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Dentine Deposition Rates in Beluga (*Delphinapterus leucas*): An Analysis of the Evidence

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Abstract

Accurately determining the age of belugas (*Delphinapterus leucas*) has been difficult and the source of considerable uncertainty in demographic studies of this species. Previous studies have predominantly assumed that two growth layer groups (GLGs) are deposited annually in beluga teeth; however, recent evidence from aquarium-raised individuals and radiocarbon dating assays of teeth lends support to the hypothesis that one dentinal GLG is deposited annually in beluga, rather than to the competing hypothesis claiming the rate is twice as large. We present the allometric relationship between female age and length at maturity among delphinoid cetaceans and suggest that estimates of beluga age at maturity based on one GLG per annum are in better agreement with this relationship than estimates based on the competing hypothesis. Our results, and a reanalysis of previously published evidence, give further support to the one annual GLG hypothesis; however, a change in the pattern of deposition rate at sexual maturity remains a possibility, and research is needed to determine whether changes in dentine deposition rates during life stages of beluga.

Key Words: age estimation, allometry, growth, life history, demography, growth layer groups, beluga, *Delphinapterus leucas*

Introduction

Determining the age of individuals from any given population is crucial in the demography, growth, and life history research of any species. Where marking large numbers of individuals at birth is impossible or too costly, indirect methods for estimating age are required. For many mammal species, this typically involves counting the number of growth layer groups (GLG) in tooth dentine or cement as it is the most cost-effective method available that provides relatively accurate estimates. Validation of the method has been performed for several odontocete species, showing that one GLG corresponds to one year of life—a pattern they share with other mammals (Klevezal, 1995). For belugas (*Delphinapterus leucas*, Pallas, 1776), evidence supporting the one GLG hypothesis was first provided by Hohn & Lockyer (1999), although Khuzin (1961) had previously suggested this might be the case. Using an increased concentration of radiocarbon (^{14}C) in many organisms as a result of nuclear tests during the 1950s and 1960s, Stewart et al. (2007) found that belugas were more accurately aged if one, rather than two, GLGs were assumed to be deposited annually. To the best of our knowledge, further direct evidence for this hypothesis is lacking. Initial support for the two GLGs hypothesis was provided by Sergeant (1959), followed by four studies claiming support for this hypothesis: Sergeant (1973), Goren et al. (1987), Brodie et al. (1990), and Heide-Jørgensen et al. (1994). Two GLGs per year are assumed in the vast majority of studies of beluga biology and ecology (e.g., O'Corry-Crowe et al., 1997; Doidge, 1990; Harwood et al., 2002; Innes et al., 2002), however, notwithstanding considerable controversy (Hohn & Lockyer, 1999).

We examine the evidence for one and two annual GLGs in belugas, considering new studies from aquarium-raised belugas and a reassessment of previous analyses. Another source of evidence which has not been considered is the predicted strong association between age at maturity and body size (West et al., 2001). Therefore, we use recently available data on delphinoid odontocete life history to provide an additional test of these competing hypotheses (one vs two GLG = one year of life), using the allometric relationship between age and length at first reproduction.

Materials and Methods

We reviewed the literature, using original sources, for evidence supporting either of the two current hypotheses regarding dentine deposition rates in beluga. In addition, the allometric relationship between body length and age at first reproduction was analyzed to determine how beluga age, determined using one or two annual GLGs, compares with other delphinoid odontocete data. Body size (e.g., body mass or length) and age at first reproduction are closely related across most mammals (Clutton-Brock et al., 1983). Therefore, we used the most recently available data (Gygax, 2000, 2002a, 2002b) to fit a linear model of delphinoid odontocete body length on age at first reproduction, excluding belugas (Table 1). More than one estimate was available for some species, representing data from different populations, so we calculated the median in these cases. Because the relationship showed strong heteroscedasticity, we used robust regression rather than least squares methods (Huber, 1964). We used the 95% CI ($\hat{\mu} \pm t^{(n-2)}_{\alpha/2}\, s_{\hat{\mu}}$, where $\hat{\mu}$ is estimated age at any given length; $t^{(n-2)}_{\alpha/2}$ is Student's t at $\alpha = 0.25$ and DF = 20; and $s_{\hat{\mu}}$ is the SE of the mean age estimate at any given length), and prediction limits ($\hat{\mu} \pm t^{(n-2)}_{\alpha/2}\, s_{\hat{\mu}}$, where $s_{\hat{\mu}}$ is the SE of the observations at any given length). These limits were used to assess the precision of the estimated regression model and to contrast the two predicted, yet excluded from the regression, beluga age estimates with those of the other odontocetes, respectively.

