the range to compute averages and differences in the paired *t*-test and *F*-test.

Table 4. Annual $\delta^{13}\text{C}$ valley to valley (autumn to autumn) baleen growth increments (cm) in young whales. Saupe and Schell (1993) also measured growth increments as the distance between $\delta^{13}\text{C}$ valleys. The year 0 increment includes all baleen grown until the whale's first autumn, including fetal baleen. The year 1 growth increment begins at the whale's first autumn.

Year	Length	Males		Length	Females		Saupe and Schell (1993)
		Std. Dev.	n		Std. Dev.	n	
0	25.92	8.00	13	21.00	6.90	12	
1	53.71	10.84	12	53.47	5.37	15	>45
2	35.45	7.23	11	34.96	7.13	14	35-45
3	26.58	6.21	12	25.38	6.50	12	27.5-35
4	22.82	4.42	11	23.00	2.12	8	<27.5
5	22.23	2.59	11	21.30	1.20	5	
6	21.86	5.20	11	25.17	2.75	3	
7	20.67	5.94	9	20.00	-	1	
8	20.60	5.64	5	17.50	-	1	
9	20.50	1.00	4				
10	21.00	2.00	4				
≥ 50	15.63	1.19	3	17.32	1.33	4	
			(13) ^a			(25) ^a	

^a There were 3 males with growth increment measurements occurring at ages ≥ 50 yrs. There were 5, 4, and 4 cycles observed in those males for a total of 13 observations in older males. There were 4 females with growth increment measurements occurring at ages ≥ 50 yrs. There were 15, 4, 4, and 2 cycles observed in those females for a total of 25 observations from older females.

Table 5. Parameter estimates and model fit statistics for NLME models using the growth increment model with fixed (sex) and random effects on G , k , or both indicate that the most parsimonious model with random effects on G was the best. For each model type (where sex effects are included or not), we show the model with random effects on G , k , or both that had the lowest BIC. Recall that G is the asymptotic baleen growth rate in cm yr^{-1} , and k is the rate of decline of the growth curve.

Model: No sex effects, random effects on G					
Parameter	Value	Standard Error	t - statistic	p -value	
G	16.66	0.67	24.95	<0.0001	df = 215
k	0.215	0.041	5.19	<0.0001	BIC = 1384.941
Correlation of G and k = 0.801					
G random effects		Std. dev. = 2.21	Residual = 3.06		

Model: Sex effect on G , random effects on G					
Parameter	Value	Standard Error	t - statistic	p -value	
G	16.47	0.95	17.40	<0.0001	df = 214
k	0.207	0.043	4.79	<0.0001	BIC = 1390.826
G_{sex}	0.178	0.859	0.21	0.836	
G random effects		Std. dev. = 2.20	Residual = 3.06		

Model: Sex effect on k , random effects on G					
Parameter	Value	Standard Error	t - statistic	p -value	
G	16.59	0.66	25.26	<0.0001	df = 214
k	0.195	0.041	4.72	<0.0001	BIC = 1390.306
k_{sex}	0.037	0.052	0.71	0.480	
G random effects		Std. dev. = 2.19	Residual = 3.06		

Model: Sex effects on G and k , random effects on k					
Parameter	Value	Standard Error	t - statistic	p -value	
G	15.58	0.71	21.83	<0.0001	
k	0.171	0.044	3.88	0.0001	df = 213
G_{sex}	2.23	0.77	2.91	0.0040	BIC = 1393.519
k_{sex}	0.152	0.065	2.36	0.0193	
k random effects		Std. dev. = 0.101	Residual = 3.21		

Table 6. Parameter estimates and model fit statistics for rate of change models with and without sex effects on G and/or k show that neither parameter has a significant sex effect.

Model				
No sex effects				
Parameter	Value	Standard Error	t -statistic	
k	0.126	0.0207	6.09	df = 14
G	29.87	10.78	2.77	RSE = 1.211
Model				
Sex effect on G				
Parameter	Value	Standard Error	t -statistic	
k	0.129	0.0275	4.68	df = 13
G	28.345	14.624	1.94	RSE = 1.256
G_{sex}	3.708	25.335	0.15	
Model				
Sex effect on k				
Parameter	Value	Standard Error	t -statistic	
k	0.293	0.322	0.910	df = 13
G	31.648	18.102	1.75	RSE = 1.254
k_{sex}	-0.165	0.308	-0.53	
Model				
Sex effects on G and k				
Parameter	Value	Standard Error	t -statistic	
k	0.260	0.772	0.34	df = 12
G	29.430	43.683	0.67	RSE = 1.305
k_{sex}	-0.132	0.773	-0.17	
G_{sex}	2.519	48.116	0.05	

Table 7. The procedure used to find estimates G and k using the growth increment and rate of change models took four iterations through each model to reach convergence.

