

Growth and maturity of belugas (*Delphinapterus leucas*) in Cumberland Sound, Canada, and in captivity: evidence for two growth layer groups (GLGs) per year in teeth

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ABSTRACT

The beluga (*Delphinapterus leucas*) is one of the few cetaceans to adapt, year-round, to an Arctic environment, one of the most challenging marine habitats, incorporating shallow estuaries, high turbidity, shifting pack-ice and extreme tidal ranges. Adaptation is attributed in part, to year-round herd integrity and synchrony, occupying a sequence of restricted seasonal habitats and calving sites, which are reflected in tooth laminae. Field research, 1966–1969, led to the conclusion that females are sexually mature at 5.75 years and males at 8.75 years, gestation is 15–16 months, reproductive cycle 3 years, with a lifespan of 30–35 years. Newborn and the first four year-classes are recognisable by length, body colour and morphology. The two-year nursing period results in rapid growth, coincident with a training period to acquire social, feeding, and crucial under-ice navigational skills. Belugas in Cumberland Sound had been reduced through exploitation, thus it is unlikely that present numbers are food limited, reflecting maximum rate of increase. We examine growth indices for captive belugas, either captured as calves, or first and second generations born in captivity, to compare known-age animals. Onset of sexual maturity in males and females is similar to findings for Cumberland Sound, which was based on two growth layer groups per year in the teeth, or GLG/2. We analyse studies where previous oral doses of tetracycline, as well as bomb radiocarbon ¹⁴C from 1958 were used to argue for single annual GLGs or GLG/1. Dedicated field studies, using appropriate dosage of intramuscular tetracycline, provide evidence for GLG/2. The ¹⁴C study appears to have been compromised by preparation technique and burdens sampled in the 1990s may have been of maternal origin, transferred during foetal growth and nursing, or from recent fallout to 1980. Fundamental to the issue of growth-at-age: arguments for GLG/1 are based on back-calculation from adults of unknown age, while GLG/2 is based on projection from newborn to known-age young and adults. Direct observations and cross-referenced parameters do not substantiate GLG/1, which requires halving the growth rate, thus doubling the age of sexual and physical maturity as well as lifespan, resulting in a 40% reduction of the intrinsic rate of natural increase, substantially lower than the present rate of recovery observed.

KEYWORDS: AGE DETERMINATION; BELUGA; BOMB RADIOCARBON ¹⁴C; CAPTIVE; DENTINAL GLGS; GROWTH; MANAGEMENT; NARWHAL; REPRODUCTION; AGE AT SEXUAL MATURITY; TETRACYCLINE

INTRODUCTION

This paper re-examines the issue as to whether one or two growth layer groups (GLGs) are deposited annually in the teeth of Arctic belugas (Brodie, 1969b; 1971; 1982; Brodie *et al.*, 1990; Goren *et al.*, 1987; Heide-Jørgensen *et al.*, 1994; Hohn and Lockyer, 1999; Lockyer *et al.*, 2007; Overstrom, 1991; Sergeant, 1959; 1973; Stewart *et al.*, 2006). The beluga has adapted to one of the most challenging marine habitats. It faces combinations of shallow estuaries, high turbidity, shifting pack-ice, extreme ranges in tides and water temperature. It tolerates many weeks without feeding and long periods of near total darkness. It demonstrates body and neck flexibility, such that it can poke its head between pack-ice to breathe, nose into small streams and back out of tight situations. It survives the extremes of an Arctic environment by shifting habitats while escorting 1–2 month old calves under the fields of pack-ice, affording protection and assistance by swimming in echelon formation (Brodie, 1985). During the calving period, the herd moves into shallow estuaries on the nearby coast which few other cetaceans can negotiate, and which provide sites for sloughing of epidermis as well as protection. Herd integrity, continuous communication, massive energy reserves and insulation, intensive parental investment and rapid growth,

may combine to offset the higher natural mortality of young which might be presumed in such a challenging habitat.

Ice extent and duration increases northward, constraining movements and feeding opportunities for Arctic populations (Brodie, 1969b). By contrast, the isolated, post-glacial, southern beluga population of the St. Lawrence River (Sergeant, 1986; Sergeant and Brodie, 1969a; 1975) is exposed to pack-ice for 2–3 months vs 9–10 months in the Arctic, a reverse ratio which allows newborns to achieve substantial growth before ice formation. This population occupies a unique habitat (47°N) having adapted to tidal and flow effects of the St. Lawrence River which widens from 25km to 60km, and to 100km entering the Gulf of St. Lawrence. It may have been affected by lowered water temperatures and seasonal changes in flow of adjoining tributary estuaries, a consequence of hydro-electric development in the 1960s, which altered qualities of traditional calving sites (Sergeant and Brodie, 1975). Feeding during winter continues in open areas within the pack-ice to the exclusion of other cetaceans (Sergeant, 1986). Unique amongst beluga habitats however, during the following 9–10 months of open water, the diversity of prey attracts numbers of an additional 12 species of mysticetes and odontocetes representative of the northwest Atlantic,

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creating a site recognised globally for whalewatching. Extralimital sightings of belugas from this population occur regularly, moving further south along the Nova Scotia coast, Bay of Fundy, to New England (Sergeant, 1986; Brodie, recent obs.; Sergeant and Brodie, 1975). Adaptions for survival by this southern population are intriguing, considering the diminishing ice cover now observed in Arctic beluga habitat. Exploitation of the St. Lawrence River population had ceased by the 1970s, so examination of carcasses is now limited to those from incidental and natural mortality. Sampling of Arctic belugas relies on landings by hunters, usually adult animals. Predictable migratory behaviour and manageable size of calves has resulted in live-capture of belugas for display and research, most originating from western Hudson Bay.

Cumberland Sound field study, 1966–1969

Background

In 1966, the Canadian Dept. of Indian Affairs and Northern Development (DIAND) commenced a harvest of belugas, using fixed nets at strategic sites in Clearwater Fjord, upper Cumberland Sound, with the intention of diversifying the hunting economy. From the beginning of July to early September 1966, all netted animals ($n = 107$) as well as those from several hunting camps ($n = 17$) were sampled by PB. The netted animals represented a cross-section of the population, i.e. no hunting selectivity. Belugas occupy Clearwater Fjord during the ice-free period of July to early September. Observations of full-term fetuses and newborns, revealed that calving took place; one birth was observed. Teeth were collected, although there were no facilities for determining age during this chance field opportunity. However, newborns and age-classes of calves were distinguishable by size, remnants of umbilical cord sheath, body colour, degree of tooth eruption, healed body scars and proximity to netted adult females of known reproductive status. While not a large sample, the spectrum of ages taken during the calving season yielded cross-referenced data, although a qualitative rather than a quantitative nature.

The range of calf sizes was presumed to represent early year-classes, based on side-by-side comparison of morphology, head profile and colour: 'Beluga in Cumberland Sound of lengths less than 300cm include newborn and as many as four year-classes' (see Fig. 2; Brodie, 1971). However, it is important to note that in this study (and others), initial colour classification can be somewhat subjective unless compared to a truly white animal. When laboratory interpretation of teeth was later applied to field data, age determination of older animals was based on continuation of the rate at which tooth laminations were deposited in younger animals i.e. those which could be ranked by year-class. Once the initial growth rate of calves to age 4 years was defined in the field, projection to 5 and 6 year-olds was considered justifiable. Based on this, two GLGs (GLG/2) were used as an index of annual growth (Brodie, 1969b).

Sergeant (1959; 1973) had earlier proposed that belugas might deposit multiple GLGs annually, based on comparison of archived teeth with the sperm whale (*Physeter macrocephalus*) and the long-finned pilot whale (*Globicephala melas*). Sergeant (fig. 4 in 1973) provided a photo illustration of beluga GLG sequence, cross-referenced

with length and status. Sergeant later stated (1981) that he was unable to explain a mechanism for the formation of GLG/2 in belugas. GLG/2 has since been rejected for the sperm whale (Perrin and Myrick, 1980).

It became evident in 1966 that the population Cumberland Sound was not as large as had been assumed as the basis for the netting project. An aerial (post hunting) near-surface count was conducted on 30 August 1967, resulting in a population estimate of 769 animals for Clearwater Fjord and upper Cumberland Sound, evidence of substantial reduction through generations of commercial and subsistence exploitation (Brodie, 1971; Sergeant and Brodie, 1975). Personal hunting experience of PB in the 1960s indicated a history of sporadic information on catches from distant camps, hunting losses and removal of young animals. This was not unusual for Arctic subsistence hunting economies at that time. However, the population decline was attributed to the high catch rates during episodes of commercial exploitation (Brodie, 1971).

Life history parameters

Despite the limitations referred to in the next section, analysis of the Cumberland Sound study (Brodie, 1971) estimated that female sexual maturity was attained at 5 years and at 85% of the physically mature length. Ovulation would occur 9–10 months later during the breeding season in early spring, at age 5.75 years. Earliest maturity was evidenced by a female with a very small (139cm) calf, thus sexually mature late in her fourth year (at 4.75 yr). Multiple ovulations and accessory corpora were typical (see also Robeck *et al.*, 2005) thus corpora numbers are unreliable indicators of production (Brodie, 1971; 1972b). Gestation was calculated to be 14.5 months (*ca.* 442 days), with births in late July–early August (Fig. 1A) followed by 24 months of lactation (Brodie, 1969a), during which time the female becomes pregnant in the spring of the second year of lactation, for a reproductive cycle of 36 months. Estimated gestation was later increased to 15–16 months (458–488 days) in Brodie *et al.* (1981).

In males, Brodie (1971) concluded that sexual maturity was attained at 8 years at 90% of physical maturity, with the first opportunity for breeding estimated to be at 8.75 years the following spring. Physical maturity of both sexes was attained after 10 years.

Tooth eruption began in the second year with partial eruption by the third. Whitening of the skin was estimated to begin after 6 years in females, 7 years in males and was used in the field to establish a minimum age. The animal is physically mature when phasing to white. An age of 21 years was used as age-for-last-birth modelling, following Kleinenberg *et al.* (1964), however belugas of Cumberland Sound were considered capable of births well after age 21. Calf production was estimated to be 43% of that estimated by Bel'kovich and Tarasevich (1964). Net reproductive rate (R_0) was estimated at 6–7 calves during the lifetime of a female (Brodie, 1971). For example, based on successful 3-year reproductive cycles, a female could produce calves at ages: 7, 10, 13, 16, 19, 22 and 25 years. Lifespan in the wild was estimated to range to 30, possibly 35 years (Brodie, 1969b).

