Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates

R.E.A. Stewart, S.E. Campana, C.M. Jones, and B.E. Stewart

Abstract: The ages of many mammals are estimated by counting growth layers in tooth sections, yet validation of age estimation techniques using free-ranging mammals has been problematic. Contrary to age estimates for most other animals in which it is assumed that one bipartite growth increment forms annually, beluga whale (*Delphinapterus leucas* (Pallas, 1776)) age estimates have been calculated assuming that two growth layer groups (GLGs) form each year. Here we report the age validation for belugas based on date-specific incorporation of atomic bomb radiocarbon into tooth GLGs. Radiocarbon assays of dentinal layers formed in belugas harvested between 1895 and 2001 indicated that radiocarbon from atmospheric testing of nuclear weapons was incorporated into growing teeth and retained for the remaining life of the animal. Comparison of age determined by bomb radiocarbon with age determined by GLG counts indicated that GLGs form annually, not semiannually, and provide an accurate indicator of age for belugas up to at least 60 years old. Radiocarbon signatures of belugas were temporally and metabolically stable and were apparently derived more from the radiocarbon content of their prey than from water. Our understanding of many facets of beluga population dynamics is altered by the finding that this species lives twice as long as previously thought.

Résumé : L'estimation de l'âge chez de nombreux mammifères se fait par l'énumération des couches de croissance dans des coupes de dents, bien que la validation de cette technique d'estimation de l'âge chez les mammifères libres en nature pose des problèmes. Contrairement à la plupart des autres animaux chez qui on présume de la formation d'un pas de croissance bipartite chaque année, on calcule les estimations d'âge chez le béluga (*Delphinapterus leucas* (Pallas, 1776)) en présupposant la formation de deux groupes de couches de croissance (GLG) chaque année. Nous présentons la validation de la détermination d'âge chez les bélugas d'après l'incorporation à des dates précises du radiocarbone provenant de bombes atomiques dans les GLG des dents. Les dosages du radiocarbone dans les couches de dentine déposées chez des bélugas capturés entre 1895 et 2001 indiquent que le radiocarbone provenant des essais atmosphériques d'armes nucléaires s'incorpore dans les dents en croissance et y demeure pour le reste de la vie de l'animal. Une comparaison des âges déterminés par le radiocarbone et par les comptages de GLG montre que les GLG se forment une fois et non pas deux fois l'an et qu'ils sont des indicateurs fiables de l'âge des bélugas jusqu'à l'âge d'au moins 60 ans. Les signatures de radiocarbone sont stables en fonction du temps et du métabolisme et elles proviennent apparemment plus du contenu en radiocarbone des proies que de celui de l'eau. Notre compréhension de plusieurs aspects de la dynamique de population des bélugas se voit modifiée par la réévaluation de cette espèce qui vit deux fois plus longtemps qu'on le croyait précédemment.

[Traduit par la Rédaction]

Introduction

Accurate age estimates are fundamental to ecological investigations of rates of individual growth, rates of population change, or rates incorporated in species-specific life-history parameters. For example, management tools such as potential biological removal (Wade 1998) and population viability analysis (Morris and Doak 2002) rely on age-specific fecundity and survival rates to calculate safe harvest levels. Life-history studies that attempt to understand the evolutionary significance of lifetime behavior (Boness et al. 2002; Winemiller 2005) rely on the timing of important events such as sexual maturation. Even population responses to climate change can be age-specific (Coulson et al. 2001). Particularly in management decisions, erroneous age estimates can have disastrous effects (Campana 2001). For example, age underestimation resulted in overly optimistic estimates of productivity and hence serious overfishing of several marine fish stocks before the inaccurate ageing was recognized (Beamish and McFarlane 1995; Smith et al. 1995; Campana 1997, 2001).

Many species are aged by examining growth lines or bands in hard structures. Bivalve shells (Lutz and Rhoads 1980), coral skeletons (Dodge and Thomson 1974), tortoise scutes (Germano 1998) and fish otoliths (Secor et al. 1995), scales (Robillard and Marsden 1996), vertebrae (Brown and

Received 15 June 2006. Accepted 1 November 2006. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 26 January 2007.

R.E.A. Stewart.[1] Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.
S.E. Campana. Fisheries and Oceans Canada, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
C.M. Jones. Center for Quantitative Fisheries Ecology, 800 West 46th Street, Old Dominion University, Norfolk, VA 23508, USA.
B.E. Stewart. Sila Consultants, 1218 Marchand Road, Howden, MB R5A 1J6, Canada.

[1] Corresponding author (e-mail: stewartre@dfo-mpo.gc.ca).

Can. J. Zool. **84**: 1840–1852 (2006) doi:10.1139/Z06-182

Gruber 1988), and fin rays (Cass and Beamish 1983) all record growth increments that have been used for age estimation. In mammals, teeth (both dentine and cementum) and bone (Johnston et al. 1987; Klevezal 1996) are the basic recording structures, although teeth show less restructuring than bone (Garlich-Miller et al. 1993; Klevezal 1996).

The beluga (*Delphinapterus leucas* (Pallas, 1776)) is a toothed whale that is exploited throughout much of its circumpolar range (Stewart and Stewart 1989). Population trajectories that serve as the basis for management decisions rely on some combination of age at maturation, age-specific fecundity, age-specific survival, and longevity (e.g., Butterworth et al. 2002; Innes and Stewart 2002). Beluga ages have been estimated routinely by counting growth layers or bands in longitudinal sections of the teeth. The term “growth layer group” (GLG) has been adopted by the International Whaling Commission (International Whaling Commission 1980) and by marine mammalogists in general to denote a repeated dyad of contrasting lines, with each pair of light and dark lines representing a growth period (International Whaling Commission 1980; Hohn 2002). The term “GLG” is functionally similar to the term “growth band” or “growth increment” used by those determining the ages of fish, reptiles, amphibians, and terrestrial mammals (Neville 1967; Secor et al. 1995). Here we use the marine mammalogy terminology, i.e., GLG.

In general, GLGs in odontocete teeth are interpreted as representing 1 year of growth, although some shorter term banding may occur (Klevezal 1996). However, the deposition rate of GLGs in belugas has been interpreted to be semiannual, with two GLGs representing 1 year of growth (Sergeant 1959). If two GLGs are deposited each year, then age is equivalent to one half the number of GLGs (GLG/2), compared with the more conventional interpretation for most animals that age = GLG/1. The assumption that belugas form two dentinal GLGs/year (Sergeant 1959) was based on previous studies of sperm whales (*Physeter macrocephalus* L., 1758) that concluded two GLGs were formed each year and the observation that the maximum number of GLGs seen in beluga teeth was about twice that apparent in long-finned pilot whale (*Globicephala melas* (Traill, 1809)) teeth. Subsequently, it has been acknowledged that sperm whales deposit only one GLG/year (International Whaling Commission 1980; Evans et al. 2002). Indeed, Sergeant (1981) noted there was no a priori justification to assume two GLGs were formed each year in belugas.

Efforts to reject either the 1 GLG/year or the 2 GLGs/year hypothesis in belugas have been equivocal at best. Allometric comparisons suggest annual, not semi-annual, deposition (Ohsumi 1979). The examination of teeth from wild-born belugas held in captivity has been inconclusive (Brodie 1982; Heide-Jørgensen et al. 1994; Hohn and Lockyer 2001). The use of tetracycline marks as a dated chemical marker in teeth is one method of calibrating age estimates (Johnston et al. 1987; Brodie et al. 1990) but has not been definitive for belugas (Hohn and Lockyer 2001).

The use of radiocarbon (^{14}C) to validate beluga ages may resolve this impasse. The atmospheric testing of atomic bombs in the 1950s and 1960s resulted in a rapid and well-documented increase in radiocarbon in the world’s oceans (Druffel and Linick 1978). The period of initial radiocarbon increase in marine carbonate structures such as corals, bivalves, and fish otoliths was almost synchronous around the world (Kalish 1993; Weidman and Jones 1993; Campana 1997), allowing the first appearance of the increase around 1958 to be used as a dated marker in growth bands of marine animals (Druffel and Linick 1978; Kalish 1993). A similar pattern of increase, lagged by several years owing to the incorporation of dietary carbon, has been documented in porbeagle shark (*Lamna nasus* (Bonnaterre, 1788)) vertebrae (Campana et al. 2002) and spiny dogfish (*Squalus acanthias* L., 1758) spines (Campana et al. 2006). Here we report the first radiocarbon assays of beluga whale teeth, using ^{14}C as a dated chemical marker, to determine whether these teeth recorded and preserved a bomb radiocarbon pulse in growth layers formed during the 1960s. We use δ^{13}C assays to test the assumption that the primary source of carbon in belugas is dietary carbon rather than dissolved inorganic carbon (DIC), and we explore the impact of the differing age interpretations on life-history parameters of belugas.

Materials and methods

Nine beluga teeth were selected from archived material (Table 1). Three of the whales (gender unknown) were from archaeological sites on Somerset Island in the high Arctic (Elwin Bay, 72.53N, 90.93W; Port Leopold, 73.90N, 90.15W; Outridge et al. 2005) and lived their whole lives before atomic bombs. The year of death for these animals was approximated as the midpoint of the whaling activity at the site (Outridge et al. 2005). Five whales (all females) were killed between 1991 and 1997 by hunters living on southeast Baffin Island at Kimmirut (62.85N, 69.88W), Iqaluit (63.75N, 68.55W), and Pangnirtung (66.12N, 65.68W), Nunavut. These whales were selected so that back-calculating from their year of death would place their birth date either before the period of atmospheric atomic bomb testing if age = GLG/1 or after bomb testing if age = GLG/2. A sixth, younger, beluga harvested in 2001, also at southeast Baffin Island, represented the recent period. Teeth were stored dry or in glycerin–alcohol–water (Pueck and Lowe 1975) until sectioning.