Model and method	Parameters pre-set	Parameters estimated	Summary statistics
Growth increments analyzed using NLME	None	$G = 16.66 \text{ cm yr}^{-1}$ (SE = 0.67) $k = 0.215$ (SE = 0.041)	$SD(G_{random}) = 2.207$ Residual = 3.062 BIC = 1384.941 logLik = -681.380 correlation(G, k) = 0.801
	$k = 0.126$	$G = 15.31 \text{ cm yr}^{-1}$ (SE = 0.39)	$SD(G_{random}) = 2.213$ Residual = 3.076 BIC = 1386.921 logLik = -685.143
	$k = 0.109$	$G = 14.99 \text{ cm yr}^{-1}$ (SE = 0.39)	$SD(G_{random}) = 2.208$ Residual = 3.083 BIC = 1389.19 logLik = -686.28
	$k = 0.107$	$G = 14.95 \text{ cm yr}^{-1}$ (SE = 0.39)	$SD(G_{random}) = 2.206$ Residual = 3.085 BIC = 1389.47 logLik = -686.42
Rate of change data analyzed using non-linear least squares	None	$G = 29.87 \text{ cm yr}^{-1}$ (SE = 10.78) $k = 0.126$ (SE = 0.021)	RSE = 1.211 logLik = -24.697 correlation(G, k) = 0.545
	$G = 16.66 \text{ cm yr}^{-1}$	$k = 0.109$ (SE = 0.019)	RSE = 1.278 logLik = -26.115
	$G = 15.31 \text{ cm yr}^{-1}$	$k = 0.109$ (SE = 0.020)	RSE = 1.311 logLik = -26.518
	$G = 14.99 \text{ yr}^{-1}$	$k = 0.107$ (SE = 0.020)	RSE = 1.320 logLik = -26.624
	$G = 14.95 \text{ cm yr}^{-1}$	$k = 0.107$ (SE = 0.020)	RSE = 1.321 logLik = -26.638
Variance-covariance matrix	G k	G 0.1521 0.00775 k 0.00775 0.0004	

Table 8. The composite age estimates based on growth increment and rate of change models using $G = 14.95\text{cm yr}^{-1}$ and $k = 0.107$ show a rough increase with body and baleen length. Data for females are italicized. We did not estimate age t and G_{random} or use the rate of change model on data from whales where there were fewer than six complete growth increments.

SE(Slope)	Growth increment model solving for t		Growth increment model solving for t and G_{random}				Rate of change model		Composite Age Estimate	
	Age	SE	Age	SE	G_{random}	SE	Age	SE	Age	SE
0.53	7.7	0.5	-	-	-	-	-	-	-	-
2.31	7.1	0.5	-	-	-	-	-	-	-	-
0.42	14.0	0.9	22.1	1.0	2.70	0.12	19.3	11.2	17.4	3.3
0.35	10.7	1.1	-	-	-	-	-	-	-	-
0.36	12.3	0.8	18.7	0.8	2.44	0.22	17.4	9.8	15.2	2.8
0.30	12.2	0.8	9.1	1.7	-1.57	0.85	10.5	5.0	11.0	1.9
1.48	7.1	0.2	4.0	1.9	-2.00	1.05	7.4	9.8	6.4	3.0
0.33	16.0	1.3	12.8	0.8	-1.30	0.45	14.6	7.7	14.9	2.4
0.30	21.8	1.7	26.3	1.4	0.94	0.12	24.0	10.0	23.4	3.3
0.25	14.4	1.1	12.8	0.8	-0.72	0.55	13.3	5.3	13.7	1.8
0.44	12.9	0.8	20.0	0.9	2.82	0.16	19.3	9.4	16.3	2.8
0.15	16.5	0.9	35.0	3.0	4.23	0.24	34.7	10.3	25.7	3.5
0.48	20.3	2.1	9.4	2.5	-4.15	0.70	13.1	7.6	15.8	3.1
0.21	13.9	0.6	22.0	1.1	3.30	0.19	21.1	7.1	17.7	2.2
0.25	18.8	1.5	15.3	0.5	-1.24	0.39	15.3	6.2	17.1	2.1
0.25	17.8	1.4	18.6	0.5	0.29	0.24	18.4	8.4	18.2	2.6