Delayed tooth eruption suggests reduced necessity for functional teeth due to extended nursing. It could also

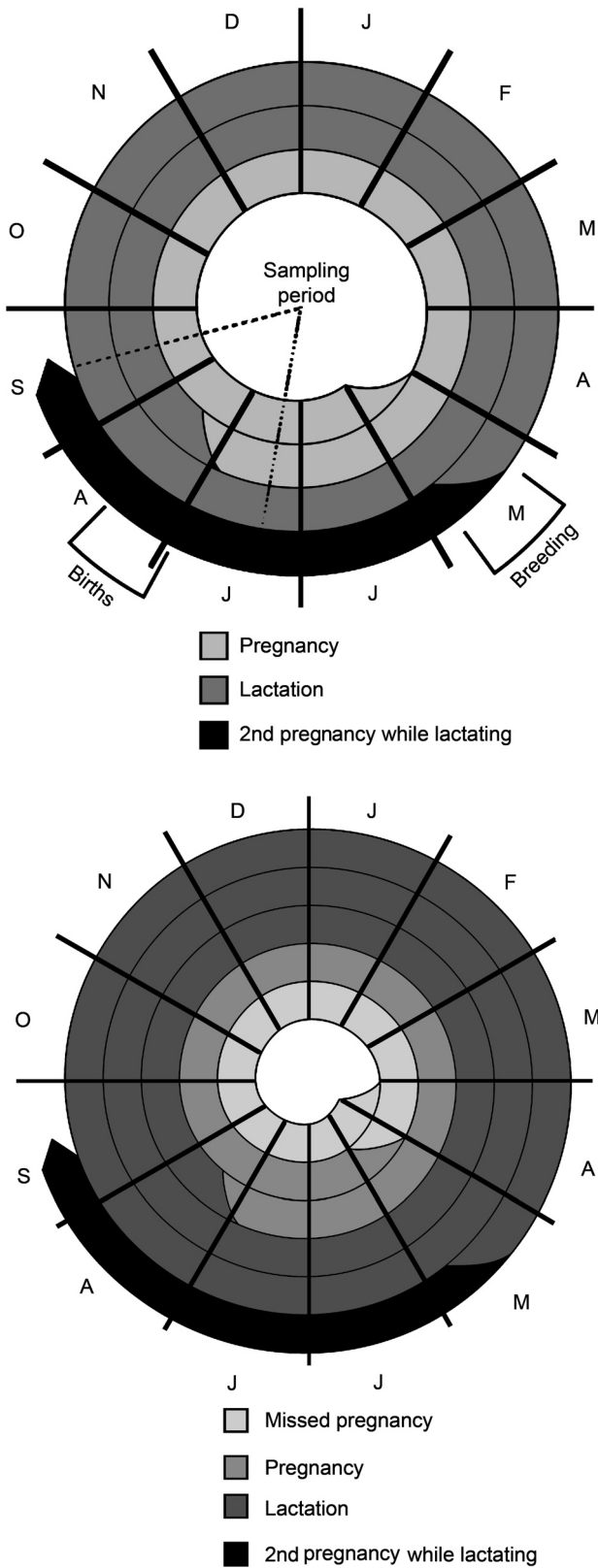


Fig. 1. Reproductive cycle:

(A) Typical of a wild population of belugas in Cumberland Sound (Brodie, 1971) encompassing 36 months. Sampling period incorporates the birthing period, while the breeding period is estimated from the foetal growth curve.

(B) Representative of the wide range of captive beluga reproductive cycles. Oestrus at ca. 6 years but without conception, followed by successful breeding in the second year of maturity. Pregnancy followed by an extended lactation period, which may last 3–7 years until conceiving (M. Haulena, pers. obs.), while continuing to nurse the older calf. Note that the sampling/observation period is year-round.

indicate a greater reliance on feeding by suction, or that teeth play a greater social role in adulthood (Brodie, 1971; 1985). Beluga teeth do not interdigitate, rather upper teeth abut lower teeth at an angle, resulting in the characteristic wear pattern and effectively sharpening contact areas.

Abundance and management in Cumberland Sound

The 1966–1969 field research and low population estimate renewed interest in the status of Cumberland Sound belugas. A booklet on beluga life-history was designed with graphics and translated into Inuktitut for the hunters, as well as distributed to northern schools (Brodie, 1972a). The Canadian Arctic Resources Committee followed the management/negotiation process (CARC, 1984).

Increased catches in 1976–1977 triggered concern, driven by the lucrative market for beluga food products. Aerial photographic surveys in 1977 (Brodie *et al.*, 1981) suggested a decline in numbers from 1967. Several surveys, by different groups, using different techniques, covering the known area of beluga distribution and relying upon the extensive knowledge and visual skills of the Inuit, did not result in substantial differences with these low estimates, 10–13 years after the 1967 survey of the same areas. The quota for 1980 was set at 40 belugas with the hunters’ agreement, a necessary concession for a hunting economy, and further justified at the 1980–82 IWC Scientific Committee sessions. Aerial surveys by DFO in 1985 and 1986 produced surface indices of 398 and 442 respectively that suggested little change since 1980. Thirteen years later, a 1999 survey (DFO, 2002) resulted in an estimated population of 1,547 whales (SD = 240) resulting in an estimated annual increase rate of 55 animals (ca. 5%) despite an annual landed catch of 15–50 animals (ca. 2–5%). The quota for 2002 was increased to 41. A 2005 update advised that the Cumberland Sound population consisted of 1,211 (932–1,574) mature individuals, above the criterion of 1,000 considered to maintain genetic diversity (DFO, 2005). The 1985–86 surveys did not detect a change after quota implementation in 1980 which is perhaps not surprising given the difficulties in detecting small changes in number. However, the later abundance estimates suggested that management intervention had initiated recovery over the following 19 years. Gross annual reproductive rate appears to be higher than belugas of the St. Lawrence River (Sergeant, 1986). The more recent surveys provided evidence that the Cumberland Sound stock was not food limited, but experienced overexploitation and subsequent increase toward recovery.

Field studies of wild belugas in temporary captivity using tetracycline

A field experiment was conducted in July 1984 and August 1985 in western Hudson Bay, using a total of seven, sub-adult belugas which were injected with tetracycline, held captive over a 10 week period, and released after a tooth extraction. Intramuscular injection of oxytetracycline provided evidence of deposition in all animals and of double deposition in three. This was not used to argue for two laminations per year, but it provided a marker for deposition rate and indicated that amongst wild beluga, there might be an interruption and acquired resources could be retained and

deposited sometime later (Brodie *et al.*, 1990). Lengths of six of the animals and their estimated ages based on tetracycline marks are included for comparison with recent, known-age captive beluga in Fig. 4. All were apparently in agreement, not varying substantially if GLG/2 counts were applied instead.

Background information on the structure of beluga teeth and difficulties in reading in the context of estimating GLG deposition rates

Before discussing the evidence for and against GLG deposition rates in belugas, it is important to review the nature and physiology of the teeth (see Plate 1) and challenges for reading GLGs.

Dentine of beluga GLGs are conical structures, the earliest being three to five-fold greater in height than more recent GLGs. Width of succeeding cones being constant, surface areas of earlier GLGs are greater accordingly. Early GLGs are observed to be thinner in cross-section than later GLGs (Brodie, 1970; figs 1 and 2 in Brodie *et al.*, 1990). However, with greater surface areas, the total volume of early GLGs

equals or exceeds more recent GLGs, unlike sperm whales. Early accessory layering may be more relevant than previously assumed. Changes in the pattern of early GLGs as they phase to a lesser cone height are observed in wild belugas. The early dentinal layering sometimes appears to be in pairs of thin laminae. Considering the above arguments, these could form a pair of GLGs should the pattern continue into adulthood. Variation in cone angle can be used to approximate GLG loss in belugas, as described later.

When analysing teeth from captive animals, several authors have relied upon the the junction nodes of dentine and cement (Goren *et al.*, 1987; Hohn and Lockyer, 1999) as evidence of pre- and post-capture growth, since the central GLG structures are sometimes obscured by irregular growth in captivity.

In examining teeth sections, a loss of early GLGs can be identified by examining the characteristics of the remaining GLG pattern and the progressive increase in total angle of deposition of the GLGs from the tip of the tooth to the base. Beluga teeth have interesting characteristics which are unlike sperm whales (illustrated in Scheffer and Myrick, 1980):

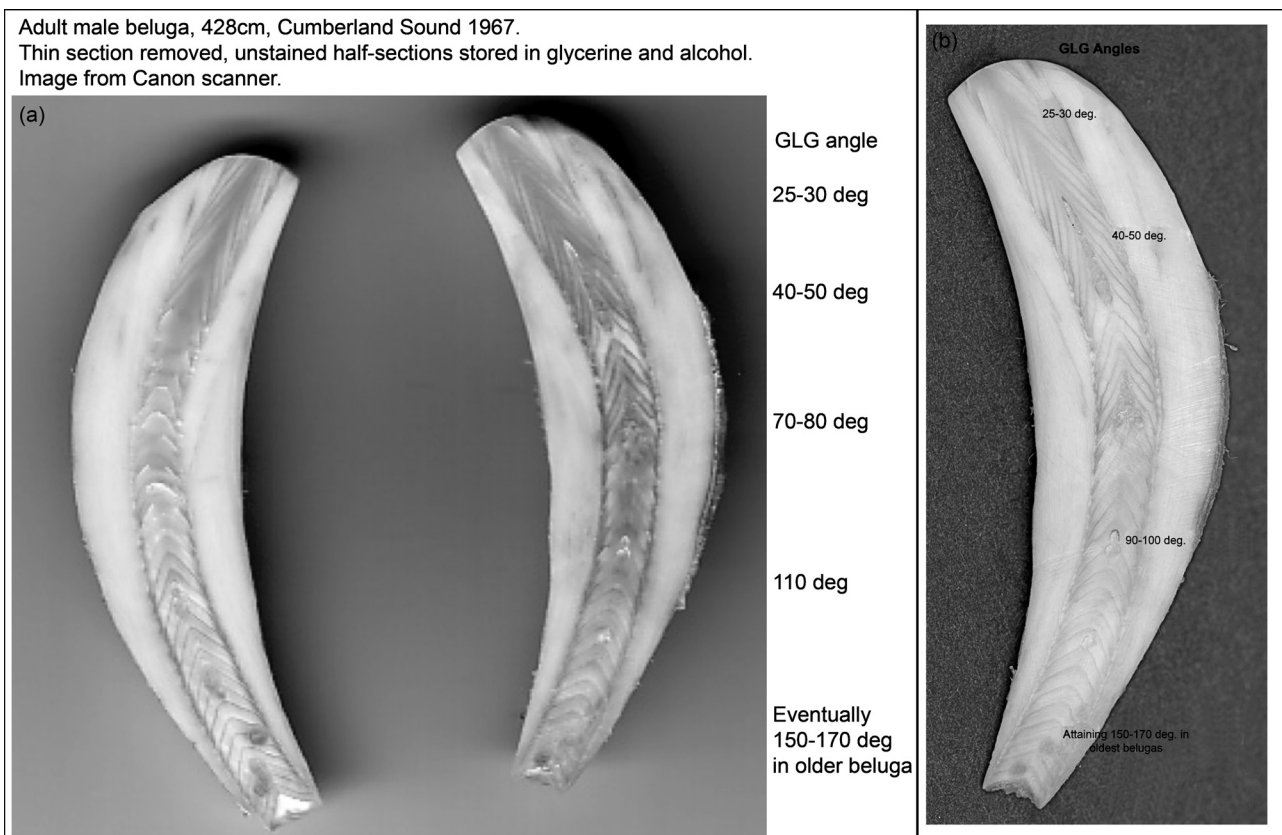


Plate 1.

(a) Tooth section.

Unstained 50 × 13 mm half-section, 428 cm beluga male, Cumberland Sound 1967. Characteristics:

- (1) obvious loss of GLGs through tip wear.
- (2) greater definition of wild beluga GLGs vs captive animals.
- (3) constant width of the dentine core (cone base).
- (4) increasing dominance of cementum in tooth volume.
- (5) three to five-fold greater height of earlier GLG dentine cones vs later GLGs.
- (6) 1–2 deg. incremental increase in total angle of subsequent dentine GLGs.
- (7) equal or greater total tissue volume of earlier dentine cones vs later GLGs.
- (8) change in pattern as GLGs phase into physical maturity.
- (9) potential to approximate earlier dentine GLG loss through wear.
- (10) male teeth larger, more robust, with generally thicker GLGs, relative to females.

(b) Right hand unstained half-section further polished and photographed at higher resolution.