Belugas have homodont dentition and teeth were identified by their position in the jaw. Preliminary feasibility analyses used teeth from the fifth position from the right mandible, designated as MNR-5. Most of our subsequent analyses used the tooth from the second position, MNR-2. Teeth of ARLHxx1003 were curved and neither MNR-2 nor MNR-5 provided a complete history, so the entire life of this animal was examined by combining data from MNR-2 and MNR-5.

Longitudinal midline sections of each tooth were prepared using a Buehler diamond-bladed saw, either after embedding the tooth in epoxy (Wainwright and Walker 1988) or after affixing it with hot-melt glue to a wooden block, without embedding. For each of belugas B92-105 and B92-108, one tooth was sectioned after being embedded and another tooth was not embedded. All GLGs visible in the dentine of wet sections were counted in 3–5 blind replicates (Stewart 1994*a*) by one reader (B.E.S.) using a binocular microscope with variable magnification and transmitted light.

Sections were digitally photographed at a minimum resolution of 1280 × 1024 and then enhanced (Photoshop®) to

Table 1. Source of belugas (*Delphinapterus leucas*) sampled for bomb radiocarbon analysis, and predicted date of growth layer group formation based on Δ^{14}C values.

Beluga or site	Year of death	Age*	Tooth[†]	Tissue[‡]	Sample span*	Sample date*	Alternative span[§]	Alternative date[§]	δ^{13}C	Δ^{14}C	Adjusted Δ^{14}C
CB 19-18	~1887	30	nd	D	1878–1880	1879	1882.5–1883.5	1883	–13.91	–88.9	–88.9
Elwin Bay				D	1862–1872	1867	1874.5–1879.5	1877	–13.90	–99.4	–99.4
CB 19-33	~1887	34	nd	D	1870–1878	1874	1878.5–1882.5	1880.5	–10.57	–74.4	–74.4
Elwin Bay				C		1872[‖]		1879.5[‖]	–12.40	–74.0	–74.0
CB 20-01	~1937	24	nd	D	1919–1923	1921	1928.0–1930.0	1929	–14.10	–83.6	–83.6
Port Leopold				D	1925–1929	1927	1931.0–1933.0	1932	–13.90	–87.3	–87.3
LH91-27	1991	51	2	D	1982–1986	1984	1986.5–1988.5	1987.5	–14.31	29.3	29.3
Kimmirut				D	1982–1991	1986.5	1986.5–1991.0	1988.75	–14.45	28.4	28.4
				D	1974–1981	1977.5	1982.5–1986.0	1984.25	–14.25	–0.5	–0.5
				D	1967–1973	1970	1979.0–1982.0	1980.5	–14.51	–36.4	–36.4
				D	1961–1966	1963.5	1976.0–1978.5	1977.25	–14.32	–65.6	–65.6
				D	1956–1960	1958	1973.5–1975.5	1974.5	–14.14	–83.7	–83.7
				D	1951–1955	1953	1971.0–1973.0	1972	–14.09	–86.7	–86.7
				D	1947–1950	1948.5	1969.0–1970.5	1969.75	–13.96	–83.5	–83.5
				D	1945–1946	1945.5	1968.0–1968.5	1968.25	–14.00	–84.9	–84.9
				D	1940–1944	1942	1965.5–1967.5	1966.5	–13.93	–97.7	–97.7
				D	1987–1991	1989	1989.0–1991.0	1990	–14.46	30.9	30.9
B92-34	1992	60	2	D	1983–1989	1986	1987.5–1990.5	1989	–16.76	–137.5	61.1
Pangnirtung				D	1969–1981	1975	1980.5–1986.5	1983	–16.81	–161.7	35.6
				D	1959–1966	1962.5	1975.5–1979.0	1977.25	–16.61	–200.8	–29.8
				D	1950–1954	1952	1971.0–1973.0	1972	–16.46	–218.7	–63.6
				C		1960[‖]		1976[‖]	–16.34	–145.1	14.9
				C		1944[‖]		1968[‖]	–16.35	–210.4	–62.2
B92-105	1992	55	5	D	1989–1992	1990.5	1990.5–1992.0	1991.25	–15.11	16.2	95.0
Iqaluit				D	1984–1988	1986	1988.0–1990.0	1989	–14.85	21.6	79.7
				D	1978–1983	1980.5	1985.0–1987.5	1986.25	–17.31	–30.4	–30.4
				D	1953–1954	1953.5	1972.5–1973.0	1972.75	–14.84	–95.8	–45.3
				D	1950–1952	1951	1971.0–1972.0	1971.5	–15.09	–96.1	–27.7
			2	D	1978–1988	1983	1985.0–1990.0	1987.5	–16.35	–112.3	54.9
				D	1946–1952	1949	1969.0–1972.0	1970.5	–16.33	–211.8	–65.5
				D	1972–1977	1974.5	1982.0–1984.5	1983.25	–16.26	–113.0	46.2
				D	1968–1971	1969.5	1980.0–1981.5	1980.75	–16.11	–128.6	15.1
				D	1965–1967	1966	1978.5–1979.5	1979	–16.07	–156.7	–20.9
				D	1963–1964	1963.5	1977.5–1978.0	1977.75	–15.92	–175.1	–53.9
				D	1961–1962	1961.5	1976.5–1977.0	1976.75	–16.22	–176.6	–32.4
				D	1958–1960	1959	1975.0–1976.0	1975.5	–16.21	–189.8	–48.7
				D	1955–1957	1956	1973.5–1974.5	1974	–16.42	–191.1	–33.6
				D	1953–1954	1953.5	1972.5–1973.0	1972.75	–16.73	–194.1	–11.5
B92-108	1992	59	5	D	1976–1989	1982.5	1984.0–1990.5	1987.25	–16.29	–122.7	37.3
Pangnirtung				D	1963–1975	1969	1977.5–1983.5	1980.5	–16.31	–187.2	–37.7
				D	1955–1962	1958.5	1973.5–1977.0	1975.25	–15.97	–201.9	–81.1
				D	1947–1954	1950.5	1969.5–1973.0	1971.25	–15.98	–200.5	–78.7
			2	D	1984–1992	1988	1988.0–1992.0	1990	–18.22	–248.1	57.6

Table 1 (*concluded*).

Beluga or site	Year of death	Age*	Tooth[†]	Tissue[‡]	Sample span*	Sample date*	Alternative span[§]	Alternative date[§]	δ^{13}C	Δ^{14}C	Adjusted Δ^{14}C
				D	1977–1983	1980	1984.5–1987.5	1986	–13.92	37.9	26.4
				D	1970–1976	1973	1981.0–1984.0	1982.5	–14.06	13.4	12.0
				D	1964–1969	1966.5	1978.0–1980.5	1979.25	–13.79	10.4	–9.6
				D	1960–1963	1961.5	1976.0–1977.5	1976.75	–14.22	–55.3	–46.0
				D	1957–1959	1958	1974.5–1975.5	1975	–14.29	–86.0	–72.4
				D	1954–1956	1955	1973.0–1974.0	1973.5	–14.06	–88.7	–90.0
				D	1951–1953	1952	1971.5–1972.5	1972	–13.97	–84.0	–91.0
				D	1948–1950	1949	1970.0–1971.0	1970.5	–14.30	–93.6	–79.5
B97-037 Kimmirut	1997	59	2	D	1985–1997	1991	1991.0–1997.0	1994	–14.50	21.4	21.4
				D	1979–1984	1981.5	1988.0–1990.5	1989.25	–14.23	11.5	11.5
				D	1972–1978	1975	1984.5–1987.5	1986	–14.21	–5.9	–5.9
				D	1967–1971	1969	1982.0–1984.0	1983	–14.23	–21.9	–21.9
				D	1961–1966	1963.5	1979.0–1981.5	1980.25	–14.22	–67.6	–67.6
				D	1956–1960	1958	1976.5–1978.5	1977.5	–14.22	–76.9	–76.9
				D	1953–1955	1954	1975.0–1976.0	1975.5	–14.35	–92.6	–92.6
				D	1949–1952	1950.5	1973.0–1974.5	1973.75	–14.31	–83.5	–83.5
				D	1943–1948	1945.5	1970.0–1972.5	1971.25	–14.54	–104.0	–104.0
				C	1985–1996	1990.5	1991.0–1996.5	1993.75	–13.81	11.6	11.6
ARLHxx1003 Kimmirut	2001	22	5	D	1979–1983	1981	1990.0–1992.0	1991	–14.14	46.6	46.6
				D	1984–1986	1985	1992.5–1993.5	1993	–14.30	39.6	39.6
				D	1987–1990	1988.5	1994.0–1995.5	1994.75	–14.39	54.8	54.8
			2	D	1999–2001	2000	2000.0–2001.0	2000.5	–14.49	14.4	14.4
				D	1996–1998	1997	1998.5–1999.5	1999	–14.35	20.2	20.2
				D	1993–1995	1994	1997.0–1998.0	1997.5	–14.66	28.1	28.1
				D	1990–1992	1991	1995.5–1996.5	1996	–14.66	40.2	40.2

*Assuming 1 GLG/year.