Whale	Sex	Body Length (m)	Baleen Length (cm)	Number of complete cycles	Sampling Interval (cm)	Slope
98KK2	<i>F</i>	8.9	144	4	2	-2.20
98KK3	M	9.2	170	3	2	-2.00
02B21	<i>F</i>	10.0	192	8	1	-0.31
98KK1	M	10.4	197	4	2	-1.40
79KK2	<i>F</i>	10.5	190	7	5	-0.36
86B7	M	10.7	200	8	2.5, 5	-0.80
79KK5	M	10.7	200	6	5	-1.00
87B3	M	11.0	195	9	2.5	-0.54
75B8	<i>F</i>	11.1	194	10	5	-0.21
89KK3	M	11.2	220	9	2.5	-0.625
76H4	M	11.2	225	9	5	-0.33
86B6	<i>F</i>	12.3	230	11	2.5, 5	-0.11
02B20	M	12.3	233	10	1	-0.67
90B8	M	12.9	243	11	2.5	-0.30
88WW3	M	13.1	210	10	2.5	-0.53
87WW2	M	13.5	215	10	2.5	-0.38

Figure captions

Figure 1. a. The $\delta^{13}\text{C}$ trace for young whale 98B24, with a cycle count based estimated age of 7.5yrs (by Lubetkin). b. The $\delta^{13}\text{C}$ trace for young whale 99B22, with a cycle count based estimated age of 5.5yrs (by Lubetkin). The distal end of the baleen is at the right end of each graph. This is the oldest baleen, grown when the whale was youngest. The upper arrows show where we could measure annual spring-to-spring growth increments, with growth increment lengths (in cm) shown between them. The lower arrows show where we could measure annual fall-to-fall growth increments, with growth increment lengths (in cm) shown between them. Partial growth increments are denoted with a “p”.

Figure 2. Age-specific annual growth increments for whale 87B1, a 9.3m male with 158cm baleen estimated to be 9 years old based on the number and lengths of cycles in the $\delta^{13}\text{C}$ from along its baleen. The regression line has a slope of -2.86 cm yr^{-2} .

Figure 3. a. Age-specific growth increments for bowheads. The dashed line is the growth increment model fit by NLME, where $G = 16.66 \text{ cm yr}^{-1}$ and $k = 0.215$. The dotted line is shows the growth increment model when the parameters are fit using the rate of change model ($G = 29.87 \text{ cm yr}^{-1}$ and $k = 0.126$). The solid line shows the growth increment model when $G = 14.95 \text{ cm yr}^{-1}$ and $k = 0.107$. b. A detail of the growth increments, focusing on growth to age 50.

Figure 4. The rate of change data vs, adjusted ages for bowhead whales. The dashed line shows the expected relationship when $G = 16.66 \text{ cm yr}^{-1}$ and $k = 0.215$. The dotted line shows the best model fit using nonlinear least squares, where $G = 29.87 \text{ cm yr}^{-1}$ and $k = 0.126$. The solid line is the hybrid model with $G = 14.95 \text{ cm yr}^{-1}$ and $k = 0.107$.

Figure 5. a. Bowhead age estimates and body lengths for males and females. Open symbols represent age estimates that came from AAR, corpora counts, and baleen cycle counting methods. Closed symbols are composite age estimates. Triangles represent males and circles females. b. A detail of bowhead body length at age up to age 35. The horizontal lines bound the body length range where male and female bowheads reach sexual maturity.

Figure 6. a. Bowhead age estimates and baleen lengths for males and females. Age estimates that were not based on baleen growth increments came from AAR, corpora counts, and baleen cycle counting methods. Symbols are the same as in Fig. 5. b. A detail of bowhead baleen length at age up to age 35. The horizontal lines bound the baleen length range where male and female bowheads reach sexual maturity.