- (1) after the initial several GLGs, the width of the dentine core remains constant;
- (2) the acute angle of the dentine, relative to the neonatal tooth at the pulp cavity, begins to open by 1–2 degree increments as GLGs are added;
- (3) the cementum GLGs are deposited at such an acute angle, almost parallel to the surface of the tooth, that they overlay each other, resulting in their dominance of the thickening tooth cross-section and total volume by 75–80% in older belugas (see fig.2 in Goren *et al.*, 1987);
- (4) the dentine layer, which is continuous with the cementum, forms a ‘W’ in cross-section, with the lengthened outer wings of the ‘W’ formed by cementum.

GLGs in longitudinal sections of beluga teeth from Cumberland Sound exhibit a general pattern, beginning with a total acute angle at the pulp cavity of 25–30°, increasing by 1–2° increments to 40–50° after 12 GLGs, 70–80° after 18 GLGs, about 110° after 30 GLGs, and then 120° and increasing thereafter until they are often compacted at 150–170° at the base of the tooth. While this could vary between populations, in figs 1 and 2 of Hohn and Lockyer (1999) and fig.1 Stewart *et al.* (2006), the growth pattern and GLG angles appear to be similar to those described here for Cumberland Sound. Of course, should data become available, these values can be adjusted for a specific population.

COMPARISON OF GROWTH RATES WITH THOSE OF CAPTIVE BELUGAS

Determination of age from size alone can be difficult, due to morphological variation in calves and adolescent belugas. Opportunities to handle hundreds of belugas during tagging in Hudson Bay (Sergeant and Brodie, 1969b) and while handling belugas from Cumberland Sound later during the same season, provided evidence of early year-classes and body-size differences between populations (Doidge, 1990; Sergeant and Brodie, 1969a). However, defining vital parameters of belugas from the collection of animals during July–September in Cumberland Sound had limitations, since breeding season and length of gestation were extrapolated from the calving period. In principle, these can be refined through year-round observation of captive belugas. A good understanding of vital rates is important for the management of wild stocks, baseline studies for environmental impact assessments, as well as captive maintenance.

In this paper, case studies based on direct observation of captive animals are compared to the findings of the 1966–1969 field studies in Cumberland Sound and those in Hudson Bay. However, inevitably evidence from tooth laminae is limited, since teeth are not often extracted from captive belugas. The approach taken therefore is to compare growth rates and age of sexual maturity of belugas of known-age, either captured as calves or captive-born.

Early observations of captive belugas for comparison with the Cumberland Sound study

Few belugas were held in captivity during the 1960s. However it is realistic to assume that observations made in the 1970s and 1980s, allow comparison with the growth and maturity estimates for Cumberland Sound in the 1960s.

Lugosi

One of the earlier captive belugas, Lugosi, a male captured in September 1967 in Bristol Bay, Alaska, was maintained at the Vancouver Aquarium (Brodie, 1982). Based on its length (229cm) it was estimated to have been 14–15 months (1.25 yr) at capture i.e. born mid-summer 1966. When Lugosi died in 1980, he had spent almost 13 of 14 years in captivity (91%) and was well known for his wide range of facial expressions and jaw-claps. As a consequence, his teeth were heavily worn, and a section of the tooth provided was too re-worked and obscure in structure for use in assessing laminae. However, body lengths, taken six times following capture, were in close agreement with those of Cumberland Sound, using GLG/2 (Brodie, 1982) suggesting physical maturity after 9–10 years. The data are included in Fig. 4 and appear consistent with growth rates of other known-age males.

As noted earlier, the age at which the body colour begins phasing to white can be a useful (although subjective, especially without direct comparison to a truly white animal) parameter when trying to determine age. It was estimated to occur after 6 years for females and 7 years for males from Cumberland Sound (Brodie, 1971). Aquarium director Murray Newman wrote:

‘According to a few dated photographs, Lugosi was very white by 1972, and according to my recollections was full, or very near to full length. The animal may have been white before this but I have no more recently dated photos to prove it.’

Turning white at six years seems early by 1–2 years, given Brodie (1971) although it is clear that no direct comparison with a truly white animal occurred in this case. According to on-site observation, Lugosi appears to have been approaching physical maturity after age six, which seems early given the case of Kayavak at the Shedd Aquarium discussed below.

The age estimate of 1.25 years at 229cm length is consistent with captive beluga calves (Brodie, 1971; Robeck *et al.*, 2005; K. Ramirez and Haulena, pers. obs.) and thus Lugosi is considered known-age. It is apparent from the growth curve in Brodie (1982), and the observations of curator M. Newman, that physical maturity was achieved by 9–10 years, consistent with GLG/2 and half the age of 18–20 years implied by proponents of GLG/1. In fact Lugosi was fully grown well before that age, when he died at 14 years.

Bella

Bella, a female was captured with Lugosi in Bristol Bay Alaska on 8 September 1967. Her length was recorded as 315cm on 26 September, 1967, however the records indicate that, 3 months later on 4 January, 1968, a length of 320cm was recorded (with the notation ‘*curv.*’ – i.e. taken over the body curve rather than linearly, ‘*lin.*’). This suggests that the initial length must have been over the body curve as well (see Doidge, 1990) which is confirmed by subsequent measurements with notation: May 14/68, 307cm (‘*lin.*’); October 16/68, 311cm; February 27/69, 320cm; May 14/69, 320cm; October 09/69, 326 cm. While not annotated, the measurements after 14 May 1968 were taken linearly. Thus the 320cm length does not appear to have been attained until 13.5 months later.

Sergeant, who examined a tooth from Bella who died in 1976 after 8.7 years in captivity, stated:

'There is a series of 14 very clear and evenly-spaced layers in early life, followed by recent extensive growth in the dentine which is very irregular. I believe I can count 9 layers in the dentinal-cement junction of this later growth, which happens to coincide with the number of years in captivity... If anyone else can reproduce this count, we have one layer equals one year.' [It is not known if he was referring only to the period in captivity]. *'In this case Bella should have been an adult at capture, which is reasonable for 10ft. 4 in length, and very light grey-white in skin colour.'*

There is no record of another reader examining this tooth, nor was there a photograph of Bella upon capture. However, as noted above, the length at capture was an overestimate as it was taken along the curve of the back. Alaskan belugas are slightly larger than those of western Hudson Bay and smaller than those of Cumberland Sound. If GLG/2 is used, Bella would have been 7 years old at capture, clearly more than 295cm, apparently less than 307cm, and sexually mature. In his fig. 10, Sergeant (1973) plots the growth of western Arctic belugas for comparison. Bella would appear to fit in the 300–310 cm range for females with 14 GLGs.

In fact, from Sergeant's description above, the total GLGs would be 23, i.e. the 14 clearly resolved, plus an estimated 9 'very irregular' GLGs. Based on GLG/1, if Bella was 7 years old at capture and had spent 8.7 years in captivity one would expect 15.7 GLGs (7 wild + 8.7 captive) and if based on GLG/2, 31.4 GLGs (14 wild + 17.4 captive). Although there was no mention of tip erosion, while the 14 clearly defined GLGs described above would almost satisfy the 15.7 GLGs to comply with GLG/1, this does not account for the additional irregular 9 GLGs.

Based on GLG/1 and assuming that the clearly defined 14 GLGs represented pre-captive growth, Bella would have been 14 years old at capture; this does not appear to be consistent with a length of only 295–307 cm. By comparison, Alex (below) was grey-white at 305cm and age estimated at 5 years; males are larger than females. Under GLG/2 and under the same assumption about pre-captive growth and regular layers, Bella could have been 7 years of age when captured, then held for 8.7 years in captivity.

Alex

Alex, a male from Bristol Bay, was captured in the company of an adult female on 24 August 1961 at 221cm length. This is consistent with the length of yearlings. The estimated weight was reported as 205kg and the estimated age 14 months (1.2 yr). He was held in captivity for 23 years. Sergeant (1973) plotted two points for Alex on a growth curve. Sergeant (fig. 10 in 1973) was advised that Alex was 305cm on 17 May 1965, weighing 448kg and grey-white in colour at 5 years and that he was white by 17 November 1966 at age 6.3 years and 335cm, although 15 months later (19 February 1968) Sergeant observed him and thought him still 'somewhat grey.'

From 28 August 1961 to 6 May 1975, he was held in an outdoor pool at the New York Aquarium. He was then moved 170km to an indoor pool with artificial lighting at Mystic

Marineland Aquarium in Mystic, Connecticut, where he remained until his death on 1 June 1984. He was 24 years, 405cm and weighed 1,200kg, and had spent 95% of his life in captivity, the oldest known captive beluga to that date (Goren *et al.*, 1987).

After his death, a well-worn tooth was examined. An estimated 40 dentinal GLGs and 37 in the cementum were identified and the photograph (fig. 2 in Goren *et al.* 1987) illustrates that the tooth section is compacted at the base, and heavily eroded at the tip. There was a loss of early GLGs, evident by the characteristics of the remaining GLG pattern, as well as the progressive increase in total angle of deposition of the GLGs from the tip of the tooth to the base (as discussed in the general section on teeth structure above).

Extrapolation, based on the pattern in Cumberland Sound belugas described above, indicates that about 10–15 GLGs had been eroded from the tip. Added to the 40 GLGs estimated, this gives 50–55 GLGs for a beluga aged 24 years (1.2 yr at capture + 23 yr captivity). Since the cementum layers join with the base of the corresponding dentine layer in a 'W' cross-section, loss of dentinal layers will include a commensurate loss of cementum. Had 10–15 cementum layers eroded, the total cementum GLGs would be 47–52. Lockyer *et al.* (2007), in their table 4, provide age estimates for two older belugas, of 42+ and 46+ GLGs, suggesting tooth erosion and compaction similar to that shown for Alex in Goren *et al.* (1987).

Alex, like Lugosi, can be considered known-age. In spite of 23 captive years of his 24 year lifespan, the pattern of GLGs could be resolved, indicating that two GLGs had been deposited, double that of the 24 GLGs that would have indicated GLG/1. Moreover, Alex's growth record (Fig. 4) and age of physical maturity appears consistent with other known-age belugas and not double the age required to conform with GLG/1.

Allua

Heide-Jørgensen *et al.* (1994) examined four teeth of a female, Allua, captured on 5 August 1969, with another female, Moby, at Seal River in western Hudson Bay. She remained in captivity for 15 years until her death on 26 July 1984 at the Duisberg Zoo, Germany. She was estimated by the captor to be 3 years old and her length on 6 September 1969 was 294cm. In their fig. 7, Heide-Jørgensen *et al.* (1994) indicate where they believe a distinct change in the GLG pattern corresponds to time of capture, although there was no means of validation. Although resolving layers was difficult due to base compaction, they estimated 30–36 GLGs and concluded that GLG/2 was most probable.

For comparison, a 295cm female from western Hudson Bay was estimated to be 5 years old by dentinal GLG/2, and 4.82 years based on tetracycline calibration as discussed below (Brodie *et al.*, 1990). Sergeant (1973) in his fig. 4e, shows the tooth of a young mature female at 295cm with 12 GLGs, aged as six years. Based on known-age belugas (Fig. 2 Robeck *et al.*, 2005), Allua could have been as much as 5.2 years old at capture. However, as discussed below, Tiqa of the Vancouver Aquarium died at known age 3.25 years and length 298cm.