[†] Right mandible position 2 or 5; nd, not determined.

[‡] D, dentine; C, cementum.

[§] Assuming 2 GLGs/year.

[||] Estimated; lines in cementum were difficult to distinguish in photomicrographs.

guide micromilling. Age interpretations used to guide micromilling were made independently (by S.E.C.) of the original age determination. To insure comparability between these two age readings, bias between the age readers was evaluated with age bias plots and precision was quantified using the coefficient of variation (CV) (Campana 2001). Bias between the age readers was absent and the CV was 4%.

Tooth samples were isolated as solid pieces with a Merchantek computer-controlled micromilling machine using steel cutting bits and burrs. Multiple samples ($n = 64$), usually representing 1–3 GLGs (Table 1), were micromilled from the dentine of each tooth. We isolated samples from near the root, representing the period just prior to death, samples from the region nearest the apical cusp, representing the oldest portion of the tooth, and multiple samples from the mid-region of each tooth. Care was taken to avoid denticles (pulp stones, cf. Heide-Jørgensen et al. 1994) that appeared as obvious inclusions in the regular growth sequence of the dentine. Four samples were micromilled from the cementum and dentine layers of three teeth to compare radiocarbon content between concurrent dentine and cementum. The date of sample formation was calculated as the year of beluga death minus the age span (GLG/1 or GLG/2) from the root of the tooth to the midpoint of the range of GLGs in the micromilled sample. Epoxy resin immediately adjacent to the embedded tooth section of belugas B92-105 and B92-108 was also isolated for radiocarbon assay.

After sonication in ultrapure (Super-Q) water and drying, each excised sample was weighed to the nearest 0.1 mg before ^{14}C assay with accelerator mass spectrometry (AMS). The carbon content of the dentine was about 10%, so the smallest sample that provided sufficient carbon in the assay was about 3 mg. AMS assays also provided δ^{13}C values (‰) that were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values are reported as Δ^{14}C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 (Stuiver and Polach 1977). The analytical precision of individual Δ^{14}C assays was about 5‰.

It became apparent during analysis that resin had permeated teeth that were embedded for sectioning. Because the isotopic composition (δ^{13}C and Δ^{14}C) of the resin was very different from that of the teeth, we used simple mixing equations to first quantify the extent of resin infiltration, then remove its effect. The δ^{13}C of the infiltrated tooth ($\delta^{13}C_E$) was first compared with that of the adjacent resin ($\delta^{13}C_R$) and a non-embedded tooth of the same animal ($\delta^{13}C_T$) to determine the extent of infiltration:

$$[1] \qquad \delta^{13}C_E = x\delta^{13}C_R + (1 - x)\delta^{13}C_T$$

where x is the proportion of resin in the infiltrated tooth. Given that δ^{13}C is normally independent of Δ^{14}C in modern samples, the δ^{13}C-based mixing proportion was statistically removed from the Δ^{14}C values of the infiltrated tooth using the resin and non-embedded tooth as Δ^{14}C endpoints for the mixing equation:

$$[2] \qquad \Delta^{14}C_E = x\Delta^{14}C_R + (1 - x)\Delta^{14}C_T$$

Variables x and $(1 - x)$ were known from the δ^{13}C mixing equation (eq. 1), allowing eq. 2 to be solved for $\Delta^{14}C_T$, the “real” Δ^{14}C of the embedded tooth:

$$[3] \qquad \Delta^{14}C_T = (\Delta^{14}C_E + x\Delta^{14}C_R)(1 - x)^{-1}$$

To assign dates of dentine deposition for belugas, we compared beluga Δ^{14}C data with a Δ^{14}C chronology based on known-age material (a reference chronology) for the northwest Atlantic derived from known-age fish otoliths formed between 1949 and 2000 (Campana et al. 2006). The Δ^{14}C chronology of fish otoliths in the northwest Atlantic parallels that of North Atlantic corals and bivalves (Campana 1997) and Arctic fishes (S.E. Campana, unpublished data), so it is a good proxy for the Δ^{14}C DIC history of the beluga environment.

Although the year of initial increase in surface marine Δ^{14}C is almost the same around the world, the year of peak values and the rate of subsequent decline are functions of water mixing rates; hence, they are region-specific (Kalish 1993; Campana 1997). Following Kerr et al. (2004) and Piner et al. (2005), we fit several sigmoid curves to the radiocarbon data to quantitatively define the year of initial increase. The four-parameter Gompertz model

$$[4] \qquad \Delta^{14}C = Y_0 + a\exp\{-\exp[-(\mathrm{YEAR} - X_0)/b]\}$$

where Y_0 is the lower asymptote, a is the upper asymptote, X_0 is the year of inflection, and b is the rate of change, had the highest adjusted r^2 value for the reference chronology and was used for the beluga as well. The year of initial increase in Δ^{14}C was defined as the year in which the fitted line was 2 standard errors above Y_0, the pre-bomb asymptote. A separate regression model was used to describe the Δ^{14}C decline since the 1980s.

Two approaches were used to evaluate the impact of using each age interpretation method (GLG/1 or GLG/2) on life-history and management models for belugas. First, data used to derive growth curves for 51 female belugas from western Hudson Bay (Stewart 1994*a*) were reevaluated using both the original GLG counts (i.e., age = GLG/1) and by assuming age = GLG/2, as in Stewart (1994*a*). Second, the ages of 191 female belugas harvested on the west coast of Hudson Bay between 1984 and 2003 (Stewart 1994*a*; Department of Fisheries and Oceans (DFO), unpublished data) were used to simulate an age distribution for life-table analysis. This population is hunted and it is unlikely that either the age distribution or the population size was unchanged over the nearly 20 years of data collection (Caughley and Birch 1971). We emphasize that the age-distribution and life-history parameters generated are illustrative only of the direction and magnitude of change depending on the way age is interpreted. They do not necessarily reflect any real beluga population. Age of maturation of females was taken as 12 (GLG/1) or 6 (GLG/2) years based on a sample comprising mostly belugas from this area (Stewart 1994*b*). The reproductive rate of mature females in this sample was 0.36/year (Stewart 1994*b*). For life-table analysis, GLG/2 ages were rounded up to the nearest full year. To determine the age structure of this simulated population, the number of newborn female calves was estimated by multiplying the number of mature females by 0.36 and dividing by 2. We

Fig. 1. Longitudinal section of tooth MNR-2 from beluga (*Delphinapterus leucas*) B92-105 under reflected light. Dots indicate each bipartite growth layer group in the dentine. Root is to the left, apical cusp to the right. Shadow around the section is embedding epoxy. (Photograph was spliced and dots were added using Photoshop®.)

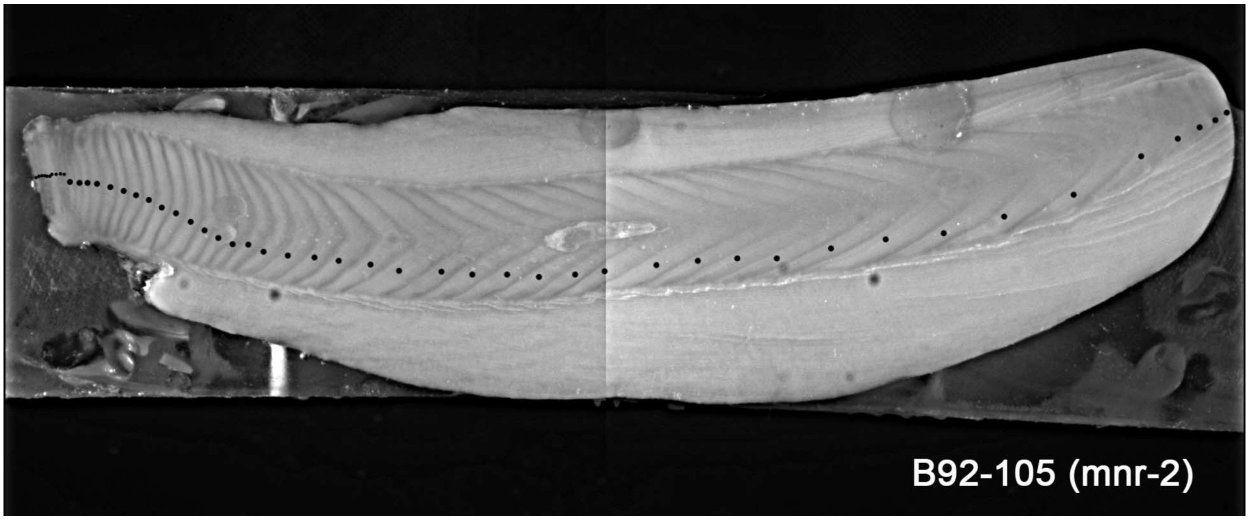
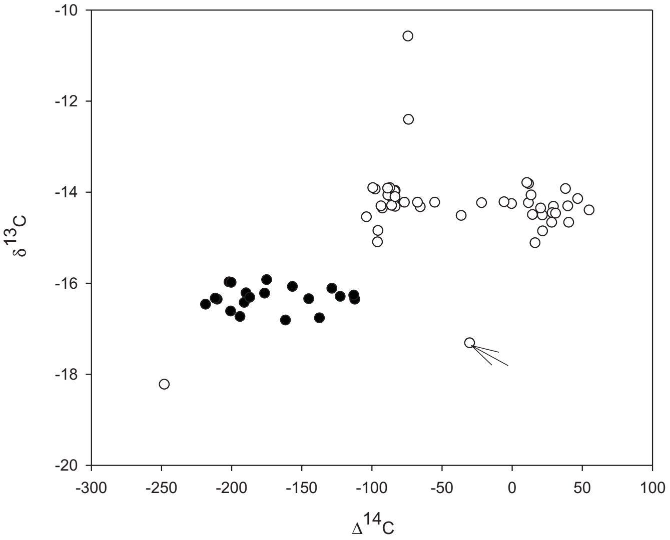


Fig. 2. $\delta^{13}C$ values as a function of $\Delta^{14}C$ for sections from teeth glued to a wooden block for sectioning (○) and sections from teeth embedded in resin (●). Arrow denotes an outlier in an MNR-5 tooth that was not resolved by applying the mixing curves. This data point was removed from further consideration.



considered full recruitment into the sample to occur at the most numerous age class, and exponential decay curves were fit to the number of newborn calves and fully recruited age classes to generate a population age structure. This population was used to explore the effects of different age estimation techniques on life-history parameters, following Pianka (1988). The instantaneous mortality rate after full recruitment was calculated for each age distribution (Ricker 1975), adding 1 to catch-at-age data to avoid the logarithm of zero.