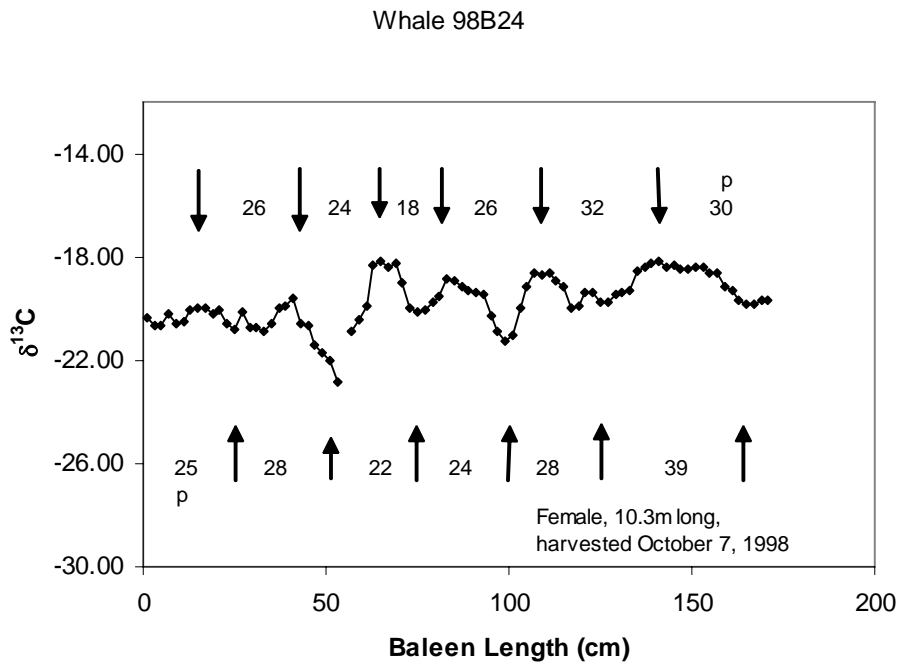


Figure 1a.

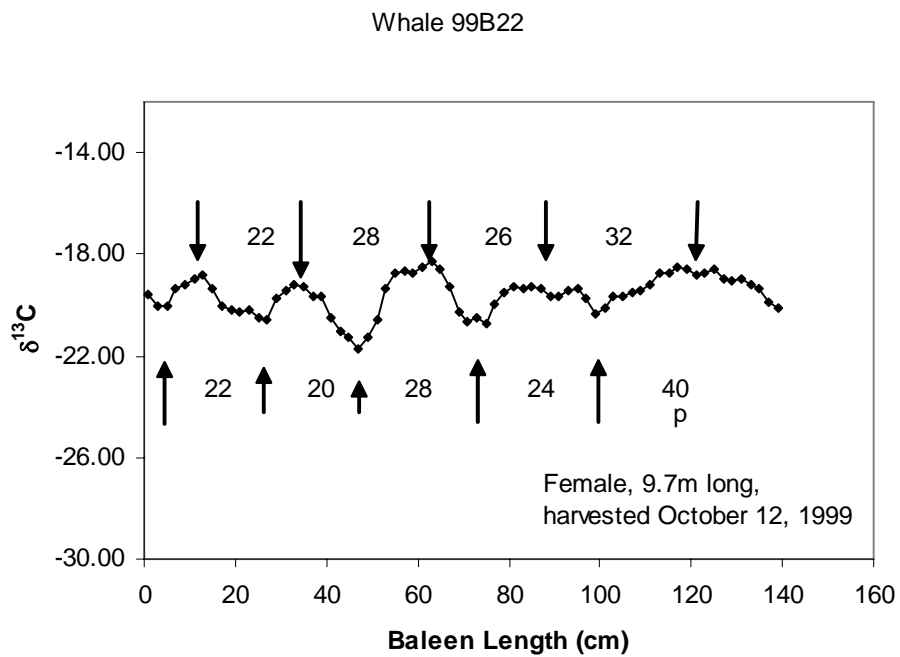


Figure 1b.