Table 1. Summary of female length (cm) and age (years) at maturity in delphinoid odontocetes; age of beluga was based on the two annual GLGs hypothesis.

Species*	Length	Age
Cephalorhynchus commersoni	130.0	6.0
Delphinus capensis	170.0	8.0
Delphinus delphis	190.0	6.0
Delphinapterus leucas	340.0	5.0
Globicephala macrorhyncus	400.0	8.0
Globicephala melas	375.0	8.0
Lagenorhyncus acutus	210.0	9.0
Lagenorhyncus hosei	215.0	5.5
Lagenorhyncus obliquidens	177.0	9.5
Lagenorhyncus obscurus	175.0	5.0
Lissodelphis borealis	200.0	10.0
Monodon monocerus[a]	380.0	7.5
Orcinus orca	495.0	15.0
Phocoena dalli	171.0	3.8
Phocoena phocoena	145.0	3.6
Pontoporia blainvillei[b]	137.5	4.0
Pseudorca crassidens	340.0	9.0
Stenella attenuata	195.0	10.0
Steno bredanensis	215.0	10.0
Stenella coeruleoalba	194.0	11.0
Stenella longirostris	165.0	4.0
Tursiops aduncus	250.0	9.5
Tursiops truncatus[c]	250.0	9.5

* Data from Gygax (2000), updated with recent data from

[a] Garde et al. (2007)

[b] Barreto & Rosas (2006)

[c] Mattson et al. (2006)

Results

The allometric relationship between body length and age at first reproduction was statistically significant ($F_{1,20} = 10.3$, $p = 0.004$) among all delphinoid odontocetes, excluding belugas (Figure 1). Variation around the estimated regression line was large, particularly for small odontocetes, so that $R^2 = 0.31$, and confidence bands and prediction intervals were relatively wide. The superimposed beluga age estimate based on the one annual GLG hypothesis was within the 95% CI for the regression, whereas that based on the competing hypothesis was not. However, both estimates were within the 95% CI for the prediction (Figure 1).

Discussion

Although support for the two GLG hypothesis has received considerably more attention in the literature than the other hypothesis, it includes important weaknesses. These include unjustified extrapolation of results from other species, inappropriate use of growth curves, circular reasoning, uncertainties due to tooth wear, and equivocal results (Hohn & Lockyer, 1999). Despite these results, management research has continued to use two annual GLGs to estimate the age of belugas (Harwood et al., 2002; Innes et al., 2002; Lesage & Doidge, 2005). A further source of skepticism regarding this hypothesis is that two annual GLGs would make belugas unique among odontocetes, which otherwise display a one annual GLG pattern (Klevezal & Kleinenberg, 1969; Klevezal, 1995). Furthermore, beluga age estimates based on the one GLG hypothesis are in better agreement with the relationship between body length and age at first reproduction for delphinoid odontocetes in general than estimates based on the competing hypothesis. These results bring additional support for the conclusions reached in Stewart et al. (2007), doubling estimates of important life history parameters such as longevity and age at first reproduction (5 vs 10 y), which are critical in studies of population ecology and conservation of this species.

Hohn & Lockyer (1999) used tetracycline marking of two belugas (male and female) of known-history, albeit of unknown age. Using length at capture and at death of their study animals, the authors calculated the expected number of GLGs at capture and at death. They used a published growth (length-at-age) curve from the population