In this case, let us assume that the estimated age at capture

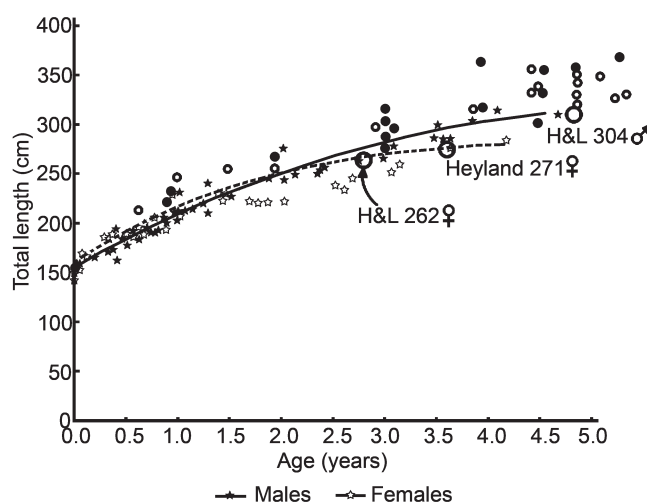


Fig. 2. Early growth rate of known-age captive belugas, based on fig. 6 from Robeck *et al.* (2005). The lengths and estimated ages of Cumberland Sound beluga (Brodie, 1971), including 16 newborn, are plotted as well to demonstrate the larger body-size of this population (females are open circles, males are dark circles). Calf ages in 1966, from Brodie (1971) were initially correlated with other parameters. A 271cm female from Heyland and Hay (1976) is plotted according to length. The 262cm female and 304cm male from Hohn and Lockyer (1999) are shown plotted according to length.

(3 yr) was an underestimate and use Sergeant's upper age of 6 years. This provides an estimated age at death of 21 years (6 yr wild + 15 yr captive) i.e. expected GLGs of 21 for GLG/1 and 42 for GLG/2.

The Heide-Jørgensen *et al.* (1994) counts were thus 9–15 GLGs in excess of the 21 required for GLG/1 and 6–12 GLGs short of the required 42 for GLG/2, both contingent upon the accuracy of estimated age at capture of six years. However, using GLG/1 and assuming that 15 of the 30–36 GLGs represented 15 years in captivity, implies that the 294 cm female would have been 15–21 years old at capture. Clearly, 15 and 21 years are excessive age estimates for 294cm and, if plotted on Fig. 4, would be off-scale in length, implying a fraction the body weight for belugas of this age. It also means that she must have spent 50–58% of her life in the wild vs the earlier estimate of 29% for this female, based on lengths of known-age captive animals and Sergeant (1973). This information suggests that the GLG/1 hypothesis is not consistent with the evidence from this female.

Using GLG/2, assuming 30 GLGs represent 15 years in captivity, Allua (with 30–36 GLGs) would have ranged from zero (newborn), to three years old (6 GLGs) at capture. The newborn category is eliminated; three years was the age suggested by the captor. However, as discussed above this may be an underestimate by 2–3 years (or 4–6 missing GLGs), for a total age of 5–6 years (10–12 GLGs) upon capture. Either way, the hypothesis of GLG/2 is not inconsistent with data for this female.

Further evidence of the lack of compatibility with the data for Allua and GLG/1 comes from consideration of her potential life history if she indeed was 15–21 years at capture and using information from Brodie (1971), Robeck *et al.* (2005), direct observations of Aurora(V) and known-age Qila in the Vancouver Aquarium (see below). At 15 years of age, she could have had the potential to produce three calves (at age 7–10–13) and become a grandmother at age 14 years, one year prior

to capture; or if 21, could have produced an additional two calves at age 16 and 19, for a total of 5, and become a great-grandmother by age 21 years, just prior to the time she was captured. Lockyer *et al.* (2007) state there is no difference between beluga growth rate in the wild and in captivity.

An age of 21 years was used by Brodie (1971) for a comparison of reproductive potential with Bel'kovich and Tarasevich (1964) whereby a female could have produced the majority of her calves. Robeck *et al.* (2005), concluded that the oldest age for conception, thus far, in a multi-parous captive beluga, was 20 years. There does not appear to be evidence from wild or captive belugas supporting Hohn and Lockyer (1999) or Lockyer *et al.* (2007) with reference to Allua, all being in the direction of GLG/2, as originally determined by Heide-Jørgensen *et al.* (1994).

Review of evidence from captive beluga groups

Robeck *et al.* (2005) combined vital parameter data from disparate groups of belugas born in captivity in nine aquaria, and of known age. From one perspective, animals in captivity have greater potential than the netted and hunted sample in Brodie (1971) for examining life history parameters since they can be repeatedly sampled/observed. However, the captive environment differs from the wild in a number of key ways including the very small number of belugas held in each facility relative to the larger numbers in the wild, which for example could affect breeding synchrony, as noted below.

Robeck *et al.* (2005) concluded that female belugas exhibited luteal concentrations of serum progesterone P at 6.9 years plus or minus 1.5 years (earliest onset at 5.4 years) and first conceived at 9.1 years plus or minus 2.8 years (earliest at 6.3 years). They state:

'In captive populations, the inconsistent availability of breeding males may artificially lengthen the period between first estrous and first pregnancy. This is supported by the observation that 67% of the captive females (n = 6) maintained in the presence of a proven breeding male became pregnant at 6 years of age.'
[Robeck *et al.* (2005) p.41].

Of six conceptions, four occurred during the first ovarian cycle at age 6 years, while the oldest age for conception in a multiparous beluga was 20 years. Females are seasonally polyoestrous, with up to two ovulations per season. The youngest male to sire a calf was 9 years old, and all males less than 8 years old were considered sexually immature. Gestation was estimated at 475 days (455–495days). They also concluded that captive belugas seem to follow similar body lengths, but not body growth patterns, when compared to their wild counterparts. Those experienced in maintaining known-age belugas are in an informed position to estimate the age of wild beluga captured as calves. The sections below summarise information on animals born in captivity.

Case studies of captive-born animals

*Aurora*⁴, *Qila*, *Tiqa*, and *Nala*

Aurora(V), a female beluga, was captured in Churchill, Manitoba, on western Hudson Bay on 15 August 1990. She

⁴Note that there is another female of the same name at Mystic, therefore Aurora (V) for Vancouver and Aurora (M) for Mystic.

was measured at approximately 2.5m on 30 August 1990. Using the growth curve for known-age females (Robeck *et al.*, 2005) suggests that she would have been 2.25–3.25 years (thus, born in the wild June 1987 or 1988). In September 1992, at age 4.3–5.3 years, she was 325cm. On 23 July 1995, at an estimated age of 7–8 years, she gave birth to her first calf, Qila. Conception would have therefore occurred *ca.* 15 months prior, at an age of 5.75–6.75 years. Thus after 2.25–3.25 years in the wild, she conceived and gave birth within the timeframe estimated for both wild belugas (Brodie, 1971) and directly observed animals in captivity (Robeck *et al.*, 2005; M. Haulena, pers. obs.). Sergeant (1973, fig. 4e) shows the tooth of a 295cm sexually mature female with 12 GLGs, initial evidence that growth to sexual maturity is not accelerated in a captive environment. Aurora(V) gave birth in 2002 to a male, Tuvaq, who died at age three in 2005.

Qila conceived in early 2001 at 5.75 years but lost the 200mm foetus in September 2001. She successfully gave birth to a female calf (Tiqqa) on 10 June 2008, one month before her 13th birthday. Thus Aurora (V) became a grandmother at age 20–21 years, although it could have been as early as 14–15 years, had Qila carried her pregnancy to term in 2002. On 7 June 2009, Aurora(V) subsequently gave birth to a female, Nala who was substantially larger than Tiqqa at birth. Nala died on 21 June 2010 at one year, larger than usual (length 243cm, max. girth 172cm and calculated weight 260–270kg). Tiqqa died at 3.25 years, length 298cm and axillary girth 189cm.

The above history shows that on a three-year cycle, Qila had the potential to produce three calves (2002, 2005 and 2008) by the age of 13 years (see also Stewart *et al.*, 2006). Had Qila given birth in 2002, the calf (if female), could have been in early pregnancy in 2008 at age six years. Carried to one more generation, that calf would have been born in 2009, making Qila a grandmother at age 14, and Aurora(V) a great-grandmother at 21–22. Examination of adult females in the field, as well as their association with newborn and older calves (Brodie, 1971) indicated that all females were in an active stage of the reproductive cycle, thus the scenario of reproduction described above may be representative of a healthy, wild population (or at least one that was recovering from overexploitation).

Kavna

Data from the Vancouver Aquarium (received in April 2012) provide a profile of a female (Kavna) captured in western Hudson Bay in July 1976. Based on a 3m length estimate and body colour, she was deemed to have been born in 1969. This is consistent with growth-at-age data from Sergeant (1973). Kavna was in early pregnancy when captured, therefore not younger than 6 years (the estimated age at sexual maturity from Brodie), born at the latest in 1970, thus probably primiparous, considering her 3m body length.

On 13 July 1977, she experienced a breech birth, a male (Tuqa) who died four weeks later. In 2009, Kavna was length 380cm and weight 850kg but although always in the presence of a proven breeding male, she had not conceived in 35 years since the single birth.

On 11 July 2007, at an estimated age of 37–38, she lost a tooth which was discovered in the pool. The slender tooth was 57mm × 9mm, some erosion near the tip, tapered to a

point at the base, with no evidence of a remaining pulp cavity. An unstained half-section was prepared by PB, allowing for curvature and erosion which required grinding past the midline close to the tip. There were no remnants of a prenatal tooth or neonatal line but the GLG angles indicated that few had been eroded. In the first 19mm there were up to 26–28 laminae of varying thickness (cone angles 25–30°), eventually phasing into 1–2 more characteristic GLGs. Thereafter, the section becomes increasingly obscure with irregular growth: osteodentine nodules, drying fractures, and possible resorption continuing to the pointed base. The interfaces between dentine and cement are visible, although somewhat irregular, while the width of the dentine core diminishes to about 35% that of early growth. There appeared to be several vague GLGs within the marbled tissue 35–45mm from the tip. The duration of irregular tooth metabolism appeared to have been extensive with an incomplete chronology culminating in tooth rejection. By shifting the angle of reflected light, the unusually complex laminae in the first 19mm appear to coalesce into 10–12 units. Allowing for some tip erosion, these may represent 6–7 years of pre-capture GLGs (as noted, changes in GLG structure or pattern may reflect transition from wild to captive, with a possible lag response related to the existing body reserves at capture). Kavna died of cancer 6 August 2012 and at a probable age of 42–43 years, considering her length estimate in 1976. A 54mm × 11mm tooth provided from the necropsy was similar in description, the base reduced to a fine point, with additional tip erosion of earlier laminae. Growth pattern of early laminae was similar to that of the ejected tooth, also being obscured by later irregular growth.

Based on two teeth examined, the laminae pattern in Kavna suggests clear, but complex growth, even prior to capture. Later depositions were obscured by irregular tooth growth and evidence of reworking, which seems to have continued throughout her life, yet she was the longest lived on record, dying at a probable age of 42–43 years. It also suggests that markers, such as tetracycline, might be redistributed during the restructuring, thus providing false readings.

Kayavak

Of the five calves successfully born in captivity at the Shedd Aquarium, Kayavak is of particular interest. She was born to Immiauyuk on 3 August 1999 (length 142cm, weight 53kg) and nine years later had reached 346cm and weighed 534kg (see Fig. 4). On 15 September 2010 at just over 11 years old she measured 343cm and weighed 552kg. The small length difference is attributed to the error incurred when measuring live animals at poolside. Observations indicate that she has not changed in size since 2008 at age nine and when compared to data in Sergeant and Brodie (1969a), this is consistent in size with mature belugas from Churchill, Hudson Bay. (K. Ramirez, pers. obs.). Kayavak was first observed to go into oestrus at 6 years of age, however she has yet to conceive. She had been isolated from the other belugas while being hand fed as a calf, and was later observed to be low in the hierarchy at Shedd; older females did not let her near the adult males. As of January 2011 (age 11.5 years) she continued to show signs of ovulation and has attracted the interest of an adult male, however females

continue to prevent her from breeding. While availability of breeding males to females in oestrus has been considered as a limiting factor in conceptions among captive belugas (Robeck *et al.*, 2005), this suggests that social complexity and the dominance of older females over subordinate females must also be considered.