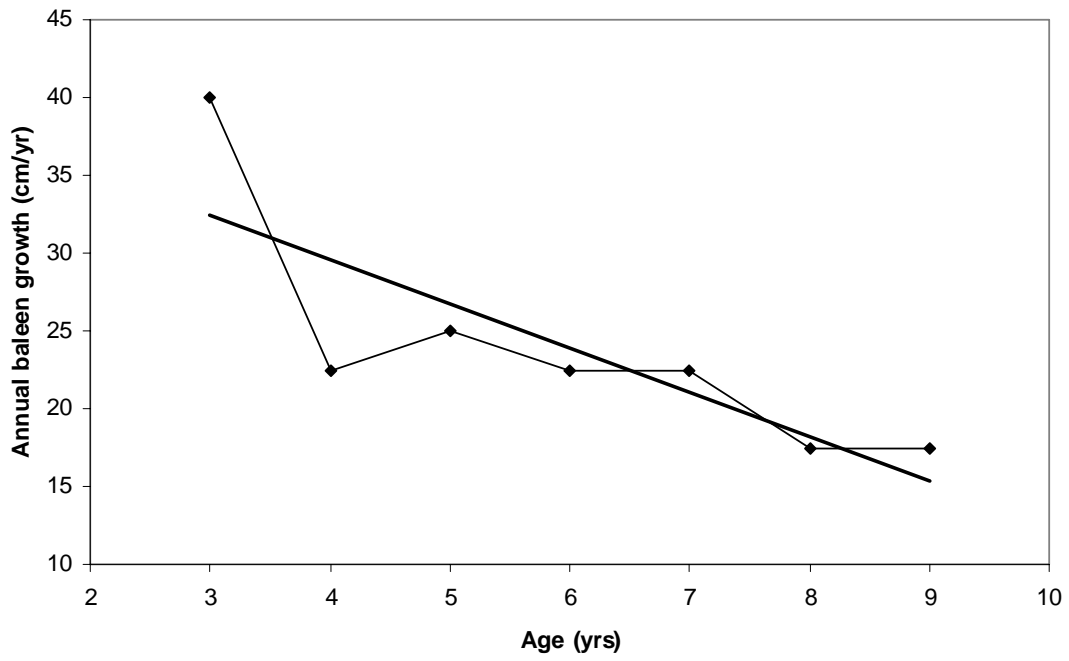


Figure 2.

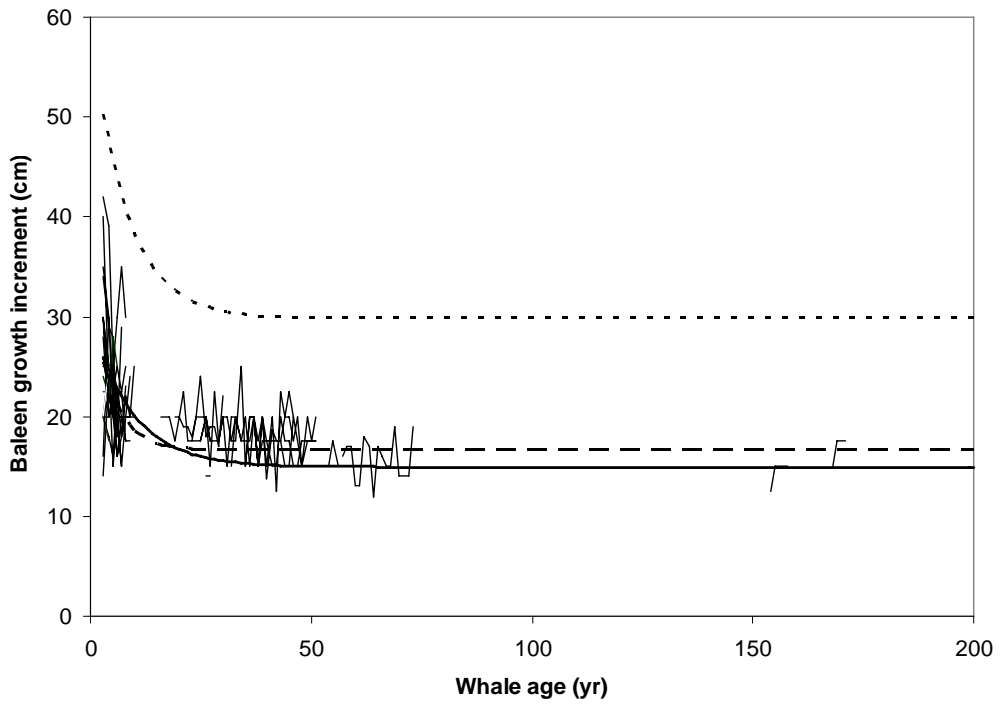


Figure 3a.