Results

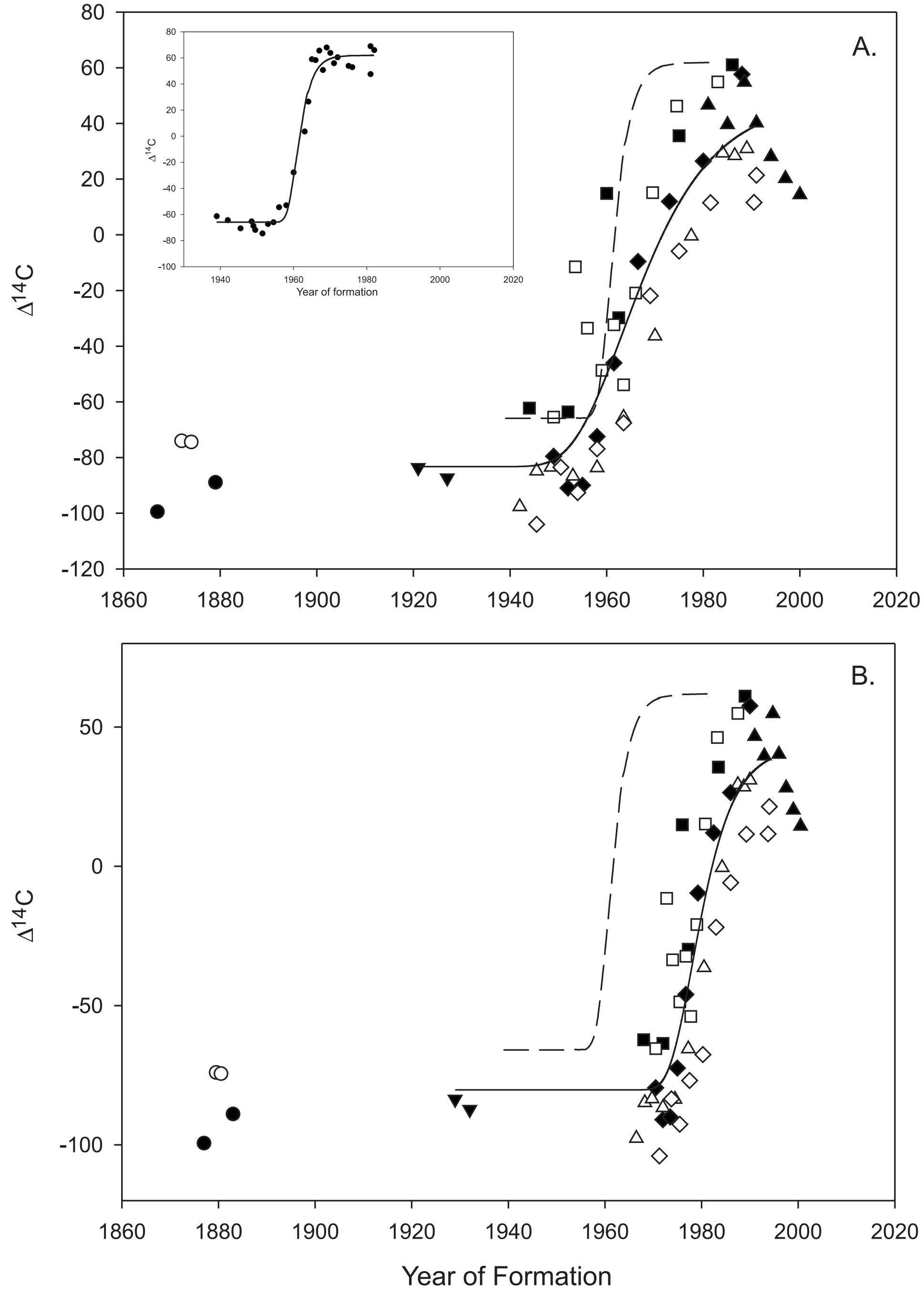
Growth layer sequences were clearly visible in beluga tooth sections and were better defined in dentine than in cementum (Fig. 1). Each GLG appeared as a bipartite structure consisting of a translucent zone and an opaque zone. Most teeth were worn distally such that no fetal dentine was present and both cementum and dentine layers had been truncated. While this precluded examination to the time of birth and maximum ages are underestimated, it did not affect our results because the year of death was used to anchor GLG counts.

Comparing non-embedded and resin-embedded teeth indicated resin infiltration into embedded teeth. Two resin samples collected immediately adjacent to the teeth were strongly depleted in both carbon isotopes, with a mean $\delta^{13}C$ of –28.05 and a mean $\Delta^{14}C$ of –974. Resin-embedded teeth were significantly depleted in $\delta^{13}C$ and $\Delta^{14}C$, to the point of physiological implausibility (Table 1, Fig. 2). Mixing-curve calculations showed that resin contributed 5%–30% of the $\delta^{13}C$ of the embedded sample. When the $\Delta^{14}C$ of each embedded tooth was corrected using the $\delta^{13}C$-based mixing curves, it became very similar to its non-embedded counterpart formed at the same time. For consistency, all samples, embedded or not, from belugas B92-34, B92-105, and B92-108 were corrected the same way using the non-embedded $\delta^{13}C$ of B92-108 as the reference. Applying the correction made little difference to the $\Delta^{14}C$ of non-embedded samples (Table 1). The adjustment for resin contamination did not change the within-tooth year of initial $\Delta^{14}C$ increase, only the magnitude of $\Delta^{14}C$ values.

The $\delta^{13}C$ of all non-embedded recent teeth ranged between –13.8‰ and –15.1‰, with an overall mean of –14.3‰ (n = 40, SE = 0.05, Table 1). $\delta^{13}C$ appeared to decline weakly but nonsignificantly with year of formation between 1942 and 2000 (P = 0.10). Although there were only four dentine–cementum matched pairs, the two tissues appeared to have similar $\delta^{13}C$ values. Only dentinal values were used in subsequent analyses.

The main limitation in analyzing beluga teeth was associated with the amount of material that could be isolated from a single GLG. To obtain sufficient material to process, it was sometimes necessary to take material from more than one GLG. The average (±1 SE) period spanned in an indi-

Fig. 3. Dentinal Δ^{14}C values from beluga teeth as a function of average year of formation (reference chronology in insert; $\Delta^{14}\mathrm{C} = -64.1 + 126.0\exp\{-\exp[-(\mathrm{YEAR} - 1960.7)/2.3]\}$, n = 21, adj. r^2 = 0.97). (A) Assuming one GLG formed each year, $\Delta^{14}\mathrm{C} = -83.3 + 131.6\exp\{-\exp[-(\mathrm{YEAR} - 1963.4)/10.5]\}$, n = 48, adj. r^2 = 0.79. (B) Assuming two GLGs formed each year, $\Delta^{14}\mathrm{C} = -80.3 + 123.0\exp\{-\exp[-(\mathrm{YEAR} - 1978.1)/4.8]\}$, n = 48, adj. r^2 = 0.74. The fitted curves are for the reference chronology (dashed line) and beluga chronologies (solid line). Individual belugas are as follows: ●, CB19-18; ○, CB19-33; ▼, CB20-01; Δ, LH91-27; ■, B92-34; □, B92-105 (MNR-2); ◆, B92-108 (MNR-2); ◇, B97-37; and ▲, ARLHxx1003 (MNR-2 and MNR-5).