Discussion

As discussed above, the growth of wild belugas has been examined based on apparent year-classes of young animals; adults have been aged (Brodie, 1971) according to dentinal laminations consistent with the lamination rate of calves and sub-adults. In considering this further in this review, captive (age estimated at capture) and born-in-captivity growth rates have also been examined.

With respect to the former, the focus was on two calf males (captured at about 1.2–1.25 years), Alex and Lugosi (see Fig. 4), held in captivity for over 90% of their lives (Brodie, 1982; Goren *et al.*, 1987). As discussed in more detail in a preceding section, information from a number of females was also considered. Bella, captured at an estimated age of 7 years and held in captivity for 8.7 years (55% of her life); Allua, a female, captured at an age ranging from 3–6 years, and held in captivity for 15 years, around three-quarters of her life (Heide-Jørgensen *et al.*, 1994); and Moby, who appeared to have lived for some 34 years, of which 30 (80%) were in captivity.

With respect to the latter, as detailed in the previous section, there are now both first and second-generation captive born animals. These represent the first belugas with a fully-known history, albeit in captivity. Age of sexual maturity for males and females in captivity is consistent with findings of wild belugas in Cumberland Sound. Primiparous belugas captured in early pregnancy, as well as calves and sub-adults later conceiving and giving birth in captivity, are consistent in size and age with those of known age in captivity and in the wild (Brodie, 1971). Pregnancies in captivity are contingent upon the availability of proven breeding males (Robeck *et al.*, 2005), and in one case, a consequence of exclusion of a mature but subordinate female, by other females. Kayavak, a female sexually mature at six and nearing 12 years old at Shedd Aquarium (Fig. 4) appears to have been physically mature since nine (K. Ramirez, pers. obs.). Beluga females appear capable of at least seven complete reproductive cycles in their lifetime, and potentially four generations, by age 28 years.

REVIEW OF PAPERS SUGGESTING GLG/1

In light of the preceding sections, the paper now considers the research and arguments that have been advanced for one GLG per year (GLG/1). The implications over GLG/2 are obvious – it doubles the duration of all life stages, including lifespan and age at attainment of sexual maturity. The focus is on a comparison of archived data to direct observations of wild and captive belugas (see Figs 2 and 4).

Hohn and Lockyer (1999)

The findings of Hohn and Lockyer (1999) have influenced subsequent studies of beluga growth and age determination (Lockyer *et al.*, 2007; Luque *et al.*, 2007; Stewart *et al.*, 2006). The authors examined tooth deposition rates based on

archived teeth of two belugas from Hudson Bay, captured at lengths of 262cm (SW-DL-7903, female) and 304cm (Churchill, male). Both animals were held in captivity for almost 8 years (7.92 and 7.83 years, respectively) until their deaths. The female had been administered tetracycline orally for clinical purposes at a dose of 9 grams, twice daily over a week period, 4.2 years before her death. The issue of tetracycline is dealt with in the discussion. This section focusses on the authors' numbers of GLGs for these two animals. Based on the best counts of GLGs and assuming GLG/1, the authors concluded that the female was 18 years old and the male 23 years old at time of death. In table 2 of a later paper by Lockyer *et al.* (2007) the average count of five readers for the male was increased to 27.8 (SD 3.63) while the average count of five readers for the female was 18.20 (SD 2.17). To avoid confusion related to this manuscript submitted in 1999, it should be noted that there exists two versions (Hohn and Lockyer, 1999⁵) with similar text, however with different figures and position of the tetracycline mark.

Assuming GLG/1, then the 262cm female was about 10.1–10.3 years old at capture, while the 304cm male was 15.2–20 years at capture. However, when compared with the growth curves (Fig. 2) for known-age captive animals (Robeck *et al.*, 2005), the implied ages are around 2.75 years for the female and 4.9 years for the male, substantially lower than those based on GLG/1 and casting doubt on that hypothesis.

However, using an estimated age of 12.7 years for the male (4.9 years wild from the growth-curve estimate plus 7.83 years in captivity), the expected number of GLGs assuming GLG/2 would be 25.4. This is comparable to the best count of 23 (Hohn and Lockyer, 1999) or the mean of 27.8 (Lockyer *et al.*, 2007).

Similarly, using an estimated age of 10.65 years for the female (2.75 years from the growth curve plus 7.9 years in captivity), the expected number of GLGs assuming GLG/2 would be 21.3. This represents a shortfall but is still comparable to their best count of 18.2 (SD 2.17) GLGs.

While the rationale is unclear, the authors rounded down the previously documented times of almost 8 years in captivity (7.92 and 7.83 years) to '7 complete years', thereby shifting the difference to the precapture age. Based on the increased precapture ages of 11 and 21 years, the annual increase in length from newborn to ages 11 and 21 would be 10cm and 7cm respectively using a growth curve from Stewart (1994) for Arviat in the western Hudson Bay. However, this represents only a small fraction of the observed growth in the first year alone based on wild (Cumberland Sound) and captive data, ranging from 60–80cm (figs 2 and 4 in Brodie, 1971). This would in fact require an almost straight-line growth trajectory from newborn to ages 11 and 21, completely inconsistent with the observed early growth of known-age belugas. In addition, the appearance and interpretation of the tooth sections for the female (figs. 1–2 in Hohn and Locker) implies that *ca.* 65%–75% of the volume of tooth deposition occurred before capture; this has not been observed in calves and sub-adults of that size.

⁵ One version was submitted at the meeting and a revised version after the meeting – both versions are available from the office of this journal.



Fig. 3. From Heyland and Hay (1976), showing Doug Heyland kneeling immediately behind a 271cm juvenile female beluga at Cunningham Inlet, Canadian Arctic. The beluga, described as brown in colour (possible sun exposure), was estimated to be three years old. For comparison, the 262cm female (from Hohn and Lockyer, 1999) was 9cm shorter and estimated 80–90% the mass of the 271cm juvenile shown. Hohn and Lockyer deduce that the 262cm juvenile was 10–11 years old at capture.

For further comparison, Heyland and Hay (1976) included a photograph (Fig. 3 here and plotted in Fig. 2) of a 271cm juvenile female beluga stranded in July 1974 in Cunningham Inlet. It was initially assessed on site to be 3–4 years old by its length, morphology and body colour. Sergeant later examined the teeth, provided by the authors, counting 5–6 GLGs. Fitting the 271cm length to the female growth curve from Cumberland Sound would place the calf at 2.5–3 years of age whereas fitting to the known-age growth curve in

Robeck *et al.* (2005) gives an estimate of 3.6 years. The difference can be attributed to a possible size difference in Cunningham Inlet belugas or to natural individual variation in age-at-length.

The female reported by Hohn and Lockyer (1999) was 9cm shorter than this 271cm stranded juvenile female. A 262cm calf in the wild (Brodie, 1971) would have some very small teeth just beginning to pierce the gum, and may have been weaned the previous year. Clearly it would not have been sexually mature whereas if it had been 11 years old at capture, based on Brodie (1971) and Robeck *et al.* (2005) it could have previously given birth at age 7 and have been multiparous by age 10. Similarly, if the male was 21 years at capture (Lockyer *et al.*, 2007) it should already have been sexually and physically mature – this seems implausible for an animal captured at a length of 304cm. Similar conclusions are reached taking into account the length-range of known-aged Nala and Tiqa, described above. We also have to consider the impractical size and weight of adult belugas when attempting live-capture in the field. Given the work of Brodie (1971) and Robeck *et al.* (2005), we believe that the pre-capture ages and histories implied by Hohn and Lockyer (1999) are considerably in error, maybe by as much as 400%.

Radiocarbon-14 dating in Stewart *et al.* (2006)

Stewart *et al.* (2006) used bomb radiocarbon 14 (^{14}C) dating from fallout in 1958 (e.g. see Levin *et al.*, 2009) to calibrate beluga age estimates. Archived teeth from nine belugas were used. Three representing the pre-bomb era (from animals of unknown sex and length) were obtained from 1890s

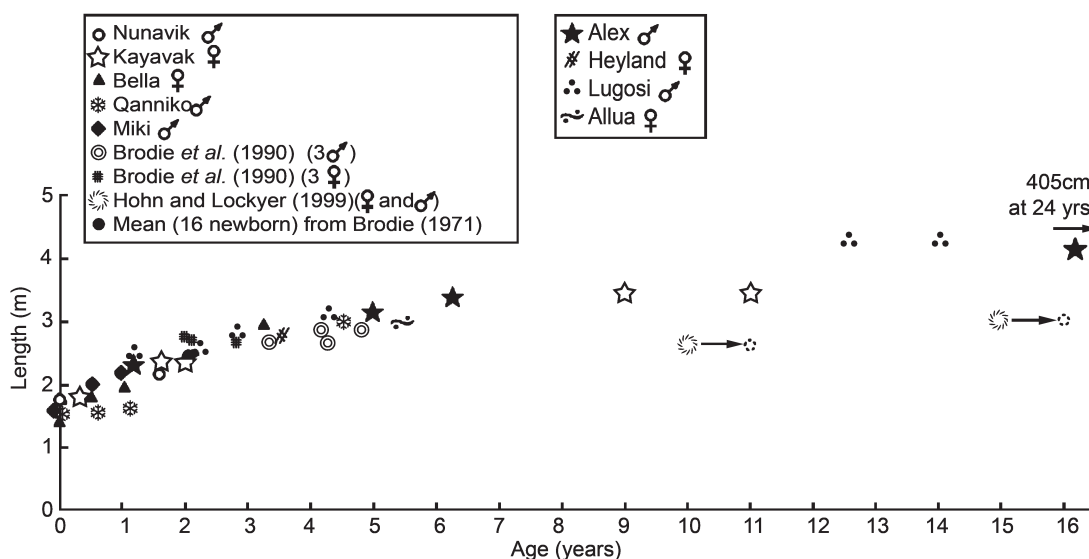


Fig. 4. Early growth rates of known-age belugas and wild belugas with estimated ages.

Kayavak, Bella, Qannik, Miki and Nunavik were born in captivity. Kayavak at age 9 years, was sexually mature at 6, of low social status, and has yet to conceive at age eleven and appears to be physically mature. Wild belugas from Brodie *et al.* (1990) are included for comparison, based on known length and their ages estimated here from tetracycline markers. The two older animals (262cm female and 304cm male) are plotted, based on known length and their extrapolated age at capture according to Hohn and Lockyer (1999). By comparison, the 262cm female which they implied was 10–11 years old is 79cm shorter than (known-age) 9 year-old Kayavak, and *ca.* 49% of her known weight. The 304cm male, based on their age estimate of at least 15 years, would be *ca.* 75% the weight of the younger, 9 year old Kayavak and 35–40% that of an adult male of that age. They imply that an annual increase in length from newborn would average *circa* 10 cm, or 15% the observed growth in the first year. If the adjusted age of ‘7 complete years’ in captivity is used for both, the points shift to 11 and 16 years respectively, as indicated. Recent data, in Table 2 of Lockyer *et al.* (2007) implies the 304cm male was 20 years old at capture (20 yr vs 5 yr), a four-fold increase in age, relative to known-age beluga. Growth data for captive Hudson Bay-origin, adult male belugas are not yet available, thus Lugosi and Alex are included here to illustrate the mature male growth curve. Both were from Alaska, intermediate between Hudson Bay and Cumberland Sound (Sergeant and Brodie, 1969b; Doidge, 1990).

archaeological sites on Somerset Island in the high Arctic. Six (5 females and 1 unknown; all unknown length) were from belugas that had been hunted in 1991–2001 from southern Baffin Island. In short, the authors concluded that belugas attain sexually maturity at twice the age and live twice the age estimated for Cumberland Sound (Brodie, 1971). Those conclusions were almost exclusively based on material micro-milled from the archived teeth of nine belugas of unknown length, with the sex known for five in the post-bomb era.