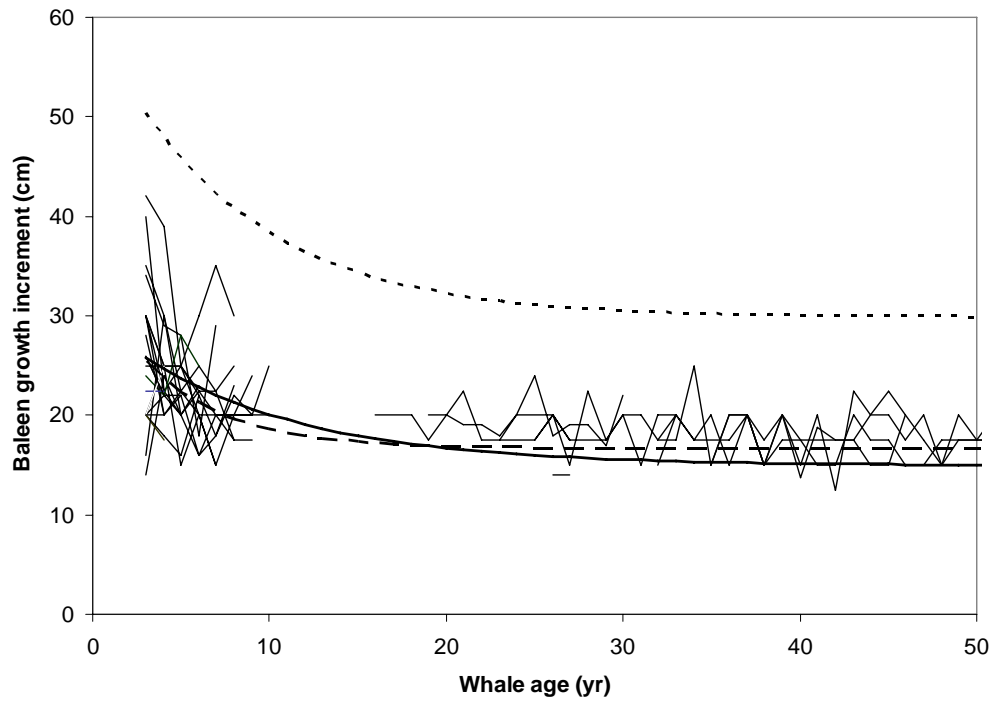


Figure 3b.

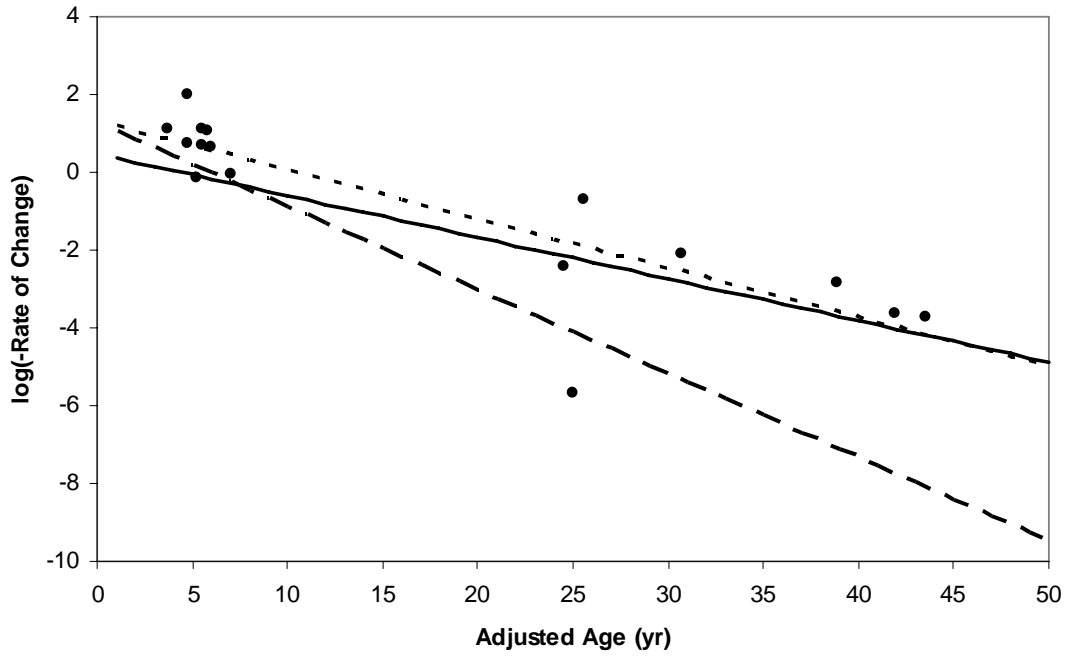


Figure 4.