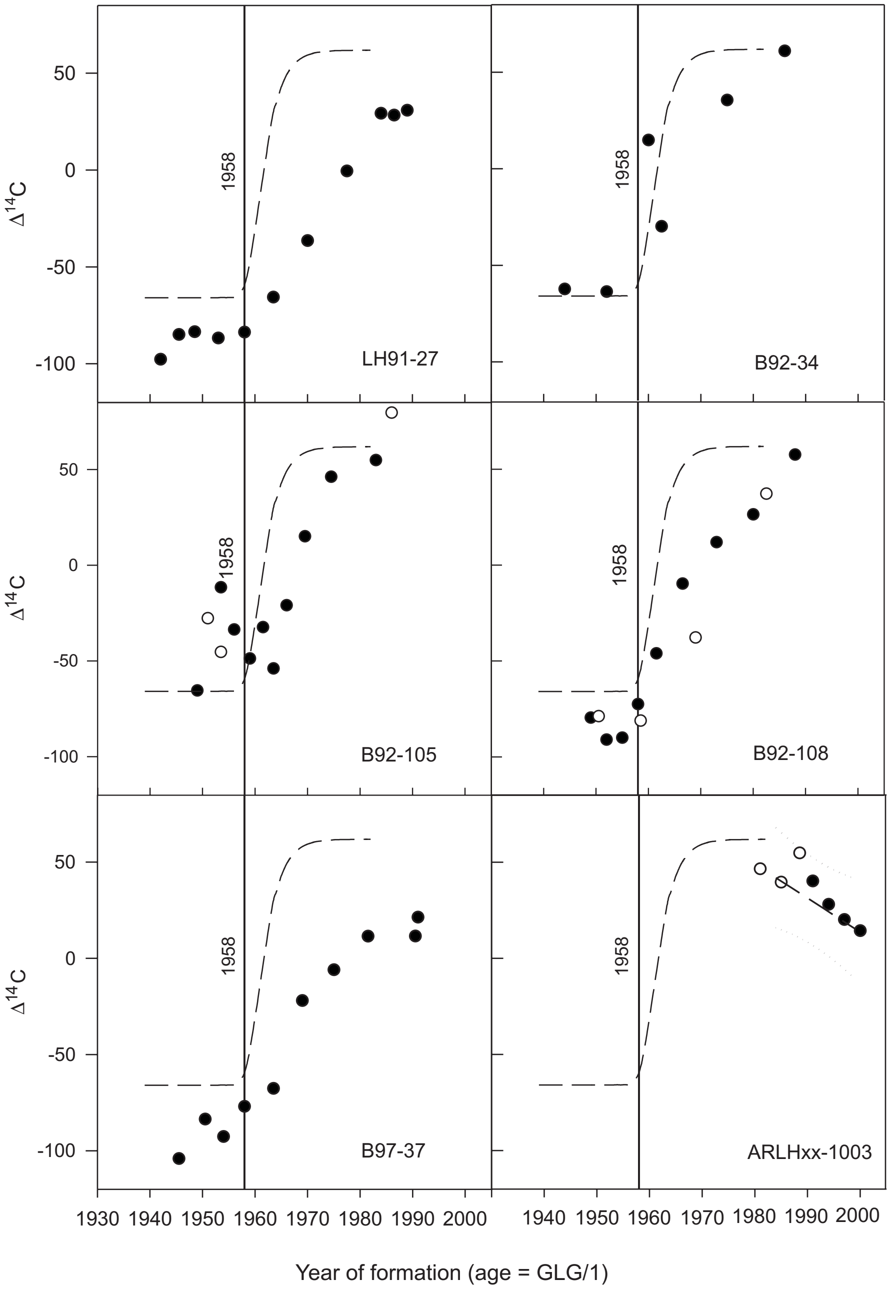


vidual sample was 4.7 ± 3.0 GLGs, allowing a sampling resolution of 2.3 years (GLG/1).

The reference chronology showed the expected sharp increase about 1958 with a decline after 1982. The post-peak radiocarbon data are uninformative with respect to date of first appearance, so the data were truncated at 1982 and the four-parameter Gompertz regression was fitted to the 1949–1982 data (Fig. 3 insert). Most beluga data were fitted to the same model but inclusion of the two whales from the 1800s introduced unequal variances (P = 0.04), so they were excluded from the final analysis. Beluga ARLHxx1003 lived entirely after the atomic bomb testing era and was not included in the Gompertz model. Post-1982 reference data were well described by a linear model ($\Delta^{14}\mathrm{C} = 3550.7 - 1.8\mathrm{YEAR}$, n = 6, adj. r^2 = 0.60).

The increase in tooth Δ^{14}C throughout the 1960s closely

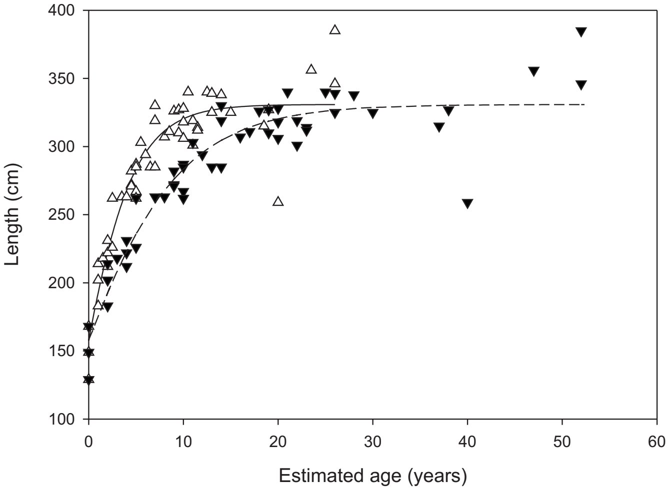
Fig. 4. Distribution of $\Delta^{14}C$ values from beluga tooth sections as a function of average year of formation assuming age = GLG/1. The year of first appearance of the bomb radiocarbon signal in the marine environment (1958, vertical line) is based on the reference chronology (dashed line). ●, teeth from position MNR-2; ○, teeth from position MNR-5.



matched the bomb signal of $\Delta^{14}C$ expected in the marine environment. The Gompertz model provided a good fit to both the 1 GLG/year and the 2 GLGs/year data (Fig. 3). Prebomb $\Delta^{14}C$ remained relatively constant in belugas at about –80 from 1865 to the late 1950s, lower than $\Delta^{14}C$ for the reference chronology (Fig. 3). The lower intercepts (Y_0) of the two beluga curves were not significantly different from each other. The year of initial increase (Y_0 + 2 SE) was 1958.5 for the reference chronology, 1955.9 for the beluga when age = GLG/1, and 1974.9 for the beluga when age = GLG/2. (Including the four data points from the 1800s altered these estimates only slightly to 1954.6 for GLG/1 and 1974.1 for GLG/2.) Given the resolution (±2.3 year) available, the GLG/1 estimate was indistinguishable from the date determined for the reference chronology, but the GLG/2 estimate was substantially and significantly different. Although the initial increase in tooth $\Delta^{14}C$ using 1 GLG/year matched that for the reference chronology, the subsequent rate of increase in $\Delta^{14}C$ using 1 GLG/year lagged behind that for marine DIC, with $\Delta^{14}C$ peaking in the 1980s rather than the late 1960s.

Bomb radiocarbon is a reliable dated marker if it remains static in a GLG throughout the subsequent life of the animal. There was little evidence of metabolic reworking of the radiocarbon signal in the tooth dentine. All nine beluga whales from which multiple GLGs were sampled showed the same

Fig. 5. A comparison of growth curves for female belugas sampled at Arviat assuming age = GLG/2 (solid line, Δ, Stewart 1994*a*) and age = GLG/1 (dashed line, ▼).



within-tooth bomb signal across years of formation as the between-tooth analysis; that is, each tooth showed an increase in the bomb radiocarbon signal around 1958 independent of the age of the beluga or the year of collection (Fig. 4). Ontogenetic effects were not evident, indicating that the bomb signal was not diluted by subsequent growth over a period of up to 40 years.

All five belugas that lived through the bomb-testing period showed an abrupt increase in Δ^{14}C within about 1–3 years of 1958, the point of reference for all bomb dating applications (Fig. 4); therefore, they must have been aged correctly (on average) based on the number of GLGs present, i.e., 1 GLG/year. Errors in age estimation would be evident as Δ^{14}C values that appeared to increase earlier or later than 1958. None of the date assignments based on 2 GLGs/year was consistent with the 1958 initiation of the bomb signal; all were delayed by almost 20 years (Fig. 3). The whale that lived after the bomb-testing era was uninformative with respect to ageing accuracy but showed the predicted decline in Δ^{14}C based on 1 GLG/year (Fig. 4).

The effect of interpreting age to be the number of GLGs counted, instead of GLG/2, on a published growth curve for female belugas from western Hudson Bay (Stewart 1994*a*) was to decrease the slope and extend the curve to older ages, with no change in asymptotic size (Fig. 5, Table 2). The changed interpretation of age has an appreciable effect on life-table parameters. In the simulated population, the number of newborn females expected from mature females was 26.6 when age = GLG/1 and 27.9 when age = GLG/2, a consequence of rounding up from 5.5 years to 6 years (n = 7) in the life table. The age structures, represented by a three-parameter exponential decay curve (Fig. 6), showed the greatest difference in survivorship among middle age classes, reflected in the age-specific realized fecundity ($l_x m_x$). Net reproductive rate, however, increased only slightly assuming age = GLG/1. The instantaneous mortality after full recruitment, the intrinsic rate of natural increase, and the finite rate of increase were all smaller under the GLG/1 hypothesis (Table 2).