The authors did provide information on technical difficulties, possible sources of error and how they accounted for these in reaching their conclusions. This information provided part of the basis for the critique presented below. The main factors considered are: (1) technical difficulties with the prepared teeth; (2) assumptions about lags in the absorption of ^{14}C ; (3) the physiology of transfer of ^{14}C from prey to beluga and from beluga mothers to calves; and (4) implications of their results in relation to population dynamics.

Technical difficulties

Stewart *et al.* (2006) stated that during their analysis it became apparent that resin had permeated teeth that were embedded for sectioning and that corrections were applied to account for this. With reference to the complexities in the use of ^{14}C vs direct observation, Ubelaker and Buchholz (2006) had stressed caution with respect to lag response, as well as the choice of tissues used, bone and hard tissues. I consulted Buchholz over the techniques used in Stewart *et al.* (2006) and he commented as follows:

‘My problems with the paper are the incomplete methods and the corrections they used to remove large amounts of dead carbon from embedded samples. None of the samples embedded in epoxy are suitable for these measurements. The corrections seem arbitrary, and can be used to obtain whatever answer you want. You can make GLG/1 fit the late 1950s rise with a suitable correction. Ignoring all data after 1982 is not justified. If the corrections are accurate, they should work for the entire curve, not just a segment. Hence, the data have significant problems.’ (Buchholz, pers. comm.)

The study seems thus to have been initially compromised in such a way as to affect the interpretation of the results although the authors point out that including the post-1982 data would change the fit very little. It also underscores the difficulties the authors appear to have in rationalising lag responses in their findings (see below).

If ^{14}C is present in the teeth, can it be assumed that the animal was alive during the radiocarbon event?

A fundamental assumption made in their analysis is that the ^{14}C originated in the lifetime of the belugas for which the teeth were examined, i.e. the late 1950s. They stated that bomb radiocarbon is a reliable dated marker if it remains static in the GLG throughout the subsequent life of the animal. They also stated that there was no evidence for ontogenetic effects, suggesting that the bomb signal was not diluted by subsequent growth over a period of up to 40 years. This fundamental assumption that animals exhibiting the signal must have been alive in the late 1950s requires serious evaluation in the light of the biology of belugas and their prey. The ^{14}C study by Stewart *et al.* (2006) did not consider

the dynamics of reproduction and the possibility of transfer of any radioactive marker from the mother to the foetus during pregnancy, nor do their citations refer to mammals.

Most fish produce large numbers of very small eggs containing genetic material and a small energy reserve. By contrast, mammals such as the beluga transfer a substantial portion of their body mass to foetal development and subsequent lactation. Where there are multiple live-births in fish and elasmobranchs, unlike belugas, individual young do not achieve 50% the weight of the mother through further transfer of resources, factors to consider in ^{14}C analysis.

Belugas produce relatively large, single calves, followed by long-term nursing. If ^{14}C is present in the beluga food-base and sequestered in their body tissue, it follows that radiocarbon in the mother would continue to be transferred and sequestered in the tissue of the foetus and nursing calf. As with all cetaceans, belugas feed more intensively during pregnancy, acquiring disproportionately large reserves (Brodie, 1975), which could further magnify their ^{14}C burden acquired during the peak fallout period.

From this perspective, foetal growth can be seen as a continuation of growth of the adult, in terms of sequestering ^{14}C from maternal tissue. This is a period when tissue is remobilised and incorporated into the foetus, including any such markers. There is no evidence that a barrier to the sub-atomic particles ^{14}C exists (Goren and Gerstner, 1965), given that there is apparently no atomic particle barrier during the sequestering of radiocarbon from prey. The forming foetal teeth would thus incorporate the radiocarbon marker in their collagen matrix (Goren and Gerstner, 1965; Liden and Angerbjorn, 1999). Beluga newborn are large (64–94kg, Brodie, 1971) relative to the muscle/skeletal body core of their mothers, being approximately 30% of her core weight at birth. By weight, as much as 40% of a beluga consists of integument and blubber, and even more in pregnant animals (Sergeant and Brodie, 1969a, fig.12). A disproportionately large amount of core tissue would therefore be transferred from the mother to the foetus during gestation.

In the wild, birth is followed by two years or more of nursing, during which the calf does not appear to rely heavily on foraging (thus a calf born in 1958 during the peak ^{14}C fallout would ingest relatively little contaminated prey). However, it is known that proportional burdens of organochlorines are transferred from mother to calf during lactation (Addison and Brodie, 1973; 1977; 1987) and there is no reason not to assume that this would also be the case for ^{14}C if present in the mother: a newborn calf gains an additional 189 kg over two years of nursing, in spite of losses through thermal maintenance and propulsion. By this stage, the total weight of a 2 year old calf would approximate the core weight of the mother and half her total weight. It seems probable that any pulse of ^{14}C acquired by females in the 1950–60s (Levin *et al.*, 2009) would be proportionately transferred to their young. We assume that subsequent tooth growth draws on tissue containing radiocarbon.

Thus the fundamental assumption of Stewart *et al.* (2006) may not be correct. A perfectly plausible (indeed more plausible) explanation is that they were actually measuring a spike of bomb ^{14}C which had been transferred across one generation and incorporated into body tissue, skeleton and forming teeth of the foetus and nursing calf. The chronology

of ^{14}C dilution and decay would continue, albeit in a second-generation animal, and would continue to be detectable against the reference background of the pre-bomb era (Levin *et al.*, 2009). Dilution of ^{14}C would be relative to the amount of body tissue transferred from the mother to the foetus and nursing calf, a probable range of 25–50%, depending on the relative size of the calf versus age-related weight of the mother. Since the total ^{14}C burden of a pregnant beluga may be magnified through disproportionate intake of prey, the actual burden transferred to the foetus and nursing calf may approximate that of a non-breeding beluga present during the peak of radiation fallout.

Stewart *et al.* (2006) concluded that GLG/2 was inconsistent with the data and could be rejected since it resulted in a delay of almost 20 years from the 1958 initiation of the bomb signal. However, as shown above that depends on an assumption, feasibly erroneous, that the animals must have been alive at the time of the signal. In addition, the atmospheric bomb test in China in 1980 produced considerable ^{14}C , and with a 1–2 year lag in its appearance in the biosphere (McNeely, 1994). Such a lag must also be taken into account for the 1958 event along with the lag response from generational transfer of radiocarbon and the more general uncertainty generated by methodological issues including the problem with resin.

In their discussion, they also noted that feeding at higher trophic levels or on long-lived prey would reduce the rate of increase of the signal and extend it over a longer period. They attributed this cause to their observation for the teeth that the radiocarbon signal initially appeared on the ‘correct’ date although subsequent incorporation extended into the 1980s rather than the early 1970s. We note that at least an equally plausible explanation is that this was a consequence of ^{14}C transfer from mother to calf, thus extending the radiocarbon signal by one or more generations.

A further general complication relates to the fact that ‘dilution’ will differ between males and females. Sexually mature females can transfer markers to the foetus and nursing calf, whereas males have no such outlet (Addison and Brodie, 1987). Thus while both male and female calves of the post-bomb era would have received similar burdens from their mothers, a female calf may later dilute her burden via reproduction. One would therefore expect dilution factor differences between the sexes over a 40 year period (of the post event samples, five were female and one was of unknown sex). A lack of change in levels reported by Stewart *et al.* (2006) of the five females sampled from the 1990s, suggests that they apparently produced few, if any, offspring during their lifetimes. This seems improbable if their ages (22 to 60 years with an aggregate productive lifespan of about 170–200 years, according to the authors with GLG/1) are correct. Dilution will occur during reproduction and it seems even less likely that that this would have occurred during a period when the animals appeared to be increasing after intensive exploitation and so would be expected to have an increased reproductive rate (see below).

Implications of their results in relation to population dynamics

In reviewing the strengths and weaknesses of their interpretation of the results in the light of the GLG/1 and

GLG/2 hypotheses, Stewart *et al.* (2006) also referred to life history parameters. They noted that an assumption that belugas live twice as long as previously assumed would necessarily result in twofold changes in growth rate, age of maturity and longevity. However, they commented that ‘differences in other life-history parameters were not so simple’. In particular, they noted that the net production rate (the average number of newborn expected over the life of a newborn female) increased by 14% in a simulated population under an assumption of GLG/1 rather than GLG/2, whereas the intrinsic rate of increase declined by almost 40% under the same assumption.

They also considered the implications for production of GLG/2 and GLG/1. Under GLG/2 they commented that a female (maturing at age 6) could have given birth to 3 calves and any daughters would have produced one calf each by the time the first female would reach maturity under a GLG/1 scenario, i.e. maturity at age 12. They further commented that although females live some 30 years longer under the GLG/1 scenario, the ‘population cannot compensate for its late start’. In fact, only the first calf (if female) would have been able to produce offspring under the above GLG/2 scenario. However, an obvious implication of their comment on the inability to ‘compensate’ (as noted above they simulated that the intrinsic rate of increase declines by almost 40% under a GLG/1 assumption) is the need to consider how populations have recovered in the wild as part of a holistic view of the merits of the two hypotheses.

In spite of the inconsistencies which they objectively described for their study, the authors concluded that the lifespan of belugas is double that proposed under GLG/2. Although not explicitly stated, one consequence is that the period of growth to sexual and physical maturity also doubled. Unfortunately, we do not consider that the authors sufficiently examined the implications of their conclusion of GLG/1 in the broader sense, i.e. relating to the whole animal and cross-reference of life history parameters with direct field observations and with known-age belugas in captivity.

In terms of the implications for growth, while recognising the inherent difficulties in estimating abundance and determining statistically significant trends in cetacean populations, it is informative to look at the available information from the Cumberland Sound population based on surveys by the Department of Fisheries and Oceans (DFO) of Canada. A substantial (>5%) annual increase in numbers has been reported (DFO, 2002; 2005); a doubling of the population since the early 1980s. There is no indication that only part of the Cumberland Sound population was observed by field observers and by experienced hunters who selected the early survey areas. More recent surveys covered the same area (DFO, 2002). It also seems unlikely that the Cumberland Sound stock has been recently augmented (doubled) by the arrival of large numbers of productive belugas from a distant population; the COSEWIC (2004) assessment of belugas, states that genetic, distributional and abundance information reinforce the historical view that the belugas of Cumberland Sound form a discrete population. This does not fit well with the population dynamics scenario provided by Stewart, *et al.* (2006) for GLG/1.