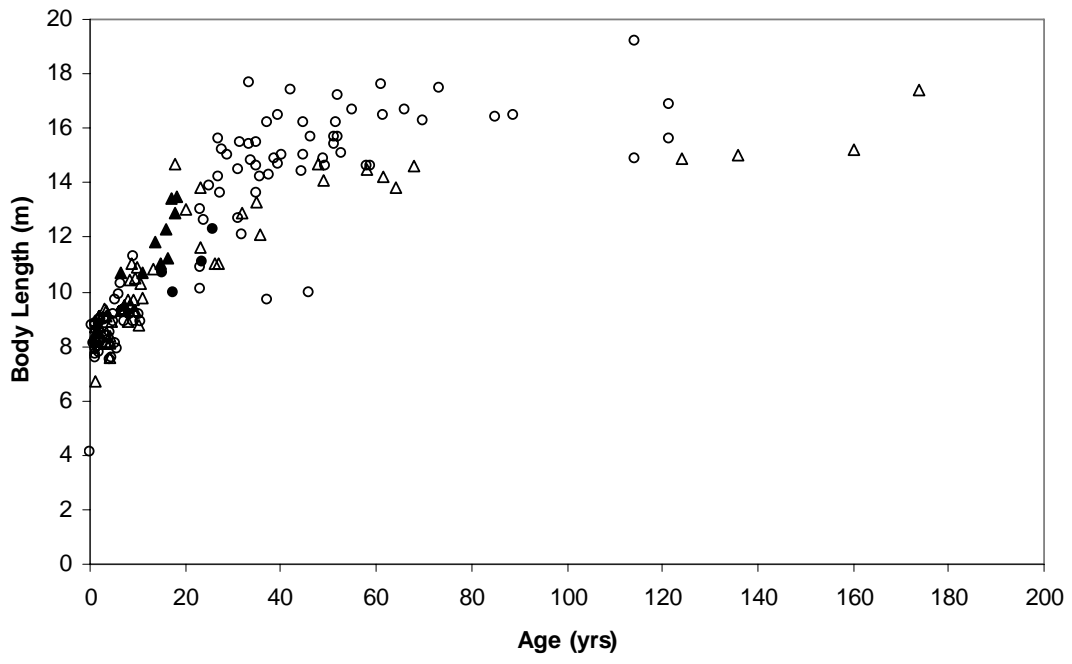


Figure 5a.

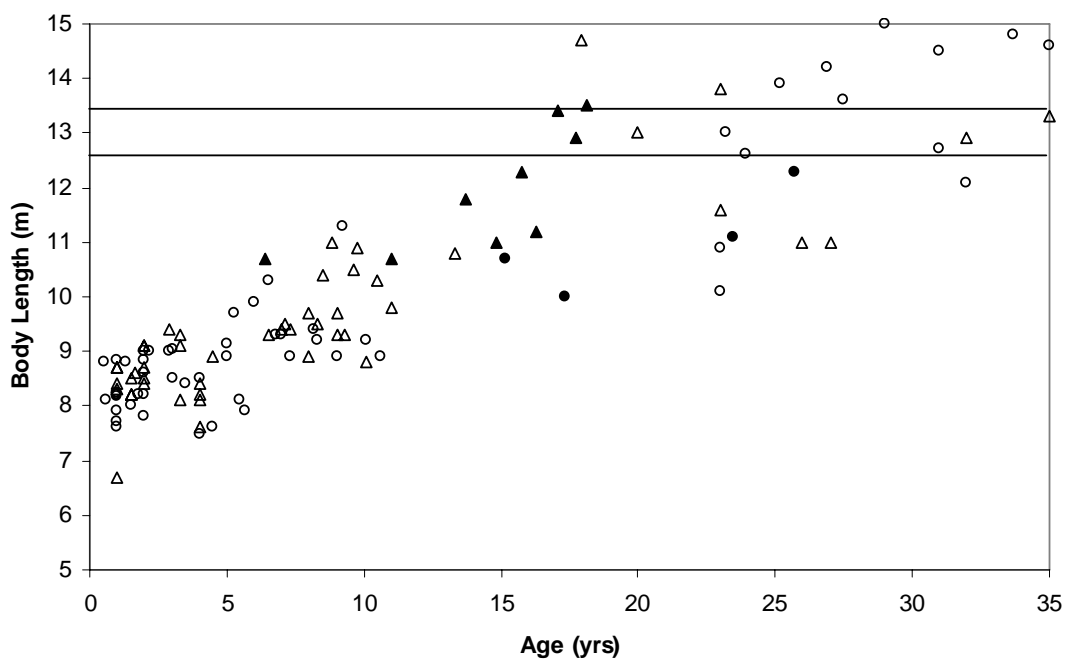


Figure 5b.