Discussion

The radiocarbon chronology recorded in tooth dentine clearly confirmed that growth layers form annually in beluga teeth and that GLG counts provide an accurate measure of beluga age. Δ^{14}C values in beluga teeth before the period of atmospheric atomic bomb testing were lower and slightly more variable than those for the reference chronology, probably reflecting differences in water masses occupied (Kalish 1993; Campana 1997), but the critical initial appearance of bomb radiocarbon in the teeth was almost identical to that observed in published marine reference chronologies (Druffel 1989; Weidman and Jones 1993; Peck and Brey 1996; Campana 1997; Druffel and Griffin 1999; Kalish et al. 2001; Ebert and Southon 2003; Kerr et al. 2004). These reference chronologies all increased markedly in Δ^{14}C around 1958 in locations as widespread as the northwest Atlantic, north and south Pacific, Arctic, and Antarctic and in surface marine DIC and organic carbonates of diverse biota including corals, bivalves, fish otoliths, and echinoderm tests. Similar chronologies have been documented in noncarbonate hard parts as well, including human teeth (Spalding et al. 2005) and shark vertebrae and spines (Campana et al. 2002, 2006). The appearance of the bomb signal in the beluga teeth at the same time as in the reference chronologies indicates that the teeth must have been aged correctly by assuming that one GLG equals 1 year's growth. The 2 GLGs/year hypothesis is rejected because it estimated the initial appearance of bomb radiocarbon to be in the 1970s, completely inconsistent with the known date of onset.

Uncertainty associated with the appropriate way to interpret beluga GLG counts has persisted for many years, but previous attempts to resolve the issue have been inconclusive (Hohn and Lockyer 1999). Examination of teeth from a beluga held captive for 23 years produced inconclusive information, presumably because teeth from captive whales produce GLGs that are less well defined and more difficult to count than GLGs of teeth from wild animals (Brodie 1982; Heide-Jørgensen et al. 1994; Hohn and Lockyer 2001). Nevertheless, the results were interpreted as supporting the formation of 2 GLGs per year (Goren et al. 1987). Post-injection tooth growth of a tetracycline-injected captive beluga was interpreted similarly despite the extrapolation of only 10 weeks of dentine growth to a full year (Brodie et al. 1990). The average age of first conception in 16 captive females (Robeck et al. 2005) can be compared with the age of maturation in wild belugas based on the two age interpretation methods, although captive animals might mature earlier in the absence of food stress. Age of maturity in captivity fell midway between the ages expected for wild animals based on 1 and 2 GLGs per year. Attempts to validate the rate of GLG formation by comparing the body size of captive and wild whales were also inconclusive (Brodie 1982). Conversely, allometric comparisons of asymptotic length (L_∞) and estimated longevity of cetaceans lead Ohsumi (1979) to conclude that GLG deposition in belugas was more likely to be annual than semiannual. Nevertheless, the prevailing wisdom was that belugas were dissimilar to other whales in that they formed 2 GLGs per year (Heide-Jørgensen and Teilmann 1994; Stewart 1994*a*; Becker et al. 2000; Boltunov and Belikov 2002). Therefore, our confirmation

Table 2. Calculation of age-related life-history parameters for belugas assuming age = GLG/1 and age = GLG/2.

Parameter	Calculation	Age = GLG/1	Age = GLG/2
Somatic growth (length)*	length = $a\exp[-\exp(kt + kt_0)]$		
asymptote, a		330.87 cm	330.87 cm
k		0.156	0.313
t_0		–1.910	–0.955
Age of maturity, α[†]		12 years	6 years
Longevity, ω			
Female[‡]		79 years	39.5 years
Male[‡]		77 years	38.5 years
Life-history parameters[§]			
Net reproductive rate, R_0	$R_0 = \sum_{x=0}^{\infty} l_x m_x$	2.55	2.24
Generation time, T (growing population, $R_0 > 1$)	$T = (\sum_{x=\alpha}^{\omega} x l_x m_x)/R_0$	24.1 years	12.6 years
Intrinsic rate of natural increase, r	$1 = \sum_{x}^{\omega} e^{-rx} l_x m_x$	0.042	0.069
Finite rate of increase, λ	$\lambda = e^r$	1.043	1.071
Instantaneous mortality, Z	ln(catch-at-age + 1) = $a + Z$age	0.05	0.12

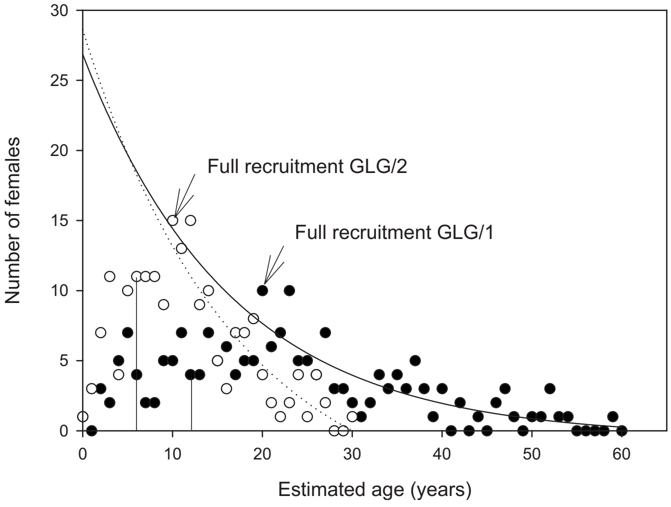
*Based on 51 females from western Hudson Bay (Stewart 1994*a*).

[†] Based on 63 females from Nunavut (Stewart 1994*b*).

[‡] Oldest of 485 female and 658 males from Nunavut (DFO, unpublished data).

[§] Based on a simulated age structure fitted to 191 females from western Hudson Bay (DFO, unpublished data) and estimated numbers of newborn females.

Fig. 6. Comparison of a hypothetical age structure based on 191 female belugas killed in western Hudson Bay, using age = GLG/2 (dotted line, ○) and age = GLG/1 (solid line, ●). Vertical lines indicate age of maturation under each ageing protocol.



that belugas produce only one growth increment per year in their teeth conforms to growth increment formation in most other marine mammals while emphasizing the difficulty of confirming the age of many whale species.

The median δ^{13}C value of the two 19th-century teeth (–13.15‰) was virtually identical to that (–13.2‰) obtained by Outridge et al. (2005), who found no evidence of diagenesis. Tooth δ^{13}C averaged –14.3‰, substantially lower than the values of –3‰ to +2‰ typically found in corals or otoliths (Druffel and Linick 1978; Campana 1999) but not as low as that found in high Artic belugas (–17.2‰, Outridge et al. 2005). Whereas the carbon source for corals and otoliths is largely DIC with a δ^{13}C close to zero (Schwarcz et al. 1998), strongly depleted values such as those observed in the beluga teeth are more characteristic of metabolic and dietary carbon, as documented for marine mammals (Tauber 1979) and sharks (Campana et al. 2002, 2006). With the carbon source for the teeth being of dietary origin, some phase shifting of the radiocarbon chronology could be expected if beluga consumed prey that were not in Δ^{14}C equilibrium with the DIC. For example, Campana et al. (2002) documented a slight phase shifting between the vertebral radiocarbon of porbeagle sharks and the DIC chronology due to the ingestion of long-lived prey that contained ^{14}C concentrations averaged across their lifetime of exposure. Thus, newly deposited porbeagle vertebral material tended to be slightly depleted in Δ^{14}C during the years of increasing bomb radiocarbon, producing a slightly lagged period of Δ^{14}C increase. A similar phenomenon almost certainly takes place in belugas, which feed at several trophic levels (Stewart and Stewart 1989). The effect of feeding at higher trophic levels or on long-lived prey would be to reduce the rate of increase of the bomb radiocarbon signal and extend it over a longer period. This was observed in the beluga teeth, whereby the radiocarbon signal initially appeared on the correct date but the subsequent incorporation extended into the 1980s rather than the early 1970s.

The life-history consequences of belugas living twice as long as previously assumed resulted in twofold changes in somatic growth rate, age of maturity, and longevity, but differences in other life-history parameters were not so simple. Net reproductive rate (R_0), the average number of newborns expected over the life of a newborn female, increased in the simulated population by 14% when reproductive life span doubled. Conversely, the intrinsic rate of natural increase (r) for the population declined by almost 40% when age was assumed to be GLG/1 rather than GLG/2. The calculation of r is greatly affected by α, which doubled (Table 2), and the "compound interest" afforded to the population when age = GLG/2. For example, when maturation occurs at 6 years (age = GLG/2), females have produced three calves each and their daughters have produced one calf each at about the time that females would produce their first calves if maturation occurred at 12 years (age = GLG/1). Although females live 30 years longer if age = GLG/1 rather than GLG/2, their numbers are reduced and the population cannot compensate for its late start.

An incorrect interpretation of age would affect management decisions for belugas because stock production models rely on various estimates of "rate of increase", which in turn rely on age-specific fecundity and survival (Reilly and Barlow 1986; Béland et al. 1988). Rates of increase are most sensitive to the inter-birth interval and non-calf survival, followed by age of maturation (Reilly and Barlow 1986). The calving interval for belugas has been determined primarily from the fraction of mature females pregnant in a sample and is independent of age estimates. Non-calf survivorship is directly linked to age estimates, and stock production models that rely on survivorship directly (Butterworth et al. 2002) or indirectly (e.g., λ; Béland et al. 1988) are vulnerable to ageing errors. However, many management plans for belugas have not determined beluga survivorship or used a point estimate of the finite rate of increase (λ), but have used a range of λ of 1.020–1.041 from Reilly and Barlow's (1986) model for dolphins (Bodaly et al. 1992; Cosens et al. 1993, 1998). Fortuitously for belugas, Reilly and Barlow assumed a longevity of 50 years, 6–12 years for the age of maturation, and 2, 3, and 4 year calving intervals in their model. These values approximate beluga values better when age = GLG/1 than when age = GLG/2. Stock production models were less sensitive to estimates of age of maturation (Reilly and Barlow 1986), but the effect of doubling this parameter on population models (e.g., Butterworth et al. 2002) requires investigation. Similarly, predecessors of Bayesian population models (e.g., Innes and Stewart 2002) can be made broad and robust to minor changes in survival but again the doubling of the age of maturation requires reexamination.