Lockyer *et al.* (2007)

In March 2001, a workshop was attended by the five authors of the resulting report (Lockyer *et al.*, 2007). Archived teeth from ten belugas, held in captivity for a range of years, were the focus of the study. The workshop focused on GLG counts, with little reference to other life-history parameters and the existing body of understanding, based on known-age captive belugas. The ten animals were originally captured in western Hudson Bay; duration in captivity was known for all as was length at capture for all except Winston. Colour reported at capture was given for 6 animals; the difficulties of interpreting these subjective colours by different people and without truly white animals for comparison have been discussed above and were recognised by the authors. The study concluded that GLG/2 was a plausible hypothesis for only four of the specimens; the six specimens for which it was deemed infeasible were Allua, Moby, Winston, No-See-Um, Big Mouth, SW-DL-7903 and Immiayuk (these are re-examined below), based largely on minimum agreed GLG counts given in their table 3 and associated estimated negative ages at capture. The authors concluded that ‘an annual deposition rate was most likely’ but also recognised that further work was required to improve age validation and standardised reading in the species. In particular, they noted the difficulties of accounting for missing layers, e.g. due to crown wear, and also mentioned that the ages for two of the animals were unrealistically large (Aurora(M) and No-See-Um) even when minimum ages were used. As noted earlier, examination of the change in total GLG angle at the pulp cavity may provide an approximation of GLG loss, e.g. when applied to the worn tooth of Alex (Goren *et al.*, 1987).

We would note that it does not seem appropriate to use ‘estimated negative ages at capture’ in conjunction with minimum estimates to rule out a hypothesis for cases when those estimates are considered minimum because of tooth wear, i.e. even the authors themselves noted it is impossible to know how many layers have been lost.

Allua

Allua was one of the animals examined in Heide-Jørgensen *et al.* (1994) and discussed above. We do not repeat the arguments above but note that the earlier discussion revealed that the case of Allua was not incompatible with GLG/2. Incidentally, Lockyer *et al.*’s table 4 (with ‘maximum’ GLGs) did not suggest incompatibility with GLG/2.

Moby

Moby was a female captured with Allua on 5 August 1969. She was 280cm long on 6 September 1969 and died in June 1999, at a length of 355cm, after 29.9 years in captivity. Even under GLG/2, this appears to have been one of the oldest belugas in captivity; 34.1 years (4.2 years wild + 29.9 years captive). Lockyer *et al.* (2007), in their table 4, estimated a maximum of 42+ GLGs (their minimum estimate in their table 3 was 38+), with evidence of tooth erosion (no neonatal line was present). Based on GLG/1, Moby would have been a minimum of 12 years old at capture (42years minus 29.9years), perhaps substantially older and probably multiparous when tooth wear is factored in. Even at 12 years this would suggest she should have been physically mature (Fig. 4). Clearly, as she grew a further 75cm in captivity, she

was not. Based on 280cm in Figs 2 and 4, she would have been about 4.2 years (births in June). Since she was almost 30 years in captivity, with little margin for error based on her age estimate at capture (see Fig. 4), thus she was realistically 34 years old at death and subject to tooth wear, as was the much younger, 24 year old Alex. It is implausible that she was 38+ years to 42+ years old (using GLG/1) since even these are substantial underestimates when tooth erosion is factored in. Interpretation is confounded by both tooth wear and perhaps complications in layer formation of animals that have spent so long in captivity.

Winston

Winston was a male who spent 14.25 years in captivity but for whom there was no length at capture. He was 380cm at death. The tooth was worn (neonatal line was not present) and thus it seems inappropriate to use this animal to rule out GLG/2. The 14.5 years in captivity is almost accounted for (using GLG/2) by the 27+ GLGs estimated. In fact, the negative ages reported in their tables 3 and 4 were minus 3.5 and minus 1.5 and thus few GLGs would need to be missing, especially if he had been captured as a calf, as were the majority in the study.

No-See-Um

No-See-Um was a male captured at 257cm who died 21.7 years later at 402cm. He also had a worn tooth (no neonatal line). While for the minimum GLG count their estimated age at capture was minus 1.4 years (their table 3), for the maximum (their table 4) the estimated age at capture was 2.6+. Rather than see this as an argument against GLG/2, the case of No-See-Um rather suggests the implausibility of the GLG/1 hypothesis due to the implausibly high ages at capture (21+ or 23+, their tables 3 and 4 respectively) this gives given the length at capture. The unrealistically high age at capture was also noted by the authors. A realistic age estimate would be: 3.2 years at capture, plus 21.7 in captivity, dying at an age of 24.9 years, thus 49.8 GLGs (GLG/2) compared to Lockyer *et al.*’s table 4 maximum estimate of 46+ indicating tooth wear.

Big Mouth

Big Mouth was a male who was 348cm at capture and whose reported colour was white. He lived 13 years in captivity and was 406cm at death. In this case there was no evidence of tooth wear and a neonatal line was seen. For the minimum GLG count the estimated age at capture for GLG/2 was minus 2; clearly implausible. However, for the maximum count the estimated age was 6 years. Alex, referred to above and believed to be captured as a yearling was estimated to be 6.3 years at 335cm. Thus while the evidence cannot be said to point strongly in favour of GLG/2 in this case, it similarly cannot be said to reject it.

The ages at capture for GLG/1 were 11 years and 19 years; if the estimated age for Alex is correct at 335cm, then an argument can be made that these are too high. In particular, if he was 19 years when captured then he would be expected to be sexually and physically mature. In fact he grew an extra 58cm. Similarly, another male Lugosi also described above died in captivity at known age 14 years at length 427cm, being 5 years younger than 19 year old Bigmouth at capture.

Alex and Lugosi were from Bristol Bay, Alaska, the nearest size category to those of western Hudson Bay. Based on Fig. 4, a realistic age for Bigmouth would be 7–8 years at capture, plus 13 years captive, dying at age 20–21 years. Furthermore, mention of manageable size of calves in the introduction alludes to a practical problem in the field, that of safely handling a captive adult male weighing 1,000–1,500kg, Lugosi and Alex as examples. Bigmouth, at supposed 19 years, would simply be too large, as well.

In summary, this case favours the hypothesis of GLG/2.

SW-DL-7903

This female was considered carefully in an earlier section of the paper reviewing Hohn and Lockyer (1999). Without repeating the discussion, we concluded that this animal favoured GLG/2 and that GLG/1 was implausible. In addition, this animal was treated with tetracycline just under 4 years after capture (Lockyer *et al.*'s table 5). The mark in the teeth was seen at GLG 14 (7 years assuming GLG/2) – this is close to expected given the earlier discussion that she was 2.75 years at capture (from the growth curve). This was not mentioned in their table 5 which commented (incorrectly) that the tetracycline information was consistent with GLG/1.

Immiayuk

Immiayuk was captured on 28 July 1989 at a length of 267cm, and was reportedly medium grey in colour. She was given tetracycline in late August 1989. She died after 10.4 years in captivity at length 388cm after 'first' calving (their table 5). No tooth wear was reported and a neonatal line was present. Lockyer *et al.* report a tetracycline mark at GLG7, 8 or 9 depending on the reader. They reported a minimum of 20 and a maximum of 27 GLGs (their tables 3 and 4, respectively).

Four possible scenarios are considered below.

- (1) *GLG/2 and 20 GLGs*. This implies that she was born in the aquarium 4.8 months after her recorded capture date and 3.8 months after her tetracycline treatment. Clearly, this is implausible.
- (2) *GLG/1 and 20 GLGs*. This implies that she was 9.6 years old at capture – this is a little greater than the maximum 9 GLG for the tetracycline mark but could be characterised as 'not inconsistent with it' given normal errors. She would be sexually mature. From known-age captive animals, a 9.6 year old female would be substantially larger than 267cm. It would also be very light grey to white in colour. Kayavak (discussed above), was born in captivity and at nine years old was 346cm and 534kg (see Fig. 4). Locker *et al.* report two males who were described as white when captured at 304cm (Churchill) and 348cm (Big Mouth). The idea that she was 9.6 years old at capture is implausible.
- (3) *GLG/1 and 27 GLGs*. This implies that she was 16.6 years old at capture. She would have been sexually mature, near physical maturity and been white in colour. The tetracycline mark would have indicated treatment 7.6–9.6 years before capture. The length-age arguments applied under scenario (2) are even more exaggerated here. This scenario is also implausible.

- (4) *GLG/2 and 27 GLGs*. This implies that she was 3.1 years at capture with tetracycline treatment occurring at 3.2 years of age or 6.4 GLGs. This is not incompatible with the minimum of 7 GLGs for the mark provided. The estimated age at capture is also consistent with information from known-age captive belugas (see Fig. 2). It also means that she reached sexual maturity while in captivity giving birth at age 13.6 years. Her estimated age at length is also consistent with the discussion of SW-DL-7903 and the juvenile depicted in Fig. 3, of the photo from Heyland and Hay (1976). From several strands of evidence this seems the most plausible scenario; indeed it is the only plausible scenario for this animal.

Discussion

The above holistic review of the ten cases in Lockyer *et al.* (2007) reveals that in fact the hypothesis of GLG/2 is consistent with a suite of information in all of the cases. In fact, there are five cases where the hypothesis of GLG/1 is either implausible or provides a much poorer explanation of the information than GLG/2: Allua, No-See-Um, Big Mouth, SW-DL-7903, Immiayuk. Thus on the basis of the ten cases alone, the hypothesis of GLG/2 is at least clearly preferable. This is discussed further under Conclusions below.

While Lockyer *et al.* did consider some additional information, this was rather limited. In particular, this relates to not fully considering information on length-at-known age from captive animals and information on the age of known animals in the early years of life from hunting data that are not dependent on teeth readings and consideration of age/length at attainment of sexual and physical maturity. In addition to the discussions of individual cases above, which reveal a number of serious inconsistencies with the GLG/1 hypothesis, Lockyer *et al.* (2007) appear largely to ignore work on captive animals without providing robust arguments to support the conclusion. This includes the work of Robeck *et al.* (2005) which is consistent with that of Brodie (1971) where they note that the authors provide 'at least a rough estimate' of length at age for 'very young' animals up to age 5 years. In fact, the estimates were not rough (they were based on known-age captive-born individuals or those identified as 1–2 years in the field) and 5 years approaches the age at which females may become sexually mature in captivity and in the wild (Brodie, 1971). In this context the 'apparent contradiction' they refer to between the monitored lengths at age for captive individuals and their (GLG/1 based) much older estimated ages relative to body length for Aurora(M) and No-See-Um disappears for the GLG/2 hypothesis as discussed above.

It is, of course, important to examine arguments related to the comparability of information from captive and wild animals. Stewart *et al.* (2006), in response to the findings of Robeck *et al.* (2005) commented that captive animals might mature earlier in the absence of food stress. That animals mature somewhat earlier (in age rather than length due to increased growth rate) in response to good food conditions is a reasonable hypothesis in line with the traditional concept of density-dependence (alongside increases in other reproductive parameters as well as increased survivorship). What is much more unlikely is that in nine separate aquaria, captive born (or captured at calf) belugas, all accelerate their

rate of growth to exactly twice the rate of free-ranging animals, without any period of adjustment to captivity. If food limitation is the ultimate governing factor determining the carrying capacity of belugas, then this would not occur at heavily-reduced population sizes when one might expect increased *per capita* food supply. If captive animals mature at earlier ages due to good food supply, then one might consider that captive animals are similar to wild animals in populations that have been reduced by overexploitation. For example, there is no evidence of food limitation or poor condition in the recovering population of Cumberland Sound belugas discussed earlier.

With respect to layering in the teeth, Lockyer *et al.* (2007), as others, discussed the possibility that GLGs in captive belugas might not reflect the extremes of feeding and migration in the wild. They noted that this may result in less defined layers in captive animals as has been noted above; tooth sections from captive animals are generally more difficult to read than from wild animals. In addition, that the tooth section from the male beluga Lugosi of the Vancouver Aquarium was difficult to resolve, could possibly attributed to wear from his social displays of jaw claps (Brodie, 1982). However, the authors then go on to suggest that this may 'preclude' using data from captive animals to calibrate GLG deposition in free-ranging ones. Given that their study was based on only a limited sample of teeth from captive animals then this could be argued to cast doubt on their own rather firmly stated conclusions. It also seems inconsistent with their recommendation that captive belugas be used for planned studies using tetracycline injections, which therefore assumes similar growth patterns of wild and captive animals.