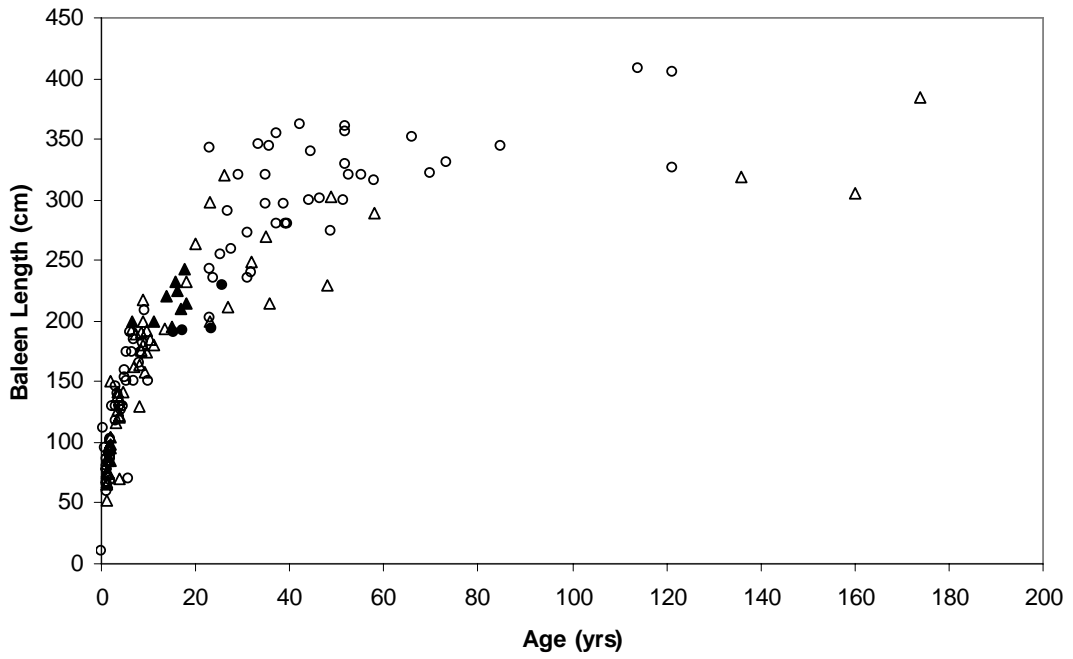


Figure 6a.

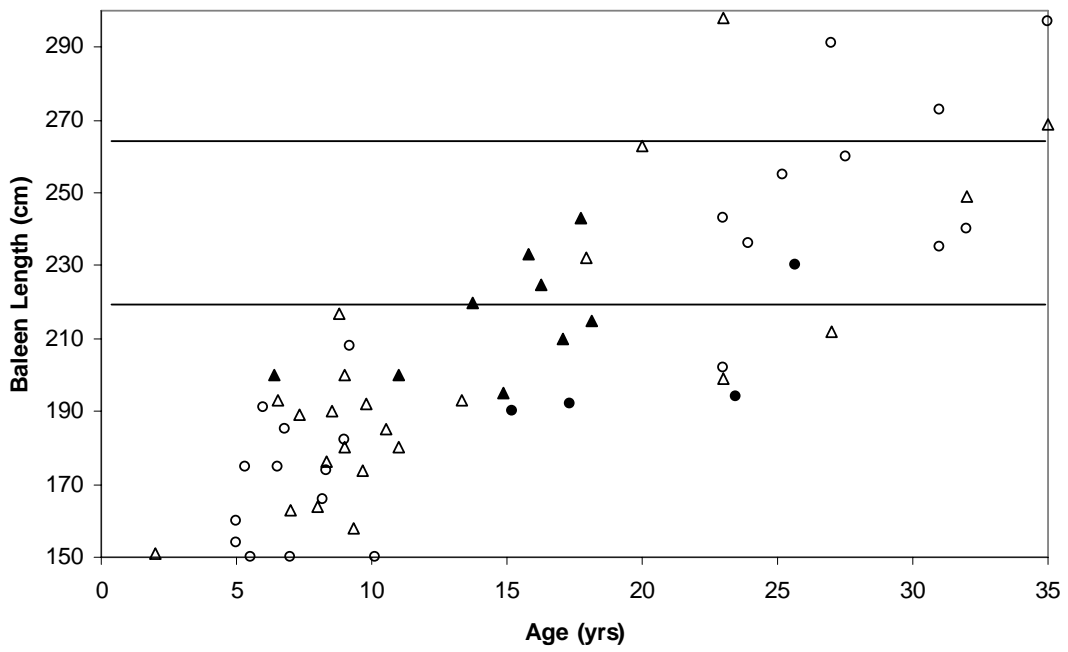


Figure 6b.