Recommendations for the management of belugas around southeast Baffin Island (Cosens et al. 1993) were based directly on the age structure of the harvest, which contained few older whales. In this harvest, it appeared that the oldest females had a reproductive life span of about 11 years ($\omega - \alpha = 17 - 6 = 11$ years), suggesting most females would die before giving birth to their fourth calf. However, had the oldest female been correctly aged at 34 years, based on 1 GLG/year, the reproductive life span would have been estimated at 22 years, with the potential to produce seven calves. Earlier management recommendations have been superseded by those based on a Bayesian model (Department of Fisheries and Oceans 2005) with its attendant caveats.

The use of bomb radiocarbon to determine age and confirm the periodicity of growth layers should be appropriate for all toothed marine mammals when some of the growth increments were formed before 1965. Although the presence of bomb radiocarbon in marine mammals in the Arctic was noted years ago, the results were not put into a chronological context (Tauber 1979; Bada et al. 1987). Yet the potential of this technique for validating the annual nature of tooth growth bands has already been demonstrated in moose (*Alces alces* L., 1758, Bada et al. 1990), humans (Spalding et al. 2005), and many fish and other marine organisms (Campana 2001). Validated ageing methods for mammals remain relatively rare (Hohn 2002), perhaps reflecting the low number of individuals aged each year relative to the roughly one million fish that are aged (Campana and Thorrold 2001). Nevertheless, the ability to sequentially sample multiple layers in a single tooth to prepare a complete Δ^{14}C chronology, confirming the age of a single mammal, is a logistical advantage of bomb radiocarbon age validation of mammals compared with fish, in which otolith size limits the amount of material available for assay (Campana 1999).

Acknowledgements

We thank the hunters of southeast Baffin Island for providing material from their subsistence hunts in several programs funded by the Nunavut Wildlife Research Trust. J. Savelle and P. Outridge kindly provided teeth from archaeological sites. B. Dunn and W. Joyce provided able assistance with tooth preparation and analysis. Thanks to the staff of the National Ocean Sciences Accelerator Mass Spectrometry Facility at Woods Hole Oceanographic Institution for their expertise in carrying out the radiocarbon assays. The manuscript was improved by comments from S. Ferguson and P. Richard and two anonymous reviewers. Funding from the DFO Nunavut Ecosystem Survey and Research Fund and the DFO Nunavut Implementation Fund made the study possible. C.M.J. was supported by National Science Foundation grant OCE-0525964.

References

Bada, J.L., Vrolijk, C.D., Brown, S., Druffel, E.R.M., and Hedges, R.E.M. 1987. Bomb radiocarbon in metabolically inert tissues from terrestrial and marine mammals. Geophys. Res. Lett. **14**: 1065–1067.

Bada, J.L., Peterson, R.O., Schimmelmann, A., and Hedges, R.E.M. 1990. Moose teeth as monitors of environmental isotopic parameters. Oecologia, **82**: 102–106. doi:10.1007/BF00318540.

Beamish, R.J., and McFarlane, G.A. 1995. A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. *In* Recent developments in fish otolith research. *Edited by* D.H. Secor, J.M. Dean, and S.E. Campana. University of South Carolina Press, Columbia, S.C. pp. 545–565.

Becker, P.R., Krahn, M.M., Mackey, E.A., Demiralp, R., Schantz, M.M., Epstein, M.S., Donais, M.K., Porter, B.J., Muir, D.C.G., and Wise, S.A. 2000. Concentrations of polychlorinated biphenyls (PCB's), chlorinated pesticides, and heavy metals and other elements in tissues of belugas, *Delphinapterus leucas*, from Cook Inlet, Alaska. Mar. Fish. Rev. **62**: 81–98.

Béland, P., Vezina, A., and Marineau, D. 1988. Potential for growth of the St. Lawrence (Québec, Canada) beluga whale (*Delphinapterus leucas*) population based on modelling. ICES J. Mar. Sci. **45**: 22–32.

Bodaly, R.A., Cosens, S.E., Shortt, T.A., and Stewart, R.E.A. 1992. Report of the Arctic Fisheries Scientific Advisory Committee for 1989/90 and 1990/91. Can. Manuscr. Rep. Fish. Aquat. Sci. **2139**: 1–91.

Boltunov, A.N., and Belikov, S.E. 2002. Belugas (*Delphinapterus* *leucas*) of the Barents, Kara and Laptev seas. NAMMCO Sci. Publ. **4**: 149–168.

Boness, D.J., Clapham, P.J., and Mesnick, S.L. 2002. Life history and reproductive strategies. *In* Marine mammal biology, an evolutionary approach. *Edited by* A.R. Hoelzel. Blackwell Science, Oxford. pp. 278–324.

Brodie, P.F. 1982. The beluga (*Delphinapterus leucas*); growth at age based on a captive specimen and a discussion of factors affecting natural mortality estimates. Rep. Int. Whaling Comm. **32**: 445–447.

Brodie, P.F., Geraci, J.R., and St. Aubin, D.J. 1990. Dynamics of tooth growth in beluga whales, *Delphinapterus leucas*, and effectiveness of tetracycline as a marker for age determination. *In* Advances in research on the beluga whale *Delphinapterus leucas*. *Edited by* T.G. Smith, D.J. St. Aubin, and J.R. Geraci. Can. Bull. Fish. Aquat. Sci. No. 224. pp. 141–148.

Brown, C.A., and Gruber, S.H. 1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. Copeia, 1988: 747–753. doi:10.2307/1445397.

Butterworth, D.A., Plagányi, É., and Geromont, F. 2002. Resource assessment and projections for the belugas off West Greenland using the population model of HITTER-FITTER. NAMMCO Sci. Publ. **4**: 211–224.

Campana, S.E. 1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock, *Melanogrammus aeglefinus*. Mar. Ecol. Prog. Ser. **150**: 49–56.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar. Ecol. Prog. Ser. **188**: 263–297.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**: 197–242. doi:10.1111/j.1095-8649.2001.tb00127.x.

Campana, S.E., and Thorrold, S.R. 2001. Otoliths, increments and elements: keys to a comprehensive understanding of fish populations? Can. J. Fish. Aquat. Sci. **58**: 30–38. doi:10.1139/cjfas-58-1-30.

Campana, S.E., Natanson, L.J., and Myklevoll, S. 2002. Bomb dating and age determination of large pelagic sharks. Can. J. Fish. Aquat. Sci. **59**: 450–455. doi:10.1139/f02-027.

Campana, S.E., Jones, C., McFarlane, G.A., and Myklevoll, S. 2006. Bomb dating and age validation using the spines of spiny dogfish (*Squalus acanthias*). Environ. Biol. Fishes, **77**: 327–336. doi:10.1007/s10641-006-9107-3.

Cass, A.J., and Beamish, R.J. 1983. First evidence of validity of the fin-ray method of age determination for marine fishes. N. Am. J. Fish. Manag. **3**: 182–188. doi:10.1577/1548-8659(1983)3<182:FEOVOT>2.0.CO;2.

Caughley, G., and Birch, L.C. 1971. Rate of increase. J. Wildl. Manag. **35**: 658–663.

Cosens, S.E., Crawford, R., de March, B.G.E., and Shortt, T.A. 1993. Report of the Arctic Fisheries Scientific Advisory Committee for 1991/92 and 1992/93. Can. Manuscr. Rep. Fish. Aquat. Sci. **2224**: 1–51.

Cosens, S.E., de March, B.G.E., Innes, S., Mathias, J., and Shortt, T.A. 1998. Report of the Arctic Fisheries Scientific Advisory Committee for 1993/94, 1994/95 and 1995/96. Can. Manuscr. Rep. Fish. Aquat. Sci. **2473**: 1–87.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., and Grenfell, B.T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science (Washington, D.C.), **292**: 1528–1531. doi:10.1126/science.292.5521.1528.

Department of Fisheries and Oceans. 2005. Recovery potential assessment of Cumberland Sound, Ungava Bay, eastern Hudson Bay and St. Lawrence beluga populations (*Delphinapterus leucas*). Canadian Science Advisory Secretariat Science Advisory Report 2005/036. Available from Regional Science Advisory Bureau, Québec Region, Fisheries and Oceans Canada, Maurice Lamontagne Institute, P.O. Box 1000, Mont-Joli, Québec, G5H 3Z4 or http://www.dfo-mpo.gc.ca/csas/Csas/status/2005/SAR-AS2005_036_e.pdf.

Dodge, R.E., and Thomson, J. 1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. Earth Planet. Sci. Lett. **23**: 313–322. doi:10.1016/0012-821X(74)90121-6.

Druffel, E.M. 1989. Decadal time scale variability of ventilation in the North Atlantic: high-precision measurements of bomb radiocarbon in banded corals. J. Geophys. Res. **94**: 3271–3285.

Druffel, E.R.M., and Griffin, S. 1999. Variability of surface ocean radiocarbon and stable isotopes in the southwestern Pacific. J. Geophys. Res. **104**: 23607–23613. doi:10.1029/1999JC900212.

Druffel, E.M., and Linick, T.W. 1978. Radiocarbon in annual coral rings of Florida. Geophys. Res. Lett. **5**: 913–916.