In fact, Sergeant and Brodie (1969a) tagged 1,700 wild beluga of which 93 were injected with tetracycline injections as discussed by Brodie (1969b) while Geraci and St. Aubin (Brodie *et al.*, 1990) held tetracycline injected belugas for several weeks, extracting a tooth before release. Length-at-age estimates from the latter tetracycline study confirm the rapid early growth of known-age belugas shown in Fig. 4.

Finally, despite Lockyer *et al.*'s (2007) conclusion that their results 'clearly indicated that an annual deposition rate was most likely', elsewhere in the paper they were more circumspect. Interestingly, they stated that the most 'compelling' evidence was the radiocarbon study of Stewart *et al.* (2006) that is critiqued above. They also recognised that loss of GLGs due to wear was an alternative explanation in several cases for which they had deemed GLG/2 implausible. Importantly, they recognised that in terms of management, the GLG/2 hypothesis should also be considered. They also made a number of recommendations to resolve 'the controversy of either one or two GLGs/y.'

Allometric relationships amongst odontocetes

Luque *et al.* (2007) briefly reviewed the then available evidence for deposition rates in beluga teeth. Their main focus was on a comparison of estimated age at maturity for 22 delphinoid odontocete species. While it is not clear how carefully they reviewed the evidence for each species, which was primarily taken from Gyax (2000, in Luque *et al.*, 2007) they used single point estimates. They then used a robust regression approach to develop an age at maturity vs length at maturity relationship. From this they took an age

at maturity value of 5 years for beluga (based on GLG/2) and a value of 10 years based apparently on Hohn and Lockyer's (1999) paper as evidence for GLG/1. They also referred to Robeck *et al.*'s (2005) estimate as 9 years stating that this may not be representative of wild populations. They concluded that while the 5-year estimate fell just within the 95% prediction limit of the allometric relationship, the 10-year estimate fell closer to the predicted line and within the 95% confidence band (in fact only 5 of the 22 species fell within the 95% band).

While the allometric approach is interesting, it does not take into account a number of factors including the confidence intervals around the ages and lengths at sexual maturity reported or the different environments of the various odontocete species which may influence life history strategies (the narwhal and beluga are almost unique in this regard). In addition, the best estimate for mean age at attainment of sexual maturity given here is 5.75 years rather than 5 years, while Robeck *et al.*'s estimate of 9 years (which they stated as giving credence to GLG/1 and an age at maturity of 10) was related to first conception and was characterised as plus or minus 2.8 years. Robeck *et al.* state quite clearly that the majority of captive females conceived at age 6 years, when in the presence of proven breeding males. In summary, despite their conclusion that the available evidence supported GLG/1, their review was not particularly informative.

Aspartic acid racemization (AAR)

One relatively new aging technique that has become more widespread is that of aspartic acid racemization (AAR). It was first tried for cetaceans in the early 1980s (Bada *et al.*, 1980; Bada *et al.*, 1983; Nerini, 1983). More recently, Garde *et al.* (2007) used AAR to examine age determination of narwhals (*Monodon monoceros*), social odontocetes that live in a similar environment to belugas. The results indicated that female and male sexual maturity in narwhals was 6–7 years and 9 years respectively, similar to the captive belugas in Robeck *et al.* (2005), wild belugas from Cumberland Sound (Brodie, 1971) and recent direct observations of captive belugas described here. However the maximum estimate of age for one female narwhal was 105–125 years, considerably higher than estimates for belugas for either GLG/1 or GLG/2. Bowhead whales have also been found to reach very high ages, but in this case corroborative evidence exists from whaling equipment found in the animals (George *et al.*, 1999; Rosa *et al.*, 2011). Rosa *et al.* reviewed a number of factors that need to be considered when interpreting results from this technique and *inter alia* stress the need for calibration work for the technique to occur for the same species and the need to recognise the relationship between racemisation rate and temperature. As several authors have noted, marine mammals demonstrate a gradient of body core temperature and there is a -2°C to $+18^{\circ}\text{C}$ temperature range in beluga seasonal habitats (Brodie and Päsche, 1985; 2001; Brodie, 1975).

CONCLUSIONS

In this paper we have examined the evidence for deposition rate in beluga from a holistic viewpoint, incorporating field-

based, life-history research, captive animal research that incorporates and cross-references the available parameters. The review highlights the value of collaborative research between field scientists and scientists maintaining animals in captivity with direct observation. It is clear that the only way to examine the question of deposition rate in tooth laminations is through such a holistic approach. Merely examining a limited suite of information or relying on new but not fully understood techniques can result in misinterpretation and lead to unjustified or overly-stated conclusions, with potentially serious consequences in terms of conservation and the provision of management advice.

We used a holistic approach to critically review: (1) evidence from the reading of a limited number of teeth of animals that died in captivity; and (2) evidence from the relatively new technique, in the context of cetaceans, of use of radiocarbon dating from specific events such as atomic weapons testing.

With respect to the former, our review shows that the hypothesis of GLG/2 is consistent with information from a number of approaches whilst the hypothesis GLG/1 revealed some serious inconsistencies with data from other sources. While it is important to try to resolve inconsistencies, it appears that the only way to do this for the GLG/1 hypothesis was for the proponents to use rather complex arguments and the application of correction factors that are not rigorously justified. Aside from the issue of radiocarbon dating, the difficulties with the Lockyer *et al.* (2007) study related to teeth can be summarised as follows:

- (i) reliance mainly on a single approach (an archived tooth) and on older belugas with greater numbers of GLGs, thus increasing the possibility of errors;
- (ii) incomplete consideration of GLG loss through erosion or behaviour in captivity – which will underestimate numbers of GLGs;
- (iii) attributing without good evidence GLGs into the pre-captive period to compensate for the apparent excess numbers produced in captivity, a portion of the tooth that is often eroded – resulting in substantially over-estimated pre-capture ages;
- (iv) use of teeth from several captive belugas with poorly understood pre-capture histories;
- (v) poor cross-referencing of real-time events recorded of known-age captive belugas.

The above factors, singly or in combination, increase the potential for compounding errors. It is possible to designate early year-classes without the use of GLGs as was done in the field (Brodie, 1971), by direct observation in captive animals (Robeck *et al.*, 2005) and as updated with more recent data in Fig. 4.

With respect to (2) above, the evidence from radiocarbon dating that was seen as the most important by Lockyer *et al.* (2007) has been shown to be problematic, especially with respect to the transfer of ^{14}C from mothers to calves as well as the influence of resin in the tooth due to the preparation method. Contaminants sequestered by belugas will continue to be transferred through several generations, unless otherwise metabolised, or diluted in the case of ^{14}C . Elevated

levels of ^{14}C may reflect the background of contamination from a previous generation. This could be examined by looking at the teeth (or bone) of earlier and recent, captive, mature belugas that could have received generational transfers of ^{14}C . These include:

Moby: Female conceived in 1964 and born in 1965, captured in 1969 and held in captivity for 29.9 years. One of the oldest verifiable belugas at 34.1 years, and born after the peak of bomb radiocarbon levels. However, her mother would have been at least 7 years old, possibly older, born in mid 1940s–1958 and exposed to bomb radiocarbon levels, feeding intensively when pregnant during the late 1950s. If 7 years old, the mother could have been born during peak ^{14}C fallout, therefore Moby's grandmother may have acquired the ^{14}C burden.

Alex: Male conceived in 1959 and born in 1960, captured in 1961 and died in 1984. Born two years after the peak of ^{14}C fallout, therefore his mother may have acquired the greater radiocarbon burden.

Lugosi: Male conceived in 1965 and born in 1966, captured in 1967 and died in 1980. Possible that his mother, if giving birth at age seven, could have been born one year after peak ^{14}C fallout, potentially a generational transfer from her mother.

Bella: Female estimated conceived in 1959 and born in 1960, captured in 1967 and died in 1976. Her mother must have been at least 7 years old, born *circa* 1940–1953, thus exposed to high levels of ^{14}C while feeding intensively when pregnant.

Kavna: Female probably conceived in 1968–1969 and born in 1969–1970, captured in July 1976, died in 2012. At birth, the youngest her mother could have been would be 7 years, born in 1962, but even at 11 years, Kavna's mother would have been born after the 1958 peak ^{14}C fallout. It is possible that Kavna's mother, or her grandmother, could have been exposed to the initial ^{14}C burden, initiating a generational transfer of radiocarbon.

Therefore, belugas of known-age, or with realistic age estimates, and having achieved adulthood during the late 1960s to the 1980s, were born after peak ^{14}C fallout. Yet, they were as old, or older, than those hunted 10–20 years later in the 1990s, and used in the ^{14}C study by Stewart *et al.* (2006). Generational transfer, later fallout to 1980, tissue contamination and application of corrections may explain the discrepancies (B. Buchholz, pers. comm.).

There are clear differences for the two deposition rate hypotheses: belugas are sexually mature by either 6 or 12 years for females and by 9 or 18 years for males. The Cumberland Sound study was based on field observations of full-term fetuses, newborns, juveniles, sub-adult, and calving adults. Often the teeth exhibited better resolved GLGs and the animals were younger with less potential for error in age determination. There are, of course, body-size differences between various populations (Sergeant and Brodie, 1969a). However, these are modest compared to the twofold and greater differences in all life processes and production being discussed. Comprehensive data on younger animals were key to understanding the initial trajectory of

the growth curve and the age of sexual maturity in females. The young age spectrum from the wild is readily compared to their counterparts of known age in captivity. The body of direct observation from wild and captive beluga established thus far, indicates mean age at attainment of sexual maturity of females at 5.75 years, and of males at 8.75 years. Physical maturity seems to occur after 10 years, and average lifespan around 30–35 years.

The implications of the two hypotheses for conservation and management are great. GLG/1 implies *inter alia* appropriate numbers of females, either pregnant and/or lactating, whose ages can be verified at 35–70 years, or greater. The implications for recovery of populations (as seen at Cumberland Sound) are quite different for the two hypotheses with GLG/1 having a much lower intrinsic rate of growth. A qualitative evaluation of the Cumberland Sound scenario supports the GLG/2 scenario. Recovery would therefore require considerably greater survivorship than considered by Stewart *et al.* (2006) and/or a decrease in the length of the reproductive cycle from three years to two.

A more sophisticated population modelling exercise would be valuable to further explore the implications of life history parameters for specific populations for which good abundance data over time are available.

While dedicated age determination studies using tetracycline can be effective if used in a controlled experiment (e.g. Brodie *et al.*, 1990), at this time we place greater confidence on direct and cross-referenced observations of known-age, wild and captive animals, in real time, rather than extrapolations.

Biological and environmental factors can clearly affect life history traits and the north circumpolar habitat does appear to have resulted in growth and behavioural adaptations, especially among highly social odontocetes. Belugas have adapted to this demanding environment, to the exclusion of most other cetaceans. The only other odontocete to survive in a similar habitat is the narwhal (*Monodon monoceros*). However, narwhals have not been successfully maintained in captivity and comparisons with free-ranging animals are not possible (Hay, 1980). Comparisons of biological parameters and teeth from high Arctic populations of beluga with those found in the quite different environment of the St. Lawrence River should be explored.

In conclusion, we believe that the suite of data now available from captive belugas and studies of younger, known-age animals, are consistent with GLG/2 and do not support GLG/1.

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