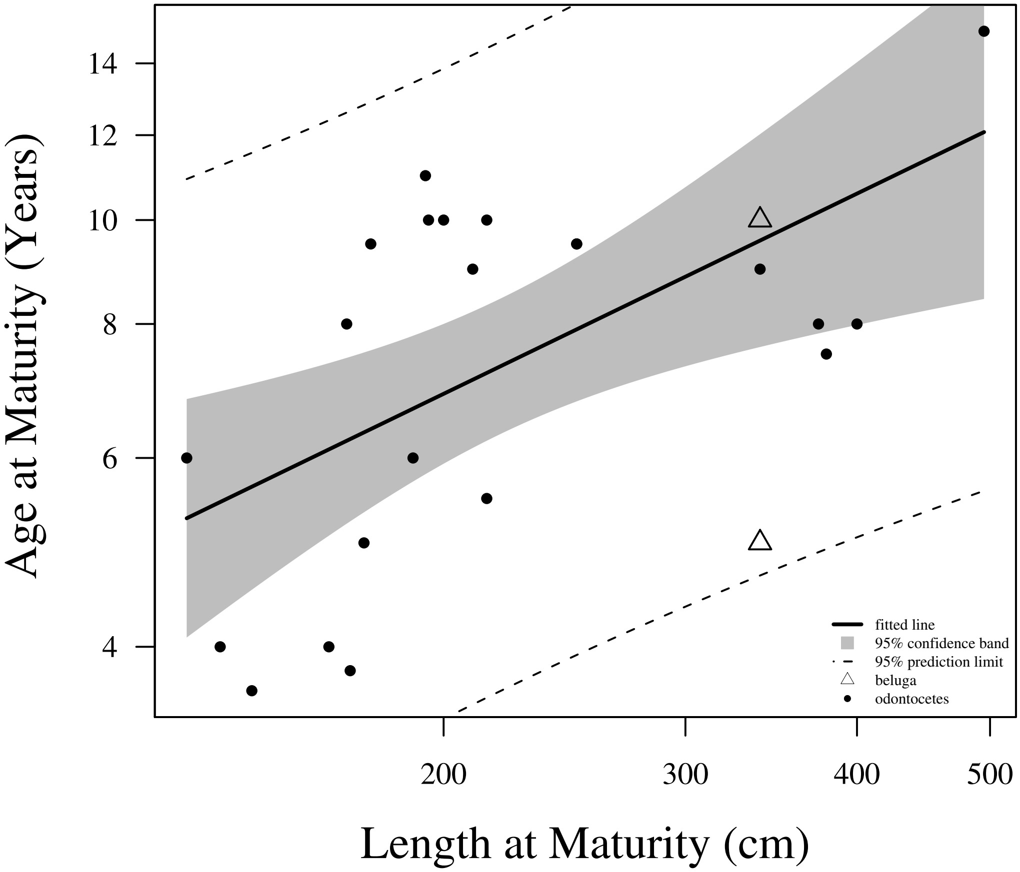

Figure 1. The age of female belugas, estimated using one annual growth layer groups (GLGs), is in better agreement with the allometric relationship between age (years) and length (cm) at first reproduction in female odontocetes (age = length · 0.62 - 0.59, $p = 0.004$, log-transformed data, excluding beluga) than estimates based on two annual GLGs. Data for beluga are shown, but were excluded from the estimated regression.

their animals came from to obtain two expected GLG counts, each based on the two presumed deposition rates, and compared them with their actual GLG count. Their actual GLG counts were closer to the number of GLGs expected under the assumption of one annual GLG than under the alternative assumption. The authors' tetracycline experiment was not as successful, but one GLG per year explained the difference in GLG counts between injection and death better than the alternative assumption.

A recent study investigating hormone changes in known-age captive belugas over several years has provided new estimates of age at first reproduction (Robeck et al., 2005). Although these estimates may not be representative of wild populations, they are based on known-age individuals and are approximately twice as large (females: 9 vs 5 y; males: 13 vs 8 y) as those previously used based on the assumption of two annual GLGs. Previous estimates were based on unknown-age animals under the assumption of two GLGs per year (Sergeant, 1973; Heide-Jørgensen et al., 1994). Therefore, Robeck et al.'s (2005) results are consistent with the one annual GLG hypothesis, although they do not support it directly.

An additional reference (Brodie, 1969) that was not considered by Hohn & Lockyer (1999), but is frequently used to support the two GLGs hypothesis, may have another interpretation, which has thus far not been considered. Brodie's Figure 3 shows that the slope of the relationship between the number of tooth layers and the number of mandibular layers is equal to two up to about 15 tooth layers. Beyond 15 tooth layers, the slope is greatly reduced, which Brodie attributed to tooth wear so that the number of tooth layers was underestimated in four teeth of his sample having at least 15 layers. Bone resorption may also have been a factor because it leads to the removal of some layers with age, and they cannot be counted (Marmontel et al., 1996). Using Brodie's (1969) assumption that one mandibular layer is deposited annually, 15 tooth layers correspond to 7 to 8 y of age, which is almost identical to the female age of first reproduction estimated by Robeck et al. (2005). Another explanation for Brodie's (1969) results is that belugas change the rate of deposition after sexual maturity from an irregular pattern to one annual GLG. Elephant seals (*Mirounga leonina*) display a qualitatively similar change at sexual maturity (Laws, 1953). Certainly, the possibility of a change in the rate of GLG deposition in belugas requires further investigation.

Although it is not clear whether a change in the pattern of deposition rate at sexual maturity occurs in beluga teeth, currently available data strongly suggest that dentine GLGs are deposited at a rate of one per annum throughout most of their lives. To summarize, data from aquarium-raised individuals, recent radiocarbon dating assays, a reanalysis of previously published evidence, and an allometric relationship lend support to the hypothesis of one dentinal GLG being deposited annually in belugas, rather than the previously assumed rate of twice this value.

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