Ebert, T.A., and Southon, J.R. 2003. Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb ^{14}carbon. Fish. Bull. (Washington, D.C.), **101**: 915–922.

Evans, K., Hindell, M.A., Robertson, K., Lockyer, C., and Rice, D. 2002. Factors affecting the precision of age determination of sperm whales (*Physeter macrocephalus*). J. Cetacean Res. Manag. **4**: 193–201.

Garlich-Miller, J.L., Stewart, R.E.A., Stewart, B.E., and Hiltz, E.A. 1993. Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walrus (*Odobenus rosmarus*). Can. J. Zool. **71**: 163–167.

Germano, D.J. 1998. Scutes and age determination of desert tortoises revisited. Copeia, 1998: 482–484. doi:10.2307/1447446.

Goren, A.D., Brodie, P.F., Spotte, S., Ray, G.C., Kaufman, H.W., Gwinnett, A.J., Sciubba, J.J., and Buck, J.D. 1987. Growth layer groups (GLGs) in the teeth of an adult belukha whale (*Delphinapterus leucas*) of known age: evidence for two annual layers. Mar. Mamm. Sci. **3**: 14–21.

Heide-Jørgensen, M.P., and Teilmann, J. 1994. Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. Medd. Grønl. Biosci. **39**: 195–212.

Heide-Jørgensen, M.P., Jensen, J., Larsen, A.H., Teilmann, J., and Neurohr, B. 1994. Age estimation of white whales (*Delphinapterus leucas*) from Greenland. Medd. Grønl. Biosci. **39**: 187–193.

Hohn, A.A. 2002. Age estimation. *In* Encyclopedia of marine mammals. *Edited by* W.F. Perrin, B. Würsig, and J.G.M. Thewissen. Academic Press, San Diego, Calif. pp. 6–13.

Hohn, A.A., and Lockyer, C. 1999. Growth layer patterns in teeth from two known-history beluga whales: reconsideration of deposition rates. Paper submitted to the IWC Scientific Committee, Grenada, May 1999, International Whaling Commission SC/51/SM4, 17 p. [unpaginated]. Available from the Secretary, International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, CB4 9NP, UK, e-mail: secretariat@iwcoffice.org.

Hohn, A.A., and Lockyer, C. 2001. Workshop to determine deposition rates of growth layers in teeth of white whales (*Delphinapterus leucas*). Draft report to NAMMCO, May 2001, SC/9/BN/4, pp. 1–12. Available from North Atlantic Marine Mammal Commission, Polar Environmental Centre, N-9296 Tromsø, Norway, e-mail nammco-sec@nammco.no.

Innes, S., and Stewart, R.E.A. 2002. Population size and yield of

Baffin Bay beluga (*Delphinapterus leucas*) stocks. NAMMCO Sci. Publ. **4**: 225–238.

International Whaling Commission. 1980. Report of the workshop. *In* Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue 3. *Edited by* W.F. Perrin and A.C. Myrick. International Whaling Commission, Cambs, U.K. pp. 1–50.

Johnston, D.H., Joachim, D.G., Bachmann, P., Kardong, K.V., Stewart, R.E.A., Dix, L.M., Stickland, M.A., and Watt, I.D. 1987. Aging furbearers using tooth structure and biomarkers. *In* Wild furbearer management and conservation in North America. *Edited by* M. Novak, J.A. Baker, M.E. Obbard, and B. Mallock. Ontario Trappers Association, Toronto, Ont. pp. 228–243.

Kalish, J.M. 1993. Pre- and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. **114**: 549–554. doi:10.1016/0012-821X(93)90082-K.

Kalish, J.M., Nydal, R., Nedreaas, K.H., Burr, G.S., and Eine, G.L. 2001. A time history of pre- and post-bomb radiocarbon in the Barents Sea derived from Arcto-Norwegian cod otoliths. Radiocarbon, **43**: 843–855.

Kerr, L.A., Andrews, A.H., Frantz, B.R., Coale, K.H., Brown, T.A., and Caolliet, G.M. 2004. Radiocarbon in otoliths of yelloweye rockfish (*Sebastes ruberrumus*): a reference time series for the coastal waters of southeast Alaska. Can. J. Fish. Aquat. Sci. **61**: 443–451. doi:10.1139/f04-009.

Klevezal, G.A. 1996. Recording structures of mammals, determination of age and reconstruction of life history. Nauka, Moscow. [Translated from Russian by M.V. Mina and A.V. Oreshkin. A.A. Balkema, Rotterdam, Netherlands.]

Lutz, R.A., and Rhoads, D.C. (*Editors*). 1980. Growth patterns within the molluscan shell: an overview. *In* Skeletal growth of aquatic organisms. Plenum Press, New York. pp. 203–254.

Morris, W.F., and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., Sunderland, Mass.

Neville, A.C. 1967. Daily growth layers in animals and plants. Biol. Rev. Camb. Philos. Soc. **42**: 421–441.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale. Rep. Int. Whaling Comm. **29**: 397–406.

Outridge, P.M., Hobson, K.A., and Savelle, J.M. 2005. Changes in mercury and cadmium concentrations and the feeding behaviour of beluga (*Delphinapterus leucas*) near Somerset Island, Canada, during the 20th century. Sci. Total Environ. **350**: 106–118. PMID:16227077.

Peck, L.S., and Brey, T. 1996. Bomb signals in old Antarctic brachiopods. Nature (London), **380**: 207–208. doi:10.1038/380207b0. PMID:8637567.

Pianka, E.R. 1988. Evolutionary ecology. Harper & Row, New York.

Piner, K.R., Hamel, O.S., Menkel, J.L., Wallace, J.R., and Hutchinson, C.E. 2005. Age validation of canary rockfish (*Sebastes pinniger*) from off the Oregon coast (USA) using the bomb radiocarbon method. Can. J. Fish. Aquat. Sci. **62**: 1060–1066. doi:10.1139/f05-082.

Pueck, Z., and Lowe, P.W. 1975. Age criteria in small mammals. *In* Small mammals: their productivity and population dynamics. IBP No. 5. *Edited by* F.B. Golly, K. Petruseweiz, and L. Ryszkowski. Cambridge University Press, Cambridge, U.K. pp. 55–72.

Reilly, S.B., and Barlow, J. 1986. Rates of increase in dolphin populations. Fish. Bull. (Washington, D.C.), **84**: 527–533.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. **91**.

Robeck, T.R., Monfort, S.L., Calle, P.P., Dunn, J.L., Jensen, E., Boehm, J.R., Young, S., and Clark, S.T. 2005. Reproduction, growth and development in captive beluga (*Delphinapterus leucas*). Zoo Biol. **24**: 29–49. doi:10.1002/zoo.20037.

Robillard, S.R., and Marsden, J.E. 1996. Comparison of otolith and scale ages for yellow perch from Lake Michigan. J. Gt. Lakes Res. **22**: 429–435.

Schwarcz, H.P., Gao, Y., Campana, S., Browne, D., Knyf, M., and Brand, U. 1998. Stable carbon isotope variations in otoliths of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **55**: 1798–1806. doi:10.1139/cjfas-55-8-1798.

Secor, D.H., Dean, J.M., and Campana, S.E. (*Editors*). 1995. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Sergeant, D.E. 1959. Age determination in odontocete whales from dental layers. Nor. Hvalfangst-Tid. [The Norwegian Whaling Gazette], **48**: 273–288.

Sergeant, D.E. 1981. On permissible exploitation rates of Monodontidae. Rep. Int. Whaling Comm. **31**: 583–588.

Smith, D.C., Fenton, G.E., Robertson, S.G., and Short, S.A. 1995. Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. Can. J. Fish. Aquat. Sci. **52**: 391–401.

Spalding, K.L., Buchholz, B.A., Bergman, L.E., Druid, H., and Frisen, J. 2005. Age written in teeth by nuclear tests. Nature (London), **437**: 333–334. doi:10.1038/437333a. PMID:16163340.

Stewart, B.E., and Stewart, R.E.A. 1989. Beluga. Am. Soc. Mammal. Spec. Issue, **336**: 1–8.

Stewart, R.E.A. 1994*a*. Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas* Pallas 1776) stocks in the eastern Canadian Arctic. Medd. Grønl. Biosc. **39**: 217–225.

Stewart, R.E.A. 1994*b*. Progesterone levels and reproductive status of white whales (*Delphinapterus leucas*) from the Canadian Arctic. Medd. Grønl. Biosci. **39**: 239–243.

Stuiver, M., and Polach, H.A. 1977. Reporting of C-14 data. Radiocarbon, **19**: 355–363.

Tauber, H. 1979. ^{14}C activity of Arctic marine mammals. *In* Radiocarbon dating. *Edited by* R. Berger and H.E. Suess. University of California Press, Los Angeles, Calif. pp. 447–452.

Wade, P.R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar. Mamm. Sci. **14**: 1–37.

Wainwright, K.L., and Walker, R.S. 1988. A method for preparing beluga (white whale), *Delphinapterus leucas* teeth for ageing. Can. Manuscr. Rep. Fish. Aquat. Sci. **1967**: 1–15.

Weidman, C.R., and Jones, G.A. 1993. A shell-derived time history of bomb C-14 on Georges Bank and its Labrador Sea implications. J. Geophys. Res. **98**: 14577–14588.

Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. Can. J. Fish. Aquat. Sci. **62**: 872–885. doi:10.1139/f05-040.